A Phytosaur from North Bergen, New Jersey

By Edwin H. Colbert

INTRODUCTION

North Bergen, New Jersey, is a township on the back slope of the westward-dipping Triassic sediments and intrusives that form the west shore of the Hudson River opposite New York City. It is about 1 mile to 1½ miles west of the river and is across from that section of Manhattan in which the American Museum of Natural History is situated. A railroad line runs northeast and southwest along the strike and at the very base of the westward-dipping Triassic beds, where they pass under the flat marshlands that border the Hackensack River, and in former years there was, within what is now North Bergen, a small stop on this railroad known as Granton. Granton was almost exactly opposite the American Museum of Natural History, the word "opposite" in this case being used to indicate a direction at right angles to the course of the Hudson River as it flows past middle and upper Manhattan. Indeed, a line projected down the middle of Seventy-seventh Street, which runs along the south front of the Museum, would, at a distance of about 3 miles northwest of the Museum, pass slightly to the south of Granton.

Immediately to the northeast of Granton there was a large hill, an outlier of Triassic sediments, in which an extensive quarry had been developed. The quarry and the hill in which it was excavated were be-

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1 Studies of the Granton Tetrapod Fauna, 1.
2 Chairman and Curator, Department of Vertebrate Paleontology, the American Museum of Natural History.
tween the railroad, already mentioned, and a heavily traveled road parallel to the railroad, this road being known as the Bergen Turnpike, or Tonnele Avenue, or Federal Highways 1 and 9. As of the present date, most of the hill containing the Granton Quarry has been leveled, to make room for stores and industrial sites along the west side of Tonnele Avenue. This development, an expression of the so-called progress of our modern culture, will eventually completely destroy an important Triassic fossil locality—a locality that, because of its special facies features, has provided information not generally available at other Triassic exposures, and incidentally a fossil locality of interest in that it is the one nearest the American Museum of Natural History.

The Granton Quarry in past years has yielded a considerable harvest of fossil coelacanth fishes of the genus Diplurus (see Schaeffer, 1952) and abundant estherians. In addition, during the course of the past decade or so, a number of tetrapods have been discovered at the Granton Quarry but as yet have not been described. The present paper is intended as the first of several contributions that will describe these tetrapods, now in the collections of the American Museum of Natural History.

The specimen, a phytosaur, described in this paper was discovered during the autumn of 1963 by Robert Salkin of Newark, New Jersey. Mr. Salkin, a good friend of the American Museum of Natural History, who for some years has been keenly interested in the Triassic reptiles of eastern North America, very kindly presented the specimen to the Museum for its paleontological collections.

Specimens from the collections of the following institutions have been studied:

A.M.N.H., the American Museum of Natural History  
A.N.S.P., the Academy of Natural Sciences of Philadelphia  
P.U., Princeton University, Princeton, New Jersey  
U.C.M.P., University of California, Museum of Paleontology, Berkeley  
Williams, Williams College, Williamstown, Massachusetts

ACKNOWLEDGMENTS

The American Museum of Natural History and the author are greatly indebted to Mr. Robert Salkin for his generous presentation of the phytosaur specimen for study and for preservation in the collections of the Museum. The author is also grateful to Mr. Salkin for advice as to the locality and level at which the specimen was found, not only through conversation but also by means of some trips together to the site. To Dr. Joseph T. Gregory of the University of California at Berkeley, the author is particularly indebted for helpful advice concerning the specimen, per-
personally examined by Dr. Gregory, and analyzed by him against the background of his extensive knowledge of phytosaurs. Likewise, the author wishes to thank Dr. Donald Baird of Princeton University, and Research Associate at the American Museum of Natural History, who has a long and abiding interest in the Triassic vertebrates of eastern North America, for his help on this problem. The photographs of the quarry (figs. 5 and 6) were generously provided by Mr. David Stager of the Newark Museum. Finally, thanks are due to various members of the Department of Vertebrate Paleontology of the American Museum, specifically to Mr. Gilbert Stucker for his careful preparation of the fossil, to Mr. Chester Tarka for the photograph of the fossil, and to Mr. Michael Insinna for some of the illustrations. Figures 2 and 9 were prepared by the Graphic Arts Department of the American Museum.

STRATIGRAPHIC RELATIONSHIPS

The hill in which the Granton Quarry was excavated was composed (as is the remnant still preserved) of Triassic sediments, dipping to the west, capped by an igneous sill. Earlier students of the eastern Triassic have placed these sediments and the overlying sill within the Stockton Formation of the Newark Series (see Shainin, 1943), but some recent studies have suggested that these particular rocks represent an eastern outlier of the Lockatong beds, which are extensively exposed in central New Jersey and along the Delaware River. It may be recalled that these two formations are elements in the three-fold sequence (the third formation being the Brunswick) into which the Newark Group of the New Jersey-Pennsylvania region has been divided. In earlier geologic literature the tripartite division of the Newark was regarded as generally a time sequence, with the Stockton as the lowest and oldest formation, the Brunswick as the uppermost and youngest, and the Lockatong as occupying a position more or less between these lower and upper formations. Within recent years, however, much evidence has been developed to indicate that there is considerable interfingering between the three formations of the Newark Series, so that they are in part contemporaneous. The Lockatong in particular has come to be regarded as a facies expression contemporaneous with a part of the Brunswick Formation, a view set forth by McLaughlin and Willard in 1949, as follows: "It is our belief that the Lockatong represents lacustrine or swamp deposition, and it is in part synchronous with the fluvitale or torrentially-formed Brunswick. The Lockatong occupies the center of the wide Newark belt in the Delaware Valley where marshy conditions
might have obtained. Lithology, stratigraphic sequence, distribution, facies changes both with and perpendicular to the strike indicate passage of the Lockatong into beds indistinguishable from the Brunswick. It is not improbable that the Stockton and Brunswick, too, are in part contemporaneous facies” (McLaughlin and Willard, 1949, p. 37).

It seems eminently reasonable to consider the sediments at the Granton Quarry as of Lockatong rather than Stockton relationships. These are predominantly black and gray, fine-grained argillites and shales, thinly bedded and highly carbonaceous. They are just the types of sediments that would have been deposited in the quiet waters of shallow lakes or ponds, or in swamps, and their topographic and stratigraphic position, west of and above the Palisades sill, would place them in the proper relation, either with the top of the Stockton or the bottom of the Brunswick, to be an eastern outlier of the Lockatong facies. Moreover the sediments at the Granton Quarry show repetitious short cycles of deposition, each darker at the bottom and lighter at the top, as is seen in the characteristic Lockatong beds farther to the west.

The sediments exposed in the Granton Quarry, before it was largely destroyed, consisted of about 60 feet of black and gray argillites and shales, with some intercalated siltstones. The predominance of the dark shales was such, however, as to make them quite characteristic of the exposure. As mentioned above, these shales and argillites are generally fine-grained and through much of the section show a considerable amount of thin bedding. Thus the shales could be split, and on the surfaces exposed by such splitting there were commonly revealed vast numbers of estherians, occasional fish, and, rarely, the bones of tetrapods. The fossils occurred at various levels throughout the sedimentary

![Fig. 2. A northwest (left) to southeast (right) section, from Granton Quarry to the Hudson River. Vertical exaggeration about five times.](image-url)
Fig. 3. A portion of the Granton Quarry as it appeared before demolition. The bedded Lockatong argillites and shales (below) are sharply separated from the volcanic sill (above).

Fig. 4. A detail of the quarry face shown in figure 3. Note the succession of dark and light sediments. In the upper left corner is the overlying sill.
FIG. 5. The remaining small section at the north end of the Granton Quarry locality, showing the succession of dark and light sediments. This is the locality for the phytosaur skull.

FIG. 6. A detail of figure 5 showing both thin-bedded shales and thicker-bedded argillites and other sediments.
sequence exposed in the quarry and thus formed a record of life in one environment, at one locality, extending through a long span of years.

On top of the sediments in the Granton Quarry were some 40 feet of igneous rocks comprising the Granton sill. These sediments and the overlying sill occurred stratigraphically above the thick Stockton sill, intruded into the sediments of the Stockton Formation, of which the eastward-facing eroded scarp comprises the long wall known as the Palisades, which forms the western border of the Hudson River for some 40 miles above its mouth.

Such, in brief, is the locale, and its stratigraphic relationships, from which the phytosaur skull, herein described, was collected.

DESCRIPTION AND COMPARISONS

*Rutiodon carolinensis* Emmons

*Rutiodon carolinensis* Emmons, 1856, pp. 302–307, figs. A, 22, pl. 6, fig. 8, pl. 5, figs. 2, 5.

**Type:** Five striated teeth, vertebral centrum, vertebrae and ribs, neural spine, and a fragment of an interclavicle.

**Horizon and Locality:** The type and various referred specimens were found in the Cumnock Formation of the Newark Group, in the Deep River coal field of North Carolina.

**Specimen Under Consideration:** A.M.N.H. No. 5500, an almost complete skull contained within a large slab of gray argillite. Associated with the skull are an apparent back portion of a mandibular ramus, a part of a vertebra, several scutes, some other bone fragments, and a coprolite. All are from a position well toward the top of the sedimentary sequence as exposed in the Granton Quarry. The specimen was discovered among the rubble that had been blasted from the quarry wall prior to removal from the quarry; nevertheless, the slab containing the skull and associated bones was obviously not far removed from its position in situ. This appears to have been about 20 feet below the contact between the sediments and the base of the overlying Granton sill.

**Discussion**

The skull here described is noteworthy because of its small size; certainly it is one of the smallest known phytosaur skulls. Unfortunately the occipital part of the skull is broken away; it is on one of the broken edges of the slab. Quite obviously the skull was originally complete, but
much diligent search in the Granton Quarry by Mr. Salkin and the author has failed to find the piece of rock that should abut against that edge of the slab that cuts across the back of the skull. Enough of the occipital region is preserved, however, to show the basal tubera of the basioccipital, an indication that only the occipital condyle itself and the back portions of the squamosals, opisthotics, quadrates, and perhaps one or two other bones of this region are missing. Consequently it is possible to estimate the original total length of this skull with a fair degree of accuracy. In a complete phytosaur skull the length from the tip of the premaxillaries to the back of the basal tubera of the basioccipital is about 85 per cent of the total length, measured to the posterior border of the squamosals. On this basis the total length of the skull of A.M.N.H. No. 5500, which has a premaxilla-basal tubera length of about 407 mm., would have been approximately 480 mm.

In the series of phytosaur skulls from Arizona described by Camp (Camp, 1930), there is a juvenile skull designated by him as *Machaeroprosopus lithodendrorum* (placed by Gregory in his revision of the genera of phytosaurs in the genus *Rutiodon*) with a total length of 678 mm. This, one of the smallest of previously known phytosaur skulls, is thus about 30 per cent larger in linear dimensions than the skull from the Granton Quarry. Another relatively small *Rutiodon* skull is A.M.N.H. No. 1, which Gregory, in a new study of the genus, has indicated as having a length of 652 mm., again exceeding the Granton specimen by the considerable margin of about one-fourth.

The above comparisons, which give an indication of the small size of the Granton skull as contrasted with other known skulls of North American phytosaurs, particularly those referred to the genus *Rutiodon*, may be supplemented by comparisons involving two incomplete specimens. In 1926 Wanner described a small phytosaur from the Newark beds of York County, Pennsylvania. This specimen was identified by him morphologically as a "part of a jaw" and taxonomically as *Rutiodon carolinensis*. There is good reason to accept the systematic assignment given by Wanner, but careful examination shows that morphologically the specimen is a left premaxilla. The specimen is interesting in the present connection because it represents a phytosaur skull that must have been almost the same size as, or perhaps slightly larger than, the one from the Granton Quarry. Probably these two specimens show us stages in phytosaurian ontogeny that may be regarded, if not as juvenile, certainly as very young adult. The Granton specimen and the fragment from Pennsylvania are important because we have too few records of growth stages in the phytosaurs, or in most fossil archosaurian reptiles.
Fig. 7. *Rutiodon carolinensis* Emmons, A.M.N.H. No. 5500, skull in containing slab of rock, with portion of lower jaw, partial vertebra, scutes, and other bones; Upper Triassic, Lockatong Formation; Granton Quarry, New Jersey. Unretouched photograph. Scale: × 3/10.

Key: A, anterior border of antorbital fenestra; Ar, articular; Ch?, chevron; Ec, ectopterygoid; Fr, frontal; LN, left naris; LO, left orbit; L Pmx, left premaxilla; MF, mandibular foramen; Na, nasal; Pof, postfrontal; Prf, prefrontal; RA, retroarticular process of mandible; RM, right ramus of mandible; RN, right naris; RO, right orbit; R Pmx, right premaxilla; S, scute; SA, surangular; Sc, scute overlying coprolite; Sk?, skull bone?; T, tooth; V, partial vertebra, Vs, vertebral spine. Numbers refer to position of teeth in premaxilla-maxilla series.
The other specimen alluded to is a very small fragment of a lower jaw, found by the present writer some years ago in the Petrified Forest Member of the Chinle Formation, at Ghost Ranch, New Mexico. An extrapolation of jaw length (which in phytosaurs is closely comparable to skull length) based on the distance separating two teeth in this jaw fragment indicates that the fossil represents a phytosaur with a skull perhaps less than 400 mm. in length, obviously somewhat smaller than the Granton skull.

Perhaps enough has been said to indicate the small size of the phytosaur from Granton, even when compared to some of the smallest phytosaurs hitherto known.

That the skull represents a young animal is further indicated by the manner of its preservation. It is crushed, and the two halves of the pre-maxillary-maxillary rostrum are cleanly separated from each other along the median suture, as if in life the sutural junction of these bones was relatively weak. The left half of the rostrum has been pushed down, and the right half up, in relation to each other, so that these two anterior halves of the skull are spread apart, scissors-fashion. The crushing of the skull has also been accompanied by twisting, so that the right external naris is seen in profile, but the left naris, the region around it, and the skull roof are seen in dorsal view. This displacement is in a sense fortunate, because it gives a profile of the rostrum on the right side, showing that the external nares are elevated on a crater-like eminence that in life almost certainly projected above the level of the skull roof. In front of the nares the rostrum is very slender. The characters of an elevated narial opening and a slender rostrum are to be expected in a small phytosaur skull; they seem to be typical of the younger stages of phytosaurian ontogeny.

The Granton specimen clearly shows the anterior border of the pre-orbital fenestra on the left side, situated directly beneath the anterior rim of the left naris. This position for the antorbital opening is quite typical for *Rutiodon carolinensis*, as shown by the skulls in the American Museum of Natural History and in the Williams College collection (this last being a skull described and figured by Emmons in 1860).

Although the front of the preorbital fenestra is thus plainly to be seen, its back border cannot be definitely determined, because of the crushing of the specimen and because of considerable destruction of some of the external skull bone surfaces in this region. Normally this opening would extend back to a position below, or perhaps slightly anterior to as well as below, the front of the orbit. Behind this anterior boundary of the preorbital fenestra the left side of the skull is a confused mass of crushed and
partially destroyed bones that makes the definition of details very difficult indeed, if not in much of its extent impossible. It is obvious that the postorbital, jugal, quadratojugal, and squamosal, at least, have been crushed down upon the pterygoid, ectopterygoid, palatine, and quadrate bones, but the delineation of any of these elements can hardly be achieved. Presumably some of the bone mass which is here seen on the left side of the skull represents some of the elements of the palate and

<table>
<thead>
<tr>
<th>R. carolinensis</th>
<th>R. lithodendorum</th>
</tr>
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<tbody>
<tr>
<td>A.M.N.H. No. 5500</td>
<td>A.N.S.P. No. 15284</td>
</tr>
<tr>
<td>Length, tip of rostrum to tubercula of basi-occipital</td>
<td>407</td>
</tr>
<tr>
<td>Total length of skull</td>
<td>480 e.a</td>
</tr>
<tr>
<td>Prenarial length</td>
<td>288</td>
</tr>
<tr>
<td>Postnarial length</td>
<td>192 e.</td>
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<tr>
<td>Ratio, prenarial/postnarial</td>
<td>150</td>
</tr>
<tr>
<td>Length, tip of rostrum to 16th tooth</td>
<td>115</td>
</tr>
<tr>
<td>Ratio, rostrum to 16th tooth/pre-narial length</td>
<td>40</td>
</tr>
<tr>
<td>Total number of upper teeth</td>
<td>43</td>
</tr>
</tbody>
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a.e., estimated.
b From Gregory (1962b).
c From Camp (1930).

perhaps the basicranium, seen from above, and showing through the opening of the lateral temporal fenestra. But any boundaries of the lateral fenestra as such are not apparent. At the back of the skull, however, on the left side, there can be seen the posterior border of the left ectopterygoid. This part of the skull is skewed in such a way that the lateral temporal bones of the right side are completely hidden beneath the skull roof.

As against these uncertainties of identification, it is possible to discern certain bones of the skull roof and the superior borders of the orbits. Here are seen the frontals and perhaps the very anterior part of the parietals, the postfrontals, with the one on the right side being rather
well shown, the prefrontals, again as seen on the right side, and the posterior borders of the nasals. The relationships of these bones to one another seem to be quite characteristic for the phytosaurs, and no particular comment is needed here with regard to their extents and boundaries.

Various teeth and alveoli are shown in the Granton skull, and it is possible to come to some conclusions concerning the development and characters of the dentition in this specimen. Of course the anterior tips of the premaxillaries form a prominent hook in which are two large teeth on each side, as is typical of the phytosaurs, these enlarged terminal premaxillary teeth being preserved in the Granton skull on the right side. Behind this anterior hook there are in the Granton skull three premaxillary teeth preserved on the left side, a considerable series on this same side of alveoli, and a number of premaxillary alveoli and bases of teeth on the right side. By extrapolation from those alveoli which are preserved in sequential series it is possible to estimate that there were approximately 43 teeth on each side in this skull. In a study of the Rutiodon skull originally described by Emmons from North Carolina, the present author determined that there were approximately 27 premaxillary teeth and 15 maxillary teeth, for a total of 42 teeth on each side (Colbert, 1947). Thus the two skulls agree very well in the matter of number of teeth. The small skull from Arizona, described by Camp as an immature specimen of Machaeroprosopus lithodendrorum (U.C.M.P. No. 2781) and referred by Gregory to Rutiodon (Gregory, 1962a), is indicated as having 46 teeth, 24 in the premaxilla and 22 in the maxilla. But Gregory has rightly pointed out: "Until much more is known of both individual and age variations in tooth frequency, this difference cannot be used reliably in systematics" (Gregory, 1962b, p. 12). Nevertheless, the number of teeth in the Granton skull is in accordance with what might be expected for an individual belonging to the genus Rutiodon. It is not possible to determine the suture between the premaxilla and the maxilla in the Granton specimen, and therefore the numbers of premaxillary and maxillary teeth cannot be given.

From the few teeth that are preserved in the Granton skull there is not much to be learned concerning details of the dentition. The two large anterior premaxillary teeth preserved on the right side are round in cross section, as might be expected. A tooth in the left premaxilla, identified as the sixth in the series, as well as two more posterior teeth, 16 and 18, also shows round cross sections. The surface of the sixth premaxillary tooth is smooth. Nothing can be said as to the surfaces of the other teeth preserved. A partial tooth exposed within the anterior part
of the preorbital fenestra on the left side, and tentatively identified as about 37 in the series, seems to be a stout tooth with an elliptical cross section, very probably with anterior and posterior carinate edges. Such a tooth would be expected in the posterior part of the tooth row, and if this particular tooth has been correctly interpreted, it gives evidence of a heterodont dentition in the Granton specimen.

In this connection mention should be made of a small phytosaur tooth, elliptical in cross section and with at least one edge finely carinate, discovered in 1946 during excavations made in the Lockatong shales for the foundation of the Firestone Library at Princeton University. The tooth (P.U. No. 18259) is of a size that would correspond very well with the Granton skull and thus supplements the evidence for our knowledge of Lockatong phytosaurs as derived from the specimen here described. It was found at a locality where literally thousands of specimens of the coelacanth fish Diplurus newarki were excavated. The association of a phytosaur tooth with coelacanth fish at Princeton parallels the presence of the phytosaur skull and coelacanths at the Granton Quarry.

In Gregory's study of the genera of phytosaurs (Gregory, 1962b) there is a key to the skulls. This key may be applied to the skull from Granton, with some difficulties, however, since the back part of the skull in question, a region of particular importance in generic distinctions among these reptiles, is missing. Even so, it is possible to use the key with definite results.

In this key, the genera Paleorhinus and Mystriosuchus are characterized, among other things, by the slightly forward position of the external nares, the upward direction of the orbits, and the homodont dentition; the genera Angistorhinus, Rutiodon, and Phytosaurus, by external nares immediately above the preorbital fenestra, the outwardly directed orbits, and the slight to marked differentiation of the teeth. On all these counts the Granton skull may be associated with the second group of genera cited above. Among these latter genera Rutiodon is characterized by a slender rostrum, never crested along its entire length, and by heterodont teeth. This is in contrast to the massive, crested rostrum of Phytosaurus and the only slightly differentiated teeth of Angistorhinus. Consequently, on the basis of such characters as can be used, it seems reasonably certain that the Granton skull can be placed within the genus Rutiodon. The type of Rutiodon is Rutiodon carolinensis, and it seems overwhelmingly probable that the other species of the genus (according to Gregory's revision, 1962a) described from eastern North America, notably R. leai and R. rostratus, are synonyms. On the basis of this argument, therefore, the Granton skull is referred to Rutiodon carolinensis.
The posterior part of a mandibular ramus, probably of the right side, is situated in the slab below and at right angles to the skull. The anterior part of this jaw extends under the premaxillae of the skull, but its front portion, which should be expected in the rock dorsal to the premaxillaries, has not been found, in spite of considerable excavation in search of it. Either the front of the jaw was broken off during fossilization or was bent to such a degree that it is far below its expected position in the matrix. It was not considered practical to continue the downward excavation in the very hard matrix in search of the anterior extension of the dentaries.

The jaw, although rather fragmentary, shows the shape and some of the bone of its posterior portion. A rather high surangular is indicated, below which can be seen parts of the border of the mandibular fenestra. There is a prominent retroarticular process, and in front of it some portions of the articular bone are preserved. Nothing else in particular can be said about this jaw; not enough of it is preserved or exposed to show the teeth.

Immediately above the anterior section of the premaxillaries a partial vertebra is to be seen. It shows a rather high spine and a long prezygapophysal process. A comparison with the vertebral series of *Machaeroprosoposaurus adamanensis* (placed within the genus *Rutiodon* in Gregory's revision, 1962a) indicates that this is probably about the eighth presacral vertebra.

In addition to the bones described above, several scutes are preserved in the slab. One of these, directly on top of a coprolite, is a rugose scute with straight edges and square corners, in other words a rather rectangular scute of the type that is found in the dermal armor of the back in phytosaurs. The dimensions of this bone indicate, however, that it is a relatively small scute of the type characteristic of *Rutiodon*; certainly it is not the large type of scute characteristic of *Phytosaurus*. This evidence reinforces the evidence of the skull for identifying the Granton specimen as *Rutiodon*. The other scutes, of which there are three, are more rhomboidal or rounded in shape and evidently were from more peripheral parts of the cuirass. One of them is very small.

Several other bones or bone fragments in the slab may be mentioned. One of these is a small, complete bone situated just above the skull and in front of the right naris. Only a part of the bone is preserved, but the remainder is shown by an impression in the rock. There is a proximal, thickened portion, which probably is divided into two articulating surfaces side by side (this part of the bone is partially hidden in the rock matrix). Beyond this, the impression in the rock shows that the bone
terminated in a very thin, rounded edge. The bone is here identified tentatively as a chevron.

The other bone fragments in the slab are so indeterminate in shape that no identifications of them have been possible.

In the foregoing description an attempt is made to describe and analyze the characters of the phytosaur skull and associated bones from the Granton Quarry, and from this description and analysis it has been argued that the specimen can without much doubt be placed within the genus Rutiodon. Moreover, if its identification as Rutiodon is correct, the specimen, because of its size and configuration, can be identified as Rutiodon carolinensis. As such the specimen is important in adding corroborative information to our knowledge of Rutiodon carolinensis, such published information being previously based (beyond the knowledge of the type) on the skull from North Carolina described by Ebenezer Emmons a century ago, on other materials now in the American Museum of Natural History, described by McGregor in 1906, and more recently redescribed and revised by Colbert (1947) and by Gregory (1962b), and on a fragmentary left premaxilla from Pennsylvania described by Wanner (1926).¹

The specimen is also important because it gives us the first record of a fairly complete phytosaur skull from the northern exposures of the Newark Group, hitherto a lack that had been keenly felt by vertebrate paleontologists interested in the details of Triassic tetrapod life in North America.

RUTIODON AND CORRELATIONS

The present study and the ones mentioned above indicate that Rutiodon carolinensis inhabited a considerable range in eastern North America during Late Triassic time, extending, on the basis of known fossils, over a latitudinal spread of more than 5 degrees. There is every reason to

¹ A fragment of the lower border of a right lateral temporal fenestra and the anterior portions of the two mandibular rami of a phytosaur were discovered at Blue Bell, Pennsylvania, a few miles north of Philadelphia, and described by the present author in 1943. The specimen, from the Lockatong Formation, was identified as Clepsysaurus pennsylvanicus and referred by Gregory in his revision of the genera of phytosaurs (1962a) to the genus Phytosaur. The identification was made at the time in part on the basis of a heterodont dentition, then regarded as characteristic of Clepsysaurus and Machaeroprosopus, in contrast to a homodont dentition, then regarded as characteristic of Rutiodon. But Gregory, in his revision and particularly in his key to phytosaur skulls (1962a), has shown that both Phytosaur (including Clepsysaurus) and Rutiodon are characterized by heterodont dentitions. Since such is the case, and since those parts of the lower jaws preserved in the specimen from Blue Bell are rather slender, it seems quite probable that this fossil may be representative of Rutiodon.
think, of course, that its range was much greater, both to the north and to the south, while the presence of phytosaurs, some of which were identified by Gregory as *Rutiodon*, in the Chinle beds of Arizona and adjacent states, indicates that these phytosaurs inhabited much of what is now North America during the final stages of Triassic history. Furthermore, the occurrence of *Rutiodon carolinensis* in the black shales of the Cumnock and Lockatong formations gives some clues as to the habitat of this phytosaur. Certainly on the basis of these discoveries it lived along the shores of quiet ponds and lakes and probably in marshes as well. There is no reason to think, however, that its habitat was limited to such environments, because the discovery of *Rutiodon* in fluvial and floodplain sandstones and siltstones, especially in western North America, gives evidence of a variety of habitats for this phytosaur. The phytosaurs were large, aggressive, and very active reptiles, and it seems very probable that, like the modern crocodilians, they lived in various environments—along large rivers and small streams, in lakes and ponds.
and swamps, and perhaps even on occasion along the strand bordering the sea.

Gregory suggested in 1962 that *Rutiodon carolinensis* was of some significance in the correlation of eastern Triassic sediments containing it, and he based his conclusion on the stage of evolutionary advancement shown by the characters of this phytosaur. "*Rutiodon carolinensis*, with its series of primitive characters [generally small size, teeth that are not strongly heterodont, relatively short squamosal processes, a posttemporal arch that is not deeply depressed, no rostral crest, no flaring of alveolar border] suggests an age later than the Popo Agie and lower Dockum faunas in which *Paleorhinus* 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*. . . . *Rutiodon carolinensis* indicates that the age of the Cumnock formation is late Triassic and probably early but not earliest late Triassic" (Gregory, 1962b, pp. 20–21).

It is now possible to extend Gregory's remarks to say that the Lockatong Formation also is "probably early but not earliest late Triassic."

**PHYTOSAURS OF EASTERN NORTH AMERICA**

Perhaps a few remarks may be made about the phytosaurs of the Newark Group. Von Huene in 1913 described a partial phytosaur skeleton, unfortunately without a skull, that had been excavated from the Stockton Formation at the base of the Palisades, opposite Manhattan. This specimen was found about a half mile south of where the west piers of the George Washington Bridge are now situated, at a horizon not far above the level of the river, and of course beneath the Palisades intrusion. It was named by von Huene *Rutiodon manhattanensis*, and in Gregory's revision of the genera of phytosaurs (1962a) was placed in the genus *Phytosaurus*.

Some years later (in 1918) Sinclair described certain phytosaurian remains consisting of two vertebrae, a left ilium and femur, some scutes, and some isolated teeth which, because of their close resemblances to the phytosaur described by von Huene, he referred to *Rutiodon manhattanensis*. These remains came from "red Triassic shales" near York, Pennsylvania, and because of their similarity to the bones from Fort Lee there is every reason to think that they are probably cospecific with the New Jersey specimens.

In a recent letter to the author, Dr. Donald Baird of Princeton University has objected to the transfer of the specimen described by von Huene to the genus *Phytosaurus*, basing his objection primarily on the

1965
form of the scutes in this fossil. The scutes are rhomboidal, of the type characteristic of *Rutiodon*, rather than broad and rectangular, of the type characteristic of *Phytosaurus*. Because of the lack of a skull in the fossil from beneath the New Jersey Palisades, the evidence of the scutes may be taken as definitive, a point to which Gregory has agreed in a letter to the author. "In the absence of critical parts of skulls I would accept the indication of the *Rutiodon* type scutes as sufficient evidence to put *C. manhattanensis* in *Rutiodon* (or both in *Clepsysaurus*)" (letter of Gregory to Colbert, February 18, 1965).

Gregory's mention of *Clepsysaurus* brings up the problem of phytosaurian genera in eastern North America, a problem that was also raised by Baird in his recent letter to the author. It might as well be discussed in this place.

Gregory, in his revision of phytosaur genera (1962a), recognized the following forms from eastern North America; *Phytosaurus pennsylvanicus* (Lea), 1851; *Phytosaurus validus* (Marsh), 1893; *Phytosaurus manhattanensis* (Huene), 1913; and *Rutiodon carolinensis* (Emmons), 1856.

These names involve an extensive series of synonyms—genera and species proposed by Emmons, Lea, Marsh, Leidy, and Cope. The synonyms need not be listed here; they have been considered elsewhere, notably by Colbert and Chaffee (1941) and by Gregory (1962a).

The three genera of phytosaurs crucial to this discussion are: *Phytosaurus* Jaeger, 1828, type: *P. cylindricodon*; *Clepsysaurus* Lea, 1851, type: *C. pennsylvanicus*; and *Rutiodon* Emmons, 1856, type: *R. carolinensis*.

The problem of particular importance is the status of *Clepsysaurus*. Gregory had reduced it to a synonym of *Phytosaurus*, as is evident from the names cited above. But previously various authors had regarded it as probably a distinct genus, evidently dating back to the monograph of Camp, published in 1930. "I see good reason for separating the Pennsylvania and New Jersey phytosaurs from the North Carolina form *Rutiodon*, and have therefore resurrected the genus *Clepsysaurus* as separate from *Rutiodon*" (Camp, 1930, p. 141). This view was essentially that taken by Gregory, many years later, except that he equated the northern genus with *Phytosaurus*. Colbert and Chaffee (1941) and Colbert (1943, 1947) accepted *Clepsysaurus* as a distinct genus.

*Clepsysaurus pennsylvanicus* was described by Lea in 1851 on the basis of some teeth, vertebrae, ribs, and other bones from Upper Milford, Pennsylvania, none of which, as we now know in the light of modern evidence, can be considered as truly diagnostic. The type was found in the lower part of the Brunswick Formation and is, to date, the only phytosaur specimen known from that formation, although phytosaur foot-
prints have been described (as *Apatopus lineatus*) by Baird (1957, p. 486) from an equivalent horizon in New Jersey. On stratigraphic grounds, therefore, the possibility remains that *Clepsysaurus* represents a taxon different from *Rutiodon*, which occurs in the underlying Lockatong and Stockton formations in this region.

*Rutiodon carolinensis* was described by Emmons in 1856 on the basis of some teeth, vertebrae and ribs, a neural spine, and an interclavicle (designated by Emmons as a “frontal”) from the Deep River coal field of North Carolina. These materials also, on the basis of our modern knowledge, can hardly be considered as truly diagnostic. However, the fossils originally described by Emmons from North Carolina were supplemented almost immediately after his original description and in subsequent years by a large body of materials, including several skulls, more or less complete. Consequently *Rutiodon carolinensis* is a well-documented species.

How can we be sure that *Rutiodon carolinensis*, though possibly specifically distinct, is not referable to the genus *Clepsysaurus*? The answer is that we cannot. There is good reason to consider the possibility that only one phytosaurian genus occurs in the Upper Triassic beds of eastern North America, and, if so, then, on the basis of priority, the genus would appear to be *Clepsysaurus*. Nevertheless, we cannot be sure of this point, and considering the nature of the type of *Clepsysaurus pennsylvanicus*, probably we never shall. So, in view of the excellent materials of *Rutiodon carolinensis* available, as contrasted with the indeterminate and truly inadequate fossils on which *Clepsysaurus pennsylvanicus* is established, it seems only good sense to use the former of these two taxa as the basis for comparisons of phytosaurs discovered in eastern North America. Consequently it is here proposed that *Clepsysaurus pennsylvanicus* be considered as a *nomen vanum*, accordingly to be disregarded in future discussions of phytosaurian relationships. The term “*nomen vanum*” was proposed by Simpson in 1945, but has not been adopted by the International Commission on Zoological Nomenclature in its latest publication of the International Code, appearing in 1961. Therefore, to be in strict accordance with the Rules, perhaps it would be appropriate to regard *Clepsysaurus pennsylvanicus* as a *nomen dubium*.

It could be said that the status of *Rutiodon carolinensis* is somewhat clouded by the name *Centemodon sulcatus* Lea, 1856, established for the designation of a phytosaur tooth found in Pennsylvania. Since Emmons, in his type description of *Rutiodon carolinensis*, referred to Lea’s genus (but not the species) in a footnote (p. 307), it might be argued that *Centemodon* has priority over *Rutiodon*. But *Centemodon* was in effect ignored in the
literature, except for a few citations without discussions, from the time of its designation until Gregory called attention to it (1962b). In view of this fact and of the inadequacy of the tooth as a diagnostic specimen, Gregory quite rightly stated that *Centemodon* is a *nomen vanum*. Again, to be in accord with the Rules it might be best to regard this form as a *nomen oblitum*, a term to be applied to a name that has remained unused as a senior synonym in the primary zoological literature for more than 50 years.

Mention should be made of the phytosaur designated as *Belodon validus* by Marsh in 1893. This specimen was based on a fragmentary scapula, found at Simsbury, Connecticut, “below the anterior trap sheet,” and therefore in the New Haven arkose according to modern terminology. Here, once again, is a phytosaur based on an indeterminate fossil, and consequently, as in the case of *Clepsysaurus pennsylvanicus*, it seems eminently reasonable to relegate the name to the status of a *nomen vanum* or, more properly, according to the Rules, as a *nomen dubium*.¹

In the light of the above considerations, it is here proposed that one genus and two species of phytosaurs, as based on skeletal remains, be recognized from the Upper Triassic deposits of eastern North America. The forms to be so recognized are: *Rutiodon carolinensis* Emmons, 1856, and *Rutiodon manhattanensis* Huene, 1913.

*Rutiodon carolinensis* occurs typically in the lacustrine facies of the Newark Group, as represented by the Cummock Formation in North Carolina, and to the north in the Lockatong Formation of Pennsylvania and New Jersey. It has also been found in the New Oxford Formation of Pennsylvania. *Rutiodon manhattanensis* was first described from the Stockton Formation of New Jersey, but has since been identified from bones found in the New Oxford Formation of Pennsylvania. Thus the two recognizable phytosaurs of eastern North America are known from sediments that make up the lower portions of the Newark Group. But the type of *Clepsysaurus pennsylvanicus* (here regarded as a *nomen vanum* or a

¹ Some confusion is possible here. In 1916 Mehl created the genus *Machaeroprosopus*, the type of which is *Machaeroprosopus validus*, based on a skull from the Chinle Formation of northern Arizona. In his revision of the genera of phytosaurs Gregory made *Machaeroprosopus* a synonym in part of *Rutiodon* and in part (but questionably) of *Phytosaurus*. Any judgment as to the relationships of *Machaeroprosopus* must ultimately rest on the type specimen of the type species of the genus. Since Gregory placed Mehl’s type species within the genus *Rutiodon* (but with a question mark) it is to be assumed that the genus *Machaeroprosopus* as judged by the type species is regarded by him as synonymous with *Rutiodon*. This being the case, *Rutiodon validus* (Mehl) may be a species distinct from *Belodon validus* Marsh, included within the genus *Phytosaurus* by Gregory. The problem is not made any easier by the fact that the species created by Marsh is based on a single fragmentary bone, while the species described by Mehl is based on a skull that seems to be irrevocably lost.
nomen dubium), as suggested above, is from the Brunswick Formation, and phytosaur tracks identified by Baird from the upper part of the Brunswick at Milford, New Jersey (Baird, 1957), give ample indication that these reptiles ranged in age through the extent of the Newark Group, in other words, through the Upper Triassic of eastern North America. Thus, in this region, as in western North America, central Europe, and peninsular India, the phytosaurs enjoyed a long reign as dominant predatory reptiles of the Late Triassic tetrapod faunas inhabiting the Northern Hemisphere.

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