

## DID "THECODONTIANS" SURVIVE THE TRIASSIC?

KEVIN PADIAN

Department and Museum of Paleontology,  
University of California, Berkeley, California 94720

**Abstract** - Late Triassic and Early Jurassic terrestrial vertebrate faunas are mainly distinguished from each other by a loss of many groups common in the Late Triassic (Norian-"Rhaetian"). Most of these groups are of archosaurs commonly named "thecodontians," a term that engenders confusion because of its uncertain definition and its paraphyletic status. The concept of "thecodontians" has also confused biostratigraphic correlations in Triassic and Jurassic horizons because it is vague and misleading. The group "Thecodontia" does not appear to be diagnosable and its use should be abandoned, but individual groups usually assigned to "thecodontians" can be diagnosed and their stratigraphic occurrences tabulated and analyzed. In terrestrial horizons shown or suspected to be of Jurassic age, records of such groups are absent or very questionable. Previously described specimens from the Moenave, Kayenta and Navajo formations of the Glen Canyon Group of the southwestern U.S. are not "thecodontians," but crocodylomorphs. Other recently described specimens from the Rock Head area of the Kayenta Formation (Early Jurassic) of northern Arizona, previously assigned to aetosaurs, a "thecodontian" group, have now been identified as scutes of the thyreophoran dinosaur Scelidosaurus, known from the middle Liassic of England. This, along with data from other vertebrate fossils, strongly suggest a Liassic age for the Glen Canyon Group.

### INTRODUCTION

Since the 1940's, the stratigraphic assignments of four formations of the Glen Canyon Group of northern Arizona and southern Utah (Moenave, Wingate, Kayenta and Navajo formations: Fig. 1) have been shifted frequently between the Late Triassic and Early Jurassic, usually based on biostratigraphic interpretations of their fossil vertebrate fauna. The purpose of this paper is to examine the basis for these changing assignments. The historical paucity of vertebrate and other fossils is only part of the reason; another, the importance of which I think has been underestimated up to now, has been the confusion engendered by using the term "thecodont" or "thecodontian" to refer to a loosely knit assemblage of non-dinosaurian, non-pterosaurian, non-crocodylian archosaurs.

Despite the vast lateral and temporal extents of the

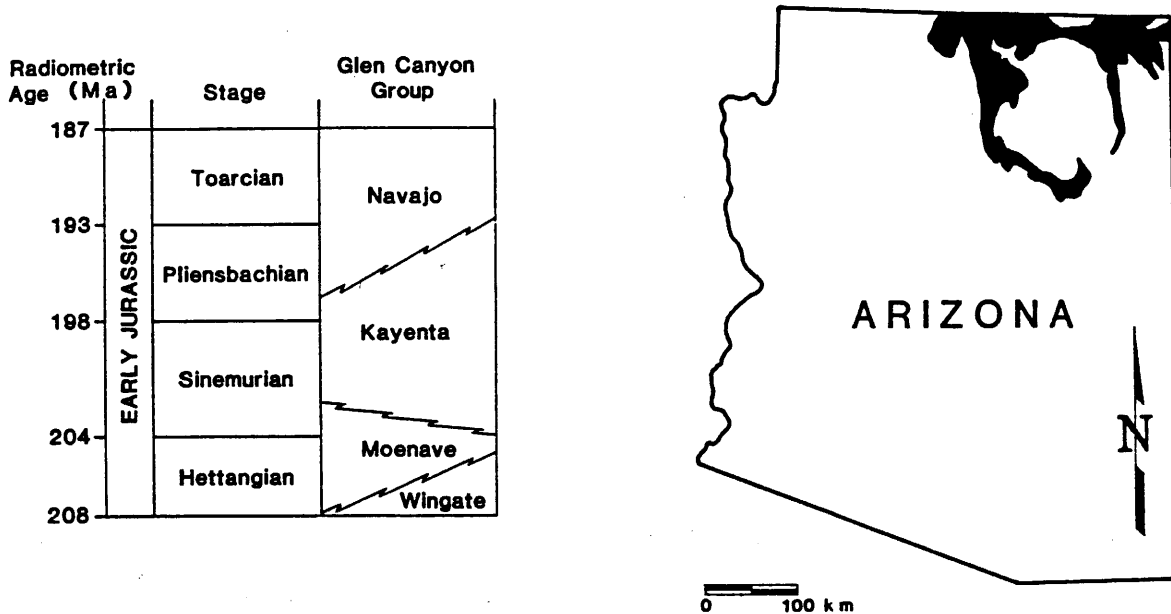


FIGURE 1. Exposures of the Glen Canyon Group in northern Arizona. Stratigraphy of component formations is given at left, along with estimated age and stage assignments (modified from Olsen and Sues, 1986, and Clark and Fastovsky, 1986).

exposures of the Glen Canyon Group, remarkably few fossil vertebrates were recovered from it until the last decade. Those that were recovered provided some contradictory implications for establishing a basis for biostratigraphical correlations. The theropod *Dilophosaurus* from the Kayenta Formation (Welles, 1984) was compared to the British megalosaurs of the Jurassic, largely on the basis of size (Welles, 1954); the latter group is still in need of extensive revision, however, and provides no useful biostratigraphic control. The crocodile *Protosuchus* (Colbert and Mook, 1951), from the Moenave Formation, bore some resemblances to the crocodylomorphs from the upper Stormberg Series of South Africa, which was at that time thought to be exclusively of Triassic age; crocodiles from horizons then known to be Early Jurassic were entirely "mesosuchian," and marine at that (e.g., those of the Holzmaden shales of West Germany and the Blue Lias of the Lyme Regis region of southwestern England). Tritylodontian cynodonts were known to occur in the Kayenta, but were not generally understood because their descriptions had not reached the published literature. "Prosauropod" dinosaurs from the Navajo Formation were compared to *Ammosaurus* and *Anchisaurus* from the Connecticut Valley (Newark Supergroup, eastern North America), also at that time thought to be exclusively of Triassic age. The small theropod *Segisaurus*, also from the Navajo, was in some respects problematic, despite Camp's (1936) description, because it was not easily compared to other theropods. There was, therefore, little basis for biostratigraphic comparison using fossil vertebrates.

Since the late 1970s, explorations in the Glen Canyon Group have vastly increased the known abundance and diversity of vertebrate fossils. Principal collections have been made by the

Museum of Northern Arizona (MNA), the Museum of Comparative Zoology of Harvard University (MCZ) and the Museum of Paleontology of the University of California, Berkeley (UCMP). Though most of this material is still under study, many significant publications have appeared (e.g., Crompton and Smith, 1980; Colbert, 1981; Jenkins et al., 1983; Padian, 1984; Welles, 1984; Sues, 1985a, b; Attridge et al., 1985; Clark and Fastovsky, 1986; Olsen and Padian, 1986; Padian, 1989). Discoveries of hundreds of macrovertebrates, microvertebrates and footprints from several different facies types in three formations now appear to be able to provide the basis for biostratigraphic correlation and age assignment for much, if not most, of the Glen Canyon Group (Padian, 1989).

In order to understand the problem of correlating the Glen Canyon Group, some background must be provided. The boundary between Triassic and Jurassic in continental strata is not easily recognized. This boundary was established on the European type section, which in the latest Triassic through the Jurassic is marine (reviewed in Colbert, 1986). Terrestrial vertebrates are generally poorly preserved in marine facies, though there are some exceptions (Padian and Clemens, 1985). However, these exceptions, such as the Early Jurassic Scelidosaurus (Owen, 1863), are few enough that they have not generally been of much help. Pollen from terrestrial plants is frequently preserved in the marine record, and is probably the best potential source for fine-scaled biostratigraphic correlation and relative chronostratigraphy. Indeed, Cornet et al. (1973) established the biostratigraphic zonation of the Newark Supergroup mostly on the basis of pollen, and Cornet (1977) continued to refine this zonation. Interfingering of marine and terrestrial sediments, and radiometric ages of terrestrial beds, are two other potentially useful sources of correlation. But it is rare to find marine-terrestrial interfingering, and it usually gives relatively coarse resolution because of the erosional effects associated with transgressions and regressions of the sea onto the land. It is equally rare to find beds amenable to radiometric dating; they are not always where we would like to have them, and the statistical margins of error in their results, while small, are enough at a distance of 200 million years to give us an estimated age range that sometimes extends across several stages (Olsen et al., 1987). This leaves us with fossil pollen as the most consistent, finest-scaled independent indicator of age. Unfortunately, the pollen record is often almost completely destroyed by oxidation of sediments (Padian et al., 1981; Clark and Fastovsky, 1986). Consequently, correlations based on fossil vertebrates often can only be poorly compared to other independent lines of evidence. However, our understanding of Triassic-Jurassic vertebrate biostratigraphy is rapidly improving as its data base grows.

#### TRIASSIC-JURASSIC BIOSTRATIGRAPHIC CRITERIA

There are really two important discoveries in the past

decade that have shifted our understanding of the Triassic-Jurassic transition in vertebrate faunas (Padian, 1986). The first is that many of the presumed Late Triassic horizons were more correctly assigned to the Early Jurassic (Olsen and Galton, 1977); the second is that in the Late Triassic horizons the dinosaurs were for the most part relatively low in diversity and abundance, compared to other Late Triassic archosaurian groups (Long and Padian, 1986). By the Carnian, both orders of dinosaurs appeared, as well as pterosaurs, sphenodontids and lissamphibians. Chelonians and crocodylians are at least as old as the Norian, and, at last count, six groups assigned to families of mammals and their closest relatives (Kuehneotheriidae, Haramiyidae, Trithelodontidae, Tritylodontidae, Morganucodontidae: Olsen and Sues, 1986, fig. 25.2, p. 328; plus Theroteinidae: (Sigogneau-Russell et al., 1986) were in place by the latest Norian, or what has traditionally been called the Rhaetian. All these groups appeared in that brief Late Triassic interval, and their descendants dominated the Mesozoic and Cenozoic. Their appearances do not define the Triassic-Jurassic boundary, however, because all these taxa were already present in the Late Triassic. Some monophyletic sub-divisions of these larger groups may yet be shown to define the boundary, but at least at the family level few so far proposed have proven reliable (and few genera are common or widespread enough to provide reliable trans-continental correlation). For example, of the taxa suggested by Olsen and Sues (1986, fig. 25.2), the sphenodontian Gephyrosauridae are known from British fissure fills of questionable age, the South African Heterodontosauridae come from sediments that cannot yet be precisely dated as Hettangian, and the Megalosauridae are as yet too poorly diagnosed to serve as a reliable taxonomic or biostratigraphic criterion (see Table 1).

If originations are not yet of much help in defining the Triassic-Jurassic boundary, what about extinctions? As recent compilations by Olsen and Sues (1986) and Benton (1986) have shown, many tetrapod groups seem to have last appeared in the Norian. These include the temnospondyl amphibian families Metoposauridae, Almasauridae (of questionable status, known only from Carnian-Norian strata of North Africa), ?Laticopidae (not clearly a valid family) and Plagiosauridae (except for a possible record in the Cretaceous of Australia: Milner, 1989); the reptilian groups Procolophonia, Trilophosauridae, Kuehneosauridae, Tanystropheidae (Protorosauria), several poorly known groups from the Italian Norian (including Drepanosaurus, Endennasaurus, and Megalancosaurus); and the archosaurian groups Rauisuchidae, Ornithosuchidae, Stagonolepididae (Aetosauria), Parasuchia (Phytosauria) and two taxa of pterosaurs from the Italian Norian. Two genera of chelonians, Proganochelys and Proterochersis, are known only from the Norian of Germany, but

TABLE 1. Taxa that have their last appearances in the Norian (latest stage of the Triassic) or their first appearance in the Hettangian (earliest stage of the Jurassic), with comments on the probable validity of such records. Modified from Olsen et al. (1986, 1987), and other sources and updated by personal communications from Drs. Paul Olsen and Hans Sues. Note that the Triassic-Jurassic boundary is mainly marked by extinctions of Norian taxa and that none of the three groups currently thought to have their first appearances in the Hettangian can be considered reliable.

Last known appearance in the Norian	
Metosauridae:	known from the Norian of Europe, North America, North Africa, and India
Almasauridae:	questionable; known only from Carnian-Norian deposits of North Africa
Plagiosauridae:	a questionable post-Triassic record from the Cretaceous of Australia (!)
Procolophonidae:	very late Norian records from the Triassic of the Newark Supergroup
Rauisuchidae:	late Norian records from Los Colorados Fm. of South America ( <u>Fasolasuchus</u> ) and from ?Norian sediments of Texas ( <u>Postosuchus</u> , from Dockum Group)
Trilophosauridae:	known from " <u>Tricuspes</u> ," found in the British Norian fissure fills and from Norian sediments of the Dockum Group, Texas; may be procolophonid (Olsen and Sues, pers.com.)
Kuehneosauridae:	known from the early Norian part of the Newark Supergroup
Tanystropheidae:	known from Norian records of Newark Supergroup, possibly western North America, and Norian of Italy
<u>Drepanosaurus</u>	known only from the Norian of Italy. Each could be referred to a
<u>Endennasaurus</u>	monotypic higher taxon. <u>Eudimorphodon</u> is related to the Early Jurassic
<u>Megalancosaurus</u>	: (Toarcian) German genus <u>Campylognathoides</u> . <u>Preondactylus</u> is the most
<u>Eudimorphodon</u>	primitive known pterosaur
<u>Preondactylus</u>	
Phytosauridae:	very late records from the Norian of Newark Supergroup and W. North America
Aetosauridae:	known from the Norian of eastern and western North America and Europe
Ornithosuchidae:	known from the Norian of South America (Los Colorados Fm.)
Proganochelyidae:	eponymous genus is from the Norian of Germany; <u>Proterochersis</u> is more closely related to <u>Kayentachelys</u> (Glen Canyon Gp.) and thus spans Triassic-Jurassic
First known appearance in the Hettangian	
Gephyrosauridae:	previously known from Jurassic fissure fills of Great Britain and Early Jurassic (Hettangian) deposits of Nova Scotia; now also recognized from the New Haven Arkose (Norian) of Connecticut (P.E. Olsen, pers.comm.)
Heterodontosauridae:	known from the Early Jurassic of South Africa, but not definitively of Hettangian age; known also from the Kayenta Formation of western North America (F.A. Jenkins, pers.comm.), but these sediments are probably no older than Sinemurian (Padian, 1989)
Megalosauridae:	Never adequately diagnosed. Most referred specimens are from Late Jurassic sediments. The earliest referred specimen is <u>Dilophosaurus</u> , from the Kayenta Formation; but the Kayenta is probably no older than Sinemurian, and <u>Dilophosaurus</u> is not properly considered a megalosaur (= carnosaur <u>sensu</u> Gauthier 1984), but a ceratosaur ( <u>sensu</u> Gauthier 1984), and ceratosaurs are known from the Late Triassic (Carnian and Norian) through the Late Jurassic or Early Cretaceous

the latter is linked phylogenetically to turtle groups of the Jurassic and later. For most of these groups it is not very clear in what part of the latest Triassic they expired. Some disappeared early on, but the fossil record of the latest Norian is not very good (Olsen et al., 1987, 1988; Padian, 1988), and there is no geographic area in which the transition to the Jurassic is established to be complete enough to address the question. As a result, the ranges of many of these groups may have extended to the end of the Triassic, but an earlier