

No gap in the Middle Permian record of terrestrial vertebrates

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ABSTRACT

During the Permian, tetrapods showed a major transition from basal synapsid-dominated faunas in the first half to therapsid-dominated faunas in the second. The transition was significant in marking the beginning of richer and more complex communities, a precursor to modern terrestrial ecosystems. This changeover may have been gradual or abrupt, but its study has been complicated by the postulated occurrence of a substantial hiatus in the fossil record, termed “Olson’s Gap”, which obscured the nature of the turnover. New evidence from redating of key tetrapod-bearing units of the American southwest and European Russia confirms that there is no gap in the fossil record of Permian tetrapods. Indeed, evidence for substantial sampling bias in the Permian tetrapod fossil record as a whole is queried.

INTRODUCTION

The Permian was a time of rapid change among terrestrial faunas, not least among tetrapods. In the Middle Permian, some 270 m.y. ago, it has long been recognized that there was a major changeover from faunas dominated by basal synapsids (= “pelycosaur”) to faunas dominated by therapsids. The therapsids are a major synapsid clade that included in the Middle and Late Permian some major subclades such as Dinocephalia, Anomodontia, Gorgonopsia, and Cynodontia. Some of these animals reached large size, as large as a hippopotamus, and Late Permian ecosystems were more complex than those of the Early Permian, with additional trophic levels. From this clade, the Anomodontia and Cynodontia diversified in the Triassic after the end-Permian mass extinction, and basal mammals emerged from among the cynodonts in the Late Triassic. Therefore, it has long been recognized that transitions in tetrapod ecosystems through the Permian are crucial for understanding the richness of modern terrestrial ecosystems dominated by mammals, direct descendants of the Late Permian therapsids (e.g., Olson, 1962, 1966, 1990; Modesto and Rybczynski, 2000).

The key to understanding the replacement of basal synapsids by therapsids is a good fossil record, and yet this has been debated, especially because the geographic location of the best fossil records switches from North America for the Lower Permian to South Africa and Russia for the Middle and Upper Permian. The question is whether the youngest North American tetrapod-bearing continental deposits overlap in time the oldest such deposits in South Africa and Russia. Work by Olson (1955, 1962, 1990) and Efremov (1956) suggested that the gap had been bridged, but this view was challenged by Lucas (Lucas and Heckert, 2001; Lucas, 2004, 2006) who identifies a global hiatus in the tetrapod fossil record, termed “Olson’s Gap”, representing most of the Roadian stage, 2.6 m.y. in duration (Gradstein et al., 2004). If “Olson’s Gap” exists, then paleontologists will be forever unable to document a remarkable terrestrial faunal replacement.

The reality of “Olson’s Gap” has been challenged (Reisz and Laurin, 2002; Amson and Laurin, 2011), and Sahney and Benton (2008) called it instead “Olson’s Extinction”, arguing that the apparently rapid replacement of Early Permian by Middle Permian tetrapods represents a turnover or extinction event. In this paper, I present evidence for the ages of deposits spanning the Middle Permian, and consider the consequences of the revised dating for understanding of ecosystem evolution and the overall quality of the Permian fossil record of tetrapods.

STRATIGRAPHY OF KUNGURIAN, ROADIAN, AND WORDIAN TETRAPOD-BEARING FORMATIONS

The crux of Lucas’ case (Lucas, 2004) was that the North American redbed successions terminated before the end of the Kungurian (and so before the end of the Early Permian), and that the Russian and South African tetrapod-bearing successions did not begin until the Wordian (Fig. 1). The stratigraphic position of these key units will be reviewed, considering the Russian succession first.

The meaning of the Russian Middle and Late Permian stratigraphic series, the Ufimian, Kazanian, and Tatarian, has changed considerably. These largely continental, redbed time divisions were used formerly (e.g., Harland et al., 1982) as the standard international divisions of the Upper Permian. With major revision to the Permian time scale (Gradstein et al., 2004), the former Upper Permian was divided into Middle and Upper Permian, and the standard stages in these were established in North America and China respectively. Further, the Middle and Upper Permian together now span some 20 m.y., compared to 10–11 m.y., as assumed before.

Opinions have been polarized about the meaning of the Russian series. On the one hand, Gradstein et al. (2004) moved the Ufimian, Kazanian, and Tatarian downward to span from late Kungurian to end-Capitanian, essentially equivalent to the latest Early Permian plus all of the Middle Permian. Menning et al. (2006) allowed the Tatarian to extend up into the Late Permian, being partly equivalent to Wuchiapingian, whereas most Russian stratigraphers (e.g., Grunt, 2005; Molostovskiy, 2005; Tverdokhlebov et al., 2005; Sennikov and Golubev, 2006) argue that the Tatarian spans the Late Permian, and so the succession extends from late Kungurian to Changhsingian. This has been confirmed by magnetostratigraphy (Taylor et al., 2009), which identified all magnetic reversals of the Illawarra interval (Fig. 1), confirming the long-established pattern determined by Russian magnetostratigraphers (e.g., Molostovskiy, 2005). It is crucial now to consider evidence for the ages of the Ufimian, Kazanian, and Tatarian Russian series, and especially to test whether these span the Roadian.

The Ufimian is widely accepted (Gradstein et al., 2004; Menning et al., 2006; Lozovsky et al., 2009) as equating with the upper part of the marine Kungurian series (Fig. 1). In a comprehensive review, Lozovsky et al. (2009) used biostratigraphic evidence from foraminifera, ammonoids, bivalves, brachiopods, ostracodes, conodonts, insects, fishes, tetrapods, macroplants, and palynomorphs to show that the Ufimian correlates with the upper part of the Kungurian; whether the Kungurian, or this upper part of it, should be regarded as entirely Early Permian (= Cisuralian) or as partly or wholly Middle Permian (= Guadalupian) is a separate debated issue (Gradstein et al., 2004; Menning et al., 2006; Lozovsky et al., 2009).

The Kazanian is widely accepted as roughly equivalent to the entire Roadian (Fig. 1): evidence comes from ammonoids and other marine taxa (Leven and Bogoslovskaya, 2006; Leonova, 2007). For example, the Kazanian in the Volga-Urals yields an ammonoid assemblage (abundant *Sverdrupites harkeri* and *S. amundseni*, and rarer *Biarmiceras* and *Medlicottia*) that indicates a Roadian age: *Sverdrupites* is exclusively Roadian, and species of *Biarmiceras* and *Medlicottia* are known from the upper Kungurian and Roadian (Leonova, 2007; Lozovsky et al., 2009).

The Tatarian, under either the restricted (Gradstein et al., 2004), intermediate (Menning et al., 2006), or extended (Taylor et al., 2009) interpretations, is the longest of the three former Russian continental series, lasting 8, 14, or 16 m.y. (Fig. 1). As noted, magnetostratigraphy (e.g., Molostovskiy, 2005; Taylor et al., 2009) strongly suggests that the Tatarian spans from Wordian to Changhsingian, as do studies of interfingering redbed and

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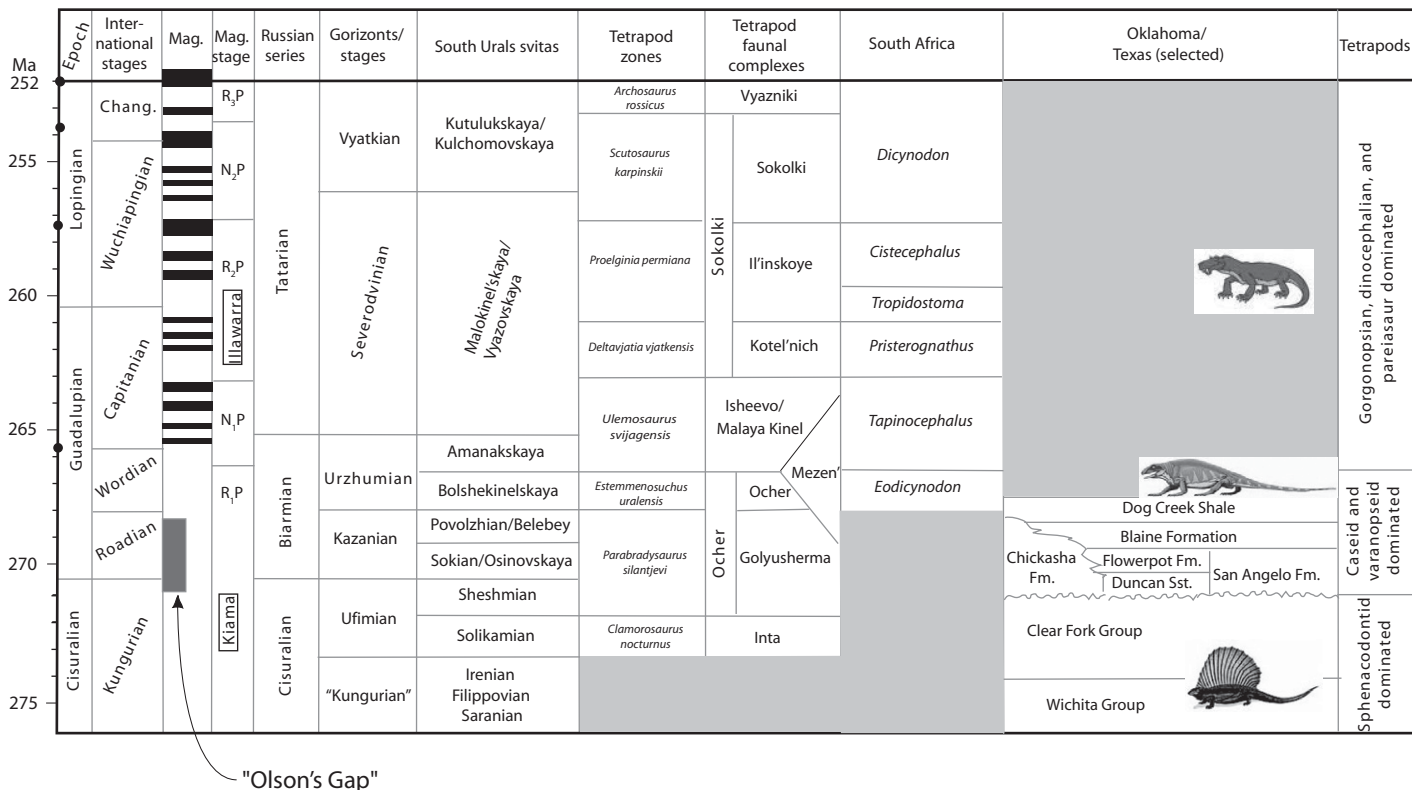


Figure 1. Stratigraphic summary of Middle Permian tetrapod-bearing formations. The key units from the late Early to Late Permian in Russia, South Africa, and North America are shown, based on evidence in Reisz and Laurin (2002), Lozovsky et al. (2009), Newell et al. (2010), and other sources. Tetrapods are, from the bottom, *Dimetrodon*, *Varanops*, and *Titanophoneus*. Chang.—Changhsingian; Fm.—Formation; Mag.—Magnetostatigraphy; Sst.—Sandstone.

marine units in the northern Kanin Peninsula (Grunt, 2006; reviewed in Newell et al., 2010).

The Permian portions of the Karoo redbed successions can be tied biostratigraphically to the Russian sequence (Fig. 1). At the base, the *Eodicynodon* Assemblage Zone is generally matched to the Ocher beds of Russia (lower Urzhumian), based on the occurrence in each of a range of basal therapsid taxa, including dinocephalians, dicynodonts, and basal anomodonts (Battail, 2000; Modesto and Rybczynski, 2000; Abdala et al., 2008; Fröbisch, 2009). The succeeding *Tapinocephalus* Assemblage Zone can be matched to the Isheevo / Malaya Kinel Russian faunal complexes by the presence of similar genera of pareiasaurs, dinocephalians, dicynodonts, and gorgonopsians (Battail, 2000; Modesto and Rybczynski, 2000) and a nycteroleterid (Cisneros and Tsuji, 2011). The later Karoo tetrapod assemblage zones are similarly matched with their Late Permian Russian equivalents (Fig. 1) on the basis of shared genera, or at least subfamilies.

Lucas (2004) moved the topmost formations in the Permian redbed successions of Texas and Oklahoma from Roadian to Kungurian, against the earlier views of Olson (1955, 1962, 1990), Chudinov (1965), Battail (2000), and others. However, Reisz and Laurin (2001, 2002) make a strong case for equivalence of the Chickasha Formation of Oklahoma and the Mezen' complex of Russia (Fig. 1). They note that the Chickasha Formation tetrapods do not include typical Early Permian sphenacodontids, ophiacodontids, or edaphosaurids, but instead *Macroleter*, caseids, and varanopseids, groups typical of the Russian Mezen' complex, dated as Urzhumian (= early Tatarian), equivalent to Roadian to Wordian, based on similarities of the tetrapods to those of the Ocher and Isheevo complexes (Ivakhnenko, 1991; Modesto and Rybczynski, 2000; Reisz and Laurin, 2001). Tetrapods are far from ideal biostratigraphic markers, but

the similarities of the Chickasha and Mezen' assemblages in terms of taxa and their relative abundances, coupled with the known rapid evolution of vertebrates, make it hard to see how the two units could be regarded as distinctly different in age.

In order to justify his identification of a worldwide absence of Roadian-age tetrapod fossils, Lucas (2004) further argued that continental Permian successions in other parts of the world, including Brazil, India, and China, also show Olson's Gap. However, the tetrapod-bearing Aceguá fauna of the Rio do Rasto Formation of southern Brazil is redated tentatively as late Roadian to early Wordian, equivalent to the Mezen' and Ocher complexes of Russia (Dias-da-Silva, 2012), based on the presence of a platyposaurine archegosaurid, as in the Ocher complex, which is suggestive but hardly conclusive evidence of age.

EFFECTS ON PERCEPTION OF THE PERMIAN TETRAPOD FOSSIL RECORD

If Olson's Gap exists, even though it might only be 2–3 m.y. long, it would create a sharp punctuation in tetrapod evolution, separating the basal sphenacodontids and relatives of the Early Permian from the therapsid expansion in the Wordian onward; indeed therapsids may already have begun to radiate before the Wordian (Amson and Laurin, 2011). The apparent dearth of fossils in the Roadian could then be interpreted as collection failure (hence Olson's Gap) or as evidence for an extinction event of some kind (Sahney and Benton, 2008) in which sphenacodontids and others died out and new taxa and new ecosystems emerged.

Equally important is the effect of the presence or absence of Olson's Gap on perceptions of fossil record quality. Many authors have used "number of formations" as a proxy for sampling in studies of the tetrapod fossil record (e.g., Fröbisch, 2008; Barrett et al., 2009; Butler et

al., 2009, 2011; Benson et al., 2010; Mannion et al., 2011), and they generally found correlations between the two metrics, and interpreted this as evidence for sampling bias. In particular, Fröbisch (2008) used his study of the anomodont fossil record as evidence for massive sampling bias in the continental Permian.

In a new analysis of the Permian tetrapod fossil record, there is no correlation (Table 1; Fig. 2A). The formation count is high at the begin-

TABLE 1. THE EFFECT OF OLSON'S GAP ON CORRELATION OF TETRAPOD GENERIC COUNTS THROUGH THE PERMIAN WITH COUNTS OF TETRAPOD-BEARING FORMATIONS (TBF)

Regular dating	Genera versus TBF	Detrended genera versus TBF
Pearson r	0.3454 ($p = 0.2074$)	0.0519 ($p = 0.8543$)
Spearman rho	0.2500 ($p = 0.3688$)	-0.0287 ($p = 0.9192$)
Kendall tau	0.1701 ($p = 0.8423$)	-0.0486 ($p = 0.4220$)
Combined time bins	Genera versus TBF	Detrended genera versus TBF
Pearson r	0.3470 ($p = 0.4000$)	0.9600 ($p = 0.0002$)**
Spearman rho	0.2994 ($p = 0.4713$)	0.9701 ($p = 0.0001$)**
Kendall tau	0.1818 ($p = 0.6180$)	0.9092 ($p = 0.0028$)*
With Olson's Gap	Genera versus TBF	Detrended genera versus TBF
Pearson r	0.6887 ($p = 0.0045$)	-0.8115 ($p = 0.0002$)**
Spearman rho	0.5131 ($p = 0.0505$)	-0.6118 ($p = 0.0154$)
Kendall tau	0.3943 ($p = 0.0512$)	-0.4327 ($p = 0.0291$)

Note: The first block shows data for formations and genera dated according to current best information ("regular dating"; see text). The second block shows data in pooled time bins. The third block shows those units dated according to Lucas (2004) showing "Olson's Gap" in the Roadian. In all cases, measures of correlation are given between raw counts of tetrapod genera versus tetrapod-bearing formations (column 2), and those data detrended (column 3). Significance levels are indicated by asterisks (* <0.05 , ** <0.01) after Bonferroni and Šidák correction for multiple comparisons.

ning of the Permian, falls toward the end of the Early Permian, peaks in the Middle Permian and again in the Late Permian. The peaks and falls are, however, out of synchrony with those in the counts of tetrapod genera; the diversity peaks are in the upper Kungurian and upper Wuchiapingian, whereas the formation count peaks are in the Roadian and lower Wuchiapingian to Changhsingian. When the data are detrended, there is also no apparent correlation because the peaks and troughs are offset in time (Fig. 2B). There is a mixed result when data are combined into longer time bins (i.e., Asselian, Sakmarian, Artinskian, Kungurian, Capitanian, and Wuchiapingian series; Roadian and Wordian combined)—there is no correlation for the raw data counts (Table 1), but the detrended data show correlation using all three tests. It is not clear why the raw and detrended data do not provide the same result, but the strong correlation for detrended data presumably reflects a close lockstep in rises and falls in diversity and formation data when they are pooled in wide time bins. This may be a general phenomenon in such studies: the averaged data suggest correlations that do not exist when data are assessed in more finely divided time bins.

When Olson's Gap is introduced by redating the 20 Roadian-age tetrapod-bearing formations according to Lucas' view (Lucas, 2004, 2006) (Appendix DR1 in the GSA Data Repository¹), 40 genera are redated upward or downward in time (Appendix DR2), and there is some correlation between the taxon and formation counts, but this is weakened when values are corrected for multiple comparisons (Table 1). This is a remarkable result, showing how labile the diversity and formation count data are, and how a result may be overturned by a single adjustment to the dating.

Apart from such lability of results, there are profound problems with such analyses for fossil record bias (Peters, 2005; Benton et al., 2011). The key problems in using formation counts as a proxy for sampling are these:

1. *A sampling proxy should be independent of the data it is meant to assess.* In this case, the two measures are intimately interdependent, in that formation counts and counts of included fossils are related by human decisions about how a rock section is divided, and this reflects rock heterogeneity and fossil occurrences, so it is not clear whether formation count determines fossil richness or vice versa.

2. *A sampling proxy must allow for nonoccurrences.* A count of formations containing tetrapod fossils excludes cases where tetrapod fossils have been sought but not found, and so sampling success and failure are not being assessed, only success. This can be circumvented by tallying all named geological formations that document the appropriate facies, whether fossiliferous or not—and yet such data are nearly impossible to obtain.

3. *Rock volume metrics may correlate with diversity because of a common cause* (Peters, 2005). Correlations may reflect an external forcing factor such as sea level change (for marine rock units) or climatic regime (for continental units) where the volume of sedimentary rock deposited and the range of habitats made available are intimately linked, and so rock volume metrics (such as formation count or map area) may not be assessing sampling at all.

It is safest then to treat all analyses in which formation counts (or other rock volume metrics) correlate with paleodiversity cautiously because such correlations may indicate any of the above explanations. The point is not that the Permian tetrapod fossil record is either good or bad, just that correlations of formation counts and fossil counts *cannot* provide a reliable demonstration of sampling bias.

The null expectation is that the data are reliable and bias is absent, so sampling bias has to be demonstrated. For the present, the Permian fossil record of tetrapods may be regarded as adequate for broad-scale phylogenetic and macroevolutionary studies.

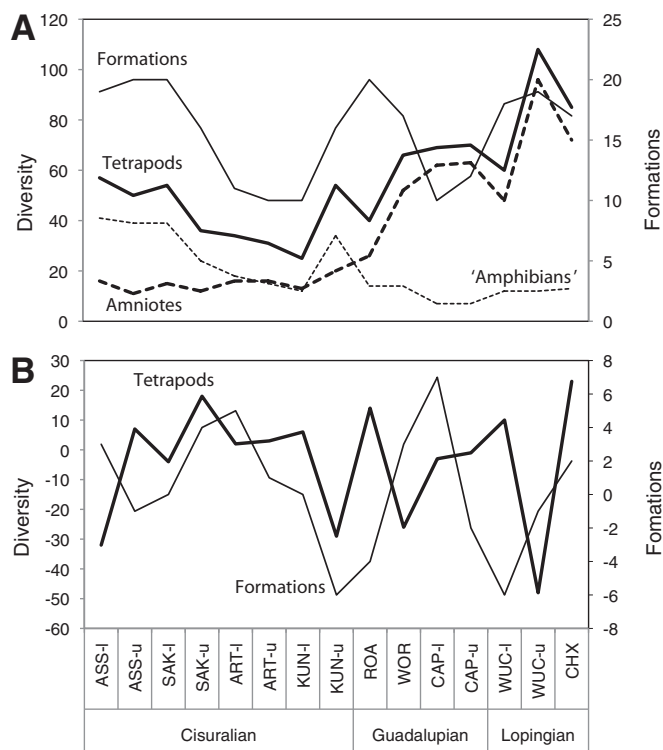


Figure 2. Diversity of Permian tetrapod genera through time. A: Raw data. B: Detrended data (calculated as first differences, the rises and falls from time bin to time bin). In both cases, number of fossiliferous formations does not parallel apparent diversity. Correlation measures reported in Table 1.

¹GSA Data Repository item 2012094, supplementary data, is available online at www.geosociety.org/pubs/ft2012.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

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