1. INTRODUCTION

The end-Permian mass extinction was the most dramatic event to impact life on Earth (Erwin 1990, 2006; Benton 2003; Benton & Twitchett 2003). On land and sea, life was nearly extinguished, ecosystems were devastated and many long-lived lineages disappeared. Most studies hitherto have focused on the effects of this extinction on marine life. It has been more difficult to determine the effects on land because rock successions are typically less complete, and only two major sedimentary basins have so far yielded extensive faunas spanning the boundary: the Karoo Basin of South Africa and the South Urals Basin of Russia.

During the last two decades, our understanding of the end-Permian extinction has increased significantly. It is now widely believed that this devastating event was caused by large-scale volcanism in Siberia, which led to major atmospheric changes and the collapse of ecosystems worldwide (Benton 2003). Earlier evidence suggested that this extinction was prolonged through the Late Permian (Erwin 1990; Teichert 1990), but hints of an earlier event, noted first among terrestrial vertebrate faunas (Benton 1985, 1989; King 1991), have been confirmed (Retallack et al. 2006) as the same end-Permian extinction of marine organisms, already noted independently (Jin et al. 1994; Stanley & Yang 1994; Rohde & Muller 2005). During both extinction events, diversity losses were not simply a reflection of increased rates of extinction but also of depressed origination rates (Benton 1998; Bambach et al. 2004).

The terrestrial vertebrate record of the Permian is also confounded by an additional earlier event, or gap, between the Kungurian and Roadian stages, 271 million years (Myr) ago. This marks the turnover between Early Permian pelycosaur-rich faunas to those dominated by therapsids and pareiasaurs and has been termed ‘Olson’s gap’ (Lucas & Heckert 2001) or ‘Olson’s extinction’ (Sahney & Benton in preparation), depending on whether it is seen as a failure of fossil preservation or a real ecological event. Frustratingly, tetrapod footprint faunas of this time show an even longer hiatus than the skeletal evidence, so that the validity of each interpretation is difficult to verify (Lucas 2004).

The impact of the end-Permian event was devastating. In the sea, the level of species loss was 80–96%, and blastoid echinoderms, tabulate and rugose corals, graptolites, trilobites, eurypterids, acanthodians and placoderms disappeared entirely (Hallam & Wignall 1997). On land, the dominant Glossopteris flora was replaced, eight orders of insects became extinct (Labandeira & Sepkoski 1993) and two-thirds of tetrapod families were lost (Benton 1989). The only tetrapod lineages to survive were procolophonoids, dicynodonts, and presumably therocephalians, cynodonts, and archosauromorphs, and their Triassic recovery was slow (Benton et al. 2004).

The return of diversity after an extinction event can be viewed in terms of taxonomy (Niklas et al. 1983; Labandeira & Sepkoski 1993; Benton 1993), ecology (Bambach 1985; Bambach et al. 2007) or morphology (Foote 1993; Roy & Foote 1997). In this study, we are concerned with the recovery of taxonomic diversity in the context of ecological diversity.

There are several meanings for the term ‘recovery’ after mass extinctions. Past studies have revealed that faunal revival after a devastating ecological event may follow a pattern similar to ecological succession (Sole et al. 2002), and recovery may be considered as the point at which the model is complete and the new ecosystem is stable.
Diversity is most commonly assessed by tallying the number of taxa on a global scale (Benton 1985, 1995, 1998; Padian & Clemens 1985); such studies provide a synoptic overview but are subject to the vagaries of sampling. This is especially true in the fossil record where patterns of global diversity often reflect patterns of fossiliferous rock availability (Raup 1972; Peters & Foote 2001; Smith 2001; Smith & McGowan 2005).

In this study, we use an alternative approach by sampling individual fossil communities (Alroy et al. 2001). By examining well-preserved and well-studied faunas, the taxonomic and ecological recovery of communities after the Permo-Triassic extinction event can be examined more accurately, and the problems of geological bias between time bins are largely avoided.

Data were collected for 69 tetrapod communities from the Artinskian to the end of the Carnian and stored in a relational database management system, the alpha diversity database (ADD). We surveyed all fossil tetrapod findings from the Permian and Triassic and chose only those localities/formations with a high quality of preservation, a completeness of community and a thorough collection and publication history. The study is therefore global and we made no geographical restrictions. Inevitably, however, we could not find suitably substantial faunas from every time bin from every continent: the Early Permian sample is dominated by North American localities, the Middle and Late Permian and Early Triassic time bins by sections in Russia (Pechora Basin, Moscow Basin, South Urals Basin) and southern Africa (Karoo Basin, Ruhuhu Valley), with additional sites from Greenland, Australia, Madagascar, Antarctica and Germany. Sampling in the Middle and Late Triassic is broader, with localities from Western Europe, Russia, South America, North America, Africa, Madagascar, India and China.

The time scale employed was that of Gradstein & Ogg (2008) and abbreviations for time units were taken from Gradstein & Ogg (2004); such studies provide a synoptic overview but are subject to the vagaries of sampling. This is especially true in the fossil record where patterns of global diversity often reflect patterns of fossiliferous rock availability (Raup 1972; Peters & Foote 2001; Smith 2001; Smith & McGowan 2005).

For this study, we use an alternative approach by sampling individual fossil communities (Alroy et al. 2001). By examining well-preserved and well-studied faunas, the taxonomic and ecological recovery of communities after the Permo-Triassic extinction event can be examined more accurately, and the problems of geological bias between time bins are largely avoided.

Figure 1. Global diversity (dashed line) and mean alpha diversity (solid line) of Permo-Triassic tetrapod families. Extinctions are labelled as 1, Olson’s extinction; 2, end-Guadalupian extinction; and 3, end-Permian extinction. Geological stages (Gradstein & Ogg 2004) are as follows: Ar, Artinskian; K, Kungurian; R, Roadian; W, Wordian; Ca, Capitanian; Wu, Wuchiapingian; Ch, Changhsingian; I, Induan; O, Olenekian; An, Anisian; L, Ladinian; Cr, Carnian.

On the scale of modern ecological recovery and recovery from mass extinction, disaster (‘weedy’ or generalist) taxa are known to insinuate themselves into empty guilds, pushing the boundaries of their geographical range and ecospace. Early Triassic terrestrial ecosystems are clearly dominated by a small number of genera, most notably the dicynodont Lystrosaurus, which accounted for approximately 90% of terrestrial vertebrates (Benton 1983). Disaster taxa then experienced rapid turnover in the time immediately following the event, later giving way to more specialized organisms (Benton 2003).

Recovery can also be viewed as a return to pre-extinction conditions, for example the numerical recovery of taxa. Globally, this type of recovery happened quickly after the end-Permian event by the Olenekian (250–245 Myr ago), but then the diversity fell again (figure 1), either as a result of displaced disaster taxa that had filled empty guilds or the devastation caused by another extinction pulse at the end of the Olenekian. In contrast, the ecological recovery of tetrapods and plants was slow, and lost guilds and trophic levels were not readily refilled (Retallack et al. 1996; Benton et al. 2004; Grauvogel-Stamm & Ash 2005).

The third interpretation defines recovery as the point when an ecological equilibrium is reached, even if this balance is unlike that of the pre-extinction fauna. Though faunal turnovers occurred continually before and after the end-Permian event, it is difficult to say when the ecosystem reached stability, i.e. a time of high biodiversity, low turnover, resistance to invaders and a complex trophic structure (Sole et al. 2002). Immediately after the end-Permian event, amphibians made a relatively quick recovery, specifically the families Capitosauridae and Trematosauridae, which filled the role of semi-aquatic predators. Among reptiles, therapsids filled disaster taxa roles but their dominance gave way to archosauromorphs.

In this paper, we present the first community-scale analysis of tetrapod recovery from the end-Permian extinction and the preceding Guadalupian extinction events.
Wuchiapingian. Globally, terrestrial vertebrates recovered the high familial diversity of the Artinskian (39 non-singleton families found worldwide) in the Changhsingian, the last stage of the Permian (figure 1), only to be devastated again by the end-Permian event.

The communities in this study are globally dispersed and despite the differences in latitude and climate, they are fairly well constrained in their diversity. Community diversity falls dramatically during Olson’s extinction and diverse Artinskian faunas, which featured large amniote predators and herbivores such as *Dimetrodon* and *Diadectes*, and a variety of semi-aquatic tetrapods, including *Eryops*, *Archeria* and *Ophiacodon*, disappear. The mean number of families in Early Guadalupian communities is reduced to a paltry 13% of the Artinskian high. A detailed look at the Russian Permian sequence confirms that the diversity drop was severe; only two families crossed the boundary from the Wordian to the Capitanian, but recovery began immediately with the origination of five families in the latter stage (Benton et al. 2004). Globally, alpha diversity does not fully recover; it slowly reaches a plateau (approx. 57% of Artinskian diversity) by the end of the Permian (figure 1). The pattern of diversification is similar at all taxonomic levels and taxonomic proportions are consistent across all time periods.

The ecological impact of the Guadalupian events is catastrophic; 8 (out of a possible 12) guilds are lost from the Artinskian high of 10 guilds. These are recovered in the last stages of the Permian before being devastated again by the end-Permian event (figure 1). During the last two stages of the Permian, there is a movement towards pre-extinction diet proportions, but again the end-Permian event disrupts this recovery. Body size is affected in a similar manner: the proportion of small, medium and large animals is thrown out of balance and recovery towards a pre-extinction balance of roughly 20% small, 60% medium and 20% large tetrapods in the Late Permian follows (figure 3a).

Olson’s extinction was a dramatic extinction ‘trough’ that is a prolonged period of very low diversity after a long and sustained diversity rise and probably the result of prolonged environmental stress. Both Olson’s extinction and the end-Guadalupian extinction experience a dramatic change in community diet proportions, body size and distinct faunal turnovers, from ‘pelycosaur’-rich communities to those dominated by the basal therapsid dinocephalians and finally giving way to more derived therapsids and pareiasaurs. Global and ecological diversities recover to pre-extinction levels by the end of the Permian. However, alpha diversity does not recover by reaching a pre-extinction balance; rather a new equilibrium is reached, significantly lower than the diversity of the Artinskian.

### 4. ACROSS THE PERMO-TRIASSIC BOUNDARY: ECOSYSTEM RESTRUCTURING AND RECOVERY

(a) A fast global recovery and a slow community recovery

The global diversity rose sharply after each extinction pulse, probably the result of disaster taxa filling empty guilds. After the end-Permian event, this rapid refilling resulted in a return to pre-extinction taxonomic diversity by the Olenekian. However, this did not last, as there was a subsequent loss of nine families (figure 1).

Until the Carnian, community diversity never reached the highest observed in Artinskian faunas. Though the end-Permian extinction pulse had the most dramatic global effect, it does not appear to have impacted the diversity within individual communities as badly as the first Guadalupian pulse. It seems to have ‘thinned out’ families rather than destroyed them completely and the average number of tetrapod families lost is only 1.5 from each community (figure 1).

A look at the community diversification rate helps explain the slow recovery of tetrapods in the Triassic.
The end-Permian event dramatically restructured communities with the loss of browsers and predators and an increase in piscivores. The loss of browsers is, no doubt, linked to changes in vegetation. A rapid loss of sediment-binding vegetation was responsible for a basin-wide change from low-energy meandering streams to high-energy braided rivers in the Early Triassic of Russia, South Africa, Australia, India and Spain (Newell et al. 1999; Ward et al. 2000; Benton in press). Also, the 7 Myr ‘coal gap’ is the result of an insufficient amount of plant material to form coal deposits, and hence little food for large browsing animals. Permian levels of plant diversity were not reached again until the Late Triassic (230 Myr ago; Retallack et al. 1996). Tracking diet proportions through the first five stages of the Triassic shows a clear trend towards reaching a pre-extinction balance of communities dominated by predators and browsers with a smaller proportion of piscivores and insectivores (figure 3b).

Overall, the recovery of the eight guilds lost in the Guadalupian occurred in 10–15 Myr, relatively quickly compared with the original 100 Myr it took to colonize them by the first tetrapods (Sahney & Benton in preparation), perhaps because sufficient representatives of the relevant lineages and guilds survived the event in some form. These broad guilds had just been refilled by them by the first tetrapods (Sahney & Benton in preparation), perhaps because sufficient representatives of the relevant lineages and guilds survived the event in some form. These broad guilds had just been refilled by the first tetrapods (Sahney & Benton in preparation). The recovery of the eight guilds lost in the Guadalupian may initially seem at odds with Botha & Smith’s (2006) analysis of the Karoo Basin, which indicates an initial rapid recovery of the tetrapod fauna after the end-Permian event. They noted that nearly half (43%) of the Early Triassic genera appeared ‘rapidly’, that is within 20 m of the Permo-Triassic boundary. As they state, however, they are documenting the onset of recovery, rather than the establishment of mature ecosystems. Botha & Smith (2006) defined recovery as a ‘new balance’ rather than a return to pre-existing conditions, something that could not be observed in the four stages following the Late Pennsylvanian extinction, an average of one family was added every 4 Myr. Then for four stages after Olson’s extinction, this rate increased to one family added every 3 Myr. But oddly, for the four stages immediately following the end-Permian extinction, a period of 35 Myr, the familial diversification rate dips in and out of the negative realm and results in an average of one additional family every 25 Myr. Outside the three mass extinction events, this is the lowest rate of tetrapod diversification since their origin in the Frasnian.

(b) Ecological recovery

Communities were slow to recover ecologically as well as numerically, and body size and diet ratios show disruptions at all extinction pulses (figure 3). The Permian extinctions created a ‘Lilliput effect’ (Urbanek 1993) in which few large species survived and, in addition, many small species were also extinguished. The large animals included the disaster taxon *Lystrosaurus* that dominated terrestrial communities, capitosaurans and *Proterosuchus*, which were populous in semi-aquatic environments. Further into the Early Triassic, larger animals became more common as dicynodonts such as *Kannemeyeria* replaced *Lystrosaurus*, and large carnivores reappeared including *Cynognathus, Garjainia* and *Erythrosuchus*.

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Karoo alone as this sequence begins in the Guadalupian, after the first extinction pulse. A longer sequence of tetrapod faunas is found in the Southern Urals of Russia, where a continuous record of tetrapod faunas spanning 30 Myr from the Kungurian to the Ladinian reveals low taxonomic and ecological diversity in the Early Triassic. Even after 15 Myr of rebuilding ecosystems, many guilds were still unfilled, such as those of small piscivores, small insectivores, large herbivores and top predators (Benton et al. 2004).

Cosmopolitanism is the degree to which a species or a clade is distributed worldwide; it can be measured simply as the mean alpha diversity ($T$) divided by global diversity ($T_i$), according to the formula $C = T/T_i$. Note the overall decline of cosmopolitanism through this time interval, perhaps related to increasing taxonomic and ecological diversity of tetrapods, but also note the coupled rises and falls in cosmopolitanism following major extinction events, especially (1) Olson’s extinction, (2) the end-Guadalupian extinction and (3) the end-Permian extinction. Abbreviations are the same as given in figure legend 2.

There is a repeated pattern of coupled rises and falls in cosmopolitanism during times of extinction, though in each case the fall is far more dramatic than the rise, creating an overall downward trend. Cosmopolitanism was slow to recover in the Triassic, rising just 7% from the Olenekian to the Carnian. There is no other time in tetrapod history that cosmopolitanism is sustained at such a low level for so long. Continued low cosmopolitanism in the Triassic is difficult to envisage owing to the existence of ecological models, which predict that when endemic/regional faunas are devastated, the survivors, especially disaster taxa, become cosmopolitan, at least in the immediate aftermath of a mass extinction (Hallam & Wignall 1997; Benton 2003; Erwin 2006). This is well illustrated among tetrapods by Lystrosaurus, a bulky herbivore that thrived in the harsh arid conditions of the Induan. Scroungers such as Lystrosaurus were then rapidly overtaken by the evolution of more stable regionally distinct faunas that were to establish the longer lasting ecosystems of the later Triassic.

Table 1. Guilds (defined by body size and diet) filled by Permo-Triassic tetrapods.

<table>
<thead>
<tr>
<th>stage</th>
<th>midpoint (Myr ago)</th>
<th>piscivores</th>
<th>insectivores</th>
<th>browsers</th>
<th>predators</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>S</td>
<td>M</td>
<td>L</td>
<td>S</td>
</tr>
<tr>
<td>Artinskian</td>
<td>280</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
</tr>
<tr>
<td>Kungurian</td>
<td>273.1</td>
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<td>Y</td>
<td>Y</td>
<td>Y</td>
</tr>
<tr>
<td>Roadian</td>
<td>269.3</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
</tr>
<tr>
<td>Wordian</td>
<td>266.9</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
</tr>
<tr>
<td>Capitanian</td>
<td>263.1</td>
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<td>Y</td>
<td>Y</td>
<td>Y</td>
</tr>
<tr>
<td>Wuchiapingian</td>
<td>257.1</td>
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<td>Y</td>
<td>Y</td>
<td>Y</td>
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<tr>
<td>Changhsingian</td>
<td>252.4</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
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<tr>
<td>Induan</td>
<td>250.35</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
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<tr>
<td>Olenekian</td>
<td>247.35</td>
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<td>Y</td>
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<tr>
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<td>241</td>
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<td>Y</td>
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<td>Y</td>
<td>Y</td>
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<tr>
<td>Carnian</td>
<td>222.25</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
</tr>
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</table>

(c) Cosmopolitanism

Cosmopolitanism is the degree to which a species or a clade is distributed worldwide; it can be measured simply as the mean alpha diversity of communities divided by global diversity. The Pennsylvanian extinction, Guadalupian pulses and end-Permian event experience significant rises in cosmopolitanism followed by dramatic losses of 40–50% (figure 4). This rise and fall of cosmopolitanism following an extinction event is in keeping with established ecological models, which predict that when endemic/regional faunas are devastated, the survivors, especially disaster taxa, become cosmopolitan, at least in the immediate aftermath of a mass extinction (Hallam & Wignall 1997; Benton 2003; Erwin 2006). This is well illustrated among tetrapods by Lystrosaurus, a bulky herbivore that thrived in the harsh arid conditions of the Induan. Scroungers such as Lystrosaurus were then rapidly overtaken by the evolution of more stable regionally distinct faunas that were to establish the longer lasting ecosystems of the later Triassic.

There is a repeated pattern of coupled rises and falls in cosmopolitanism during times of extinction, though in each case the fall is far more dramatic than the rise, creating an overall downward trend. Cosmopolitanism was slow to recover in the Triassic, rising just 7% from the Olenekian to the Carnian. There is no other time in tetrapod history that cosmopolitanism is sustained at such a low level for so long. Continued low cosmopolitanism in the Triassic is difficult to envisage owing to the existence of ecological models, which predict that when endemic/regional faunas are devastated, the survivors, especially disaster taxa, become cosmopolitan, at least in the immediate aftermath of a mass extinction (Hallam & Wignall 1997; Benton 2003; Erwin 2006). This is well illustrated among tetrapods by Lystrosaurus, a bulky herbivore that thrived in the harsh arid conditions of the Induan. Scroungers such as Lystrosaurus were then rapidly overtaken by the evolution of more stable regionally distinct faunas that were to establish the longer lasting ecosystems of the later Triassic.

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Figure 4. Cosmopolitanism of tetrapods through the Carboniferous, Permian and Triassic. Cosmopolitanism ($C$) is measured as mean alpha diversity ($T$) divided by global diversity ($T_i$), according to the formula $C = T/T_i$. Note the overall decline of cosmopolitanism through this time interval, perhaps related to increasing taxonomic and ecological diversity of tetrapods, but also note the coupled rises and falls in cosmopolitanism following major extinction events, especially (1) Olson’s extinction, (2) the end-Guadalupian extinction and (3) the end-Permian extinction. Abbreviations are the same as given in figure legend 2.
the global supercontinent, Pangaea and equable climates: terrestrial organisms should have been able to migrate nearly worldwide without major barriers.

5. CONCLUSIONS
The Permo-Triassic extinction events halted the growth of tetrapod communities. Extinction in the Guadalupian had a much more severe impact at the community level than the terminal end-Permian event. Faunas were recovering from the Guadalupian events at reasonably high rates and ecologically communities had recovered when the end-Permian event hit. Though globally tetrapods recovered quickly, the dramatic restructuring that occurred at the community level was not permanent and communities did not recover numerically or ecologically in the Early and Middle Triassic. It would not be until the great diversity of the Late Triassic, which included dinosaurs, pterosaurs, crocodylians, rauisuchids, aetosaurs, rhynchocephalians, triloboids, sphenodonts, amphibians and mammals, some 30 Myr after the end-Permian event, that terrestrial tetrapod community diversity was restored.

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