

A PHYLOGENETIC ANALYSIS OF PHYTOSAURIA FROM THE LATE TRIASSIC OF  
THE WESTERN UNITED STATES

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Abstract - A review of the group Phytosauria shows that the group Rutiodon is restricted to the lower unit of the Petrified Forest Member of the Chinle Formation (Late Carnian). Another group, previously referred to Rutiodon and now revised as Pseudopalatus, is restricted to the upper unit of the Petrified Forest Member of the Chinle Formation (early Norian). Examination of phytosaur skulls and lower jaws, using a cladistic method, has helped revise the systematics of each group. Recognized species of Rutiodon are R. carolinensis, R. crosbiensis, R. adamanensis and R. gregorii. Recognized species of Pseudopalatus are P. buceros and P. pristinus, in addition to a the new species, Pseudopalatus mccauleyi.

INTRODUCTION

During the early Mesozoic the swampy, fluvial environments of Arizona, New Mexico and Texas were inhabited by archosaurs with "crocodile-like" forms and habits. These were the semi-aquatic, quadrupedal phytosaurs, whose remains have been discovered in Late Triassic sediments of North America, Europe, India and Africa. The western North American sediments range in age from the late Carnian to the early Norian (Olsen and Sues, 1986). Two genera of phytosaurs, Angistorhinus and Paleorhinus, are restricted to the Carnian. These early phytosaurs display characters that are more primitive than in other phytosaur taxa, such as completely dorsal supratemporal fenestrae and nares that are anterior to the antorbital. Several taxa have been established on characters more derived than those of Angistorhinus and Paleorhinus. The names assigned to these taxa depend upon interpretations of the great amount of variation seen in the specimens, which often consist of complete skulls with lower jaws. Some of the confusion of phytosaur taxonomy becomes apparent when the historical literature is reviewed.

The first phytosaurs were discovered in early 19th century Europe. In North America the first remains of phytosaurs were found as scrappy remains of jaws, skulls and teeth in eastern North America (Newark Supergroup). In the western United States, early workers include McGregor (1906), who revised some of the taxonomy by synonymizing several genera into one genus, Rutiodon, and Mehl, who established three new genera: Angistorhinus (1913), Machaeroprotopus (1916) and Pseudopalatus (1928). Camp's (1930) monograph was the first attempt to classify all the North American phytosaurs into major groups and to comment on their evolutionary and biostratigraphic histories. In Camp's (1930)

classification, North American phytosaurs were geographically separated into the eastern genera Clepsysaurus and Rutiodon, the southwestern genus Machaeropsopus and the southern genus Leptosuchus. Camp also recognized the more "primitive" taxa Paleorhinus, Angistorhinus, and Promystriosuchus. Gregory (1962a) recognized no differences among Machaeropsopus, Leptosuchus and Rutiodon other than the variation that he attributed to growth, sex or individual differences. He therefore synonymized Machaeropsopus and Leptosuchus with Rutiodon because of the latter's priority of name. Gregory referred all species of Machaeropsopus to Rutiodon except M. gregorii, which he assigned to the genus Phytosaurus because of its similarity to the European Phytosaurus kapffi. Gregory (1969) later referred P. gregorii to Nicrosaurus gregorii because of the large crest and robustness of the skull, and that name has been retained until now.

Paleorhinus and Angistorhinus are easily recognized and diagnosed because they retain a suite of primitive characters but also have a few derived ones. It has been more difficult to distinguish among specimens and taxa that have derived characters. Often specimens were referred to a particular genus because of general similarity of characters, regardless of differences (e.g., Gregory's referral of R. gregorii to Nicrosaurus). And, many times diagnoses turned out to be mere descriptions, not establishing characters that would define the taxon. This occurred easily because polarities of characters were not established. The phylogenies that were postulated were influenced by geographic provenance, stratigraphic placement, comparison with European material without adequate diagnoses of genera and species or characters that are more reasonably attributed to some type of non-taxonomic variation. In this study, I have applied a phylogenetic systematic method to establish character polarity. A suite of derived character states can now be used to diagnose the genera Rutiodon and Pseudopalatus, and other phytosaur taxa can be linked to these.

The systematic relationships of European phytosaurs to North American phytosaurs are outside the scope of this paper. However, derived characters observed in the type specimens of Belodon plieningeri and Nicrosaurus kapffi can also be discerned in many North American specimens referred to the genus Rutiodon. Only through a complete character analysis of all European and North American phytosaurs could their taxonomy be fully revised and any common species or genera between the two continents determined. As a preliminary step, the task of this paper is to redefine and diagnose the North American genera Rutiodon and Pseudopalatus and to revise the species belonging to them.

#### Rostral Morphology as a Taxonomic Character

Problems in phytosaur taxonomy can be largely reduced to differences in the interpretations of the systematic value of some characters. One such character that has caused a great deal of confusion in determining phytosaur relationships is rostral morphology. The morphology of the phytosaur rostrum varies from

slender and uncrested to wide and partially or fully crested. This morphological variation has been attributed to specific difference (Camp, 1930), to growth and sexual variation (Colbert, 1947) and to size (Gregory, 1962b).

Camp (1930, p.28) was the first to infer that the development of a rostral crest was a species-specific character. He placed 17 skulls from the Chinle Formation of Arizona into stratigraphic position and observed that the uncrested, partially crested and fully crested forms were segregated through successive horizons. From this he concluded that the crest differences represented different species because if the difference was sexually dimorphic, then there would be skulls of the various forms in each horizon. Two problems plague Camp's model. First, seven of the skulls that he used are too fragmentary to determine rostral type, so his sample size is too small; and second, the relative stratigraphic position of each skull is in doubt. Fifteen of the skulls were collected from the Petrified Forest National Park, where relative stratigraphic position is known at only a few of Camp's localities. Therefore, correlations among lithologic units cannot be made.

The material collected from the Petrified Forest National Park (PFNP) has a distribution of partially crested forms throughout the lower Petrified Forest Member (late Carnian: Litwin, unpub.). Other than Rutiodon gregorii, it is not clear which phytosaurs Camp meant to include as "fully crested," although I assume he meant the skulls that he assigned to Rutiodon lithodendrorum. Therefore, of the skulls collected from Petrified Forest National Park, none are fully crested. Rutiodon gregorii was collected north of the PFNP, near Round Rock, Arizona, and is the only fully crested North American phytosaur. The several partially crested phytosaurs from the Petrified Forest National Park (lower Petrified Forest Member) are referred to two species, Rutiodon crosbiensis and Rutiodon adamanensis, based on shared characters (Fig. 1). R. gregorii has not been collected in association with R. crosbiensis or Rutiodon adamanensis. Correlation among the various localities of these three species has not been made, therefore Camp's suggested segregation of crested and uncrested forms is not supported by the available evidence.

Colbert (1947) inferred that the rostral variations reflected both growth and sexual dimorphism; he concluded that all adult phytosaurs have rostral crests and young males have crests, but young females do not. His determination of "adult" specimens was based only on size skull length, and the "sex" of the specimens was based on whether the external nares were elevated or not (1947, table 3, p.71). Skull length is not always by itself a good criterion for determining the age of a specimen. Degrees and sequences of fusions in postcranial material (e.g., vertebrae and pectoral and pelvic girdles) could document shared ontogenetic stages among specimens; however, very little associated postcranial material is available for most North American skulls described up to now.

It is also difficult to justify the inference of sexual

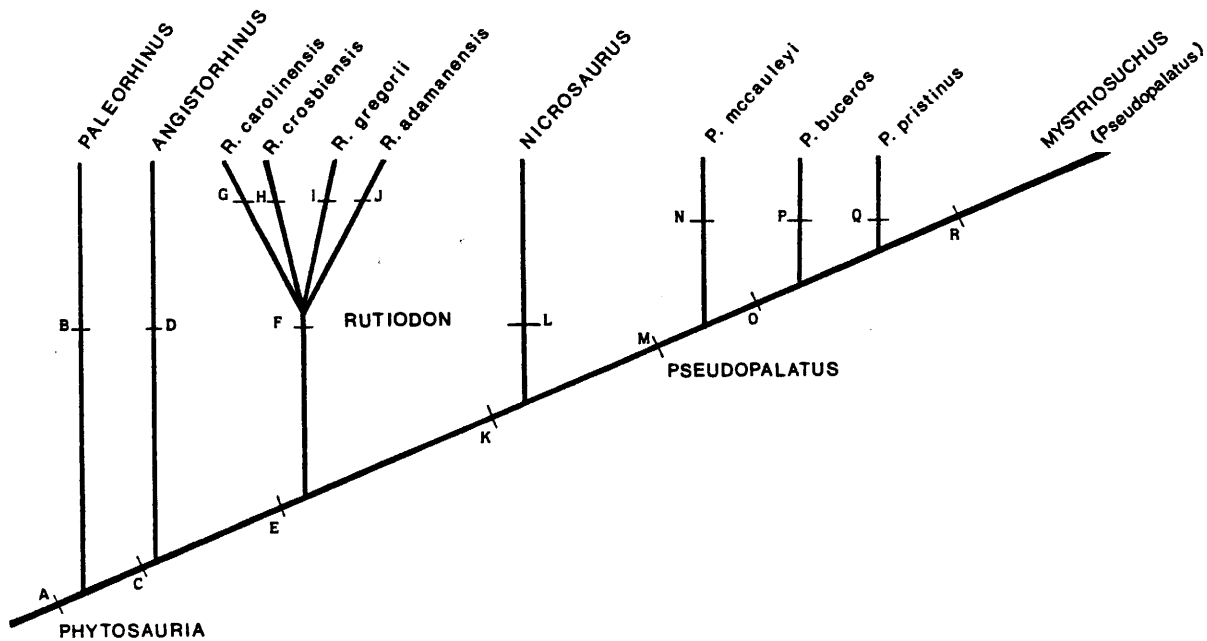


FIGURE 1. Cladogram of western United States phytosaurs. Nodes are defined by the following characters:

A. Phytosauria

1 - A posterior elongation of the premaxillaries.

2 - Nares are not terminal.

3 - Nasal bones that completely surround the narial openings, except where a septomaxillary has been identified.

4 - Squamosals are divided into dorsal and lateral planes by anteroposterior ridges.

B. Paleorhinus

5 - Nares face anteriorly.

6 - Orbits face dorsally.

7 - The posterior borders of the narial openings lie directly above or slightly in front of the antorbital fenestrae.

8 - The posterior borders of the narial openings lie directly above or slightly in front of the anterior borders of the antorbital fenestrae.

C. Angistorhinus, Rutiodon, and Pseudopalatus

9 - The posterior borders of the narial openings lie superior and posterior to the anterior borders of the antorbital fenestrae.

10 - The ventral extension of the squamosal forms a hook-like process.

11 - Nares face dorsally.

12a- The squamosal has a posterior process (laterally deep in Angistorhinus and Rutiodon).

D. Angistorhinus

13 - Long parietals remain united for more than half the length of the supratemporal fenestra.

14 - Combination of dorsal supratemporal fenestrae and posterior nares (above antorbital).

E. Rutiodon and Pseudopalatus

15 - Combination of posteriorly depressed supratemporal fenestrae

and posterior nares (above antorbital).

F. Rutiodon

16a- The supratemporal fenestrae have wide anterior semicircular borders with depressed posterior portions.

17a- The parietal extensions angle obliquely from the skull roof to the internal medial squamosal ridge and can be seen in dorsal view.

18a- The parietal extensions are long, thin bones that lie dorsal to the supraoccipital.

19a- The parietal-supraoccipital complex forms an inverted "V" shape.

20 - The posttemporal fenestrae are dorso-ventrally wide.

G. Rutiodon carolinensis

21 - The rostrum is cylindrical and without a crest.

H. Rutiodon crosbiensis

22 - The quadrates are pulled in toward the midline of the skull.

23 - The squamosals are laterally vertical.

24 - In lateral view, the squamosals comprise more than half the height of the skull.

25 - The region extending from the orbits and along the parietal crest is almost a straight line.

I. Rutiodon gregorii

26 - Full crest, not above skull level.

27 - The rostrum lies along a midline of the skull, halfway between the dorsal and ventral surfaces.

28 - The jugal no longer meets the quadrate in a lateral plane; the quadrate has angles upward and inward.

29 - Lateral temporal fenestra opens dorsolaterally.

30 - The posttemporal extends more laterally because the opisthotic is not completely fused to the internal squamosal.

31 - Anterior shift in tooth pattern.

J. Rutiodon adamanensis

32 - The rostrum is partially crested; the uncrested, anterior portion is cylindrical in shape.

33 - The squamosals are distinct, with deep, rounded posterior processes.

K. Nicrosaurus, Pseudopalatus, and Mystriosuchus

16b- The supratemporal fenestra has recessed further below the skull deck causing the anterior portion to become very compressed.

34 - The postorbital bar is broad and stout.

12b- The squamosal is laterally compressed.

35 - The posterior portion of the jugal is a much thinner bone before it meets the quadratojugal.

L. Nicrosaurus

36 - A flange extends along the lower premaxillary.

37 - A bulbous snout constricts just behind the terminal end.

38 - Squamosals are compressed, yet rounded.

39 - Parietal-supraoccipital complex has inverted V-shape as in Rutiodon, but with steeper sides and not as splayed.

M. Pseudopalatus

40 - External nares are raised above the level of the skull roof.

41 - The squamosal is compressed and without a rounded, posterior process.