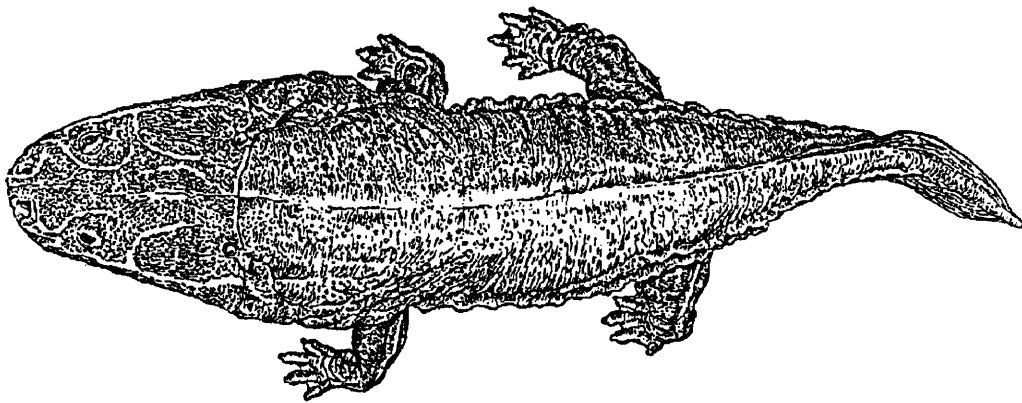


# FAUNAL ANALYSIS AND BIOCHRONOLOGY



## LATE TRIASSIC TETRAPODS OF THE NORTH AMERICAN SOUTHWEST

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**Abstract** - The Upper Triassic Chinle and Dockum formations are broadly contemporaneous sequences of sediments deposited in adjacent continental basins in the southwestern United States. The tetrapod faunas of these formations and their biostratigraphic ranges are reconsidered in light of new discoveries. A previously hypothesized division of the Chinle vertebrates into stratigraphically separate lower and upper vertebrate faunas is still supported by the available evidence. However, many of the taxa (principally aetosaurs and phytosaurs) known from both basins appear to have broader temporal ranges in the Dockum basin. Several interpretations of these data are considered in this report. Finally, paleoecological interpretations of the faunas of the two basins are briefly reviewed.

## INTRODUCTION

The Upper Triassic exposures comprising the Dockum and Chinle basins of the southwestern United States are one of the most areally extensive sequences of continental rocks of this age in the world, with discontinuous exposures stretching west to western Nevada, east to eastern Texas, south to the southern parts of New Mexico and Arizona and north to northern Colorado and Utah. Despite being broadly contemporaneous in age, numerous faunal differences seem to categorize the two formations, which were deposited in adjacent tectonic basins (Dubiel, 1989). This contribution briefly reviews tetrapod faunas of the two formations and compares and contrasts the endemic assemblages in terms of paleoecology, environments of deposition and biostratigraphy.

## FAUNAL COMPOSITION

## Amphibia

To date, the Late Triassic amphibian fauna differs from those in correlative Late Triassic beds in Eurasia and South Africa, and in the Newark Supergroup (Olsen and Sues, 1986) primarily in that it is dominated by metoposaurid labyrinthodonts and lacks any record of capitosaurids. One of the dominant faunal elements in the Late Triassic of the Southwest is the metoposaurid amphibian Metoposaurus. This genus is abundant throughout the stratigraphic extent of the Dockum Formation, and in the lower parts of the Chinle

Formation, although its stratigraphic range in the latter formation may be a result of facies restriction (Parrish, in press). A small metoposaurid that seems to be morphologically distinct from Metoposaurus has been found in the Chinle Formation throughout its stratigraphic range and from the Cooper Member of the Dockum. This material has been referred by Davidow-Henry (1989) to Dictyocephalus, a genus erected by Leidy (1856) on material from the Newark Supergroup of New Jersey. The enigmatic amphibian Laticopus was described by Wilson (1948) from the lower part of the Dockum Formation. The single skull is very poorly preserved and its affinities are uncertain. A second skull of a similar animal was found by Chatterjee in the Post quarry of the Dockum (Chatterjee, 1986a) and is currently under study by J.R. Bolt at the Field Museum of Natural History.

### Amniota

The amniote fauna is made up of fragmentary anapsids (procolophonids), diverse diapsids (a few lepidosaurs and many archosauromorphs) and relatively rare synapsids (dicynodont therapsids and cynodonts).

### Anapsida

Baird and Take (1959) and Murry (1986) concur that the fragmentary jaw material described by Case (1928) as the fish Colognathus instead has procolophonid anapsid affinities. Jacobs and Murry (1980) mentioned a jaw fragment that was an apparent procolophonid from the Downs quarry of the lower unit of the Petrified Forest Member of the Chinle near St. Johns, Arizona. Procolophonids are well known from Late Triassic exposures in the eastern United States and in Europe, occurring almost up to the Triassic/Jurassic boundary (Fraser, 1988).

### Diapsida

The Diapsida form two divergent monophyletic clades, the Lepidosauromorpha (with modern members lizards, snakes and Sphenodon) and Archosauromorpha (with modern members birds and crocodilians), that diverge early in diapsid history (e.g., Gauthier, 1984). As is characteristic of the Late Triassic worldwide, the dominant elements of the fauna both in terms of abundance and diversity are members of the Diapsida, and in particular of the Archosauromorpha.

Murry (1982, 1986) has described fragmentary lepidosauromorphs, consisting of jaw material of a sphenodontid and a ?lepidosaur, from the Dockum Formation. Additional small lepidosauromorph material has been described from the Chinle Formation near St. Johns by Tannenbaum (1983) and by Murry (1987), who referred some material to the families Sphenodontidae and Kuehneosauridae. These small lepidosauromorphs remain

relatively poorly known, mostly from jaw fragments. Although similar animals are also known from more complete material in correlative beds in Great Britain (e.g., Robinson, 1967; Fraser, 1988, and references therein).

The recent studies of Carroll (1976), Brinkman (1981), Gauthier (1984, 1986) and Benton (1984) have shown that a number of amniotes that previously were thought to have lepidosauromorph affinities are instead much more closely related to the Archosauria. These taxa, comprising the Protorosauria and Rhynchosauria, are the sister groups of the Archosauria in the Archosauromorpha (e.g., Benton, 1984, Gauthier, 1984).

The protorosaurian archosauromorph Trilophosaurus was named by Case (1928) from a fragmentary maxilla. A complete osteological description was published by Gregory (1945) based on much better material, including one nearly complete skeleton from a single site in the lower part of the Dockum Formation, Howard County, Texas. Additional trilophosaur material is known from the lower unit of the Petrified Forest Member of the Chinle Formation in northeastern Arizona, including small material that Murry (1987) used to designate a new species of Trilophosaurus.

A second protorosaurian, the small protorosaurid Malerisuchus, was reported from the Post quarry of the Dockum Formation by Chatterjee (1986b). Although Chatterjee erected a new species for the Dockum form, he considered it congeneric with another species from the Maleri Formation of India.

Rhynchosaurians have been noted, but not extensively described, from the Dockum Formation by Elder (1978; 1987) and Murry (1986). The presence in the Chinle Formation of large archosauromorph limb bones that are probably rhynchosaurians has been noted by Parrish (in press). To date, the Late Triassic material known from the southwestern United States is relatively incomplete, although unquestionable rhynchosaur material is known further north from the Popo Agie Formation of Wyoming (N. Hotton, pers. comm., 1988) and from Nova Scotia (Baird, 1963). As opposed to the situation in the Late Triassic of South America and Scotland, rhynchosaurians seem to have been a relatively rare or at least rarely preserved part of the Late Triassic fauna in the southwestern United States.

The Archosauria are the dominant elements of the continental fauna during most of the Mesozoic. Later in the Mesozoic, the dinosaurs become the dominant elements of the fauna. In the Late Triassic, the bulk of the archosaurian fauna is made up of groups more closely related to the Crocodylia, including the phytosaurs, the aetosaurs, the poposaurians and primitive members of the Crocodylomorpha. These groups were united by Parrish (1987) as the crocodile-normal archosaurs.

The Parasuchia, or phytosaurs, are an entirely Late Triassic group of archosaurs with a very specialized skull form characterized by an elongate gavial-like rostrum. Despite overall similarities in skull form, individual specimens of phytosaurs exhibit a wide variety of differences in morphological detail. Sorting out the sources of variation, which

include species differences, postmortem crushing, intraspecific variation and probably sexual dimorphism, is an ongoing problem.

The phytosaurs are the dominant faunal elements throughout the Late Triassic of the American Southwest, and represent a diverse assemblage that is badly in need of systematic review. The most recent monographic treatment was by Westphal (1976). Recent studies have included Ballew (1986), who concentrated on Chinle forms from the Petrified Forest National Park region and Shelton's (1984) description of new specimens from the Post quarry of the Dockum Formation. A new interpretation of the biostratigraphy of North American phytosaur genera is offered by Murry and Long (1989).

Paleorhinus and Angistorhinus are two genera that commonly occur at the same stratigraphic horizons. They occur together in the Popo Agie Formation of Wyoming (e.g., Mehl, 1928), the Dockum Formation of Howard County, Texas (reviewed by Murry, 1986) and the Argana Formation of Morocco (Dutuit, 1977a, b). These are the first phytosaur genera that appear (excluding the questionably dated and now destroyed single specimen of Mesorhinus: Jaekel, 1910). They were initially thought to be entirely separated stratigraphically from the genus Rutiodon (e.g., Gregory, 1962), but instances of co-occurrence have been noted in both the Dockum and Chinle formations.

Nicrosaurus is a stratigraphically persistent, large-headed phytosaur that is distinguished by the following characters: (1) narial crest and skull-roof form an essentially flat horizontal surface, (2) elongate antorbital fenestrae that open anterodorsally and (3) persistently broad snout that is characterized by a ventrally expanded "step" in the tooth row on the premaxilla near its junction with the maxilla. The genus Rutiodon was erected by Emmons (1856) on material from the Newark Supergroup of North Carolina. Gregory (1962) expanded the amount of Chinle material referred to this genus by synonymizing Mehl's (1916) genus Machaeroprotopus with Rutiodon. With this one taxonomic reassignment, Rutiodon became the most common archosaur fossil in the Chinle Formation and the upper part of the Dockum Formation.

Camp noted that the existing species of Chinle phytosaurs could be divided into two stratigraphically separate groups, comprising a series of species of Rutiodon [Machaeroprotopus] below the Sonsela Sandstone and Rutiodon [Machaeroprotopus] tenuis above the Sonsela. Pending formal reconsideration of the taxonomic affinities of these genera, Long and Ballew (1985) and Parrish and Carpenter (1986) put these two groups into the informal groups Rutiodon A and Rutiodon B, respectively. Ballew (1986) contemplated placing the specimens of Rutiodon B into another genus, although this has not yet been formally proposed. The strong possibility exists that this taxon may be synonymous with the German genus Mystriosuchus, as both share a number of derived characters, including the presence of elongate, very narrow snouts and large numbers of small, isodont teeth. In any event, Rutiodon B is stratigraphically restricted, being limited to the Chinle Formation above the lower unit of the Petrified Forest Member and the Redonda Member of the Dockum Formation