

**PALEOECOLOGY AND VERTEBRATE FAUNAL RELATIONSHIPS
OF THE UPPER TRIASSIC DOCKUM AND CHINLE FORMATIONS,
SOUTHWESTERN UNITED STATES**

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Abstract-The Dockum and Chinle formations of the southwestern United States serve as a model for establishing the structure of Upper Triassic vertebrate communities and environments. The dominant sediment type of the southwestern Triassic consists of red shales. Although some of the coloration may be due to diagenetic factors, gray coloration of sediments believed to be deposited within lacustrine or backswamp environments indicates that some coloration of Triassic sediments may be primary. The vertebrate trophic categories of the southwestern Triassic include aquatic omnivores (hybodont sharks, lungfish, redfieldiid fish), aquatic carnivores (palaeoniscid, semionotid, coelacanth fishes; xenacanth sharks, metoposaurid amphibians, phytosaurs), terrestrial herbivores (procolophonid, trilophosaurid, stagonolepidid, kannemeyeriid, rhynchosaurid reptiles), terrestrial carnivores and omnivores (laticopid amphibians; sphenodontid, eolacertilian/lacertilian, protorosaurid, podokesaurid saurischian, poposaurid/rauisuchid, cynodont reptiles) and possibly aerial carnivores (kuehneosaurs, pterosaurs). The differences in faunal composition and abundance indicate a complex and changing community structure in the southwestern Upper Triassic.

SEDIMENT COLORATION - PALEOECOLOGY AND DIAGENESIS

Probably the single-most sedimentary feature associated with Permo-Triassic sediments worldwide is red beds. The origin of this red coloration has been much-debated and is probably not yet resolved. The controversy seems to be divided as to whether the coloration is primary (of detrital origin) or secondary (a diagenetic effect). As this field conference will involve a considerable drive through unrelenting exposures with red coloration, a review as to the significance of this feature seems in order.

Krynine (1949, 1950) considered the origin of red beds as a direct result of wet-dry seasonality in tropical climates. The formation of the red coloring was believed to be due to the incision of laterites and hematite-rich rock by highland streams during the rainy seasons, the admixture being deposited as red beds downstream. However, Van Houten (1961) and Walker (1967a, 1967b) noted that in areas where red lateritic soils were mixed with fresh detritus the resulting alluvium was a brown or yellowish-brown color, not red as Krynine speculated. No modern red beds are known to form within humid climates. However, it has been suggested that if red beds deposited in such climates were later subjected to oxidizing ground water regimes, a common

situation where water tables are lowered, the red beds may form by diagenetic alteration (Reading, 1986). Miller and Folk (1955) believed that the formation of red coloration was only indirectly dependent on climate or depositional environment and that the key to the origin of red beds was in the proximity of the depositional environment to an igneous or metamorphic source from which magnetite or ilmenite could be derived. Although the presence of iron-bearing detrital grains was also considered to be important by Walker (1967a, 1967b), other factors were believed to be equally important in formation of the red coloration. This included postdepositional conditions in which interstratal alteration of limonite to hematite could be achieved and by the maintenance of a proper Eh-pH environment in which ferric oxides could form. Also, time was considered a factor for alteration of beds to a red color although no specific temporal boundaries were suggested. Study of alluvial fan and tidal flat sediments in Baja California by Walker et al. (1978) showed that formation of red beds in that region involved the slow transformation of colors of granite-derived sediment from gray (Recent) to yellow (Pleistocene) and finally to red (Pliocene-age sediments). The most important controlling feature seemed to be the presence of water provided by ephemeral rains and runoff, although the elevated temperatures in the region also assisted in the process and the proximal occurrence of biotite- and hornblende-rich source rocks (to supply the iron) was critical. In view of this evidence, the diagenetic origin of red beds seems convincing.

Although the origin of red beds has generally been thought of as occurring primarily in distal flood plains or to a lesser extent within lacustrine environments, Clemmensen (1979) has suggested that red beds in the Lower Triassic Buntsandstein of Helgoland and the Upper Triassic Malmros Member of East Greenland were formed within playa lake sediments. Many of the Dockum and Chinle mudstones show the same characteristics as those noted by Clemmensen for formation of red beds in a playa. For example, work by McGowen (1980), McGowen et al. (1979, 1983), Seni (1978), Boone (1979), Handford et al. (1980), Granata (1981), Johns and Granata (1987) and Dubiel (1987) indicates the persistence of relatively large, very shallow ephemeral lakes with greatly fluctuating water levels. However, there are gray mudstones at Kalgary (Crosby County, Texas), a locality believed to represent an ephemeral lacustrine environment, and at the Dying Grounds, Crocodile Hill and Placerias/Downs quarries (Arizona), all of which probably represent backswamp or similar environments. The persistence of the gray color in these deposits as opposed to the red coloration found within the deltaic and ephemeral lake environments within the Dockum and Chinle provides some evidence for a syndepositional, as opposed to a postdepositional, origin of coloration for at least some of the southwestern Triassic beds. We will be seeing other indications of gray (mostly interpreted as lacustrine or swampy environments) versus red (mostly fluvial overbank deposits, playas (?), etc.) coloration within the Dockum and Chinle, seemingly within similar-textured sediments. Therefore, it may be that not all Dockum and Chinle colorations are due to diagenesis but include some primary

"grays" (and "reds" ?) within the finer-grained facies of the southwestern Triassic.

VERTEBRATE COMMUNITIES AND PALEOECOLOGY OF THE SOUTHWESTERN TRIASSIC

To obtain a better understanding of paleoecological relationships of localities within the southwestern Triassic, screen sieving techniques have begun to be utilized at sites in Texas, New Mexico and Arizona (Jacobs and Murry, 1980; Murry, 1981, 1982, 1986, 1987a, b, 1989a, b; Lucas and Oakes, 1988). By this method, many of the smaller members of the fauna are recovered and a better picture of paleoecological relationships of the southwestern Triassic obtained. These studies have resulted in the establishment of a framework for understanding community structures in the Upper Triassic, although many problems remain to be solved. The fragmentary nature of the material dictates that the analysis should be approached with caution and intensely scrutinized thereafter.

The biological analysis of a paleocommunity may often be rather complex, especially regarding vertebrates. Kauffman and Scott's (1976) stages of ecological analysis include data collection at closely spaced intervals, assembling mental constructs from the data, interpreting the taxa sets and ranking the ecological units. Although this may be practical in interpretation of marine organisms, it may not be possible for vertebrate communities. For example, most vertebrate localities do not have closely spaced fossiliferous units, and this is especially true in Permo-Triassic red beds. Also, interpreting and ranking vertebrates as concerns their paleoecology is considerably more complex than for invertebrates, since vertebrates are much more complex in their ecological and behavioral interactions, and their environment is often subject to greater fluctuation of environmental conditions. This is evident in each of the Triassic vertebrate localities discussed herein where elements of both aquatic and terrestrial vertebrate communities are present. Temporal and taphonomic problems arise when defining a community since a congregation of interacting, contemporaneous organisms is not generally preserved as fossils, even under ideal conditions. Most fossil deposits are assemblages of more than one community, such as that seen in essentially all of the localities in the southwestern Triassic. Sites in which large numbers of well-preserved bones are found, such as the Metoposaurus bakeri collection from Scurry County, Texas (Case, 1932a), may be essentially contemporaneous but often contain only a single or very few species preserved. Therefore, neither can they be classed as a community in the neoecological sense. However, although most members of each fauna are not likely to be contemporaneous and do not belong to a single community, their interrelationships should not be ignored. There was interaction between the aquatic and terrestrial paleocommunities in a given area within the southwestern Triassic as is the case in essentially all ecosystems. This is illustrated by the presence of vertebrates which were probably found in both habitats, such

as the phytosaurs. Triassic paleocommunity structure will be substantiated only by establishing a trend of recurring distribution among the taxa, a process which will involve more intense research on the biota as well as the physical and chemical parameters which control their distribution.

One primary method by which we can obtain an overall view of the changing ecologies of the southwestern Triassic is to review what is known concerning these animals, especially from the viewpoint of functional morphology. Therefore, I include herein a number of trophic "groups" in which I have categorized the fishes and tetrapods of the southwestern Triassic in terms of what has been inferred concerning their habits. It is much simplified, and a number of the taxa do not fit neatly into a particular category. I do not mean to infer by these discussions that there was a single "southwestern Upper Triassic community." Instead, a mosaic of taxonomic groups are present, of which some are seemingly rare and some common, and their presence in our samples fades in and out through the stratigraphic intervals.

Aquatic Omnivores

Within this category I include the hybodont (and neoselachian?) sharks, lungfish and redfieldiid fishes. However, the morphology of the redfieldiids suggest they may also have been carnivores.

Lissodus humblei, a small hybodont shark, has been recovered from the lower portion of the Dockum Group in Texas and the lower Petrified Forest Member (Chinle Formation) in Arizona (Murry, 1981, 1982, 1986, 1987a, 1989a, b, this volume). All of the species of Lissodus that have been recovered are evidently of freshwater origin. This provides strong evidence that this particular group of hybodont sharks was well adapted to a freshwater existence. According to Freeman (1975), the flat, low-crowned teeth of Lissodus found within the English Wealden (Cretaceous) were adaptations for a malacophagous diet. Lissodus humblei was probably also feeding on some variety of hard-shelled prey or grinding food between the upper and lower jaws since many teeth exhibit extreme wear. The teeth are heterodont with shorter, higher crowned teeth laterally and posteriorly. Therefore, one might surmise that the front teeth were probably used for grasping and the laterals for crushing prey.

Acrodus teeth described in this volume by Murry from the upper Petrified Forest Member (Chinle Formation) and Owl Rock Member are quite similar to the ptychodont genus Hylaeobatis, a taxon believed to have been derived from Acrodus (Patterson, 1966; Cappeta, 1987). The teeth of the new species also exhibits many ptychodont features, although parallel evolution of malacophagous taxa cannot be ruled out. Flat, wide teeth present on some species of Ptychodus (P. latissimus, P. polgyrus) similar to the Chinle Acrodus were probably utilized for crushing thick-shelled, benthic molluscs. The presence of many unionid bivalves and pulmonate snails in the upper unit of the Petrified Forest Member probably provided ample prey for both the lungfish and the hybodontiform sharks. The new shark fed on such