

Invited review

Permian tetrapod extinction events

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ARTICLE INFO

Keywords:

Permian
Tetrapods
Mass extinctions
Best sections
Genus-level diversity
Olson's gap
Dinocephalian extinction event
Permo-Triassic boundary

ABSTRACT

Four substantial tetrapod extinctions have been identified during the Permian, but only one of these is an apparent mass extinction. Analyses of global compilations of the family-level diversity of Permian tetrapods have been confounded by incorrect and compiled correlations. Instead, analyzing diversity patterns at the genus level in “best sections” identifies only one apparent mass extinction of Permian tetrapods. Much evolutionary turnover took place among tetrapods during the latter part of the early Permian and had been identified as a single mass extinction at the Artinskian-Kungurian boundary. However, the only stratigraphically dense tetrapod record of the late early Permian, from the southwestern USA, indicates a succession of extinctions spread out from Redtankian through Littlecrotonian (Kungurian) time, not a single mass extinction. Olson's gap remains a hiatus in the global record of Permian tetrapods equivalent to part of the Kungurian-Roadian. Across the gap, eupelycosaur-dominated assemblages were replaced by therapsid-dominated assemblages, but the claim that this is associated with a mass extinction (“Olson's extinction”) has been based on compressing all of the extinctions of the Redtankian-Littlecrotonian and Olson's gap into one event. Recognition of Olson's gap does not preclude the possibility of an extinction at the early-middle Permian boundary (“Olson's extinction”). However, the gap in the tetrapod fossil record makes it impossible to establish the magnitude, precise timing and structure of the extinctions that took place across Olson's gap.

The only Permian mass extinction of tetrapods is the dinocephalian extinction event during the Gamkan (near the end of the Guadalupian), which saw the total extinction of dinocephalians and major diversity drop in therocephalians. In the Karoo basin of South Africa, this extinction is the loss of at least 64% of generic diversity. The changeover from dinocephalian assemblages to assemblages without dinocephalians in other parts of Permian Pangea suggests that the dinocephalian extinction event was a global event. The late Permian tetrapod extinctions are older than the end-Permian marine extinctions. Furthermore, the magnitude of the diversity drop and ecological severity of the end-Permian tetrapod extinctions have been greatly overstated. Best sections analysis in the Karoo basin indicates a stepwise late Permian tetrapod extinction during deposition of the upper *Dicynodon* Assemblage Zone that took at least 250,000 and perhaps more than a million years. The culmination of this stepwise extinction, across the highest occurrence of *Dicynodon* (= boundary of Platbergian and Lootsbergian land-vertebrate faunachrons) is a loss of genera not much above an inferred background extinction rate of Permian tetrapod genera and resembles the amount of turnover seen at several other boundaries of Permian and Triassic land-vertebrate faunachrons. The case for coeval land plant, insect and tetrapod extinctions during the Permian is a weak one. The first coeval marine and nonmarine mass extinctions of the Phanerozoic were likely the end-Guadalupian extinction. Climate change, notably greenhouse climates, may have driven Permian tetrapod extinctions, but that hypothesized relationship needs better documentation.

1. Introduction

The Permian Period of Earth history, about 299–252 million years ago, was a Pangean world where the vast supercontinent stretched nearly from pole to pole (Fig. 1). The late Paleozoic ice ages culminated in southern Gondwana, ending with the collapse of the major ice sheets during the early Permian. In the Pangean tropics, the extensive right lateral fault system along which the Gondwanan and Laurussian

supercontinents were sutured encompassed a series of orogenic belts—Hercynian (Variscan), Alleghanian and ancestral Rocky Mountain. The nonmarine sedimentary basins associated with these orogenic belts accumulated fluvial and lacustrine sediments that contain almost all of the fossil record of early Permian tetrapods (amphibians and amniotes). By middle Permian time, the focus of nonmarine deposition shifted to the vast intracratonic Paraná basin of Brazil, the Karoo foreland basin of southern Africa, the extensional basins of central and eastern Africa, the

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<http://dx.doi.org/10.1016/j.earscirev.2017.04.008>

Received 6 February 2017; Received in revised form 17 April 2017; Accepted 17 April 2017
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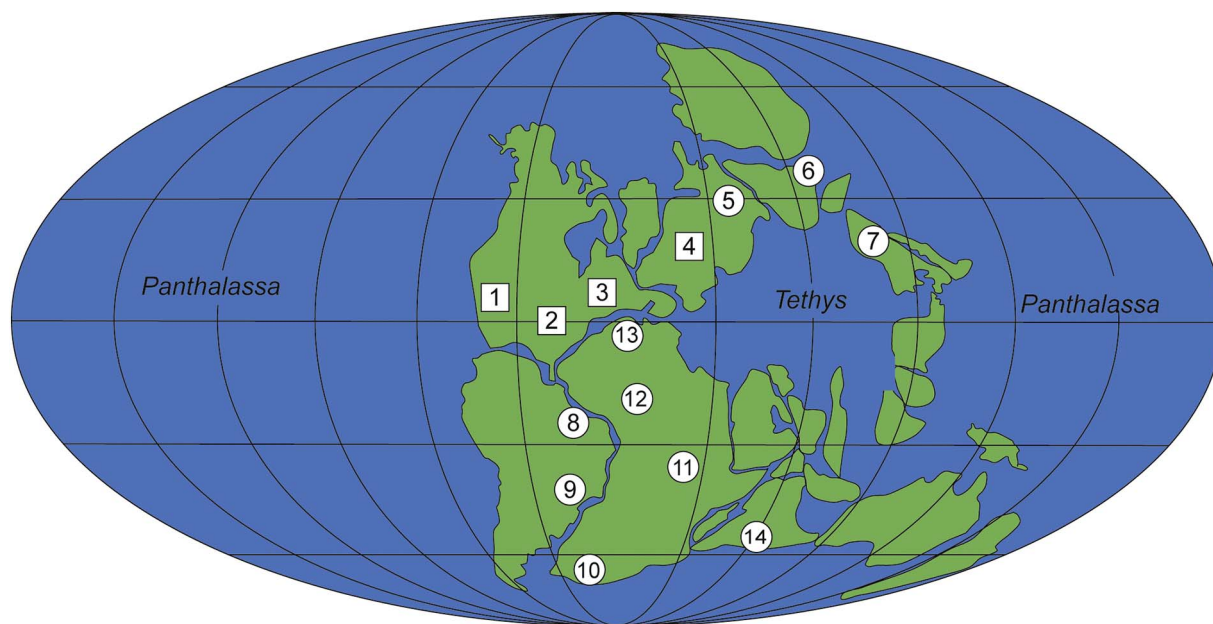


Fig. 1. Map of Permian Pangea at ~270 Ma (modified from Golonka et al., 1994) showing principal tetrapod fossil localities. Boxes are lower Permian localities, circles are middle-upper Permian localities. 1 = western USA (New Mexico/Texas/Oklahoma); 2 = eastern USA (Dunkard); 3 = eastern Canada; 4 = Western Europe (Rotliegend basins); 5 = Russian Urals; 6 = Junggur basin, China; 7 = Ordos basin, China; 8 = Parnaíba basin, Brazil; 9 = Paraná basin, Brazil; 10 = Karoo basin, South Africa; 11 = Ruhuhu basin, Tanzania-Malawi and Luangwa basin, Zambia; 12 = Niger; 13 = Morocco; 14 = Pranhita-Godavari Valley, India.

Russian Ural foreland basin and the Junggur, Turpan and Ordos foreland basins of the Chinese microplates. The fluvial and lacustrine deposits in these basins contain almost all of the fossil record of middle and late Permian tetrapods.

Tetrapod vertebrates emerged on land during the Middle Devonian, and amniotes (“reptiles”) first appeared about 60 million years later during the Late Carboniferous (Pennsylvanian). About 20 million years after that, during the early Permian, the first truly terrestrial tetrapod communities appeared, in which tetrapod predators fed on tetrapod herbivores in a freshwater/terrestrial setting (Olson, 1971). Indeed, the Permian was the time when amniotes rose to dominate terrestrial tetrapod faunas.

The end of the Permian witnessed the most substantial marine extinction of the Phanerozoic. The structure and timing of this extinction is well documented (see Payne and Clapham, 2012, and Hoffman, 2016 for relatively recent reviews). A coeval mass extinction of terrestrial tetrapods is widely accepted. Furthermore, three mass extinctions of tetrapods earlier in the Permian have been posited (Fig. 2). Here, I critically review the record of Permian tetrapods to argue that it identifies only one mass extinction, and that is not a mass extinction at the Permo-Triassic boundary (PTB).

2. Some terminology and abbreviations

The standard global chronostratigraphic scale (SGCS), which is depicted in the International Chronostratigraphic Chart (www.stratigraphy.org), consists of the series and stages that provide the framework for ordering geologic time (Fig. 2). Sometimes paleontologists refer to it as the “marine timescale.” Land-vertebrate faunachrons (LVFs) are intervals of geologic time characterized by distinctive vertebrate fossil assemblages (“faunas”). They are biochronological units, and their beginnings are defined by biochronological events, namely the first appearance of a tetrapod genus or species (Lucas 1998a, 2006, 2010, 2017). The LVFs provide a temporal framework for the correlation of Permian tetrapod assemblages to each other independent of the SGCS (Fig. 3).

I make an important distinction here between biostratigraphic datums and biochronological events. Biostratigraphic datums are the

lowest occurrence (LO) and highest occurrence (HO) of a fossil taxon in a stratigraphic section. Biochronological events are the first appearance datum (FAD) and last appearance datum (LAD) of a taxon, its evolutionary origination and extinction, respectively. These biochronological events are abstractions of evolutionary events that may never actually be captured by the fossil record. LO and HO, to some extent, operationalize the identification of the FAD and LAD of a taxon. However, the incompleteness of the fossil record often undermines the hoped for correspondence between LO and FAD and between HO and LAD, an important consideration in any analysis of changing diversity. Indeed, great emphasis is placed here on using LOs and HOs as the datum points by which changing tetrapod diversity is identified with the knowledge that the incompleteness of the fossil record makes these datum points somewhat unreliable and unstable.

3. The “best sections” method

Mass extinctions have mostly been studied by analyzing global diversity patterns compiled from the published literature. Such compilations chart changing diversity, typically at the taxonomic level of family (e.g., Sepkoski, 1984; Benton, 1987; Sahney and Benton, 2008; Ruta and Benton, 2008). Nevertheless, the age data (correlations) used to order the diversity data in geologic time strongly influence the analysis of such compiled diversity. Both the temporal precision and the accuracy of correlations can change the perception of changing diversity. Thus, incorrect correlations confound diversity analysis by temporally equating taxa that were actually separated in geologic time, or vice versa. I refer to this problem as the incorrect correlation effect and discuss below how it has created the false appearance of a mass extinction of tetrapods at the early-middle Permian boundary.

The temporal ranges of taxa based on literature compilations are only as precise as the relative geological ages of the taxa being compiled. Most published ages are not resolved below the level of stage/age, so the temporal ranges of taxa within stage/ages are not resolved. This artificially concentrates extinctions at stage/age boundaries so that a complex series of extinctions during the time interval of a stage/age is made to appear as a mass extinction at the end of a stage/age. Put differently, compiling diversity for long time intervals into

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