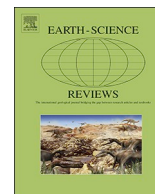




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Invited Review

Early Triassic terrestrial tetrapod fauna: a review

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ARTICLE INFO

Keywords:

Tetrapods
Early Triassic
Late Permian
Permo-Triassic mass extinction

ABSTRACT

The Permian-Triassic mass extinction (PTME, ca. 252 Mya) was one of the most severe biotic crises of the Phanerozoic, eliminating > 90% of marine and terrestrial species. This was followed by a long period of recovery in the Early and Middle Triassic which revolutionised the structure of both marine and terrestrial ecosystems, triggering the new ecosystem structure of the Mesozoic and Cenozoic. Entire new clades emerged after the mass extinction, including decapods and marine reptiles in the oceans and new tetrapods on land. In both marine and terrestrial ecosystems, the recovery is interpreted as stepwise and slow, from a combination of continuing environmental perturbations and complex multilevel interaction between species in the new environments as ecosystems reconstructed themselves. Here, we present a review of Early Triassic terrestrial tetrapod faunas, geological formations and outcrops around the world, and provide a semi-quantitative analysis of a data set of Early Triassic terrestrial tetrapods. We identify a marked regionalisation of Early Triassic terrestrial tetrapods, with faunas varying in both taxonomic composition and relative abundance according to palaeolatitudinal belt. We reject the alleged uniformity of faunas around Pangaea suggested in the literature as a result of the hot-house climate. In addition, we can restrict the “tetrapod gap” of terrestrial life in the Early Triassic to palaeolatitudes between 15°N and about 31°S, in contrast to the earlier suggestion of total absence of tetrapod taxa between 30°N and 40°S. There was fairly strong provincialism following the PTME, according to cluster analysis of a taxon presence matrix, entirely consistent with Early Triassic palaeobiogeography. Unexpectedly, the overall pattern for Early Triassic terrestrial tetrapod faunas largely reflects that of the Late Permian, suggesting that the recovery faunas in the Early Triassic retained some kind of imprint of tetrapod distributions according to palaeogeography and palaeoclimate, despite the near-total extinction of life through the PTME.

1. Introduction

The mass extinction at the Permian–Triassic boundary (PTB; ca. 252 Mya) eliminated > 90% of marine and terrestrial species (Erwin, 1993; Song et al., 2013, 2015; see Stanley, 2016 for a slightly lower estimate) and is widely considered the most severe biotic crisis in Earth's history (Sepkoski, 1984; Raup and Sepkoski, 1982; Sheldon and Retallack, 2002; Benton and Twitchett, 2003; Smith and Botha-Brink, 2014; Ward et al., 2005; Lehrmann et al., 2006; Knoll et al., 2007; Isozaki et al., 2007; Roopnarine et al., 2007, 2018; Sahney and Benton, 2008; Lucas, 2009; Metcalfe and Isozaki, 2009; Korte et al., 2010; Chen and Benton, 2012; Hermann et al., 2011; Song et al., 2011; Chen et al., 2015; Roopnarine and Angielczyk, 2015; Song et al., 2018; Dineen et al., 2019). The long period of recovery in the Early and Middle Triassic

revolutionised the structure of both marine and terrestrial ecosystems (Chen and Benton, 2012), influencing the course of evolution in the remainder of the Mesozoic and Cenozoic eras (Sepkoski, 1984; Benton, 2010). Entire new groups emerged after the crisis, including new tetrapods on land and decapods and marine reptiles in the oceans (Chen and Benton, 2012). Several lineages of sauropsids diversified rapidly during the 5 Myr of the Early Triassic both on land (Butler et al., 2011; Nesbitt et al., 2010a; Gower et al., 2014) and in the sea (Scheyer et al., 2014; Motani et al., 2015a, 2015b). Cynodonts and archosaurs came to prominence during the Triassic recovery and, among archosaurs, avemetatarsalians (the lineage including dinosaurs and pterosaurs) originated during this time (Brusatte et al., 2010; Nesbitt et al., 2010b, 2017; Chen and Benton, 2012; Benton et al., 2014).

Taking into consideration the great importance of the Early Triassic

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<https://doi.org/10.1016/j.earscirev.2020.103331>

Received 27 March 2020; Received in revised form 19 August 2020; Accepted 24 August 2020

Available online 31 August 2020

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for the re-structuring of ecosystems after the Permo-Triassic mass extinction (PTME), and following the approaches adopted by [Bernardi et al. \(2017\)](#) in their analysis of the Late Permian, in this contribution we provide a review of terrestrial vertebrate faunas around the world at the beginning of the Mesozoic Era. Early Triassic tetrapod assemblages, known from both body fossils and footprints, have been reported from Antarctica, Argentina, Australia, Brazil, Canada, China, England, Germany, Greenland, India, Italy, Japan, Kenya, Laos, Mongolia, Morocco, Madagascar, Niger, Pakistan, Poland, Russia, Scotland, Spain, the United States and South Africa (see detailed references below). For the present analysis, 11 geographic regions were selected on the basis of geological domains and palaeolatitudes and a comprehensive dataset has been generated to provide a semi-quantitative analysis of faunal composition in the Early Triassic. For each region, a short review is provided of the geology and fossiliferous formations and outcrops, along with the percentage occurrences for the principal clades.

2. Causes of the PTME and its effects on the marine realm

2.1. Siberian Traps eruptions and their consequences

Over the last three decades several hypotheses have been proposed to explain the PTME, including the eruption of the Siberian Traps and Emeishan Traps ([Campbell et al., 1992](#); [Renne et al., 1995](#); [Bowring et al., 1998](#); [Chung et al., 1998](#); [Courtillot, 1999](#); [Jin et al., 2000](#); [Wignall, 2001](#); [Lo et al., 2002](#); [Kamo et al., 2003](#); [Racki and Wignall, 2005](#); [Reichow et al., 2009](#); [Saunders and Reichow, 2009](#); [Grasby et al., 2011](#); [Konstantinov et al., 2014](#); [Shen et al., 2019](#)), and a bolide impact ([Kaiho et al., 2001](#); [Becker et al., 2001, 2004](#); [Basu et al., 2003](#)). However, the evidence for a bolide impact has been criticized ([Isozaki, 2001](#); [Erwin, 2003](#); [Koeberl et al., 2002, 2004](#); [Farley et al., 2005](#); [Xie et al., 2007](#)) and considered both unnecessary and inadequate to explain the biotic crisis ([Ward et al., 2005](#); [Tohver et al., 2012, 2013, 2018](#)). In this regard, [Ward et al. \(2005\)](#) stressed how the detailed geological record from the South African Karoo Basin testifies to a protracted catastrophic ecosystem collapse rather than a sudden crisis from a bolide impact (also see [Irmis and Whiteside, 2011](#); [Smith and Botha-Brink, 2014](#); [Viglietti et al., 2018](#)). Further, the evidence for two equally serious pulses of marine extinction (see below), separated by perhaps 60,000 years, or even a prolonged extinction episode is more plausibly explained by pulses of volcanic eruption than by one or more bolide impacts ([Shen et al., 2011, 2019](#); [Burgess and Bowring, 2015](#)).

Several physical environmental shocks have been proposed as proximal killers, and so triggers of the PTME, including increased atmospheric CO₂ concentrations, ocean acidification, ocean anoxia, hypercapnia, global warming and acid rain ([Chen and Benton, 2012](#); [Benton, 2018](#)). The Permo-Triassic crisis is characterized by an end-Permian sulfur event ([Kaiho et al., 2006a, 2006b](#); [Riccardi et al., 2006](#)) and by a consistent negative carbon isotopic excursion reported from both marine and terrestrial carbonates, and marine and terrestrial organic matter (e.g., [Holser and Magaritz, 1987](#); [Holser et al., 1989](#); [Magaritz et al., 1988](#); [Baud et al., 1989](#); [Holser et al., 1989](#); [Oberhänsli et al., 1989](#); [Chen et al., 1991](#); [Morante, 1996](#); [Wignall et al., 1998](#); [Heydari et al., 2000](#); [Jin et al., 2000](#); [Krull et al., 2000](#); [Krull and Retallack, 2000](#); [Dolenec et al., 2001](#); [Kaiho et al., 2001](#); [Musashi et al., 2001](#); [Twitchett et al., 2001](#); [Cao et al., 2002](#); [Sephton et al., 2002](#); [de Wit et al., 2002](#); [Payne et al., 2004](#); [Thomas et al., 2004](#); [Xie et al., 2005, 2007](#); [Hansen, 2006](#); [Algeo et al., 2007](#); [Coney et al., 2007](#); [Horacek et al., 2007](#); [Riccardi et al., 2007](#); [Grasby and Beauchamp, 2008](#); [Korte et al., 2010](#); [Chen et al., 2015](#); [Rey et al., 2016](#)).

Several authors (e.g., [Benton and Twitchett, 2003](#); [Chen and Benton, 2012](#); [Benton and Newell, 2014](#); [Shen et al., 2019](#)) considered the best-supported causative model to include an initial eruption of the Siberian traps large igneous province, a megascale eruption with more than 1000 Gigatonnes (Gt) of erupted lava ([Grasby et al., 2011](#)), which released a huge amount of sulphate aerosols and methane from

clathrate reservoirs (see [Bernier, 2002](#)). In turn, this led to global warming and to the production of acid rain that caused plant die-offs and associated intensive soil erosion (see [Wignall, 2001](#); [Benton, 2003, 2018](#); [Benton and Twitchett, 2003](#); [Sephton et al., 2005](#); [Knoll et al., 2007](#)). Studies conducted on conodont bioapatite stable oxygen isotopes ([Joachimski et al., 2012](#); [Sun et al., 2012](#)) highlight an increase in sea surface temperature of about ~9 °C from Bed 24e to Bed 27a in the Meishan section (South China). The global warming, starting at the extinction horizon and continuing into the Early Triassic ([Joachimski et al., 2012](#); [Sun et al., 2012](#); [Schobben et al., 2014](#); [Song et al., 2015](#)), probably also triggered the release of methane from coals and deep ocean sediments, with additional greenhouse gases released by interactions between the Siberian traps and local limestones, permafrost soils, and other organic-rich sediments ([Krull et al., 2000](#); [Dorritie, 2002](#); [Racki, 2003](#); [Racki and Wignall, 2005](#); [Retallack and Jahren, 2008](#); [Grasby et al., 2011](#)). [Konstantinov et al. \(2014\)](#) stress how the Siberian LIP was underlain by a really thick succession of Permian- and Carboniferous-aged carbonates, coal-bearing deposits and evaporites, which could produce large volume of poisonous and greenhouse gases (see [Svensen et al., 2009](#); [Ganino and Arndt, 2009](#)), and they hypothesize a great influence of huge and fast injections of magma into such underlying sediments as the key driver of the Permo-Triassic crisis. Together, it is estimated that 30,000 to 40,000 Gt of carbon were released ([Clarkson et al., 2015](#)), potentially overwhelming climate-regulating mechanisms of the time and causing positive feedback that exacerbated ocean anoxia, increased global warming, and sustained ocean acidification (see [Wignall, 2001](#); [Chen and Benton, 2012](#); [Clarkson et al., 2015](#); [Kump, 2018](#)). In the marine realm, [Song et al. \(2014\)](#) propose a model where the spectrum of extinction selectivity is explained by a combination of lethally warm shallow waters and anoxic deep waters, which led to a consistent restriction of habitable area to a narrow mid-water refuge zone. According to these authors, shallow water organisms like corals, large foraminifers and radiolarians intolerant to high temperature were the first to be eliminated, whereas ostracods tolerant of high temperatures were not affected. On the other hand, temperature-intolerant but hypoxia-tolerant foraminifers likely moved to dysoxic slope margins from shallow waters, and only molluscs that could survive both high temperatures and hypoxia were able to thrive in the mass extinction aftermath ([Song et al., 2014](#)).

It has been suggested that the Siberian Trap eruptions were part of a wider phase of massive eruptions. For example, the Emeishan Plateau basalts in the South China Block, smaller than the Siberian Traps, were linked to the PTME ([Lo et al., 2002](#); [Luppo et al., 2018](#)). However, these have been dated to 260 Ma, linking them instead to the Middle-Late Permian transition, and the possible end-Guadalupean mass extinction, not to the PTME ([He et al., 2007a, 2010a](#); [Fan et al., 2008](#); [Xu et al., 2010](#); [Luppo et al., 2018](#)). Part of the evidence for longer-term eruptions comes from the Choyoi Province, located on the southwestern margin of Gondwana ([Kleiman and Japas, 2009](#); [Rocha-Campos et al., 2011](#); [Sato et al., 2015](#); [Spalletti and Limarino, 2017](#); [Luppo et al., 2018](#)), comprising acidic lavas with a total thickness up to 2 km and an areal extent of 500,000 km² ([Strazzere and Gregori, 2005](#)). Available age constraints indicate almost continuous magmatic activity from the Early Permian to the Early Triassic ([Kleiman and Japas, 2009](#); [Spalletti and Limarino, 2017](#)), driving, according to some authors ([Henry et al., 2013](#); [Limarino et al., 2014](#); [Spalletti and Limarino, 2017](#)), the major climatic shift from an icehouse regime characterizing the Late Carboniferous–Early Permian to a greenhouse regime in the Late Permian–Triassic. According to [Luppo et al. \(2018\)](#), the PTME represents a punctuated extreme event in the framework of a long-term magmatic process that started in the Early Permian. Further, on the basis of new radiometric dating, [Luppo et al. \(2018\)](#) were able to refer the large volcanic Los Menucos Complex, exposed in NW Patagonia, to the 10 Myr around the PTB, whereas formerly it had been ascribed to the Middle or Late Triassic. Taking into account wider links, [Luppo et al. \(2018\)](#) argue that the La Esperanza-Los Menucos Plutono-Volcanic

Complex might have had a substantial effect on the PTME.

Massive soil erosion and mobilization (Newell et al., 1999, 2010; Ward et al., 2000; Sephton et al., 2005; Xie et al., 2007; Cao et al., 2019) is thought to have been triggered by a combination of stripping of forests by acid rain (Benton and Newell, 2014), increased chemical weathering due to elevated temperature (Sheldon, 2006), and huge wildfires in some places promoted by prevailing arid conditions (Shen et al., 2011). This led to a steady increase in sedimentation rates, with a major influx into the oceans of terrigenous sediments and nutrients (Retallack, 1999; Algeo and Twitchett, 2010; Algeo et al., 2011; Song et al., 2015). The increased input of nutrients into the sea, together with the generalized global warming, are highlighted in the sedimentary record by very common sulfides and black sediment, testifying to widespread oceanic anoxia (Wignall and Twitchett, 1996; Chen and Benton, 2012).

2.2. Scaling and timing of the crisis

The best record for the PTB in the marine realm is the sedimentary succession in south China, with exposures extending from Zhejiang to Yunnan provinces, up to 2000 km from east to west. Particular effort has been dedicated to studying the Meishan section in South China (e.g., Mundil et al., 2001, 2004; Cao et al., 2002; Kaiho et al., 2006b; Jiang et al., 2007; Shen et al., 2007; Wang and Visscher, 2007; Cao and Zheng, 2009; Song et al., 2009; Shen et al., 2011; Chen et al., 2015), as it contains the best marine record of the PTME and is the Global Stratotype Section and Point (GSSP) for the PTB (Yin et al., 2001; Chen et al., 2015), defined by the first appearance of the conodont *Hindeodus parvus* in shallow-marine strata of Bed 27c (Nicoll et al., 2002). Based on zircon U–Pb analyses bracketing ash beds, the GSSP is dated at 251.495 ± 0.064 Ma (Burgess et al., 2014), while it is dated to 251.902 ± 0.024 Ma on the basis of a cyclostratigraphic analysis to spectral gamma-ray logs of multiple Permian-Triassic conodont-zoned marine sections on the South China carbonate platform (Li et al., 2016a, 2016b).

In the Meishan section it has been calculated that 280 marine invertebrate species out of a total of 329 disappeared close to the PTB. This evidence led some authors to hypothesize a single, abrupt extinction event (Jin et al., 2000). However, other studies conducted at Meishan, and in other correlated sections of South China, noted a more complex pattern of extinction with two major events separated by 60–200 thousand years (Xie et al., 2005, 2007; Chen et al., 2009; Shen et al., 2011; Chen and Benton, 2012; Song et al., 2013; Chen et al., 2015).

In particular, Song et al. (2013) recognize two extinction events in the Chinese body fossil record, separated by a 180,000-year recovery phase. The first phase comprises extinction of 57% of marine species, including rugose corals, fusulinids, algae and all plankton. A second phase, in the earliest Triassic, marked the extinction of 71% of the remaining marine taxa, deeply changing the structure of marine ecosystems (Song et al., 2013). Likewise, Chen et al.'s (2015) analysis of ichnofabric proxies such as tiering level, bioturbation level, burrow size, along with ichnodiversity and fossil fragment content, in the uppermost Changhsing to Yinkeng formations, clearly indicate two separate and discrete phases for the PTME. The two-step extinction at the PTB also has been reported from Iran (Korte et al., 2004) and Austria (Schönlaub, 1991).

Beyond the extinction of large numbers of species, the PTME had profound effects on marine ecosystems. The event has long been recognized as playing a role in the transition between the so-called Paleozoic Evolutionary Fauna, dominated by groups such as trilobites, rugose and tabulate corals, brachiopods and crinoids, to a Modern Evolutionary Fauna characterized by previously less diffused clades like malacostracans, echinoids, scleractinian corals, gastropods and bivalves (e.g., Sepkoski, 1981; Sepkoski and Sheehan, 1983; Sepkoski and Miller, 1985; Song et al., 2018). New types of communities and

ecological interactions accompanied these changes in taxonomic dominance in both the immediate aftermath of the extinction and the long-term recovery (e.g., Bambach et al., 2002; Knoll et al., 2007; Chen and Benton, 2012; Hofmann, 2016; Brayard et al., 2017; Muscente et al., 2018; Song et al., 2018; Dineen et al., 2019).

2.3. Continuing environmental perturbations in the Early Triassic

Stressful environmental conditions in the Early Triassic are indicated by the absence of coal deposits on land, known as the 'coal gap' (Retallack et al., 1996a, 2011; Rees, 2002), and in the marine environment by the contemporaneous disappearance of shallow-water reefs made by colonial metazoans (the 'coral gap'; Alroy et al., 2008, Algeo et al., 2011).

At least five greenhouse crises have been reported in the 5 Myr following the PTB (Induan–Anisian), indicated by consistent negative excursions in carbon isotope ratios (Kidder and Worsley, 2004; Payne et al., 2004; Retallack et al., 2005; Retallack, 2009; Retallack, 2013; Grasby et al., 2011; Retallack et al., 2011; Sun et al., 2012; Chen and Benton, 2012). In the ocean, extended euxinia with ocean stratification and sulfur enrichment, is testified by pyrite framboid sizes, Ce anomalies, S-isotopic compositions and biomarkers, which indicate free H₂S and the loss of dissolved oxygen in the water column (Riccardi et al., 2006; Shen et al., 2007; Wang and Visscher, 2007; Algeo et al., 2011). Anoxic conditions have been interpreted as a recurring element in Early Triassic oceans (see Wignall and Twitchett, 1996, 2002; Payne et al., 2004; Grice et al., 2005; Chen and Benton, 2012), with a major anoxia peak in the early Induan (*parvus* and *isarcica* zones, see Wignall and Twitchett, 2002). In addition, upwelling CO₂ from the deep ocean and associated acidification of surface waters likely contributed to high mortality in invertebrates and may explain some patterns of extinction selectivity (Bambach et al., 2002; Knoll et al., 2007; Chen and Benton, 2012).

Further evidence of harsh environmental conditions comes from peculiar and unusual biosedimentary features including seafloor carbonate precipitates, wrinkle structures, and very abundant and widespread microbialites in shallow marine settings of both Panthalassa and Tethys (Sano and Nakashima, 1997; Baud et al., 1997, 2005; Kershaw et al., 1999, 2002; Lehrmann, 1999; Lehrmann et al., 2003; Pruss and Bottjer, 2004a; Pruss et al., 2004; Metcalfe and Isozaki, 2009). The abundance of microbialites is evidence of global environmental deterioration after the PTME, where the microbiota overwhelmed the severely affected metazoans (Metcalfe and Isozaki, 2009). A consistent reduction in diversity, size and tiering in fossil traces (Twitchett and Wignall, 1996; Twitchett, 1999; Ausich and Bottjer, 2002; Pruss and Bottjer, 2004b; Hofmann, 2016) further attests to a reduction in metazoan activity in the aftermath of the extinction. Together, these data indicate a combination of episodes of high chemical precipitation and anoxia, with the disappearance of metazoans in marine environments (Algeo et al., 2011; Chen and Benton, 2012).

2.4. Recovery of life after the PTME

Recovery, both in marine and terrestrial ecosystems, is generally thought to have been slow and stepwise (e.g., Erwin, 1993, 1994, 2000, 2001; McGhee Jr. et al., 2004; Tong et al., 2007; Roopnarine et al., 2018, 2019), although some exceptions to this pattern are known (Brayard et al., 2017). The delay likely stems from a combination of continuing environmental perturbations (Pruss et al., 2006; Erwin, 2007) and biotic drivers such as the multilevel interaction between species in the new environments and ecosystems (Chen and Benton, 2012; Song et al., 2018; Dineen et al., 2019).

The duration of the recovery interval is debated, with much of the confusion depending on the definition of 'recovery' (Chen and Benton, 2012). If the term refers simply to a basic rebuilding of species numbers, then recovery of some clades was quick, maybe within the first

1–3 Myr after the PTME (Song et al., 2011; Brayard et al., 2010, 2011, 2017). Hofmann et al. (2011) suggested global recovery of benthic ecosystems in the late Griesbachian, less than 1 My after the extinction, on the basis of ichnofossils from the Lower Triassic Werfen Formation (Dolomites, Italy). In fact, these early phases of recovery through the Early Triassic were stopped by the repeated flash warming events, and usually the definition of ‘recovery’ has included an assumption of ‘lasting recovery’ or stability of the recovered ecosystems. Under this definition, the recovery in the Early Triassic is usually estimated as lasting 5–9 Myr (Hallam, 1991; Erwin, 1992, 2001; Payne et al., 2004, 2011; Algeo et al., 2011; Whiteside and Ward, 2011), with complex ecosystems totally restored only at the beginning of the Middle Triassic (Chen and Benton, 2012; Dineen et al., 2014; Roopnarine et al., 2019).

Different clades responded differently to continuing heat shocks during the Early Triassic. Fast-evolving groups such as conodonts and ammonoids experienced three to four cycles of extinction and recovery over 8–9 Myr (Hallam, 1991; Erwin, 1992, 2001; McGowan, 2004, 2005; Payne et al., 2004, 2011; Orchard, 2007; Brayard et al., 2009; Metcalfe and Isozaki, 2009; Stanley, 2009; Meyer et al., 2011; Chen and Benton, 2012; Bai et al., 2017), whereas more slowly evolving plants and tetrapods took 8–9 Myr or longer (Benton et al., 2004; Sahney and Benton, 2008; Irmis and Whiteside, 2011; Chen and Benton, 2012). Brachiopods were slow to recover also; they were very common in Permian marine ecosystems but only reached substantial diversity in the Middle Triassic (Chen et al., 2005a, 2005b), even if a first recovery started already in the immediate aftermath of the PTME according to Wang et al. (2017). Another slowly evolving group, the benthic foraminifera, started to recover in the Early Triassic, just 1 Myr after the PTME, but needed 10 Myr to reach a pre-extinction level of diversity (Song et al., 2011). Amongst echinoderms, ophiuroids underwent a geographic radiation and increase in diversity in the immediate aftermath of the PTME (Chen and McNamara, 2006), whereas crinoids were virtually absent in earliest Triassic marine ecosystems, and radiated only in the Spathian (Twitchett et al., 2005). Corals were severely affected by the PTME and re-appeared in the fossil record only in the middle Anisian (Flügel, 2002), thus with a prolonged delay in recovery till Middle Triassic (Kiessling et al., 2002; Chen and Benton, 2012; Bai et al., 2017).

An ecological aspect characterizing both the PTB crisis and the entire Early Triassic in marine ecosystems is a substantial reduction in overall body size (Twitchett, 2007), a dwarfing process known as the ‘Lilliput Effect’ (Urbanek, 1993). This process can be linked to several biotic and abiotic stresses, including increasing ecological pressure, shortage of food resources, and greenhouse crises leading to reductions in oxygen levels (see Chen and Benton, 2012). Although conflicting patterns have been suggested for some groups (e.g., compare Payne, 2005 to Brayard et al., 2010 for gastropods), several marine and terrestrial invertebrate clades in the Early Triassic show the Lilliput Effect (e.g., Hayami, 1997; Fraiser and Bottjer, 2004; Chen et al., 2005a, 2019; Payne, 2005; Twitchett et al., 2005; He et al., 2007b, 2010b, 2015; Twitchett, 2007; McGowan et al., 2009; Fraiser et al., 2011; Song et al., 2011; Chu et al., 2015; Schaal et al., 2016; Zhang et al., 2016, 2017). A smaller body size in the Early Triassic has also been documented for vertebrates in both the marine and terrestrial realms (e.g., Smith, 1995; Tverdokhlebov et al., 2003; Mutter and Neuman, 2009; Huttenlocker, 2014; Romano et al., 2016).

3. The PTME and tetrapod recovery on land

Early Triassic tetrapod assemblages were therapsid-dominated, as was the case for most Middle–Late Permian tetrapod assemblages (Lucas, 2009). There is thus a question about recovery and the eventual establishment of archosauromorph-dominated tetrapod communities in the Middle Triassic, as many of the Early Triassic therapsid survivors of the PTME were ‘holdover’ taxa that soon went extinct. Thus, even if local diversity on land recovered quite fast for tetrapods, well-balanced

and stable ecosystems emerged only in the Middle Triassic (Chen and Benton, 2012). In a study based on trophic network analysis, Roopnarine et al. (2007) stressed that terrestrial vertebrate communities in the Early Triassic were substantially less stable when compared to those characterizing the Late Permian. Roopnarine et al. (2007) show how the amphibian dominated *Lystrorhynchus* zone communities were characterized by a greater number of connections per guild when compared to the Late Permian communities dominated by amniotes. The greater connectance of the *Lystrorhynchus* metanetwork also implies a greater dynamic amplification of perturbations (including feedback) among the detected guilds, resulting in a greater level of combined secondary extinction, and overall instability (Roopnarine et al., 2007).

The Triassic recovery of tetrapods marked the largest ecosystem reconstruction on land, with the origins of crucial modern groups such as lizards, crocodiles, frogs, turtles and mammals, including the evolution of dinosaurs (Chen and Benton, 2012). The PTME had wiped out the well-structured latest Permian ecosystems characterized by carnivorous gorgonopsian therapsids and herbivorous pariaesaur and dicynodonts. The latter survived the crisis, passing the through bottleneck along with thercephalians and procolophonids (Chen and Benton, 2012). Early Triassic terrestrial ecosystems testify to an unbalanced ‘disaster fauna’, lacking top predators and diverse herbivores and characterized by very abundant specimens of the dicynodont *Lystrorhynchus* and temnospondyl amphibians (Benton, 1983; Benton et al., 2004; Sahney and Benton, 2008; Chen and Benton, 2012). Sahney and Benton (2008) report a lower level of vertebrate cosmopolitanism for the Early Triassic, compared to the condition in the Late Permian.

The best-studied records of the effects of the PTME on terrestrial tetrapods come from three geographically-separated areas, the Karoo Basin of South Africa (e.g., Ward et al., 2005; Smith and Botha, 2005; Botha and Smith, 2006; Botha-Brink et al., 2014, 2016; Viglietti et al., 2018), the fore-Ural region of the Russia Platform (e.g., Benton et al., 2004; Sennikov and Golubev, 2005, 2006, 2012; Newell et al., 2010; Sennikov, 2017), and the flanks of the Bogda Mountains in western China (e.g., Metcalfe et al., 2009; Liu and Abdala, 2017). In addition to these areas, tetrapod assemblages that may span the PTB are known from the Luang-Prabang Basin of Laos and the Norte Basin of Uruguay, but the significance of these records for studies of the PTME is uncertain. The Laotian Purple Claystone Formation has produced a fauna of chroniosuchian and dicynodontoid-grade dicynodonts (Arbez et al., 2018; Olivier et al., 2019), and radiometric dating of volcanoclastic strata within the formation gives dates that span the PTB (Rossignol et al., 2016). However, the error-ranges on the dates are relatively broad and the tetrapod taxa do not facilitate an unambiguous biostratigraphic correlation with Late Permian or Early Triassic assemblages from South Africa, Russia, or China. A more diverse assemblage is known from the Buena Vista Formation of Uruguay, including lauderiid, mastodontosaurid, rhinesuchid, and dvinosaurian temnospondyls (Marsicano et al., 2000; Piñeiro et al., 2007a; Piñeiro et al., 2007b; Piñeiro et al., 2007c; Piñeiro et al., 2012), procolophonoid parareptiles (Piñeiro et al., 2004), putative varanopid and sphenacodontid synapsids (Piñeiro et al., 2003), and basal archosauromorphs (Ezcurra et al., 2015). The age of this assemblage, known as the Colonia Orozco Local Fauna, is controversial. The Buena Vista Formation has been correlated with the Brazilian Sanga do Cabral Formation (Bossi and Navarro, 1991), which is thought to be of Induan age based on the presence of the parareptile *Procolophon* (Dias-da-Silva et al., 2006a). However, the “transitional” morphologies of some taxa from the Buena Vista Formation (Piñeiro et al., 2012) and disputes over the identifications and biostratigraphic significance of the taxa (Dias-da-Silva et al., 2006a; Modesto and Botha-Brink, 2010) have suggested a generalized “Permo-Triassic” age for the Colonia Orozco Local Fauna (e.g., Ezcurra et al., 2015).

The most complete record for tetrapod faunas across the PTB is from the Karoo Basin of South Africa (Smith and Botha, 2005; Botha and Smith, 2006; Lucas, 2009; Modesto and Botha-Brink, 2010). Botha and

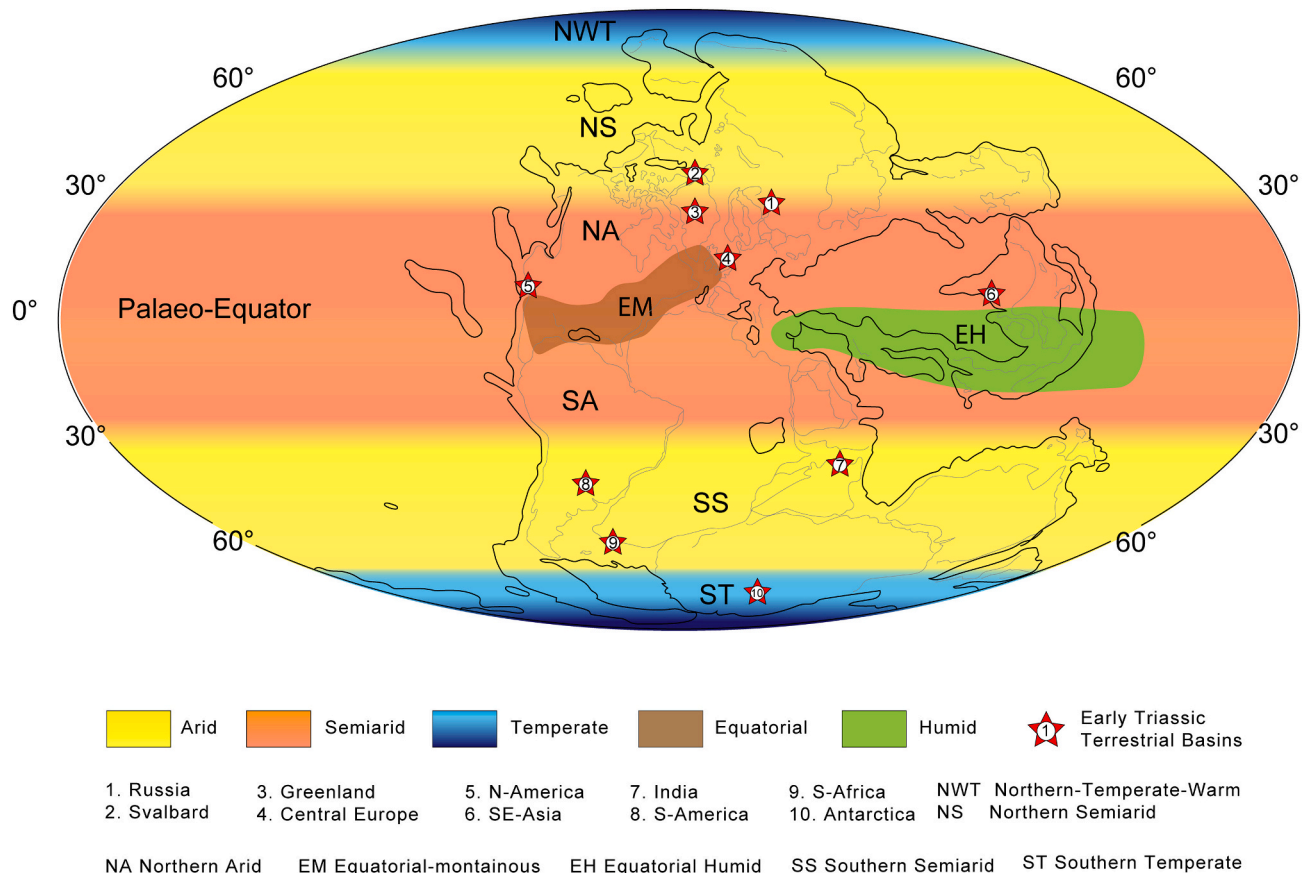


Fig. 1. Simplified palaeoclimatic reconstruction for the Early Triassic showing the inferred distribution of the Northern Arid, Equatorial-mountainous, Equatorial Humid, Southern Semi-arid, Southern Temperate belts. Principal Early Triassic Terrestrial basins indicated with a star.

Smith (2006) proposed three categories for the PTB tetrapod fauna, an extinction fauna characterized by only Permian tetrapods, a survivor fauna with three species that were able to cross the bottleneck of the mass extinction, and a recovery fauna with only Triassic tetrapods.

In the Karoo, the PTB is characterized by an extinction phase in the upper *Daptocephalus* Assemblage Zone (Viglietti et al., 2016), with the final extinctions of biarmosuchians and gorgonopsians and consistent extinction of dicynodonts (Lucas, 2009). Parareptiles seem to be less affected, with the loss of four to six taxa (Botha et al., 2007; Lucas, 2009). Lucas (2009) defined this faunal turnover as the “PTB tetrapod extinction event”. In the Karoo Basin the PTB tetrapod extinction event is represented by only a 60 m thick stratigraphic interval, from the upper part of the Balfour Formation, through the basal portion of the overlying Katberg Formation (Smith and Ward, 2001; Retallack et al., 2003; Ward et al., 2005; Smith and Botha, 2005; Botha and Smith, 2006, 2007; Lucas, 2009). For this stratigraphic interval, Ward et al. (2005) report a loss of ten genera, one passing the crisis and the appearance of five new genera; for the same interval Smith and Botha (2005) and Botha and Smith (2006, 2007) report nine genera that disappear, two passing through the crisis, and six new genera that appear after the crisis. The 60 m thick PTB stratigraphic interval represents a time span within 100 kyr (but see Gastaldo et al., 2009 for a different interpretation and a reply by Ward et al., 2012).

The recovery fauna in the Early Triassic of the Karoo Basin includes small insectivorous cynodonts, medium-sized dicynodonts, small procolophonoids, proterosuchian archosauromorphs and small amphibians (Smith and Botha, 2005). Apart from gorgonopsians that went extinct in the Late Permian crisis (although already in decline well before the end of the Permian, see King, 1993; Smith and Botha, 2005), dicynodonts represent the therapsid group most severely affected by the mass extinction, with a 83% generic extinction rate (Smith and Botha, 2005).

According to Smith and Botha (2005), the predominance of burrowing therapsids in the earliest Triassic, including *Lystrosaurus*, *Thrinaxodon*, *Galesaurus*, and probably also *Progalesaurus* (as the sister taxon of *Galesaurus*), suggests that either habitual or obligate burrowing behaviour might have been a means to tolerate the Early Triassic aridification that characterised southern Gondwana (see below). Smith and Botha (2005), Botha and Smith (2006) and Smith and Botha-Brink (2014) claim a rapid vertebrate recovery in the Karoo, faster than in the South Urals Basin in Russia (see Hancox and Rubidge, 2001; Benton et al., 2004; Smith and Botha, 2005).

Newer studies explore the diversifications of tetrapods in the Triassic by means of phylogenetic comparative analyses (Sookias et al., 2012). As an example, Ezcurra and Butler (2018) analyse patterns of early archosauromorph biodiversity change through the PTME. The analysis shows major phylogenetic diversification of archosauromorphs in the Olenekian, with significantly elevated evolutionary rates in the diversification of archosaurs, erythrosuchids, rhynchosaurs and tanystropheids (Ezcurra and Butler, 2018). The initial diversification of archosauromorphs is interpreted as a response to vacant ecological space, emptied by the PTME, but with a species richness that remained quite low for all the Olenekian, and similar to that of the Induan. Ezcurra and Butler (2018) find a diversity-first model of evolution for basal archosauromorphs, involving a first fast diversification of disaster taxa to occupy the vacant ecospace, and a subsequent more steady adaptive evolution exploring new portions of morphospace, with late stabilization of communities and ecosystems.

4. Early Triassic climate

Early Triassic climates have been reconstructed from a variety of proxies, including isotopic composition, palaeosols, peculiar

sedimentary structures, and biological evidence (see Benton and Newell, 2014 for a complete review). Conditions were unusual for the Phanerozoic, with anoxic and alkaline oceans and migration of warm temperature and desert expansion to high southern hemisphere latitudes (Woods, 2005) (Fig. 1). Levels of CO₂ substantially increased in the Early Triassic, whereas levels of atmospheric O₂ decreased (Berner, 1989, 1994, 2001; Graham et al., 1995; Sheldon and Retallack, 2002; MacLeod et al., 2017), generating harsh environmental conditions that very likely had a strong influence on the tempo and mode of biotic recovery from the PTME (Woods, 2005; MacLeod et al., 2017). A general trend in global warming in the Early Triassic is interpreted as the cause of a shift of the deciduous forests (typical of warm climates) to polar regions in the southern hemisphere (Taylor et al., 1992, 2000), deposition of extensive evaporitic deposits (Gordon, 1975), and an expansion of desert belts between 15° and 45° and possibly as high as 60° latitude (Kidder and Worsley, 2004). At the equator, temperatures between 32 and 35° have been estimated for the earliest Triassic (Joachimski et al., 2012), and Sun et al. (2012) calculated temperatures of up to 40° at the Smithian–Spathian boundary. According to Retallack et al. (2011), the long recovery from the PTME was caused not only by the severity of the biological crisis, but also by repeated greenhouse crises during the Early Triassic (see also Knoll et al., 2007; Chen and Benton, 2012).

Early Triassic global warming has been linked to an increase in levels of CO₂ and other greenhouse gases (Berner, 1989, 1994, 2001; Graham et al., 1995; Sheldon and Retallack, 2002), with the expansion of harsh arid climates in the Northern Hemisphere up to high latitudes (Embry, 1991; Ziegler et al., 1993; Wang, 1996; McLoughlin et al., 1997; Beauchamp and Baud, 2002; Kidder and Worsley, 2004).

The increase in CO₂ has been explained in a number of ways: a decline in the silicate weathering rate linked to curtailed orogenesis in the final assemblage of Pangaea (Kidder and Worsley, 2004); a shift from terrestrial to marine settings for the burial of organic carbon (Broecker and Peacock, 1999; Berner, 2002); a decline in the photosynthesis CO₂ drawdown, linked to a decline in oceanic productivity and global reduction of global forest coverage (Kidder and Worsley, 2004); the decay of large amounts of biomass derived from mass mortality (Berner, 2002); CO₂ release via Siberian Traps eruption at the PTB (Renne et al., 1995); and release of CH₄ from methane hydrates in marine sediments and CH₄ oxidation to CO₂ (Erwin, 1993; Krull and Retallack, 2000; MacLeod et al., 2000; Krull et al., 2004).

One of the first major factors influencing Early Triassic climate was the north to south extension of the Pangaeian supercontinent (see Woods, 2005), which led to marked seasonality (Parrish, 1993) and consistent dry climates (Parrish et al., 1982; Dickins, 1993; Trotter et al., 2015). In particular, modelling studies that considered the increase in CO₂ during the PTB interval, indicate a possible increase in the global air temperature of 6–8 °C (Royer et al., 2004).

On the basis of evidence for moist and warm polar climates (Taylor et al., 1992; Retallack, 1999), it has been proposed that the Early Triassic climate was characterized by a consistent reorganisation in the atmosphere, with polar cells totally disappearing or abruptly weakened (Kidder and Worsley, 2004). This new general circulation configuration of the atmosphere would have allowed temperate palaeosols (Retallack, 1995, 1999) and deciduous forests (Taylor et al., 1992, 2000) to develop at high latitudes, as well as the deposition of evaporitic deposits (Gordon, 1975) and the development of consistent desert belts (Ziegler et al., 1993; Wang, 1996; McLoughlin et al., 1997). Polar regions in the Early Triassic have been considered as totally ice-free, with deposits of the Late Permian characterised by soils, plant and coal deposits typical of cool temperate latitudes (Retallack et al., 2006). The temperate condition of the poles has also been linked to a reduced albedo, from the lack of permanent land ice and unrestricted ocean transport of heat toward the poles (Kiehl and Shields, 2005).

The almost symmetrical configuration of Pangaea around the equator, with an essentially pole-to pole distribution of land masses

(Benton and Newell, 2014), would have caused marked monsoonal conditions via a breakdown in zonal circulation (Kutzbach and Gallimore, 1989; Parrish, 1993), with a climate dominated by strongly seasonal rainfall (Kutzbach and Gallimore, 1989; Golonka et al., 1994; Wilson et al., 1994). This Pangaeian ‘megamonsoon’ (Kutzbach and Gallimore, 1989; Parrish, 1993; Sellwood and Valdes, 2006; Preto et al., 2010; Trotter et al., 2015) was associated with extreme seasonality, with dry winters and wet summers, and is corroborated by the vast deposition of red bed facies (Parrish, 1993; Woods, 2005). Intense global warming in the Early Triassic occurred in tandem with an increase in both frequency and intensity of winter storms and hurricanes (Marsaglia and Klein, 1983; Duke, 1985; Barron, 1989; Ito et al., 2001; Kidder and Worsley, 2004). This is supported by an increase in hummocky cross-stratification wavelength across the Permian-Triassic sedimentary interval (Ito et al., 2001).

Climate models confirm the megamonsoon. Crowley et al. (1989) and Kutzbach and Gallimore (1989) were pioneers in modelling the Early Triassic energy balance based on the peculiar plate configuration of Pangaea. Their models indicate the possibility of extreme seasonal temperature variation for the vast continental interiors of Pangaea and very arid climates for the western margin of Laurussia and Gondwana. The models also predict intense monsoonal circulation and high precipitation on the Tethys coast.

Kiehl and Shields (2005) developed a model based on the coupling of oceanic and atmospheric circulation, obtaining cool temperate polar regions via a flow into high latitudes of warm water. Roscher et al. (2011) present a model where an episode of global cooling around the PTB was predicted, which would have resulted in a more successful process to explain the climate belt changes with respect to global warming.

On the basis of two marine sedimentary sequences at Chaohu and Daxiakou, South China, Li et al. (2016a, 2016b) stressed a million-year-scale astronomical forcing of Early Triassic climate. Their sedimentary sections indicate a dominant obliquity-scale cycling, with 1.2 myr. Periodicity of weathering intensity linked to models of Earth's obliquity modulations and variations in both ocean redox conditions and temperature. They argued that the extreme climate changes in the Early Triassic were essentially obliquity-forced, with major changes affecting the transfer of moisture and heat and the eustasy of continental aquifers, with a strong influence on global ecosystems (Li et al., 2016a, 2016b). More details on Early Triassic climate can be found in Appendix 1.

5. Material and methods

Early Triassic tetrapod faunas, represented by both body fossils and footprints, have been reported and described from Antarctica, Argentina, Australia, Brazil, Canada, China, England, Germany, Spain, Greenland, India, Italy, Japan, Kenya, Laos, Mongolia, Morocco, Madagascar, Niger, Pakistan, Poland, Russia, Scotland, United States and South Africa. Plant fossil assemblages are known from Antarctica (Axsmith et al., 1998; McManus et al., 2002; Escapa et al., 2010), Argentina (Ottone and Garcia, 1991), Australia (Balme, 1963; Ash, 1979; Foster, 1982; Scott and Playford, 1985; Cantrill and Webb, 1998; Retallack, 1999; Michaelsen, 2002; Retallack, 2002; Northwood, 2005; Haig et al., 2015), China (Peng et al., 2006; Yu et al., 2007; Peng and Shi, 2009; Schneebeli-Hermann et al., 2012), Spain (López-Gómez et al., 2005), Kenya (Hankel, 1991, 1992), and Russia (Nauogolnykh, 2012).

A comprehensive Dataset of Early Triassic terrestrial tetrapods (Supplementary Material) was compiled starting with data from the Paleobiology Database (PBDB, <http://fossilworks.org/>, downloaded 07 February 2019). The occurrences derived from the PBDB were integrated with other published material and large museum collection databases. In particular for South Africa we used the Karoo vertebrate database, which includes all catalogued vertebrate specimens from the

principal South African collections (i.e. Albany Museum, Grahamstown; American Museum of Natural History, New York; Bremner Collection; Council for Geoscience, Pretoria; Evolutionary Studies Institute, University of the Witwatersrand; Field Museum of Natural History, Chicago; Iziko South African Museum, Cape Town; National Museum, Bloemfontein; Rubidge Collection; Stellenbosch University; Transvaal Museum, Pretoria; University of California Museum of Paleontology, Berkeley), made up of more than 21,000 specimens. In addition to the body fossil record, the global ichnological record was incorporated using the dataset presented by [Bernardi et al. \(2018\)](#), supplementary material) with updates to account for recently published material.

The new dataset has been subdivided into eleven regional palaeo-latitudinal bins: Russia (32°-58.61° N; including the Lower Triassic Heshanggou Formation and Hongyanjing Formation of northern Gansu Province, China); Svalbard (55.72°-55.94° N); Greenland (43.93°); North America (18.56°-39.53° N; including specimens from USA and Canada); Central Europe (25.26°-31.73° N; including specimens from Germany, Spain, England, Poland, Scotland and Italy); South America (32.08°-35.01° S; including Argentina and Brazil); India (30.3°-49.28° S; including Madagascar, Kenya and Pakistan); Southeast Asia (15.81° N to 46.55° S; including China and Japan); South Africa (49.54°-51.93° S); Antarctica (71.96°-72.48° S); and Australia (51.11°-82.66° S).

For each of the eleven selected regions we provide a short review of the geological setting and outcrop data for all formations that preserve Lower Triassic terrestrial tetrapods. We also provide a list of all recognized taxa at the species level whenever possible, with the number of described or catalogued specimens for each taxon in our database used to provide relative abundance estimates for the following major clades: Archosauromorpha, Chroniosuchia, Cynodontia, Dicotyrodontia, Procolophonomorpha, Salentia, Temnospondyli and Therapsida. The relative abundances, with standard errors, were compared to highlight statistically significant differences presented in the Discussion section. A second abundance estimate was derived including also the ichnological dataset using more inclusive higher taxa: Archosauromorpha, Chroniosuchia, Lepidosauromorpha, Non-temnospondyl Amphibia, Procolophonomorpha, Temnospondyli and Therapsida. We used the latter percentages to build a presence matrix (see Supplementary Material) where all taxa for each region are scored according to their relative abundance (based on number of specimens for each taxon) in the analysed fauna. The scores applied to each clade are as follows: 1) Absent or unknown: 0% (score = 0); 2) Rare: 0–10% (score = 1); Moderate abundance: 10–30% (score = 2); Abundant: > 30% (score = 3). To quantify similarities in faunal composition between the different regions, we subjected the data matrix to a Cluster analysis using the Paired Group Algorithm (UPGMA) and the Euclidean Similarity Index in PAST 3.10 ([Hammer et al., 2001](#)).

6. Early Triassic tetrapod faunas

6.1. Antarctica

Early Triassic terrestrial tetrapods from Antarctica are known from body fossils ([Owen, 1876](#); [Elliot et al., 1970](#); [Colbert, 1970](#); [Kitching et al., 1972](#); [Colbert and Cosgriff, 1974](#); [Colbert and Kitching, 1975, 1977, 1981](#); [Hammer and Cosgriff, 1981](#); [Cosgriff et al., 1982](#); [Cosgriff and Hammer, 1984](#); [Colbert, 1986, 1987](#); [Hammer, 1990](#); [Gow, 1992](#); [Warren and Marsicano, 2000](#); [Miller et al., 2001](#); [Debraga, 2003](#); [Retallack et al., 2005](#); [Collinson et al., 2006](#); [Collinson and Hammer, 2007](#); [Sidor et al., 2007, 2008a](#); [Fröbisch et al., 2010](#); [Hasiotis et al., 2004](#); [Smith et al., 2011](#); [Huttenlocker and Sidor, 2012](#); [Peecook et al., 2019](#)), and a poor ichnological fossil record ([Macdonald et al., 1991](#); [Sidor et al., 2008b](#)).

Early Triassic terrestrial tetrapods have been found and collected since the late 1960s from the Fremouw Formation ([Fig. 2](#)), outcropping at Graphite Peak, and other localities in the central Transantarctic Mountains. On the basis of vertebrate biostratigraphy and correlation

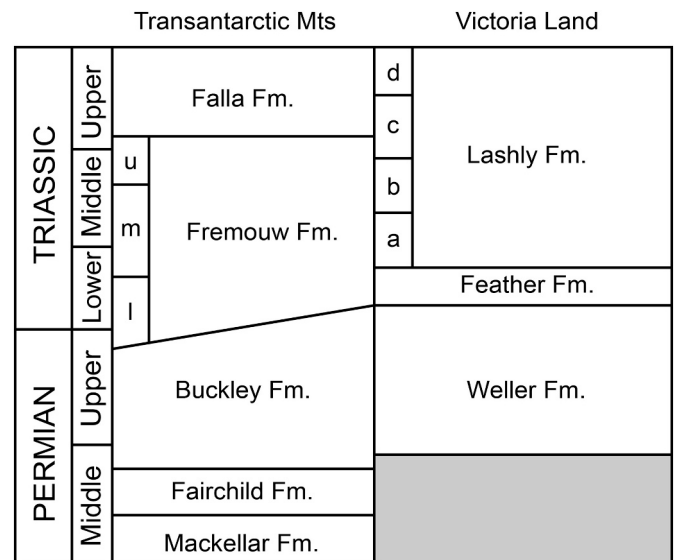


Fig. 2. Overview of the Permian and Triassic stratigraphy of Antarctica. For further details see [Sidor et al. 2008](#) with bibliography.

with the Karoo Basin in South Africa, sedimentary deposits outcropping in the Transantarctic Mountains can be referred to the Lower Triassic, Middle Triassic, Upper Triassic, and Lower Jurassic ([Elliot et al., 1970](#); [Hammer et al., 1987, 2004](#); [Sidor et al., 2008a, 2013, 2014](#); [Peecook et al., 2019](#)). The Beacon Supergroup sedimentary sequences in the central Transantarctic Mountains represent the fill, from Early Permian through Early Jurassic, of a series of retroarc foreland basins that developed on the continental side of the rising Gondwanide mountains ([Collinson, 1991](#); [Isbell, 1991](#); [Collinson et al., 1994](#); [Peecook et al., 2019](#)). Filling of the Beacon Supergroup starts, as observed in the Karoo Basin, with diamictites of the Pagoda Formation recording different cycles of Gondwanan glaciation in the Permo-Carboniferous, followed by melt-out black shales of the Mackellar Formation, passing upward to the Permian deltaic systems of the Fairchild Formation ([Peecook et al., 2019](#)) ([Fig. 2](#)). Upward the deltas coalesce, forming large alluvial plains with a large-scale distributary fluvial channel running northwards, essentially parallel to the mountain range ([Isbell, 1991](#); [Peecook et al., 2019](#)).

The nonmarine Triassic rocks of Antarctica are represented by the the Fremouw and Falla formations and by the Feather and Lashly formations in Victoria Land ([Elliot, 1975](#); [Collinson et al., 1994](#)) ([Fig. 2](#)). The Fremouw Formation is over 600 m thick, with a distribution ranging laterally from approximately 83° to 86° S latitude in the proximity of the Beardmore and Shackleton glacier regions of the central Transantarctic Mountains ([Barrett et al., 1986](#); [Huttenlocker and Sidor, 2012](#)). Sedimentary rocks of the Fremouw Formation indicate low-sinuosity braided systems, with a setting dominated by sub-angular quartzose clasts in coarse channel sands ([Barrett et al., 1986](#); [Isbell and MacDonald, 1991](#)). The formation is subdivided informally into lower, middle, and upper members ([Collinson and Elliot, 1984](#); [Barrett et al., 1986](#); [Huttenlocker and Sidor, 2012](#)) ([Fig. 2](#)).

The lower Member of the Fremouw Formation, well-exposed in the Shackleton Glacier region, is represented by green-grey or red rooted siltstone beds and stacked fining-upward cycles of medium- to coarse-grained fluvially deposited sandstone ([Peecook et al., 2019](#)). According to [Collinson et al. \(2006\)](#), the base of the Fremouw Formation can be identified by the first cliff-forming channel sandstone ([Barrett, 1969](#)), but it is diachronous in the Beacon Basin particularly the Shackleton Glacier region, ranging in age from latest Permian at some sites to earliest Triassic at others (see also [McManus et al., 2002](#)). [Collinson et al. \(2006\)](#) positioned the PTB in the lower Member, within a 7–10 m interval above a level with a glossopterid flora ([McManus et al., 2002](#))

in the Shackleton Glacier area. The middle Member of the Fremouw Formation is composed of green-grey or red beds, while fine- to medium-grained sandstone and isolated coal beds characterize the upper Member (Barrett, 1969; Peacock et al., 2019). Most terrestrial vertebrate remains come from the lower Member, with rare elements recovered from the middle Member at Shenk Peak (Fröbisch et al., 2010). At Gordon Valley and at Fremouw, the upper Member of the Fremouw Formation yielded a vertebrate fauna comparable to that of the *Cynognathus* Assemblage Zone of the Karoo Basin (Hammer, 1990; Hammer et al., 1990; Fröbisch et al., 2010).

On Graphite Peak, the Fremouw Formation shows an abrupt change in palaeosols characterised by the total disappearance of carbonaceous shale and the appearance of white-weathering claystone-lined root moulds, which, according to Retallack et al. (2005), testify to a severe and fast climatic drying associated with the PTME. Triassic palaeosols of the Fremouw Formation were formed essentially in woodland settings, on a seasonally well-drained and wet floodplain, and suggest warmer climate with respect to palaeosols described from the upper Buckley Formation (Retallack et al., 1996b; Retallack and Krull, 1999; Krull and Retallack, 2000; Collinson et al., 2006). In fact, palaeosols in the underlying Buckley Formation indicate a humid climate and an environment of swampy floodplains and woodlands, with seasonal snowfall (Retallack et al., 1996b; Retallack and Krull, 1999; Krull and Retallack, 2000).

On the basis of several shared taxa (e.g., *Lystrosaurus curvatus*, *Procolophon trigoniceps* and *Thrinaxodon liorhinus*), the Fremouw Formation has traditionally been correlated with the *Lystrosaurus* Assemblage Zone (LAZ) of the Karoo Basin (Colbert, 1970; Elliot et al., 1970; Kitching et al., 1972). More recently however it has been shown that some taxa of the lower Fremouw Formation, including brachyopoid temnospondyls, the enigmatic reptile *Palacrodon*, and the dicynodont *Kombuisia*, appear only later in the Karoo Basin and thus are not known from the LAZ (see Peacock et al., 2019). Similarly, a possible gomphodont cynodont, *Lystrosaurus maccaigi* and large-bodied archosauriforms are not present in the South African LAZ, but occur in the lower Fremouw (Peacock et al., 2019). Thus, to date, the lower Fremouw Formation assemblage is characterized by a combination of taxa showing non-overlapping stratigraphic distributions with the Karoo Basin of South Africa. Taxa characterizing the lower Fremouw Formation, such as brachyopoid temnospondyls, the dicynodont *Kombuisia* and *Palacrodon browni*, appear in the South African Karoo Basin record only in the *Cynognathus* Assemblage Zone (Sidor et al., 2008a; Peacock et al., 2019).

Fröbisch et al. (2010) proposed that Antarctica could have served as a high-latitude refuge during the PTME, as already suggested for temnospondyl amphibians (Yates and Warren, 2000), explaining why taxa such as *Lystrosaurus maccaigi* and *Kombuisia* cross the boundary and persist into the Lower Triassic. The idea arose because the climate of Antarctica was cooler than that of the Karoo Basin, but warm enough to allow the survival of terrestrial vertebrates, thus representing a refuge for the “postapocalyptic greenhouse” identified by Retallack (1999). However, on present evidence, Peacock et al. (2019) concluded that the lower Fremouw vertebrate assemblage cannot simply be interpreted as a taxonomic subset of the LAZ, being characterized by taxa not shared with the LAZ in the main Karoo Basin of South Africa such as *Palacrodon*, *Kombuisia*, Lapillopsidae, Brachyopoidea, early members of the Gomphodontia, and by the occurrence of unique forms such as the large archosauriform *Antarctanax shackletoni*.

Smith et al. (2011) stressed that the presence of large archosauriforms from the lower Fremouw Formation indicate that one or more lineages reached large body size comparable to later members of the clade soon after the PTME, thus contrasting with the ‘Lilliput effect’ often characterizing post-extinction terrestrial communities. According to Collinson and Hammer (2007), a first dispersal of terrestrial tetrapods to modern-day Antarctica during the Early Triassic was allowed by a combination of general global warming and the northward movement

of Pangaea.

On the basis of the newly compiled dataset (Supplementary Material) the fauna is dominated by Temnospondyli represented by Brachyopoidea and unidentifiable Stereospondyli (30.9%), followed by Archosauromorpha with two genera *Prolacerta* and *Antarctanax* (21%), Cynodontia with the galesaurid *Thrinaxodon* (19.8%), Procolophonomorpha with the single, quite abundant genus *Procolophon* (13.6%), Dicynodontia with the genera *Kombuisia*, *Myosaurus* and *Lystrosaurus* (8.6%) and Theriocephalia as the least abundant clade, represented by the genus *Eriocolacerta*, and four unidentifiable specimens referable to Akidnognathidae, Baurioidea, and Eutherocephalia (6.2%).

The ichnological record includes generic dicynodont tracks from the Induan Fremouw Formation (middle Member) in the Gordon Valley of Antarctica (MacDonald et al., 1991).

Including the ichnological record, the fauna is dominated by Therapsida (39.4%), followed by Temnospondyli (30%), Archosauromorpha (20.5%), and Procolophonomorpha (14.5%).

6.2. South America (Argentina + Brazil)

Early Triassic tetrapod faunas of South America, known from both body fossils and footprints, have been described from Argentina (Bonaparte, 1978; Melchor and De Valais, 2006; Ezcurra et al., 2010), and Brazil (Lavina, 1983; Abdala et al., 2002; Cisneros and Schultz, 2002; Dias-da-Silva et al., 2005, 2006a, 2006b; Langer et al., 2007; Dias-da-Silva and Schultz, 2008; Da-Rosa et al., 2009; Dias-da-Silva and Ilha, 2009; Dias-da-Silva and Milner, 2010; Dias-da-Silva and Da-Rosa, 2011; Pinheiro et al., 2016; Eltink et al., 2017).

Traditionally, Early Triassic terrestrial vertebrate remains from Argentina are known from the Puesto Viejo Formation (Fig. 3), which may be divided into the Quebrada de los Fósiles Formation and the Río Seco de la Quebrada Formation (Stipanovic et al., 2007; Ezcurra et al., 2010). However, more recently Ottone et al. (2014) ascribe the unit to the Late Triassic. According to Bonaparte (1966a, 1966b, 1967, 1981, 2000), the Quebrada de los Fósiles Formation can be considered equivalent to the LAZ of Induan–early Olenekian age, based on both radiometric dating (Valencio et al., 1975; Ramos, 1993) and the correlation of the Río Seco de la Quebrada Formation to the *Cynognathus* Assemblage Zone (CAZ), sharing the cynodonts *Cynognathus craternotus* and *Diademodon tetragonus*, and on the basis of the fossil content (see Ezcurra et al., 2010). Zavattieri et al. (2003) described a typical microfloristic Gondwanan Permian assemblage associated with less common Middle and Late Triassic components from the Quebrada de los Fósiles Formation, which led the authors to refer the Formation to the PTB, if not to the uppermost Permian. On the basis that no representatives of the *Dicroidium* flora (typical of the Middle and Late Triassic assemblages) had been found in the Puesto Viejo Group, Stipanovic et al. (2007), referred the Quebrada de los Fósiles Formation to the oldest Early Triassic (Induan) or the youngest Late Permian. Based on a preliminary reappraisal of the dicynodont material from the Quebrada de los Fósiles Formation (Domnanovich and Marsicano, 2010), Ezcurra et al. (2010) consider the unit to be Early Triassic in age. The Quebrada de los Fósiles Formation hosts the first archosauriform *Koilemasuchus gonzalezdiazii* from the Early Triassic of Argentina, from the Agua de los Burros locality, 35 km south of the city of San Rafael (Mendoza Province).

Early Triassic terrestrial vertebrates from Brazil are known from the Paraná Basin, a huge intracratonic depocentre extending over Brazil, Uruguay, Argentina, and Paraguay (Milani et al., 1998), that was filled from the Ordovician to the Cretaceous by marine, continental and volcanic rocks (Zalán et al., 1991). According to Zeffass et al. (2003), the Early Triassic Sanga do Cabral Formation represents a second-order supersequence which includes also the Uruguayan Buena Vista Formation. In contrast, Pinheiro et al. (2016), in describing the new archosauromorph *Teyujagua paradoxa*, refer to the Sanga do Cabral

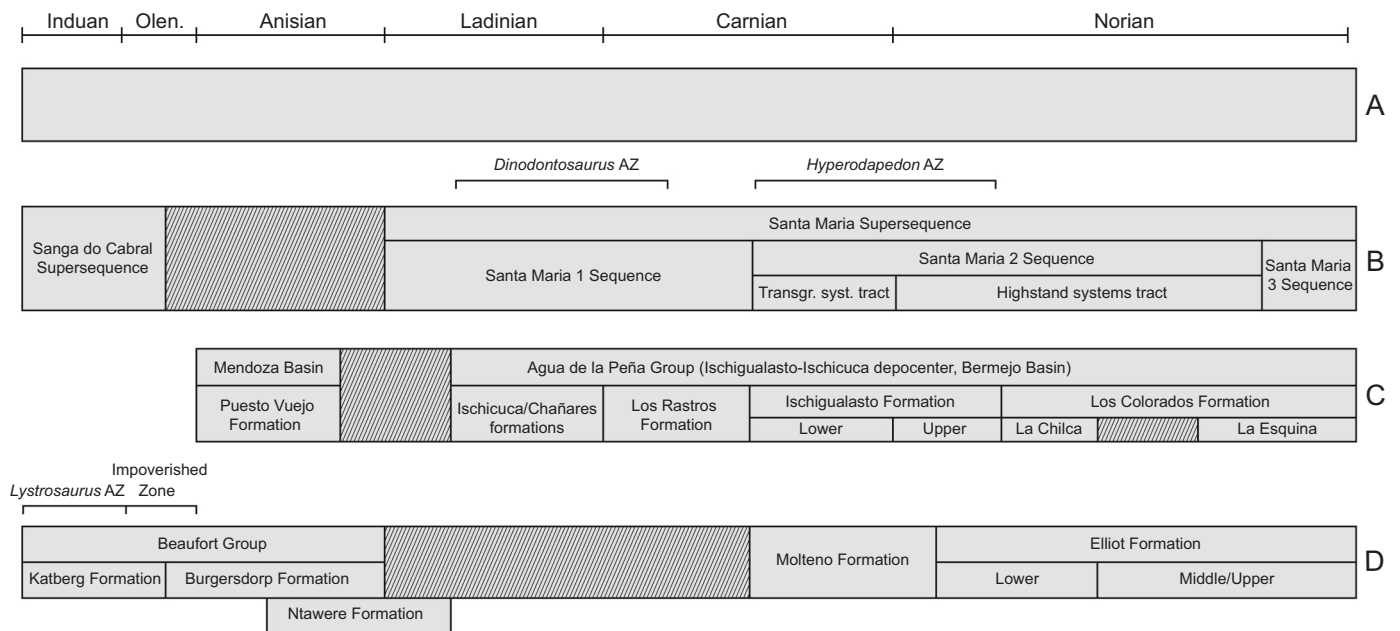


Fig. 3. Comparison of the lithostratigraphy (A) and sequence stratigraphy (B) of the Rosário do Sul Group with synthetic stratigraphic schemes of the Triassic tetrapod-bearing units of Argentina (C) and southern Africa (D). From Langer et al. (2007), with bibliography.

Formation as being Induan to early Olenekian (Lower Triassic) in age, based on the occurrence of *Procolophon trigoniceps*, which is restricted to the LAZ of the Karoo Basin of South Africa (upper Katberg Formation). Recently, Ernesto et al. (2020) dated the Buena Vista Formation in Uruguay as Late Permian, a reason to exclude it from our dataset.

In Brazil, the Sanga do Cabral Supersequence lies above the aeolian sandstones of the Pirambóia Formation, and is overlain by the Santa Maria and Caturrita formations, which together constitute the Santa Maria Supersequence, which is Middle to Late Triassic in age (Eltink et al., 2017) (Fig. 3). The Sanga do Cabral Supersequence, which is 50 to 100 m thick (Zerfass et al., 2003), comprises horizontally bedded fine-grained massive to trough cross-stratified sandstones and intraformational conglomerates, which were deposited in poorly confined braided channels characterized by a low gradient (Holz and Souto-Ribeiro, 2000; Eltink et al., 2017). The upper part of the unit is characterized by interbedded laminated mudstone lenses interpreted as the deposits of lakes and small ponds (Scherer et al., 2000; Zerfass et al., 2003; Dias-da-Silva et al., 2006a; Eltink et al., 2017). Vertebrate fossils are typically found associated with intraformational conglomerates, showing evidence of breakage and reworking (Dias-da-Silva and Ilha, 2009; Pinheiro et al., 2016).

Dias-da-Silva and Da-Rosa (2011) described a new fossiliferous site (Granja Palmeiras), where the Sanga do Cabral 'Formation' is about 12 m thick, and is composed of orange and reddish fine sandstones, characterized by fossiliferous intraformational conglomerates and calcareous concretions. According to Dias-da-Silva and Da-Rosa (2011), the precipitation of carbonate in coarse (cementation) and finer levels (nodularization), evidence of laterally persistent hydromorphic discoloration, and very frequent iron oxide (red colours) and hydroxide (orange colours), indicate low accommodation rate in a semi-arid to sub-humid alluvial plain.

On the basis of isolated vertebrae, Piñeiro et al. (2015) suggest a Late Permian age for the Sanga do Cabral Formation. However, Eltink et al. (2017) argue for an Early Triassic (Olenekian) age based on the phylogenetic position of the capitosaurid *Tomeia witecki*, sister taxon of the Olenekian *Edingerella madagascariensis* and *Watsonisuchus magnus*.

The Early Triassic terrestrial tetrapod record for South America is quite poor, being represented by only 34 specimens (Supplementary Material). The fauna is dominated by Procolophonomorpha with a

single genus *Procolophon* (38.2%), followed by Temnospondyli with the genera *Tomeia* and *Sangaia* and indeterminate Plagiosauridae and Rhytidosteidae (23.5%), indeterminate Cynodontia (20.6%), and Archosauromorpha, with the genera *Koilamasuchus* and *Teyujagua* (17.6%).

The ichnological record from South America includes the ichnogenera *Rhynchosauroides* (Lepidosauromorpha) and *Synaptichnium* (non-dinosauromorph archosaurs) and by Chirotheriidae indet. (non-dinosauromorpha archosaur) from Argentina. The faunal composition, including footprints, is dominated by Procolophonomorpha (34.2%), followed by Archosauromorpha (21.1%), Temnospondyli (21.1%), Therapsida (18.4%), and Lepidosauromorpha (5.3%).

6.3. Australia

Early Triassic terrestrial tetrapods from Australia are known to a large extent on the basis of body fossils (Cosgriff, 1965, 1969, 1974; Cosgriff and Garbutt, 1972; Howie, 1972; Camp and Banks, 1978; Bartholomai, 1979; Thulborn, 1979; Warren, 1980, 1981, 1985a, 1985b; Warren and Black, 1985; Warren and Hutchinson, 1987, 1988, 1990; Damiani and Warren, 1996; Retallack, 1996; Damiani, 1999, 2001; Yates, 1999, 2000; Northwood, 2005; Nield et al., 2006; Warren et al., 2006; Fröbisch, 2009; Kear, 2009; Haig et al., 2015), with a single ichnological record (Retallack, 1996).

Early Triassic terrestrial vertebrates are known from the Arcadia Formation (Rewan Group; Bowen Basin) (Fig. 4), the Blina Shale (Canning Basin), Bulgo Sandstone (Narrabeen Group, Sydney Basin), Cluan, Knocklofty Formation (Tasmania Basin), the Kockatea Shale and the Rewan Formation (Galilee Basin).

The Arcadia Formation of the Rewan Group (Bowen Basin) is dominated by red-brown massive mudstones, forming thick sequences of overbank deposits that are interbedded with less abundant, well-defined channel sandstones (Jensen, 1975; Kassin and Fielding, 1996; Warren et al., 2006). These sedimentary rocks were deposited by meandering and anastomosing river systems in the context of huge vegetated alluvial plains developing under warm to subarid climatic condition, characterised by strongly seasonal rainfall (Cantrill and Webb, 1998). According to Warren et al. (2006), on the basis of the peculiar composition of the fauna characterized by very rare

Chronostratigraphy			SE Galilee Basin	SW Bowen Basin	Karoo Basin
Period	Stage	Spore Units			
Early Triassic	Spathian	APT2	Clematis Sst.	Glenida Fm.	Cynognathus AZ
	Nammalian		Dunda Beds	Arcadia Fm.	Lystrosaurus AZ
	Griesbachian	APT1	Rewan Fm.		
Late Permian	Changhsingian	APP6	Bandanna Fm.	Bandanna Fm.	
	Wuchiapingian	APP5	Black Alley Shale	Black Alley Shale	

Fig. 4. Stratigraphic correlation scheme showing the approximate stratigraphic position of the Early Triassic localities in the southeastern Galilee and Bowen (central Queensland, Australia) compared with those of Karoo Basins (South Africa). Permian assemblage zones of the Karoo Basin are not included. Abbreviations: AZ – Assemblage Zone; Fm. – Formation; Sst. – Sandstone. From Warren et al. (2006) with bibliography.

dicynodonts and reptiles, and a consistent dominance of aquatic stereospondyls, the environment had to be substantially different from those dominated by *Lystrosaurus*. In particular, in contrast to the dry floodplains of the Karoo LAZ, the depositional setting of the Arcadia Formation represented a wet floodplain habitat. A Griesbachian age for the Arcadia Formation has been proposed by several authors (Warren, 1980; Thulborn, 1983, 1986; McLoughlin et al., 1997), whereas Battail (1988) suggested a Smithian age.

Based on coprolite analysis from the Crater, Queensland Museum and Duckworth Creek localities of the Arcadia Formation, Northwood (2005) showed that even if a variety of arthropods are recovered in the coprolites, invertebrates did not represent a major food source for the coprolite producers. On the other hand, dipnoans represented a crucial seasonal resource of food (Northwood, 2005). In addition, on the basis of cyanobacteria preserved in one coprolite, Northwood (2005) suggested that when the local water sources dried up periodically the environment of the Arcadia Formation could have been dry and warm.

The Bulgo Sandstone Formation, the lowermost subdivision of the Narrabeen Group, is well exposed at Long Reef, New South Wales (Australia). The unit represents at Long Reef. It is overlain by the Bald Hill Claystone and Garie Formation (Retallack, 1977; Kear, 2009). The Bulgo Formation is made up from a basal pebbly sandstone facies, followed by volcanic sandstones and granule conglomerates. The top of the unit consists of thin interbedded sandstone/lutite deposits (Kear, 2009). Based on a sequence stratigraphic analysis, plant macrofossils, and palynological data, the unit has been ascribed a mid-Early Triassic age (i.e. Dienerian–early Spathian range; Helby, 1973; Retallack, 1977, 1980; Balme and Foster, 1996; Herbert, 1997). Vertebrate remains from the unit are commonly disarticulated, abraded, and highly fragmented, indicating energetic stream transport prior to final burial (see Kear, 2009). The basal coarse clastic portion of the Bulgo Sandstone Formation has been interpreted as an alluvial plain braided stream system (Herbert, 1997), whereas the uppermost clay-dominated strata indicate a low-energy coastal floodbasin and/or estuarine environment (Herbert, 1997).

The Knocklofty Formation (Tasmania Basin) of Early Triassic age outcrops extensively across southeastern Tasmania (Cosgriff and DeFauw, 1987). The type section, located at Mount Knocklofty (West Hobart), is divided into three informal members, with a total thickness

of 180 m (Cosgriff and DeFauw, 1987). The lower member (about 90 m thick), and the upper member (about 50 m thick), both comprise massive sandstones. In contrast, the middle member, which is about 40 m thick, is characterised by more variant lithologies, dominated by varicoloured shales and siltstones (Cosgriff and DeFauw, 1987).

The sandstones are well-sorted and quartz-rich, with bedding planes characterized by mica and graphite (Camp and Banks, 1978). The sandstones show frequent cross-stratification at different scales, varying from few millimetres to 3–4 m. According to Camp and Banks (1978), the deposits can be referred to a high-sinuosity meandering stream system.

The Kockatea Shale outcrops in several isolated sections along the northern margin of the Perth Basin in Western Australia (Playford et al., 1976a, 1976b). The unit lies unconformably on the crystalline Precambrian basement and is overlain disconformably by Jurassic strata (Playford et al., 1976a, 1976b). The lower part of the Kockatea Shale is characterized by a mixture of both terrestrial and marine taxa, including acritarchs, organic-cemented agglutinated foraminifera, lingu-lids, ammonoids, small gastropods and bivalves, spinicaudatans, insects, austriocaridid crustaceans, actinopterygians, a temnospondyl-like mandible, plant remains, and spores and pollen (Haig et al., 2015). The deposits comprise essentially fresh, grey, laminated, pyritic mudstone at the base, followed upward mainly by shale (Haig et al., 2015). The unit can be interpreted to have been deposited on the margin of an Early Triassic shallow interior sea, characterized by variable estuarine-like water conditions. The mixture of marine and terrestrial taxa suggests variation in water conditions or transport of terrestrial and fresh/brackish-water organisms from adjacent biotopes (Haig et al., 2015). On the basis of spores and pollen of the *K. saeptatus* Zone, Haig et al. (2015) consider the unit no younger than Smithian, referring the lower section of the Kockatea Shale to the early Olenekian.

Palaeogeographical reconstructions for the Early Triassic have positioned the northern Perth Basin from 45°S (Blakey, 2005) to 50°S (Scotese, 2001), 55–60°S (Torsvik et al., 2012), up to 70°S (Veevers, 2000), thus stressing a general middle to high latitude for the basin (see Haig et al., 2015).

According to Warren et al. (2006), the Rewan Formation of the Galilee Basin (central Queensland) can be correlated to the Rewan Group of the Bowen Basin, and to the basal part of the LAZ of the Karoo

Basin of South Africa, on the occurrence of *Lydekkerina huxleyi*. In the northern part of the Galilee Basin, the Rewan Formation overlies the Permian Blackwater Group (Betts Creek Beds) and is characterised by tuff beds that can be correlated to the Burngrove Formation (Bowen Basin), thus extending the formation down into the Permian (see Warren et al., 2006).

Based on the new compiled dataset (Supplementary Material) the vertebrate fauna is dominated by Temnospondyli, which represent 95.9% of specimens. Recognised genera include *Acerastea*, *Banksiops*, *Batrachosuchus*, *Bulgosuchus*, *Chomatobatrachus*, *Deltasaurus*, *Derwentia*, *Erythrobrachius*, *Keratobrachyops*, *Lapilopsis*, *Lydekkerina*, *Nanolania*, *Plagiobatrachus*, *Rewana*, *Rotarisaurus*, *Tirratuhrinus*, *Warrenisuchus*, *Watsonisuchus* and *Xenobrachyops*. Archosauromorpha (3.3% of specimens) are represented by *Kalisuchus* and *Tasmaniosaurus*. These are followed by Dicynodontia (0.37%) and Procolophonomorpha (0.37%), both represented by a only a single unidentified specimen.

The ichnological record (Retallack, 1996) is two occurrences of the ichnogenus *Dicynodontipus* (Therapsida) from the Early Triassic of the lower Coal Cliff Sandstone at Bellambi (Wollongong, New South Wales). The faunal composition, including the ichnological record, is still dominated by Temnospondyli (96.6%), followed by Archosauromorpha (3.3%), Therapsida (0.7%), and Procolophonomorpha (0.4%).

6.4. North America (United States + Canada)

Early Triassic tetrapod faunas of North America and Canada are known from both body fossils and footprints (Brown, 1933; Lull, 1942; Peabody, 1948, 1956; Baird, 1951, 1954, 1957, 1962, 1963, 1964; Brinkman, 1988; Welles, 1993; Lucas and Schoch, 2002; Pruss and Bottjer, 2004b; Nesbitt, 2005; DeBlieux et al., 2006; Mickelson et al., 2006; Santucci et al., 2006; Klein and Lucas, 2010; Lovelace and Lovelace, 2012).

The majority of both body and trace fossils from the Lower Triassic of United States come from the Moenkopi Formation/Group (Fig. 5). The unit outcrops extensively in the southwest United States (Arizona, Utah, New Mexico, Nevada, Wyoming, Idaho), and has a total thickness of about 700 m. The unit comprises a thick sequence of red beds inter-fingered, in the northwest and west, with marine deposits of the Thaynes Group (Klein and Lucas, 2010). All the identifiable vertebrate remains come from the Wupatki and Holbrook members of the Moenkopi Formation (Fig. 5), and mainly from the Holbrook Member

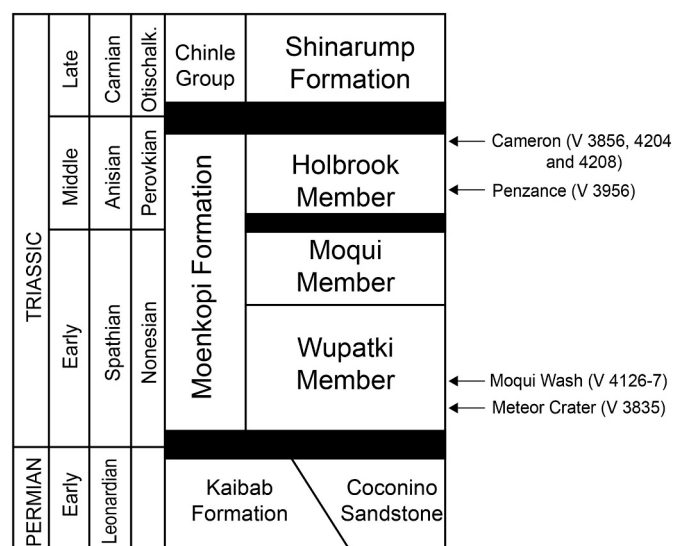


Fig. 5. Stratigraphic distribution and age of the Moenkopi Formation tracksites in northern Arizona (USA). From Klein and Lucas (2010).

(Heckert et al., 2005). Most of the Wupatki outcrops and fossiliferous localities are in the Meteor Crater area (Welles, 1947; Morales, 1993). Holbrook Member fossiliferous sites are more common, including the areas around Joseph City, Geronimo, Radar Mesa and several sites near Holbrook (Welles, 1947, 1993; Welles and Cosgriff, 1965; Welles and Estes, 1969; Morales, 1987, 1993; Cuny et al., 1999; Hunt et al., 2000; Nesbitt, 2000, 2003; Nesbitt and Angielczyk, 2002; Nesbitt and Whatley, 2004; Heckert et al., 2005).

The Moenkopi Formation is known to provide an abundant and very well preserved tetrapod ichnofauna, with the best material coming from different horizons from the upper part of the unit, represented by the Wupatki and Holbrook members in northern Arizona and by the Upper Red Formation in south-central and southwestern Utah (Klein and Lucas, 2010). On the basis of regional stratigraphy and the body fossil record, Klein and Lucas (2010) suggested a late Olenekian (Spathian) age for the Wupatki Member and an Anisian age for the Holbrook Member.

Tracksites of the Moenkopi Formation were originally described by Peabody (1948) from: i) Arizona, with the localities Meteor Crater (Wupatki Member), Moqui Wash (Wupatki Member), Cameron (Holbrook Member), and Penzance (Holbrook Member); ii) Utah, with the localities Hurricane (Upper Red Formation, see Klein and Lucas, 2010), Rockville (Upper Red Formation, see Klein and Lucas, 2010) and in the upper red formation near Paria (locality V 5054, see Klein and Lucas, 2010), Capitol Reef (locality V 5366, see Klein and Lucas, 2010) and near Fruita (locality V 5059, see Klein and Lucas, 2010); iii) Colorado, with the single locality of Pat's Hole in Moffat County (UCMP locality V 4622 in Klein and Lucas, 2010).

As stressed by Klein and Lucas (2010), while the body fossil fauna from the Moenkopi Group/Formation is represented mainly by temnospondyls, with quite rare body fossils of archosaurs or other reptiles, the described ichnofauna is dominated by archosaurs. As already noted elsewhere (e.g., Lockley and Hunt, 1994; Lockley, 1999; Lucas et al., 2003), Klein and Lucas (2010) linked this faunal inconsistency to the different facies of preservation within the Moenkopi Formation, with body fossils recovered from channel lag or bar deposits (Boy et al., 2001) and footprints from sandstone/siltstone beds interpreted as unchannelized flow events developed on both river floodplains and tidal flats. The ichnofauna from the Moenkopi Formation/ Group is similar to that of corresponding stratigraphic levels (Olenekian-Anisian) of central Europe (Klein and Lucas, 2010), especially on the basis of the shared ichnogenera *Chirotherium*, *Isochirotherium*, *Synaptichnium*, *Rotodactylus*, *Rhynchosauroides* and *Procolophonichnium*. The tetrapod communities from North America and Europe are characterized by both primitive and advanced forms and represent the transition to ichnofaunas typical of the late Middle and Late Triassic, which are characterised by more dinosauriform footprints (Klein and Lucas, 2010).

In addition to the Moenkopi, a Lower Triassic ichnological record from is also known from Red Peak Formation of the Chugwater Group in central Wyoming, a unit that has yielded no vertebrate body fossils. The Chugwater Group of central Wyoming comprises four formations (Picard, 1978), extending from the Lower Triassic (Dienerian) to the lower-Upper Triassic (Carnian). In Wyoming, the earliest Triassic is represented by the syndepositional conodont-rich Dinwoody Formation and continental Goose Egg Formation, which is Griesbachian in age (Boyd and Maughan, 1972; Paull and Paull, 1983, 1994). The Red Peak Formation, which represents the basalmost unit of the Chugwater Group, overlies the Dinwoody and Goose Egg formations (High and Picard, 1967; Picard, 1967), with a thickness of roughly 200 m in central Wyoming up to 700 m in eastern Idaho (Picard, 1967; Pipiringos and O'sullivan, 1978; Lovelace and Lovelace, 2012).

Traditionally the Red Peak Formation was divided into three facies (High and Picard, 1967; Picard, 1978), namely alternating facies, upper platy facies, and sandy facies. This traditional subdivision was retained by Lovelace and Lovelace (2012), who provided a sedimentological analysis. The majority of the tracks come from the upper platy facies,

interpreted by Lovelace and Lovelace (2012) as fluvial and proximal floodplain deposits, with the upper part characterised by abundant crevasse splays, weakly developed palaeosols, small-scale fluvial deposits and shallow lacustrine deposits, consistent with a semi-arid fluvio-lacustrine depositional environment. The unit is no younger than upper Spathian.

According to Lovelace and Lovelace (2012), the vertebrate ichnofauna from the Red Peak Formation matches the *Procolophonichnium* ichnocoenosis of Hunt and Lucas (2007), and correlates with analogous Lower–Middle Triassic fluvio-lacustrine strata from Argentina (Melchor et al., 2006; Marsicano et al., 2010), Germany (Diedrich, 2008, 2009), Greenland (Bromley and Asgaard, 1979) and Italy (Sirna et al., 1994; Avanzini et al., 2001; Avanzini and Mietto, 2008).

In Canada, the only Early Triassic fossil vertebrate is the eosuchian *Wapitisaurus problematicus* from the Vega-Phroso Member of the Sulfur Mountain Formation. The Vega-Phroso Member comprises flaggy-weathering shale at the base, followed upwards by a sequence of rusty brown siltstones (Gibson, 1971, 1975; Brinkman, 1988). The unit has been dated as Lower Triassic, ranging from the Griesbachian to the Spathian, with the large part of the collections referable to the Smithian. The depositional environment has been interpreted as restricted and relatively deep-water (Brinkman, 1988).

The new dataset (Supplementary Material) confirms that the terrestrial tetrapod body fossil record for North America is poor, being represented by only nine specimens. The fauna is dominated by Temnospondyli including the genera *Cosgriffius*, *Parotosuchus*, *Stanocephalosaurus* and *Wellesaurus* (66.7%), followed by Archosauromorpha with a single genus *Wapitisaurus* (22.20%), and a single unidentified therapsid (11.1%).

In contrast, the tetrapod ichnological record from North America is more abundant, with a total of 49 specimens. The record is dominated by the ichnogenera *Chirotherium* (28.6%) and *Rhynchosauroides* (20.4%), followed by *Rotodactylus* (14.2%), *Synaptichnium* (10.2%), *Ischirotherium* (6.1%), and *Chelonipus* (6.1%). The faunal composition including footprints is dominated by Archosauromorpha (61.5%), followed by Lepidosauromorpha (19.2%), Temnospondyli (13.5%), and Therapsida (5.8%).

6.5. South East Asia (China + Japan)

Early Triassic tetrapod faunas of South East Asia, recorded from both body and trace fossils, are known from China (Young, 1935, 1936, 1939, 1952, 1963, 1973; Koh, 1940; Sun, 1964, 1980; Li, 1983; Lucas and Hunt, 1993; Liu et al., 2002; Matsukawa et al., 2006; Li and Sun, 2008; Gao et al., 2010; Nesbitt et al., 2010a; Maisch and Matzke, 2014; Liu and Abdala, 2017) and Japan (Nakajima and Schoch, 2011).

In China, terrestrial deposits stretch across the country north of a line drawn through the Kunlun Shan (Xinjiang) and Dabie Shan (Hubei-Anhui) (Meyerhoff et al., 1991; Yin, 1991; Lucas, 1993). The whole Chinese Triassic tetrapod record comes from two basins, the Junggar (Zunggar) Basin in northern Xinjiang and the Ordos Basin in Shaanxi, Shanxi, Nei Monggol, Ningxia and Gansu (Cheng, 1981; Lucas, 1993). The oldest terrestrial Mesozoic vertebrate remains from China are from the upper part of the Guodikeng Formation and the lowermost Jiucaiyuan Formation of the Cangfanggou Group (Fig. 6), outcropping in the vicinity of Jimsar (northeast of Urumqi) in western Xinjiang (Lucas, 1993). The vertebrate assemblage from this unit is essentially equivalent to the ‘*Lystrosaurus* fauna’ of northwestern China of Sun (1972), and to the Jimsarian faunachron proposed by Lucas (1993). Early Triassic terrestrial vertebrates are also known from the Heshanggou Formation in north-central China.

The Guodikeng Formation encompasses the terrestrial Permian–Triassic transition sequence in China (Fig. 6), with outcrops in the Dalongkou, Jimsar and Xinjiang, that have yielded remains of the dicynodonts *Lystrosaurus* and *Jimusaria* (Sun, 1963; Yuan and Young, 1934a, 1934b; Liu and Abdala, 2017). The southern part of the

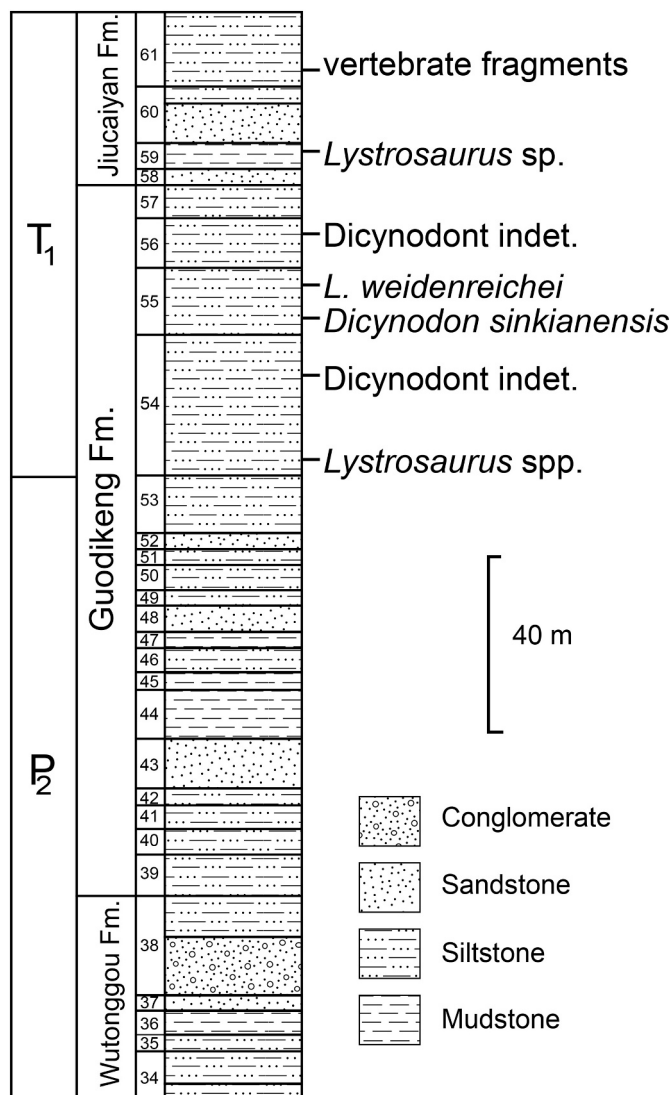


Fig. 6. Stratigraphic distribution of vertebrate remains from the Guodikeng and Jiucaiyuan formations (China). From Lucas (1993).

Dalongkou anticline section (SLS) has been indicated as a possible candidate for the global non-marine PTB reference section (Cheng and Lucas, 1993; Liu, 1994). Traditionally, the PTB has been located at the base of the Jiucaiyuan Formation, but it might be in the uppermost Guodikeng Formation, based on the first appearance datum (FAD) of *Lystrosaurus* (Yang et al., 1986). More recently, Kozur and Weems (2011) considered the continental extinction event horizon to be in the middle part of the Guodikeng Formation at the Dalongkou anticline section, using the FAD of *Falsisca verchojanica* about 25 m below the base of the Jiucaiyuan Formation as a marker for the PTB (but see Liu and Abdala, 2017 for a more exhaustive stratigraphic discussion).

Early Triassic terrestrial tetrapods from Japan are represented by a single capitosauroid temnospondyl, described by Nakajima and Schoch (2011) from the lower Hiraiso Formation (Inai Group) in northeastern Honshu. The specimen is from a pebbly sandstone bed outcropping on Karashima Island (Tsuya area, Miyagi Prefecture, northeastern Japan). The fossiliferous bed is enclosed in conglomerates and cross-stratified sandstones, and the unit has been assigned a Smithian age on the basis of ammonoid biostratigraphy (Nakazawa et al., 1994).

The site is referable to the South Kitakami Terrane (SKT), a tectonostratigraphic unit which comprises sedimentary strata of Silurian and younger age (Nakajima and Schoch, 2011). The SKT sedimentary sequence includes Triassic–Jurassic shallow-marine clastic deposits, and a

particular shared brachiopod assemblage indicates that this unit, at least during the Permian and possibly for longer in the late Palaeozoic, was positioned near the North or South China Block (Kobayashi, 1999; Ehiro, 2001; Tazawa, 2002; Nakajima and Schoch, 2011). The SKT represented a microcontinent fragmented from a lost continent (Saito and Hashimoto, 1982), detached from Pacifica or Gondwana during the Silurian–Devonian, with a successive drift in the Carboniferous through the equatorial area of Tethys and was close to East Asia during the Permian (see Nakajima and Schoch, 2011). More recently, based on both geophysical and paleobiogeographical evidence, it has been proposed that the SKT shows close tectonostratigraphic relationships with either South China (Yangtze Craton) or North China (Sino-Korea Craton) (Ehiro, 2001; Tazawa, 2004).

According to Nakajima and Schoch (2011), the single specimen from the Hiraiso Formation, which is also the only non-marine vertebrate from the Triassic of Japan, indicates that large aquatic tetrapods could cross the distance between SKT and the adjacent continental blocks of South or North China. This also confirms that capitosauroids were able to tolerate fluctuating salinity and to cross shallow marine waters.

The dataset (Supplementary Material) suggests that the body fossil record of terrestrial tetrapods from South East Asia is quite poor, being represented by a total of 20 specimens, of which 19 are from China and only one from Japan. This terrestrial tetrapod fauna is dominated by Archosauromorpha with the recognized genera *Chasmatosaurus*, *Prolacertoides*, *Santaisaurus* (35%), and *Dicynodontia* (35%) represented by *Lystrosaurus* and a single specimen of the kannemeyeriiform *Sungeodon*, followed by Temnospondyli (20%), a single bauriid Theriocephalia ascribed to the genus *Urumchia* (5%) and one specimen referable to the *Chroniosuchia* (5%).

The ichnological record is a single occurrence of *Chirotherium* sp. from the Olenekian of Guizhou, China. The faunal composition including ichnological data is similarly dominated by Archosauromorpha (38.1%) and Therapsida (38%), followed by Temnospondyli (19%) and *Chroniosuchia* (4.8%).

6.6. Central Europe (Germany + Spain + England + Italy + Poland + Scotland)

Early Triassic tetrapod faunas of Central Europe, both as body fossils and fossil footprints, are known from Germany (Huene, 1902; Huene, 1932; Haubold, 1966, 1967; Charig and Sues, 1976; Demathieu and Haubold, 1982; Morales and Kamphausen, 1984; Demathieu and Mueller, 1987; Hunt and Lucas, 1991; Werneburg, 1993; Fichter and Kunz, 2004, 2013; Klein and Haubold, 2007; Schoch et al., 2007; Säilä, 2008; Butler et al., 2011; Schoch, 2011a, 2018), Spain (Calafat et al., 1987; Mujal et al., 2016), Italy (Mietto, 1986; Conti et al., 2000), England (Girard, 1846; Beasley, 1904; Wills and Sarjeant, 1970; King and Benton, 1996; King, 1997; Tresise and Sarjeant, 1997; King et al., 2005), Scotland (Clark et al., 2002; Clark and Corrance, 2009), and Poland (von Huene, 1942; Fuglewicz et al., 1990; Evans and Borsuk-Bialynicka, 1998; Borsuk-Bialynicka et al., 1999; Ptaszyński, 2000; Borsuk-Bialynicka and Evans, 2002; Borsuk-Bialynicka and Evans, 2003; Borsuk-Bialynicka and Evans, 2009a, 2009b; Ptaszyński and Niedzwiedzki, 2004; Borsuk-Bialynicka and Lubka, 2009; Borsuk-Bialynicka and Sennikov, 2009; Evans, 2009; Evans, 2009a, Evans, 2009b; Shishkin and Sulej, 2009; Brusatte et al., 2011; Klein and Niedzwiedzki, 2012; Sulej and Niedzwiedzki, 2013).

Early Triassic tetrapod faunas from Germany are known from the Bernburg Formation of the Lower Buntsandstein and from the Volpriehausen, Hardegsen and Solling Formations of the Middle Buntsandstein (Fig. 7). The Central European Buntsandstein, spanning 6–7 Myr between the Early and Middle Triassic, can be considered to cover a key period for the evolution of terrestrial tetrapods (Schoch et al., 2007), with a classic sequence of continental red beds producing several terrestrial vertebrates including archosaurs, basal diapsids,

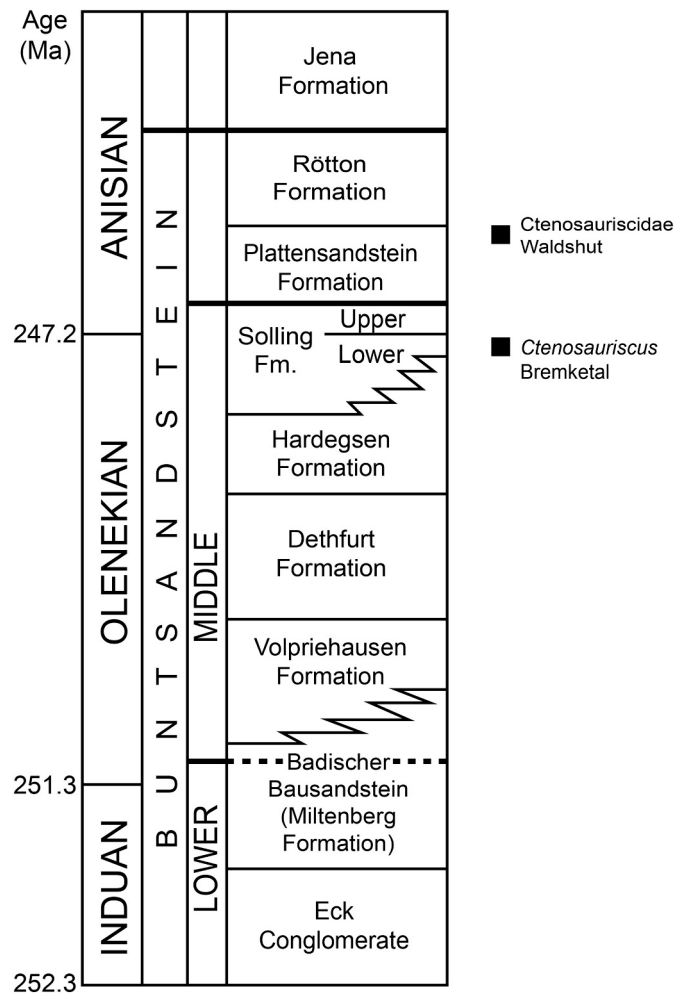


Fig. 7. Stratigraphic distributions of the German ctenosauriscid specimens. From Butler et al. (2011).

pareiasaurs, procolophonids and temnospondyls (von Meyer, 1858; Jaekel, 1910; Huene, 1914; Huene, 1920; Wild, 1998; Schoch et al., 2007).

The Lower Buntsandstein (Induan) is almost devoid of terrestrial vertebrates, with only some large tetrapod tracks in the southern Black Forest (see Schoch, 2011a). In contrast, the Middle Buntsandstein is comparatively rich, with the majority of Lower Triassic tetrapod remains being known from this unit (Schoch, 2011a). Classic fossiliferous regions include the Black Forest and surrounding areas (Wepfer, 1923; Kamphausen, 1989), the Vosges in Alsace-Lorraine (Heyler, 1969; Gall, 1971), northern Hesse (Huene, 1932; Schoch et al., 2007), Heligoland in the North Sea (Schroeder, 1913; Staesche and Wolff, 1934) and eastern Saxony-Anhalt (Meyer, 1855; von Meyer, 1858).

The Solling Formation, which forms the top of the Middle Buntsandstein, is exposed at Merkel's Quarry on the western periphery of Bernburg an der Saale (Saxony-Anhalt, Germany), and this represents the richest tetrapod lagerstätte in the Buntsandstein and coeval sequences across Europe (Schoch, 2018). The Formation was traditionally ascribed to the late Olenekian, but the upper portion of the Solling Formation was referred to earliest Anisian by Kozur and Bachmann (2005) and Szurlies (2005). On the basis of magnetostratigraphy, the Solling Formation, as well as the lower part of the Röt Formation, can be referred to the Olenekian (Menning and Käding, 2014). Another important outcrop of the Solling Formation is in the area of Bremke dell in Niedersachsen (Lower Saxony, northern Germany), known as "Solling-Bausandstein" (upper Middle Buntsandstein: Solling Formation)

which produced the holotype of the sail-backed archosaur *Ctenosauiscus koeneni* (Butler et al., 2011). Quarries with outcrops of the Solling-Bausandstein are scattered southeast of Göttingen, between Reinhausen and Bremke, on the western flank of the Eichsfeld-Altmark Swell. This unit has a total thickness of 40–45 m (Kallies, 1963; Rettig, 1996; Butler et al., 2011). The lower part of the Solling Formation (Wilhelmshausen Beds, Trendelburg Beds and Karlshafen Beds) is characterised by coarse fluvial deposits referred to the latest Olenekian (late Spathian) on the basis of palaeomagnetic data, palynomorphs and conchostracans (Kozur and Bachmann, 2005, 2008; Szurlies, 2007; Kozur and Weems, 2010; Hounslow and Muttoni, 2010; Kürschner and Hergreen, 2010; Butler et al., 2011). The lower to middle parts of the Solling Formation were deposited in a meandering to braided river system, dominated by sandstones, siltstones and claystones (Rettig, 1996; Weber and Lepper, 2002). The Solling-Bausandstein in the northeastern Eichsfeld area has been correlated with the Trendelburg and Karlshafen beds of the nearby Reinhardswald Trough (northern Hesse) (Butler et al., 2011).

A review of the temnospondyl fauna from southern Germany by Schoch (2011a) highlighted the occurrence of large aquatic predators already in the Early Triassic and demonstrates an increase in the diversity of aquatic predators from Induan to Anisian. The Induan tetrapod fauna includes small aquatic predators from the Eck Conglomerate (Bernburg Formation), which inhabited rivers in the peripheral regions of the basin (Schoch, 2011a). The central parts of the basin were covered by large playa lake systems, characterised by intense aridity and high salinity, making the general environment quite hostile (Paul, 1999).

In contrast, the appearance of large temnospondyl predators by the early Olenekian time (i.e., *Parotosuchus*, *Sclerotherax*) indicates that climates in southern Germany during the Early Triassic were sufficiently moist to, at least periodically, enable the formation of small river ecosystems for large stereospondyls to inhabit (Schoch, 2011a). During the late Olenekian, the rivers evolved from braided systems with small channels to larger channels covering larger areas (Mader, 1981), and opened niches for large faunivorous aquatic tetrapods (Schoch, 2011a).

Early Triassic terrestrial tetrapods from Spain are known only from the ichnological record of the Catalan Pyrenean Basin (NE Iberian Peninsula, Southern Europe). This extensional basin (Fig. 8), comprising several depocenters filled by red-bed Buntsandstein facies deposited by meandering and braided fluvial systems, was formed during the break-up of Pangaea via strike-slip tectonics, in the last phases of the Variscan Orogeny (Torsvik and Cocks, 2013; Mujal et al., 2017). Fluvial deposits cover the Variscan basement and Carboniferous-

Permian volcanosedimentary sequences with a basal erosive angular unconformity. These Buntsandstein facies are in turn overlain by post-rift Muschelkalk and Keuper facies (Mujal et al., 2017). The Buntsandstein facies are divided into three main units (Saura, 2004): i) a basal conglomerate unit, comprising oligomictic conglomerates of quartz pebbles and coarse sandstone; ii) an intermediate shale and sandstone unit composed of greenish to greyish and reddish medium-coarse sandstones, with discontinuous conglomerate levels; and iii) an upper shale unit, characterized by reddish shales and occasional thin sandstone. Mujal et al. (2017) recognize 13 lithofacies, grouping them into seven facies associations referable to a range of channel to floodplain sedimentary environments.

The deposits assigned to the red-bed Buntsandstein in the Catalan Pyrenees were deposited by high-energy braided systems that evolved through time to low-energy meandering and floodplain systems, filling the depocenters of the Triassic rifting (Mujal et al., 2017). The sections described by Mujal et al. (2017) include Buntsandstein facies characterized by a fining-upwards sequence culminating in Muschelkalk-type facies, representing a marine transgression. Palynological data from the shale unit suggested an early Anisian age for the Buntsandstein facies (Calvet et al., 1993), but ichnological and palynological data indicate a late Olenekian age (Mujal et al., 2016).

The Pyrenean ichnoassemblage described by Mujal et al. (2017) matches those from the Early Triassic of Central Pangaea, with small archosauromorph tracks dominating the assemblage and being present in several facies from the Triassic Pyrenean Basin.

Early Triassic terrestrial tetrapods from Italy are known from only a few isolated and quite badly preserved tracks from the Olenekian of the Southern Alps (Mietto, 1986; Conti et al., 2000; Avanzini and Mietto, 2008; Avanzini et al., 2011). In the Southern Alps, the PTB was originally placed close to the top of the Bellerophon-Werfen Formation (Bosellini, 1964; Assereto et al., 1973; Posenato, 1988), but subsequently it has been considered to fall within or at the top of the Tesero Member (Pasini, 1985; Broglio Loriga et al., 1986; Visscher and Brugman, 1988; Wignall et al., 1996; Farabegoli and Perri, 1998; Farabegoli et al., 2007), which represents the lower portion of the Werfen Formation. All footprints from the Early Triassic of Italy come from the terrigenous and terrigenous-carbonate units of the Werfen Formation, which is Olenekian in age. The overlying Middle Triassic (Anisian) units include the Gracilis Formation, Voltago Conglomerate, Richthofen Conglomerate, and Morbiac Dark Limestones. The Anisian units are characterized by rich and well-preserved ichnoassociations in lagoonal-peritidal to continental sediments (Avanzini et al., 2011). The Werfen Formation, which may be divided into nine members, comprises a complex succession of carbonate, terrigenous and mixed sedimentary strata, with a fossil content that enables the formation to be divided into six large sedimentary cycles of generally regressive character (Pisa et al., 1978; Broglio Loriga et al., 1983; Neri and Posenato, 1988; Broglio Loriga et al., 1990). The sedimentary environment was shallow shelves with low-energy, mud-dominated sediments, offshore deposits and shallow tidal plains characterized by emerged sub-environments, isolating areas of strong evaporation and restricted circulation (Avanzini and Mietto, 2008). Tetrapod tracks are preserved only in the upper three members of the Werfen Formation, namely the Campil, Cencenighe and San Lucano members (Avanzini et al., 2011).

Only two ichnospecies have been described from the Werfen Formation, namely *Rhynchosauroides palmatus* and *R. schochardti* (Avanzini et al., 2001; Conti et al., 2000). These come from sites near Recoaro, in Val Trivignolo and in Val Gardena (Mietto, 1986; Conti et al., 2000; Avanzini et al., 2011), which represent the “Scythian-*Rhynchosauroides schochardti* Assemblage” Faunal Unit, in the zonation proposed by Avanzini and Mietto (2008). The very low ichnodiversity in the lowermost Triassic of the Southern Alps has been explained by three hypotheses: unfavourable environmental conditions (Avanzini and Mietto, 2008; Avanzini et al., 2011); the occurrence only of coastal vertebrates, able to live in ephemeral emerged lands; or a genuine

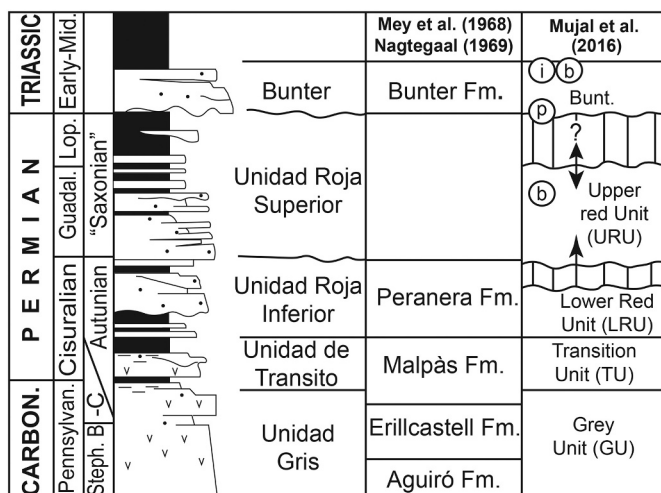


Fig. 8. Lithostratigraphic correlation chart of Permian-Triassic stratigraphic sections from Central-Eastern Pyrenees (Spain). From Mujal et al. (2016).

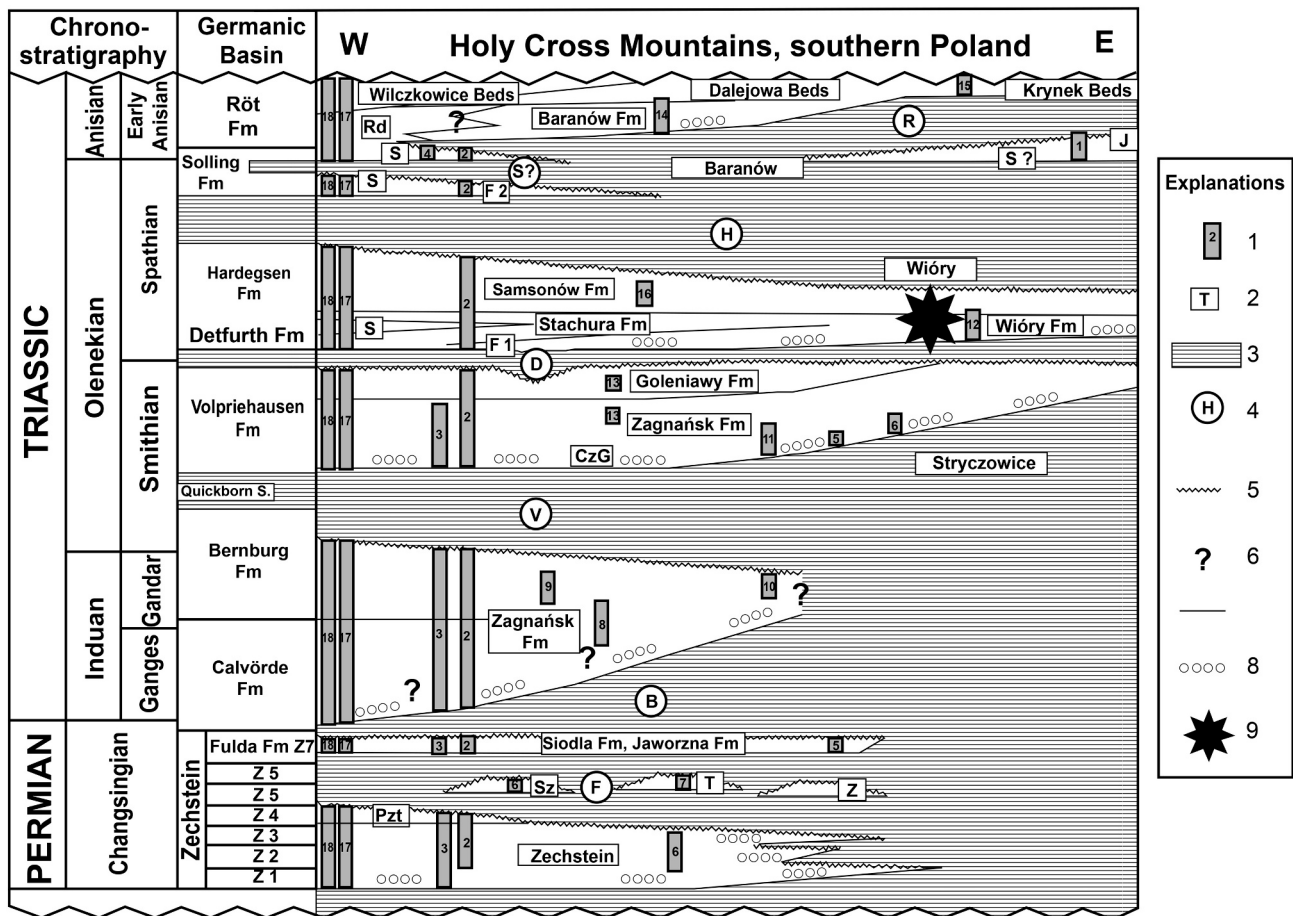


Fig. 9. Chronostratigraphic scheme of the Buntsandstein in the Holy Cross Mountains and its lithostratigraphic correlation with units in the Germanic Basin. Boreholes and outcrops: 1, Bukowie; 2, Cierchy IG 1; 3, Jaworzna IG 1; 4, Paegi; 5, Zachemie; 6, Jaworzna; 7, Tumlin and Sosnowica; 8, Gaezice; 9, Zajczków; 10, Czerwona Góra, Lower Buntsandstein; 11, Czerwona Góra, conglomerates from Czerwona Góra; 12, Wióry; 13, Jaworz; 14, Baranów; 15, Witulin; 16, Samsonów; 17, Opoczno IG 2; 18, Ruda Strawczyńska. Lithostratigraphic units: J, marly limestones from Jarugi Member; S, Samsonów Formation; Rd, Lower Roetian; F1, Cierchy Sandstone Member, F2-sandstone layer; CzG, Czerwona Góra Conglomerate Member; Pzt, Top Terrigenous Series; Sz, Szczukowice Formation at the Jaworzna quarry; Z, Zachemie Conglomerate member; T, Tumlin sandstones. Discordances: F, in the bottom of the Upper Fulda Formation; B, local discordance in the bottom of the Buntsandstein; V, Volpriehausen; D, Detfurth; H, Hardegsen; S, Solling; R, local discordance within the Roetian. Explanations: 1, borehole profiles and outcrops; 2, lithostratigraphic units; 3, stratigraphic gaps; 4, unconformities; 5, erosional boundaries; 6, presence of the formation not certain; 7, boundaries (without erosion); 8, conglomerates; 9, lithostratigraphic position of Wióry tracksites. From Klein and Niedźwiedzki (2012) with bibliography.

evolutionary pattern testifying the slow recovery of tetrapod diversity after the PTME (Avanzini et al., 2011).

In Poland, Early Triassic terrestrial tetrapods are known from both body fossils and a rich ichnological record, from the fluvial deposits of the Wióry Formation, which is late Olenekian, early Spathian in age (Ptaszyński and Niedźwiedzki, 2006; Niedźwiedzki and Ptaszyński, 2007; Becker et al., 2007; Sulej and Niedźwiedzki, 2013) (Fig. 9). The Wióry site is noted for its very well-preserved tetrapod trace fossils (Fuglewicz et al., 1981, 1990; Ptaszyński, 2000; Niedźwiedzki and Ptaszyński, 2007; Brusatte et al., 2011), including evidence of some of the earliest members of the dinosaur stem-lineage. The site may correspond in age to the Spathian/late Olenekian Detfurth Formation of the Germanic Basin (Sulej and Niedźwiedzki, 2013).

The Wióry Formation, informally named by Kuleta and Zbroja (2006), comprises the Labyrinthodontidae beds and the Hieroglyphic beds of Senkowiczowa (1970), which may be correlated to the lower part of the Middle Buntsandstein (Gervillia beds, Goleniawy Formation; see Kuleta and Zbroja, 2006; Sulej and Niedźwiedzki, 2013). The stratigraphic sequence includes sandstone, mudstone and claystone, with an inferred depositional environment of channels and floodplains of a braided river system (Mader and Rdzanek, 1985; Fuglewicz et al., 1990). The sequence yields two species of conchostracans, plant

remains, and abundant invertebrate and vertebrate fossil tracks (Mader and Rdzanek, 1985; Fuglewicz et al., 1990; Machalski and Machalska, 1994; Rdzanek, 1999; Ptaszyński, 2000; Ptaszyński and Niedźwiedzki, 2006; Niedźwiedzki and Ptaszyński, 2007). The conchostracan taxa allow the age of the Wióry Formation to be determined as late Olenekian and early Spathian (Bachmann and Kozur, 2004; Kozur, 2005; Kozur and Bachmann, 2005; Ptaszyński and Niedźwiedzki, 2006; Becker et al., 2007; Kozur and Weems, 2010; Sulej and Niedźwiedzki, 2013), an age congruent with the vertebrate ichnotaxa from Wióry and those of the Detfurth Sandstein and lower Hardegsen Formation in Germany (see Sulej and Niedźwiedzki, 2013), both assigned to the Spathian (Bachmann and Kozur, 2004; Kozur and Bachmann, 2005). This age attribution is corroborated by the lower Anisian *Chirotherium* ichnofauna that lies above the Wióry Formation (Sulej and Niedźwiedzki, 2013).

Body fossils are quite rare with the exception of the well-known fissure infillings at Czatkowice in southern Poland, which are Olenekian in age. Here one of the most diverse tetrapod assemblages from the Germanic Buntsandstein has been found (Borsuk-Bialynicka et al., 1999; Borsuk-Bialynicka and Evans, 2003; Paszkowski, 2009; Sulej and Niedźwiedzki, 2013). The karst systems developed in the Lower Carboniferous limestone of the Kraków region (Paszkowski and Wieczorek,

1982; Paszkowski, 2009), with the bone-bearing sedimentary infill represented by fine grained sandy limestone and rare clasts (Shishkin and Sulej, 2009). The fauna has been interpreted as that of a low upland setting during the Early Triassic (Borsuk-Bialynicka et al., 1999; Paszkowski, 2009; Shishkin and Sulej, 2009).

Other fragmentary and isolated vertebrate remains from Buntsandstein strata of Poland are known from the northern margin of the Holy Cross Mountains (Senkowiczowa and Ślącza, 1962; Senkowiczowa, 1970; Fuglewicz et al., 1981, 1990; Sulej and Niedźwiedzki, 2013), with four recognized lithostratigraphic units outcropping at four localities (Sulej and Niedźwiedzki, 2013).

At the end of the late Olenekian, the rivers changed from small local gullies, within braided river systems, into larger meandering and fast-changing rivers that cover larger regions (Mader, 1981; Mader and Rdzanek, 1985; Fuglewicz et al., 1990). According to Sulej and Niedźwiedzki (2013), this major environmental change in the marginal parts of the Germanic Basin generated new niches for large aquatic temnospondyls in small lakes and large rivers, triggering the origin and early radiation of large capitosaurids such as *Meyerosuchus*, *Odenwaldia* and *Parotosuchus*.

Brusatte et al. (2011) described footprints from the Early–Middle Triassic Holy Cross Mountains of Poland referable to Dinosauromorpha using a synapomorphy-based taxonomic approach. Although quite rare, dinosauromorph footprints have been described by Brusatte et al. (2011) from three sites: i) the Stryczowice tracksite, referable to the Smithian (Early Olenekian) on the basis of palynomorph and conchostrachan data, and characterized by a diverse ichnological assemblage including the basal dinosauromorph ichnogenus *Prorotodactylus*; ii) the Wióry tracksite, already discussed, also preserving rare traces referable to *Prorotodactylus*; iii) and the Baranów tracksite, which is latest Olenekian–early Anisian in age, and which preserves the two dinosauromorph ichnogenes *Rotodactylus* and *Sphingopus*. This ichnological evidence shifted the origin of the dinosaur stem lineage to the early Olenekian, about 14 Myr earlier than the oldest body fossils. In particular, Brusatte et al. (2011) were the first to suggest that the early radiation of the Dinosauromorpha was part of the recovery from the PTME.

Early Triassic terrestrial tetrapods from Scotland are known only from rare ichnological data from the Auchenhew Beds on the Isle of Arran (Clark and Corrance, 2009) (Fig. 10). Individual chirotheriid footprints and several *in situ* trackways have been found from several sites on the southern coast of the Isle of Arran, namely Annan (Dumfriesshire, Harkness, 1850a, 1850b; Haubold, 1971), Levencorroch Hill

(Clark et al., 2002), Cleiteadh nan Sgarbh (Clark et al., 2002), Kildonan (SE Arran, Clark and Corrance, 2009), the coastal exposures between Port Dearg and Port Buidhe (Clark and Corrance, 2009), Bannan Head, and the coast south-east of Port Mór (Clark and Corrance, 2009).

The Permo-Triassic sequence of Arran is divided into three lithostratigraphic units, the Brodick Beds, Lamlash Beds and Auchenhew Beds (Craig, 1965; Warrington, 1973). The Triassic rocks are represented by the Lamlash Beds overlain by the Auchenhew Beds (McGregor, 1983; Clark et al., 2002) (Fig. 10). The Lamlash Beds comprise fluvial and aeolian sandstones and occasional caliche horizons (Pollard and Lovell, 1976). The unit has been referred to fluvial-lacustrine environments, developed under arid conditions (based on the presence of halite pseudomorphs), and is considered as approximately equivalent in age to the Sherwood Sandstone Group (Warrington et al., 1980). The Lamlash Beds are subdivided into the Lamlash Sandstone Formation and the Glen Dubh Sandstone Formation (Warrington et al., 1980; McGregor, 1983). The Auchenhew Beds are subdivided into the Lag a'Beith Formation, Auchenhew Mudstone Formation and Levencorroch Mudstone (Warrington et al., 1980) and are the units that yielded the trace fossils (Pollard and Lovell, 1976; Pollard and Steel, 1978, 1981; Lovell, 1981). Based on miospores, the Auchenhew Beds are late Scythian to Anisian in age (Warrington, 1973).

The terrestrial tetrapod record of Central Europe is fairly abundant, being represented by 738 body fossil specimens and about 150 ichnological specimens. The body fossil record is dominated by Archosauromorpha (38.8%) and includes the genera *Collilongus*, *Ctenosauriscus*, *Czatkowiella*, *Microcnemus* and the very abundant euparkeriid *Osmolskina* (260 specimens), followed by Lepidosauromorpha represented by the quite abundant genera *Pamelina* and *Sophineta* (27%), Temnospondyli with the genera *Batrachosuchoides*, *Meyerosuchus*, *Odenwaldia*, *Parotosuchus*, *Sclerothorax*, and *Trematosaurus* (21.8%), Salientia (Amphibia, Batrachia) with the really abundant genus from Poland *Czatkobatrachus* (10.3%), and Procolophonomorpha with *Anomoiodon* and *Procolina* (2.2%).

The ichnological record from Central Europe is dominated by *Chirotherium* (28.9%), followed by *Protochirotherium* (20.1%) and *Rhynchosauroides* (15.4%). Other ichnogenes are “*Capitosauroides*” referable to a primitive non-amphibian tetrapod or reptiliomorph, *Brachychirotherium* from the Olenekian of Lauterbach in Germany (non-dinosauromorph archosaurs), *Charaichnos* from the upper Olenekian Wióry Formation of Poland (tetrapod indet.), *Chelichnus* from the Olenekian of Hessberg in Germany (therapsid), *Procolophonichnium* from the Olenekian of Britten in Germany and the Wióry Formation of Poland, *Prorotodactylus* from the late Olenekian Detfurth Formation in Germany, the late Olenekian Bunter Formation of Spain and late Olenekian Wióry Formation of Poland (Dinosauromorpha), *Rotodactylus* from the late Olenekian Solling Formation, Detfurth Formation and Harras (Eisfeld) of Germany, and from the middle-upper Scythian Wildmoor Sandstone Formation of England (Dinosauromorpha), *Saarichnium* from the Olenekian Middle Buntsandstein of Britten in Germany (basal Neodiapsida), and *Synaptichnium* from the late Olenekian Wióry Formation of Poland and from Lauterbach in Germany (non-dinosauromorph archosaurs).

The faunal composition including ichnological data is dominated by Archosauromorpha (45.5%), followed by Lepidosauromorpha (26%), Temnospondyli (17.5%), non-temnospondyl Amphibia (8.3%), Procolophonomorpha (2.2%), and Therapsida (0.5%).

6.7. Greenland

Early Triassic terrestrial tetrapod faunas from Greenland are known from body fossils (Säve-Söderbergh, 1935; Nielsen, 1954; Schoch and Milner, 2000) represented by Temnospondyli (40 available specimens), and include *Luzocephalus* (Lydekkerinidae), *Selenocara* (Mastodontosauridae), *Stoschiosaurus* (Trematosauridae), *Tupilakosaurus* (Tupilakosauridae) and 25 unidentified temnospondyls.

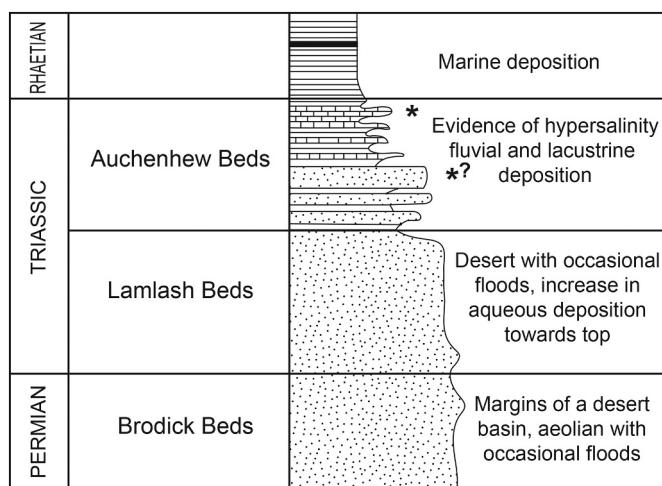


Fig. 10. Stratigraphy and palaeoenvironment of the Permo-Triassic of the Isle of Arran, Scotland. Asterisks indicate possible footprint-bearing levels. From Clark and Corrance (2009).

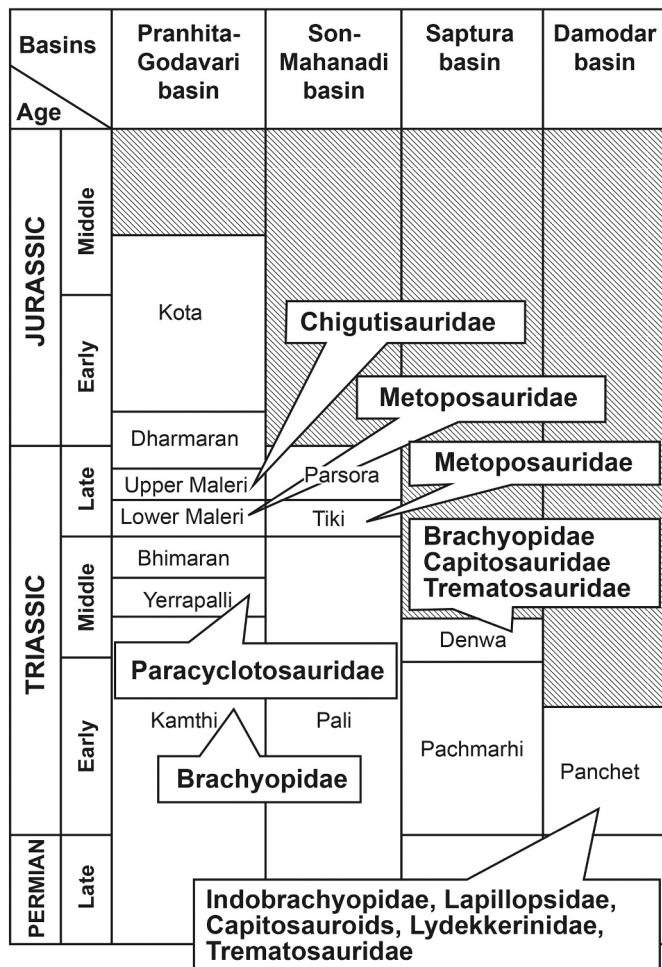


Fig. 11. Lithological successions of the major Gondwana basins of India. Temnospondyl bearing formations are highlighted. From Sengupta (2003).

No ichnological data are available from Greenland.

6.8. India 'block' (India + Madagascar + Kenya + Pakistan)

Early Triassic tetrapod faunas based only on body fossils are known from India (Owen, 1855; Lydekker, 1882; Dasgupta, 1928; Huene and Sahni, 1958; Jain et al., 1964; Huxley, 1865; Tripathi and Puri, 1961; Tripathi and Satsangi, 1963; Satsangi, 1964; Tripathi, 1969; Cosgriff et al., 1982; Yates and Sengupta, 2002; Sengupta, 2003; Ray, 2005; Gupta and Das, 2011; Das and Gupta, 2012), Madagascar (Swinton, 1956; Lehman, 1961, 1966, 1979; Rage and Roček, 1989; Hewison, 1996; Schoch and Milner, 2000; Steyer, 2002, 2003; Ketchum and Barrett, 2004; Maganuco and Pasini, 2009; Maganuco et al., 2009, 2014; Falconnet et al., 2012; Fortuny et al., 2018), Pakistan (von Huene, 1920) and Kenya (Harris and Carroll, 1977).

Early Triassic terrestrial vertebrates from India include body fossils from the Panchet Formation of the Damodar Valley, in the West Bengal area (Das and Gupta, 2012) (Fig. 11). The Panchet Formation is underlain by the Raniganj Formation and overlain by the Supra Panchet Formation (Gupta and Das, 2011). The unit is subdivided into two (Dasgupta, 1922, 1926; Tripathi, 1962): a lower part characterized by red argillaceous strata alternating with pale yellow, greenish yellow, and greenish grey arenaceous beds rich in mica and containing abundant remains of the dicynodont *Lystrosaurus*; and an upper part that is sandstone dominated, with the Deoli Sandstone unit containing abundant temnospondyl remains, actinopterygian fish scales, teeth of dipnoan lung fish and tooth plates referred to perleidid fish (Gupta,

2007, 2009; Das and Gupta, 2012).

On the basis of its tetrapod fauna, the Panchet Formation has been correlated to the Looptenbergian Land Vertebrate Faunachron of Lucas (1998). It is Induan in age, equivalent to the lower Jiucaiyuan and upper Goudikeng formations of the Junggur Basin of China, the Heshanggou Formation of the Ordos Basin of China, the lower part of the Fremouw Formation of Antarctica and the Balfour, Katberg and Burgersdop (lower part) formations of the Karoo Basin of South Africa (Groenewald and Kitching, 1995; Lucas, 1999; Das and Gupta, 2012).

Early Triassic terrestrial tetrapods from Madagascar are known from body fossils and the fauna is dominated by temnospondyls (Steyer, 2002, 2003; Maganuco and Pasini, 2009; Falconnet et al., 2012; Maganuco et al., 2014). All material comes from the Sakamena Group, a thick sequence of terrestrial clastic deposits that outcrops along the northwestern and western borders of Madagascar in the Diego, Majunga and Morondava basins (Boast and Nairn, 1982; Wescott and Diggins, 1998; Piqué et al., 1999; Smith, 2000; Ketchum and Barrett, 2004). The Sakamena Group has abundant fossiliferous nodules that include vertebrate remains including many tetrapods (e.g., Piveteau, 1955; Lehman, 1966; Besairie, 1972; Currie, 1981; Arduini, 1993; Meckert, 1995; Smith, 2000; Steyer, 2002, 2003; Ketchum and Barrett, 2004; Maganuco et al., 2009).

The Sakamena Group as a whole is dated as Late Permian to Middle Triassic on the basis of palynomorphs, invertebrates, and vertebrate biostratigraphic correlations (Besairie, 1972; Battail et al., 1987; Wescott and Diggins, 1998). The occurrence of the conchostracan *Euestheria* (*Magnietheria*) *truempyi* in the Middle Sakamena Formation (Shen et al., 2002) dates this unit as early Smithian (Olenekian, Early Triassic; see Yanbin et al., 2002), based on correlation with the well-constrained Triassic strata of the Germanic Basin (Kozur and Weems, 2010). Further, an ammonite fauna in the Middle Sakamena "Couches à Poissons et Ammonites" is referred to the Induan (local Gyronitien Stage, Besairie, 1972). Similarities with the fauna from the Karoo Basin of South Africa, combined with palynological evidence (Wescott and Diggins, 1998) indicates that the Middle Sakamena Formation is intermediate in age between the *Lystrosaurus* and *Cynognathus* Assemblage Zones (Battail et al., 1987).

The Lower Sakamena Formation, referred to the Upper Permian, yields a quite diverse vertebrate fauna largely from the Morondava Basin (Ketchum and Barrett, 2004). The unit is overlain by the Middle Sakamena Formation referred to the Lower Triassic; vertebrate body fossils include abundant fish remains including actinopterygians, coelacanths and dipnoans, as well as abundant temnospondyls (Ketchum and Barrett, 2004). The greater part of the vertebrate material from the Middle Sakamena comes from the Diego Basin (Lehman, 1966; Besairie, 1972; Battail et al., 1987; Rage and Roček, 1989; Beltan, 1996; Hewison, 1996; Steyer, 2002; Ketchum and Barrett, 2004). In contrast, exposures of the Middle Sakamena Formation in the Majunga Basin are quite rare and scattered (Besairie, 1972) and are depauperate in vertebrate fossil remains.

The majority of tetrapod specimens from the Diego Basin come from the "Couches à Poissons et Ammonites" (Besairie, 1972). These are sandy shales with intercalations of sandstone lenses with terrestrial detritus, deposited in shallow-water marine environments (Ketchum and Barrett, 2004), envisaged to have been coastal lagoonal to deltaic, under tidal influence (Maganuco et al., 2014). This contrasts with the wide floodplains within braided and meandering river systems of the contemporaneous Karoo Basin, and because it was closer to the Equator the climate may have been wetter and warmer (Péron et al., 2005). According to Falconnet et al. (2012), the tetrapod association in the Middle Sakamena Formation that survived the PTME, along with more typical vertebrates from the Early Triassic (Steyer, 2002, 2003; Ketchum and Barrett, 2004; Maganuco et al., 2009; Falconnet et al., 2012), indicates that Madagascar probably represented a refuge during the PTME.

Early Triassic terrestrial tetrapods in Kenya are represented by a

single specimen of the tangasaurid eosuchian *Kenyasaurus mariakaniensis*, collected about 40 km north of Mombasa (Harris and Carroll, 1977). The specimen comes from the upper part of the Maji ya Chumvi Beds, represented by khaki-coloured fissile micaceous sandstone. The middle part of the unit preserves marine fish remains (Harris and Carroll, 1977). This rock unit is part of the Middle Duruma Sandstone Series (Caswell and Baker, 1953; Harris and Carroll, 1977), which has been dated as Early Triassic on the basis of lithological correlations with the sedimentary units outcropping in Madagascar and Tanzania (Harris and Carroll, 1977).

Early Triassic terrestrial tetrapods from Pakistan are represented by a single specimen of the trematosaurid temnospondyl *Aphaneramma kokeni* from the *Prionolobus rotundatus* Beds of the Salt Range of Pakistan (Huene, 1920b; Welles, 1993; Schoch and Milner, 2000; Novikov, 2018). It was named by Huene (1920b) and has been discussed subsequently (e.g., Schoch, 2006, 2011b; Fortuny et al., 2015; Novikov, 2018).

The fauna of the India 'block' (India + Madagascar + Kenya + Pakistan) is dominated by Temnospondyli including *Aphaneramma*, *Brachyops*, *Deltacephalus*, *Edingerella*, *Indobrachyops*, *Mahavisaurus*, *Manubrantlia*, *Tertremoides* and *Wantzosaurus* (36.9%) and Dicynodontia represented by the very abundant genus *Lystrosaurus* (35%), followed by Archosauromorpha with the genera *Hovasaurus*, *Kenyasaurus* and *Proterosuchus* (23.6%), Procolophonomorpha with two genera *Barasaurus* (Owenettidae) and *Lasasaurus* (Procolophonidae) (3.2%), Salientia (Amphibia, Batrachia) with a single specimen of the genus *Triadobatrachus* (0.6%), and Cynodontia represented by a single specimen of the brasilodontid genus *Panchetocynodon* (0.6%).

No ichnological data are available for the India 'block'. The fauna considering the broader taxonomic category for the abundance matrix is dominated by Temnospondyli (36.9%) and Therapsida (35.7%), followed by Archosauromorpha (23.6%), Procolophonomorpha (3.2%) and very rare non-temnospondyl Amphibia (0.6%).

6.9. Svalbard

Early Triassic tetrapod faunas from Svalbard are known only from body fossils (Woodward, 1904; Wiman, 1910, 1914, 1916, 1917; Nilsson, 1943, 1946). As with Greenland, the terrestrial tetrapods of the Early Triassic of Svalbard are exclusively Temnospondyli (46 specimens), with the genera *Aphaneramma* (Trematosauridae), *Lyrocephaliscus* (Lyrocephaliscidae), *Peltostega* (Rhytidosteidae), *Platystega* (Platystegidae), *Tertrema* (Trematosauridae), nine unidentified Mastodontosauridae and five unidentified generic temnospondyls.

No ichnological data are available for the Svalbard area.

6.10. Russia

Early Triassic terrestrial tetrapods from Russia are known entirely from body fossils (Yakovlev, 1923; Efremov, 1940; von Huene, 1940, 1960; Vjushkov and Chudinov, 1956; Chudinov and Vjushkov, 1956; Ochev, 1958, 1978, 1979; Shishkin, 1960, 1961, 1967; Ivakhnenko, 1973, 1974, 1975, 1983, 2008, 2011; Tatarinov, 1978; Novikov, 1990, 1991, 2007, 2010, Novikov, 2012a, Novikov, 2012b, Novikov, 2016; Sennikov, 1990, 1992, 1999, 2005, 2008, 2011, 2012; Novikov and Orlov, 1992; Shishkin and Novikov, 1992; Benton and Allen, 1997; Battail and Surkov, 2000; Gower and Sennikov, 2000; Novikov and Shishkin, 2000; Schoch and Milner, 2000, 2014; Shishkin et al., 2000a, 2000b, 2006, 2014; Spencer and Benton, 2000; Lozovsky et al., 2001; Spencer and Storrs, 2002; Damiani, 2001; Damiani and Yates, 2003; Tverdokhlebov et al., 2003; Benton et al., 2004; Novikov and Sues, 2004; Zakharov et al., 2004; Surkov et al., 2005; Arkhangel'skii and Sennikov, 2008; Fortuny et al., 2011; Naugolnykh, 2012; Ezcurra et al., 2018; Fernández-Coll et al., 2018).

More than 1000 body fossil specimens have been recovered, making the area, along with the Karoo Basin in South Africa, one of the most

crucial to understanding the early recovery of tetrapods after the PTME. On the basis of the really abundant fossil record and species level diversity, Shishkin et al. (2006) proposed the differentiation of three realms for European Russia. The first realm is represented by the northern and central regions of the East European Platform (Moscow-Mezen Syncline) and the Timan-North Ural Region. The second is the southern Fore-Urals, which includes the Obshchii Syrt Plateau, and the third is the southern regions of the East European Platform (Voronezh Anticline slope). From a climatic point of view, all regions were at the periphery of the northern arid belt (Tucker and Benton, 1982; Lozovsky, 1993) and were homogeneous with respect to the degree of aridity (Shishkin et al., 2006).

From comparisons of faunal taxonomic composition, Shishkin et al. (2006) found that the Southern Fore-Ural Realm (Obshchii Syrt Highland) was characterised by marked faunal links with Gondwanan regions. In addition, the territory of Obshchii Syrt was the possible centre of origin of three closely related Early Triassic temnospondyl lineages, the families Benthosuchidae, Capitosauridae and Trematosauridae (Novikov, 2011, 2016). In contrast, a connection with the Germanic Basin and more western Euramerican areas is inferred for the Southern Realm, represented by late Olenekian units formed in coastal marine settings. Shishkin et al. (2006) also stressed a marked differentiation in the terrestrial vertebrate fauna for the entire Early Triassic of the East European Platform, with a heterogeneity overprinted on a background of essentially similar seasonal semiarid climate conditions. Amphibians show the greatest spatial differentiation in taxonomic composition in the Induan, whereas the greatest spatial differentiation of reptiles was in the late Olenekian (Shishkin et al., 2006). In particular, the increase in reptile diversity during the Early Triassic was linked by Shishkin et al. (2006) to a gradual trend from an initial arid climate towards milder conditions.

The Russian Early Triassic tetrapods are differentiated into three intervals, the Induan, the lower Olenekian, and the upper Olenekian (Shishkin and Ochev, 1999; Shishkin et al., 2000b; Shishkin et al., 2006). The Induan (Early Vetlugian) and lower Olenekian (Late Vetlugian) intervals, the Vokhmian Gorizont (*Benthosuchus*–*Wetlugasaurus* Fauna), are characterized by four consecutive faunal episodes. The Vokhmian was a time of maximum aridification with regional differences (Shishkin et al., 2006). The early Olenekian, represented by the Rybinskian–Ustmylian Horizons (*Benthosuchus*–*Wetlugasaurus* Fauna) corresponds to an eustatic maximum (Lozovsky, 1992), leading to expansion of lake systems in Eastern Europe, which in turn led to a great radiation and differentiation of tetrapods living in lakes. The late Olenekian (Yarenskian) interval includes two divisions, the Fedorovskian and Gamskian, corresponding to the *Parotosuchus* Fauna. This was a time of milder seasonal semi-arid climate, inferred both on the basis of faunal composition and sedimentology, matching the shift of the Arctic shelf and northern margin of the European continent into the humid belt by the end of the Early Triassic (Mangerud and Romund, 1991; Shishkin et al., 2006).

Even though the Early Triassic terrestrial tetrapod record of European Russia has been subdivided into three different heterogeneous realms, with three major time intervals characterized by five-to-six successive fauna episodes, in this work we have chosen to consider the Induan and Olenekian time bins and the three realms together, since such a refined division was not possible for all recognized biomes around the world.

Early Triassic terrestrial tetrapods from Russia are known from several formations (or svitas) including: the Admiralty Fm. (Ivakhnenko, 1983), Bogdo Fm. (Shishkin, 1960; Novikov, 2007), By-zovaya Fm. (Sennikov, 1990), Charkabozh Fm. (Tatarinov, 1978; Novikov, 1990; Novikov and Orlov, 1992), Gamskaya Fm. (Shishkin et al., 2014), Gostevskaya Fm. (Tverdokhlebov et al., 2003), Kamennyi Yar Fm. (Novikov, 2016), Kopanaskaya Fm. (Ochev, 1978; Tverdokhlebov et al., 2003; Novikov, 2016), Kzylsaiskaya (= Kzylsai) Fm. (Tverdokhlebov et al., 2003), Lestanshor Fm. (Novikov, 1991;

Sennikov, 2011), Lipovskaya Fm. (Chudinov and Vjushkov, 1956; Shishkin, 1967; Ivakhnenko, 1973; Sennikov, 1999, 2011, 2012; Ivakhnenko, 2008; Arkhangelskii and Sennikov, 2008; Novikov, 2010; Shishkin et al., 2014), Mechet Fm. (Novikov and Shishkin, 2000; Tverdokhlebov et al., 2003), Nyadeytinskaya Fm. (Novikov and Shishkin, 2000; Schoch and Milner, 2014), Petropavlovskaya (= Petropavlovka) Fm. (Ochev, 1958, 1979; Huene, 1960; Novikov, 1991; Tverdokhlebov et al., 2003; Novikov and Sues, 2004; Sennikov, 2005; Ivakhnenko, 2011), Pizhmomezenskoi Fm. (Novikov, 1991), Rybinsk Fm. (Damiani, 2001; Damiani and Yates, 2003; Fernández-Coll et al., 2018), Sludka Fm. (Ochev, 1978), Staritskaya Fm. (Sennikov, 1990; Novikov and Shishkin, 2000; Tverdokhlebov et al., 2003), Sukhorechka Fm. (Tverdokhlebov et al., 2003; Novikov, 2016), Teryutekh Fm. (Schoch and Milner, 2000), Ustmylian Fm. (Sennikov, 1990), Vetlugian (= Vetluga) Series (Efremov, 1940; Schoch and Milner, 2000; Tverdokhlebov et al., 2003; Novikov, 2016; Fernández-Coll et al., 2018), Vokhmian horizon (Battail and Surkov, 2000); Vokhminskaya (= Vokhma) Fm. (Shishkin, 1961; Tatarinov, 1978; Shishkin and Novikov, 1992; Sennikov, 1992; Spencer and Benton, 2000; Ivakhnenko, 2008; Sennikov, 2008; Naugolnykh, 2012), Yarenskian horizon (Ivakhnenko, 1975; Ochev, 1979; Gower and Sennikov, 2000; Damiani, 2001; Spencer and Storrs, 2002; Novikov, 2010; Schoch and Milner, 2014), and Zhitkov Formation (Zakharov et al., 2004) (Fig. 12).

Considering the distribution of land masses in the Early Triassic we include the Heshanggou and Hongyanjing formations of China with the Russian block. The Early Triassic Heshanggou Formation of north-central China is known for the occurrence of several terrestrial vertebrates including temnospondyls ascribed to Capitosauridae and Benthosuchidae (Cheng, 1980), the procolophonids *Eumetabolodon bathycephalus* (Li, 1983) and *Pentaedrusaurus ordosianus* (Li, 1989), the archosauriform *Fugusuchus hejipanensis* (Cheng, 1980), the therapsids *Hazhenia concava* (Sun and Hou, 1981) and *Shaanbeikannemeyeria xilougouensis* (Cheng, 1980), later considered a synonym of *Kannemeyeria* by King (1988) and Renault (2001), and an undescribed *Proterosuchus*-like specimen (Nesbitt et al., 2010a). Based on its fauna, Lucas (1998) ascribed the Heshanggou Formation to the Lootsbergian land-vertebrate faunachron, correlated to the *Lystrosaurus* Assemblage Zone of the Karoo Basin, thus confirming an Early Triassic age for the unit. According to Rubidge (2005), the age of *Xilousuchus sapingensis* and its associated vertebrate fauna must be older than early Anisian, thus further constraining the Heshanggou Formation to an Olenekian age (see also Nesbitt et al., 2010a).

Richly fossiliferous beds are exposed at Beishan Hills (northern Gansu Province, China) and are represented by dark shales referable to a lacustrine environment in an intermontane graben setting (Gao et al., 2010). The beds occur within the Beishan Minor Region of the Northern Xinjiang–Beishan Mountains Stratigraphic Region (Yang et al., 1982, 2000; Yin, 2003). The locality produced a variety of vertebrate remains, including actinopterygians, coelacanths, hybodont sharks, a trirachodontid eucynodont (*Beishanodon youngi*), a lizard-like reptile, and lepospondyl and aquatic temnospondyl amphibians (Gao et al., 2004, 2005, 2010). On the basis of lithology, Gao et al. (2010) refer the Beishan fossil beds to the Hongyanjing Formation, with a fossil composition indicating an Early Triassic age.

The terrestrial tetrapod record for the Russia biome (including the Lower Triassic Heshanggou and Hongyanjing formations of China) is abundant, being represented by a total of 1110 body fossil specimens. The fauna is dominated by Temnospondyli with the genera *Angusaurus*, *Aphaneramma*, *Batrachosuchoides*, *Benthosphenus*, *Benthosuchus*, *Boreopelta*, *Eryosuchus*, *Komatosuchus*, *Inflectosaurus*, *Luzocephalus*, *Melanopelta*, *Parotosuchus*, *Prothosuchus*, *Quantas*, *Rhinesuchus*, *Rhytidosteus*, *Samarabatrachus*, *Selenocara*, *Syrtosuchus*, *Thoosuchus*, *Trematosaurus*, *Trematotegmen*, *Tupilakosaurus*, *Vladlenosaurus*, *Volgosuchus*, *Vyborosaurus*, *Wetlugasaurus*, and *Yarengia* (58.9%), followed by Archosauromorpha represented by the genera *Augustaburiania*, *Blomosaurus*, *Boreoprincea*, *Bystrowisuchus*,

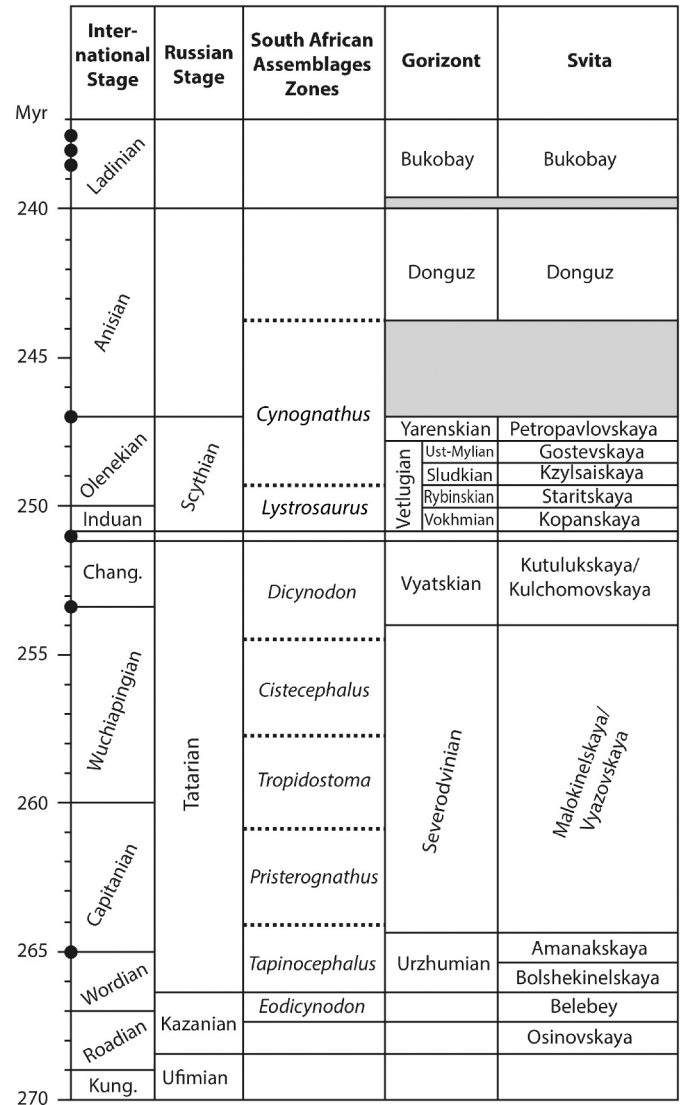


Fig. 12. Permo-Triassic tetrapod vertebrates from Russia. From Benton et al. (2004).

Chasmatosuchus, *Coelodontognathus*, *Doniceps*, *Garjainia*, *Microcnemus*, *Scythosuchus*, *Vitalia*, *Vonhuenia*, *Vrtramimosaurus*, *Vytshgedosuchus* and *Xilousuchus* (29.1%), Procolophonomorpha with the genera *Eumetabolodon*, *Kapes*, *Orenburgia*, *Phaanthosaurus*, *Pentaedrusaurus*, *Tichvinskia*, and *Timanophon* (7.9%), Chroniosuchia with the by-strowianid genera *Axitectum*, *Bystrowiana*, *Dromotectum*, and *Vyushkoviana* (2.43%), four generically unidentified Amphibia (0.36%), Cynodontia represented by two unidentified galesaurids and by the trirachodontid *Beishanodon* (0.27%), Lepidosauromorpha with the genus *Scharschengia* and two unidentified Rhynchocephalia (0.27%), Dicynodontia represented by the genera *Lystrosaurus*, *Putillosaurus* and *Kannemeyeria xilougouensis* (*Shaanbeikannemeyeria* in Cheng, 1980) (0.27%), Therocephalia represented by the genera *Scalopognathus* (Scalopognathidae), *Silphedosuchus* (Ericiolacertidae) and *Hazhenia* (Bauriidae) (0.27%) and two unidentified Batrachomorpha (0.18%).

No ichnological data are available for Russia. The fauna, considering the broader taxonomic category for the abundance matrix, is dominated by Temnospondyli (59%), followed by Archosauromorpha (29.2%), Procolophonomorpha (7.9%), Chroniosuchia (2.4%), Therapsida (0.8%), non-temnospondyl Amphibia (0.4), and Lepidosauromorpha (0.3%).

6.11. South Africa

Early Triassic terrestrial tetrapods from South Africa are known from a huge collection of body fossils and subordinate ichnological material (Huxley, 1859; Owen, 1860, 1884; Seeley, 1878, 1894, 1905; Broom, 1903a, 1903b, 1903c, 1905, 1915, 1930, 1936, 1937, 1941, 1946; Broili, 1908; Watson, 1913, 1962; Haughton, 1915, 1924, 1925, 1965; Van Hoepen, 1915, 1916; Broili and Schröder, 1934, 1937; Broom and Robinson, 1948; Parrington, 1948; Crompton, 1955; Brink, 1958, 1959, 1965; Estes, 1961; Sigogneau, 1963; Hoffman, 1965; Carroll, 1976, 1982; Kitching, 1968, 1977; Cruickshank, 1972, 1975; Mendrez, 1972; Cluver, 1974; Colbert and Kitching, 1977; Cosgriff and Zawiskie, 1979; Carroll and Lindsay, 1985; Groenewald, 1991; Shishkin et al., 1996, 2004; Warren, 1998; Welman, 1998; Gow, 1999; Neveling et al., 1999; Damiani et al., 2000, 2001, 2003; Hancox, 2000; Shishkin and Rubidge, 2000; Damiani and Welman, 2001; Groenewald et al., 2001; Modesto et al., 2001, 2002, 2003, 2010; Damiani and Jeannot, 2002; Reisz and Scott, 2002; Bender and Hancox, 2004; Damiani, 2004; Modesto and Sues, 2004; Sidor and Smith, 2004; Schoch and Rubidge, 2005; Abdala et al., 2006, 2014; Abdala, 2007; Botha et al., 2007; Fourie and Rubidge, 2007; Cisneros, 2008; Modesto and Botha-Brink, 2008; Botha-Brink and Modesto, 2011; Botha-Brink and Smith, 2011; Gaetano et al., 2012; Novikov, 2012a; Sigurdson et al., 2012; Huttenlocker and Botha-Brink, 2013; Gower et al., 2014; Ezcurra and Butler, 2015; Jasinowski and Abdala, 2017; Butler et al., 2019).

The South African Karoo Basin represents one of the few stratigraphic sequences in the world that preserves a complete record of the terrestrial PTME (Smith and Botha-Brink, 2014; MacLeod et al., 2017; Viglietti et al., 2018) and subsequent recovery in the Early Triassic (Rubidge et al., 2016). Decades of fossil collecting and fieldwork in the Bethulie and the Graaff-Reinet districts of the southern and central Karoo Basin (Smith, 1995; Smith and Botha, 2005; Botha and Smith, 2007; Botha-Brink et al., 2014; Smith and Botha-Brink, 2014; Viglietti et al., 2017), have improved understanding of the major changes in the vertebrate and floral composition across the PTB. While the exact position of the PTB and causes for extinction have been challenged (Gastaldo et al., 2015, 2017, 2018; Li et al., 2017), the documentation of the PTME is pivotal in understanding the recovery of Early Triassic Gondwanan ecosystems (Neveling et al., 2005; Botha and Smith, 2006; Botha-Brink et al., 2016; Kammerer et al., 2019).

The Karoo Supergroup comprises a thick (maximum thickness ~ 6 km; Lindeque et al., 2007, 2011; Scheiber-Enslin et al., 2015) succession of sedimentary rocks deposited in southwestern Gondwana in the framework of a large intracratonic retroarc foreland basin, recording continuous sediment accumulation from the Permo-Carboniferous to the Early Jurassic (Catuneanu et al., 1998; Viglietti et al., 2017). The Karoo Supergroup succession is dominated by the Beaufort Group (Fig. 13), represented by more than 4000 m of fluvio-lacustrine deposits. The Karoo deposits were formed in both fluvial and lacustrine settings under a semi-arid climate (Smith and Botha-Brink, 2014; MacLeod et al., 2017; Viglietti et al., 2018).

The upper Beaufort Group succession contains the PTB highlighted both by a change in the composition of the tetrapod faunas and floras, and also a major change in fluvial style (Smith and Botha-Brink, 2014). The extinction event across the inferred PTB in the Karoo Basin was phased, documented in both the Graaff-Reinet and Bethulie sections, by the same lithological, taphonomic, and biostratigraphic changes through the Permian *Daptocephalus* Assemblage Zone (Viglietti et al., 2016) and Triassic *Lystrosaurus* Assemblage Zone and inferred PTB (see further detail in Smith and Botha-Brink, 2014).

In the lower portion of the Palingkloof Member (upper Balfour Formation, Fig. 13), three extinction phases are documented over a 70 m interval (Smith and Botha-Brink, 2014). However, the attenuation of the stratigraphy, documented by Viglietti et al. (2016, 2017) from south to north, as well as faunal changes below Smith and Botha-Brink's (2014) phased extinctions (Viglietti et al., 2018), means the extinction

interval likely occurs over a more expanded interval in the south (Graaff-Reinet) than in the north (Bethulie) due to fewer depositional hiatuses.

In the post-extinction earliest Triassic, a distinctive taphonomic change occurs. In the latest Permian, fossils are commonly preserved as isolated skeletons and skulls, and there is generally a greater diversity of fossil taxa (Smith and Botha-Brink, 2014). In the Triassic, fossil abundance does not drop, but there is a significant increase in the abundance of one taxon, *Lystrosaurus*, frequently preserved as numerous bonebed accumulations, with several disarticulated skeletons (almost sub-adult individuals). Smith and Botha (2005) interpreted these as drought-induced aggregations formed by mass mortality of individuals around shrinking waterholes. However, Viglietti et al. (2013) suggested they might be behavioural aggregations under climatic extremes such as droughts or sudden cold snaps caused by a destabilised global climate.

Overall, field data indicate a massive faunal turnover in the Karoo Basin at the PTB, with only 17% of genera surviving and 41% of new taxa appearing in the Early Triassic. A total of 23 vertebrate taxa have been reported by Smith and Botha (2005) from the terrestrial PTB sections of the central Karoo Basin, of which nine became extinct in the uppermost 40 m of the Permian deposits, four taxa crossed the mass extinction and ten taxa originated in the recovery phase in the Early Triassic. This corresponds to a 60% mass extinction for Late Permian terrestrial vertebrates, with a calculated duration around 300 kyr and terminating at the PTB, and a subsequent smaller extinction pulse (31%) affecting the four survivors in the Early Triassic (Smith and Botha, 2005). Dicotylids, which were really abundant in the latest Permian, were the clade most affected by extinction, with a calculated 83% generic extinction rate, pareiasaurs disappear and Gorgonopsia are totally absent from the Early Triassic and were likely already in decline well before the end of the Permian (King, 1993). Among the ten taxa collected from the earliest Triassic, seven originated within the first 30 m above the PTB, and the archosauriform *Proterosuchus* was the first new taxon to appear (Smith and Botha, 2005; Botha and Smith, 2006), followed by the amphibian *Micropholis*, the procolophonoid *Owenetta*, the cynodonts *Thrinaxodon* and *Galesaurus* and the dicynodonts *Lystrosaurus murrayi* and *L. declivis*; the procolophonoid *Procolophon*, the therocephalian *Scaloposaurus* and the amphibian *Lydekkerina* (first appearance 37 m above the boundary) appear higher in the Katberg Formation (Smith and Botha, 2005).

It has been suggested that some surviving tetrapods burrowed beneath the floodplain to escape harsh environmental conditions (Smith and Botha, 2005). For example, burrowing behaviour has been inferred in *Lystrosaurus murrayi*, *L. declivis* (King, 1990) and *L. curvatus* (Smith and Botha, 2005) based on the morphology of humerus and claws. This is corroborated by articulated *Lystrosaurus* skeletons preserved in burrow casts filled by sand, found in floodplain mudrocks of the Katberg Formation (Groenewald, 1991; Miller et al., 2001; Retallack et al., 2003; Botha and Smith, 2007). Burrowing behaviour has also been inferred in the post-extinction cynodonts *Thrinaxodon liorhinus*, *Galesaurus* and *Progalesaurus* and the therocephalian *Tetracyonodon* (Damiani et al., 2003; Botha and Smith, 2006; Fernandez et al., 2013; Iqbal, 2015; Jasinowski and Abdala, 2017; Butler et al., 2019). These examples indicate that a fossorial lifestyle enabled terrestrial tetrapods to survive in southern Gondwana during the Early Triassic aridification, and likely represents an adaptation to tolerate low oxygen and high carbon dioxide levels during the PTME (Retallack et al., 2003; Smith and Botha-Brink, 2009, 2014; Lyson et al., 2016; Botha-Brink, 2017; Huttenlocker and Farmer, 2017; Jasinowski and Abdala, 2017; Fontanarrosa et al., 2018).

The Lower Triassic fauna is dominated by Dicotylia represented in large part by *Lystrosaurus* and by less abundant genera including *Myosaurus* (60.8%), followed by Procolophonomorpha with the genera *Coletta*, *Kitchingnathus*, *Owenetta*, *Phonodus*, *Procolophon*, *Saurodektes* and *Sauropareion* (11.9%), Temnospondyli with the genera

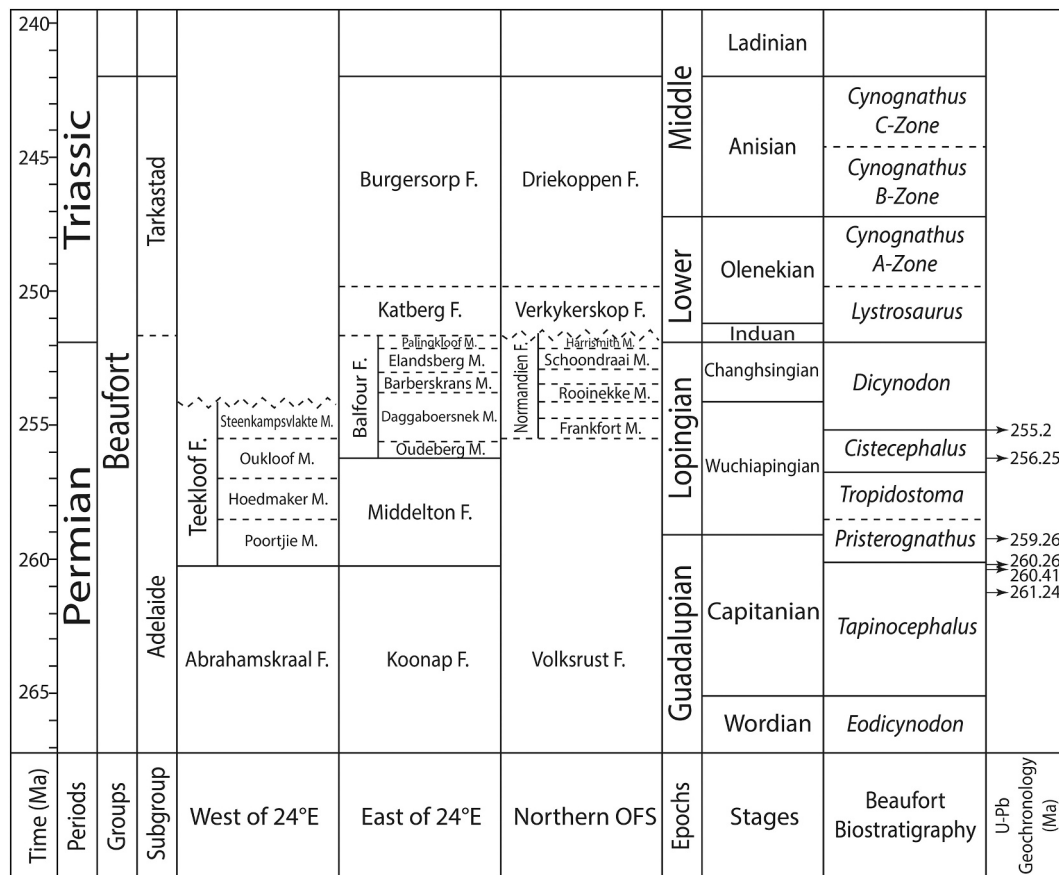


Fig. 13. Stratigraphic chart of the Main Karoo Basin and tentatively correlated to the Assemblage zones and the marine stages. Boundaries without absolute ages are represented with dashed lines. From Rubidge et al. (2016) with bibliography.

Bathignathus, *Broomistega*, *Eolydekkerina*, *Kestrosaurus*, *Lydekkerina*, *Micropholis*, *Phonodus*, *Pneumatostega*, *Rhytidosteus*, *Sauropareion*, *Thabanchuia*, *Trematosuchoides*, *Trematosuchus* and *Watsonisuchus* (9.3%), Cynodontia with the recognized genera *Langbergia*, *Nanictosaurus*, *Platycraniellus*, *Progalesaurus* and *Thrinaxodon* (6.5%), Archosauromorpha, represented by the recognized taxa *Garjainia*, *Noteosuchus*, *Prolacerta* and *Proterosuchus* (4.9%), Therocephalia with the genera *Erioclacerta*, *Moschorhinus*, *Olivierosuchus*, *Promoschorhynchus*, *Regisaurus*, *Scalopsaurus* and *Tetracynodon* (3.5%), basal Diapsida represented by the genus *Palacrodon* (3.5%) and Lepidosauromorpha with a single specimen of *Paliguana* (0.02%, not considered in the graphs). Early Triassic ichnological material from South Africa has been reviewed (Marchetti et al., 2019) from the Palingkloof Member of the Balfour Formation (Adelaide Subgroup), Beaufort Group. The recognised ichnogenes are *Dicynodontipus* referred to cynodonts, *Dolomitipus* referred to large dicynodonts, *Procolophonichnium* ascribed to procolophonid parareptiles, and *Rhynchosauroides* referred to non-archosauriform neodiapsids.

The faunal composition including ichnological data is dominated by Therapsida (73%), followed by Procolophonomorpha (12.2%), Temnospondyli (9.7%), Archosauromorpha (5.1%) and Lepidosauromorpha (0.05%).

7. Result of the semi-quantitative analysis

The result of the semi-quantitative analysis based on the relative abundance of specimens for each clade is reported in Figs. 14–16. For Temnospondyli, the highest percentage of presence is found in Greenland and Svalbard where the clade represents 100% of the recovered and described terrestrial tetrapods, followed by Australia (95.6%),

Russia (59%), India (36.9%), Antarctica (30%), South America (21.1%), SE Asia (19%), Central Europe (17.5%), North America (13.5%) and South Africa (9.7%). When arranged according to palaeolatitude (Fig. 15), the highest concentrations of Temnospondyli in terrestrial tetrapod faunas occur at high latitudes in both the north and south, while low latitudes show statistically significant lower abundance.

The Archosauromorpha show a greater percentage abundance in North America (61.5%), Central Europe (45.5%) and SE Asia (38.1%), followed by Russia (29.2%), India (23.6%), South America (21.1%), Antarctica (20.5%), South Africa (5.1%), and Australia (3.3%), whereas no members of the clade have been recovered from Lower Triassic deposits of Greenland or Svalbard. The latitudinal spread of Archosauromorpha (Fig. 15) shows the highest concentration at mid-low latitudes, up to a palaeolatitude of about 40° North and South, and a statistically significantly lower abundance at higher latitudes.

The Lepidosauromorpha are in general very poorly represented in all regions, with a maximum percentage presence in Central Europe (26%), based on the ichnological record, and in North America (19.2%), followed by South America (5.3%); the percentage presence is very low in Russia (0.3%) and South Africa (0.05%), whereas there is no record from India, SE Asia, Greenland, Svalbard, Australia or Antarctica. Lepidosauromorpha are distributed mainly around medium low paleolatitudes with a maximum between 25° and 40° North (Fig. 15).

The Procolophonomorpha show greater percentage abundance in South America (34.2%), followed by Antarctica (14.5%), South Africa (12.2%), and Russia (7.9%). Very low presences have been detected in India (3.2%), Central Europe (2.2%) and Australia (0.4%), and the clade is absent from the Lower Triassic of SE Asia, North America,

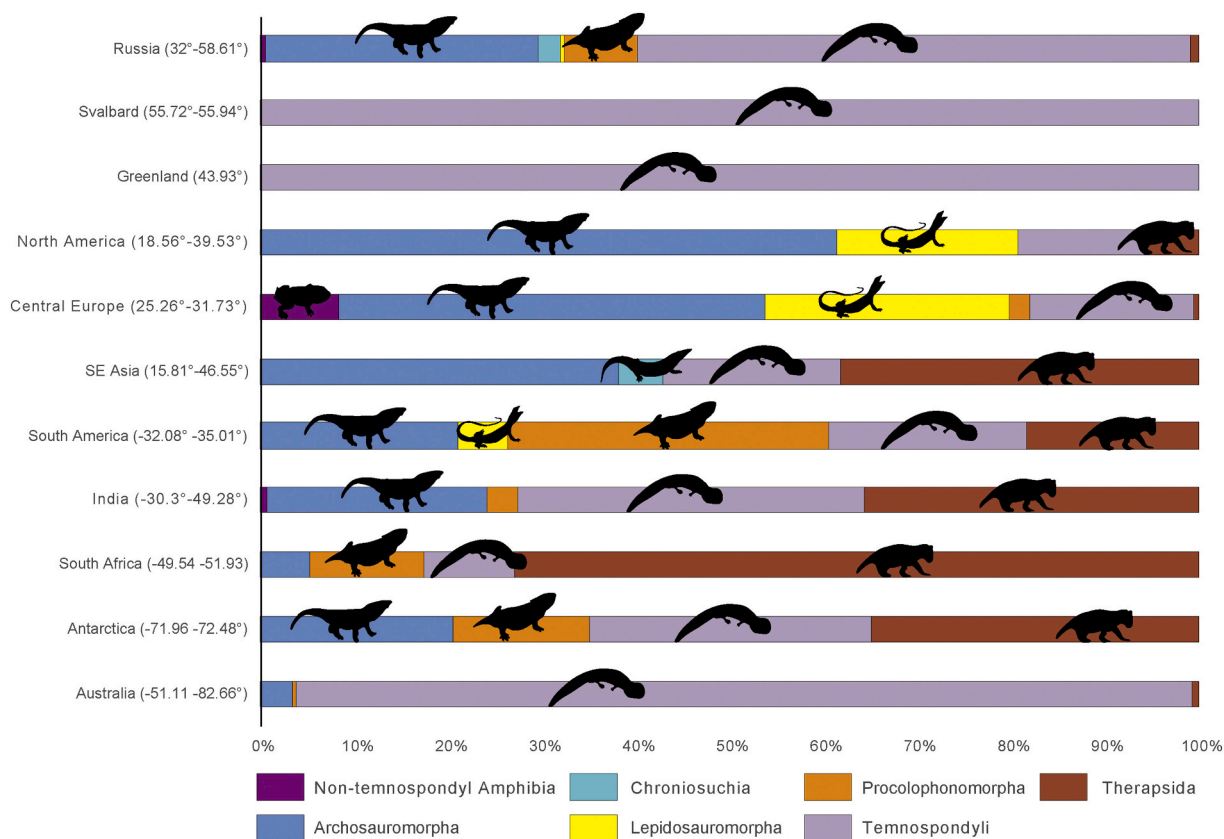


Fig. 14. Tetrapod composition and relative abundances in the 11 best-documented Early Triassic terrestrial ecosystems, plotted against palaeolatitudes.

Greenland and Svalbard. The latitudinal distribution of Procolophonomorpha (Fig. 16) shows highest abundance in the southern hemisphere (apart from a 7.9% presence in Russia), with a statistically significant peak at mid-palaeolatitudes in the south (from 32 to 35°S).

The Therapsida show a dominant percentage of abundance in South Africa (73%), followed by SE Asia (38%), India (35.7%), Antarctica (34.9%), South America (18.4%), and North America (5.8%); they are much rarer in Russia (0.8%), Australia (0.7%) and Central Europe (0.5%), and are absent from Greenland and Svalbard. The distribution for Therapsida during the the Early Triassic (Fig. 16) is concentrated in the southern hemisphere, especially between 30° and 72° palaeolatitudes. The maximum percentage is in the Karoo Basin of South Africa at palaeolatitudes between 49.54° and 51.93° South, where their abundance is statistically significantly higher than in any other region.

The result of the cluster analysis that takes account of the faunal list and relative abundance of different taxa is shown in Fig. 17. Our results show a pairing of the faunas of Svalbard and Greenland (connected by a dominance of Temnospondyli), and two major clusters representing the northern and southern hemisphere. The northern cluster comprises North America, Central Europe and Russia. The southern cluster consists of two sub-clusters, one pairing SE Asia and India, the other South Africa, South America and Antarctica. North America, Central Europe and Russia are united by the dominance of Archosauromorpha, a discrete presence of Temnospondyli and Lepidosauromorpha and rare Therapsida and Procolophonomorpha. SE Asia and India cluster together with a dominance of Therapsida, abundant Archosauromorpha and Temnospondyli, and no Lepidosauromorpha. Antarctica, South America and South Africa are clustered by the dominance of Therapsida, abundant Procolophonomorpha, Temnospondyli and Archosauromorpha, and very rare Lepidosauromorpha.

8. Discussion

The relative species richnesses (based on number of specimens for each taxon) of Early Triassic tetrapods of the world (Fig. 14) and by major groups and palaeolatitude (Figs. 15, 16) show some variation. As noted in the regional descriptions above (Section 6), the relative proportions are generally based on a combination of body and trace fossil data, but dominated by body fossils, except in North America, where skeletal fossils are less abundant than in other regions.

The obtained distribution of Temnospondyli (Figs. 14–16) could be explained by the extremely hot climate and arid environments of the Early Triassic. Temnospondyli depended on the stability of bodies of water for survival, and the cooler and more humid climates at high latitudes may have favoured stable freshwater tables, operating as shelters for the clade during the time of greatest warming and aridity. In fact, according to several studies, global warming in the Early Triassic led to temperate conditions in polar regions (Taylor et al., 1992, 2000; Retallack, 1995, 1999; Sun et al., 2012).

Although the large amphibian percentages reported for Greenland, Svalbard and Australia could be explained by a bias in sampling, the low percentage for example in South Africa must be considered as genuine, considering the intensive sampling in the Karoo Basin for well over 150 years.

The substantial percentage presence of Therapsida between the medium and high southern palaeolatitudes probably indicates a tolerance to a broad spectrum of environmental conditions. However, it must be emphasized that often the great majority of therapsids are *Lystrosaurus*, which were likely in some way adapted to the extreme climatic conditions of the Early Triassic (i.e., Retallack et al., 2003, 2006; Smith and Botha, 2005; Botha and Smith, 2006, 2007). In particular, Retallack et al. (2003, 2006) stressed how *Lystrosaurus* had a barrel-like chest probably hosting expanded lungs, a muscular diaphragm, and an improved efficiency of blood flow by a four-chambered

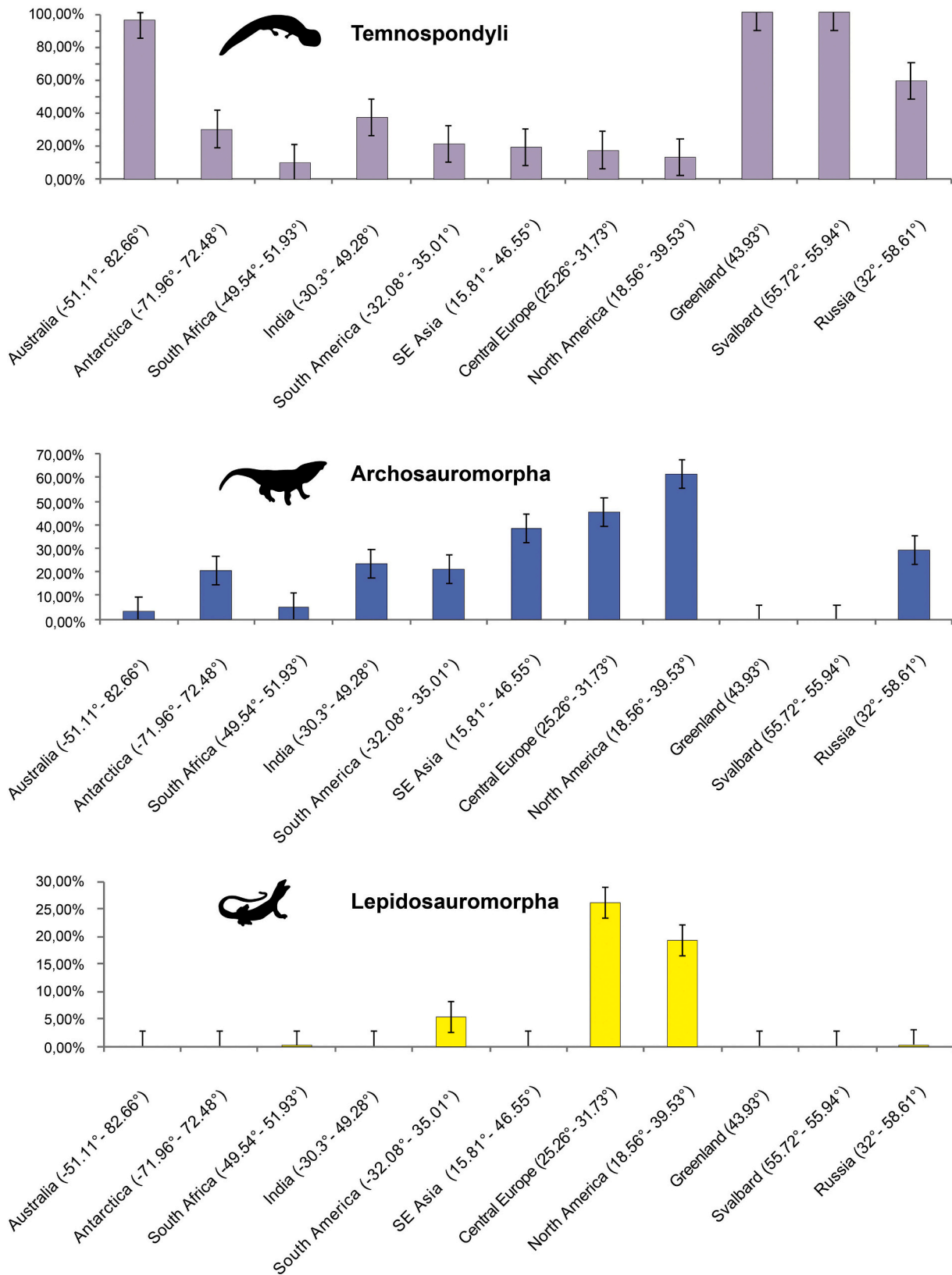


Fig. 15. Temnospondyli (purple), Archosauromorpha (light blue) and Lepidosauromorpha (yellow) relative abundance (percentage with standard error bars) in relation to the selected paleolatitudes.

heart, all features which allowed greater survival in an environment with declining oxygen concentration.

In addition, as already stressed in the text, other post-extinction

therapsid taxa such as the cynodonts *Thrinaxodon*, *Galesaurus* and *Progalesaurus* and therocephalian *Tetracynodon* were characterized by a fossorial lifestyle (Damiani and Yates, 2003; Botha and Smith, 2006;

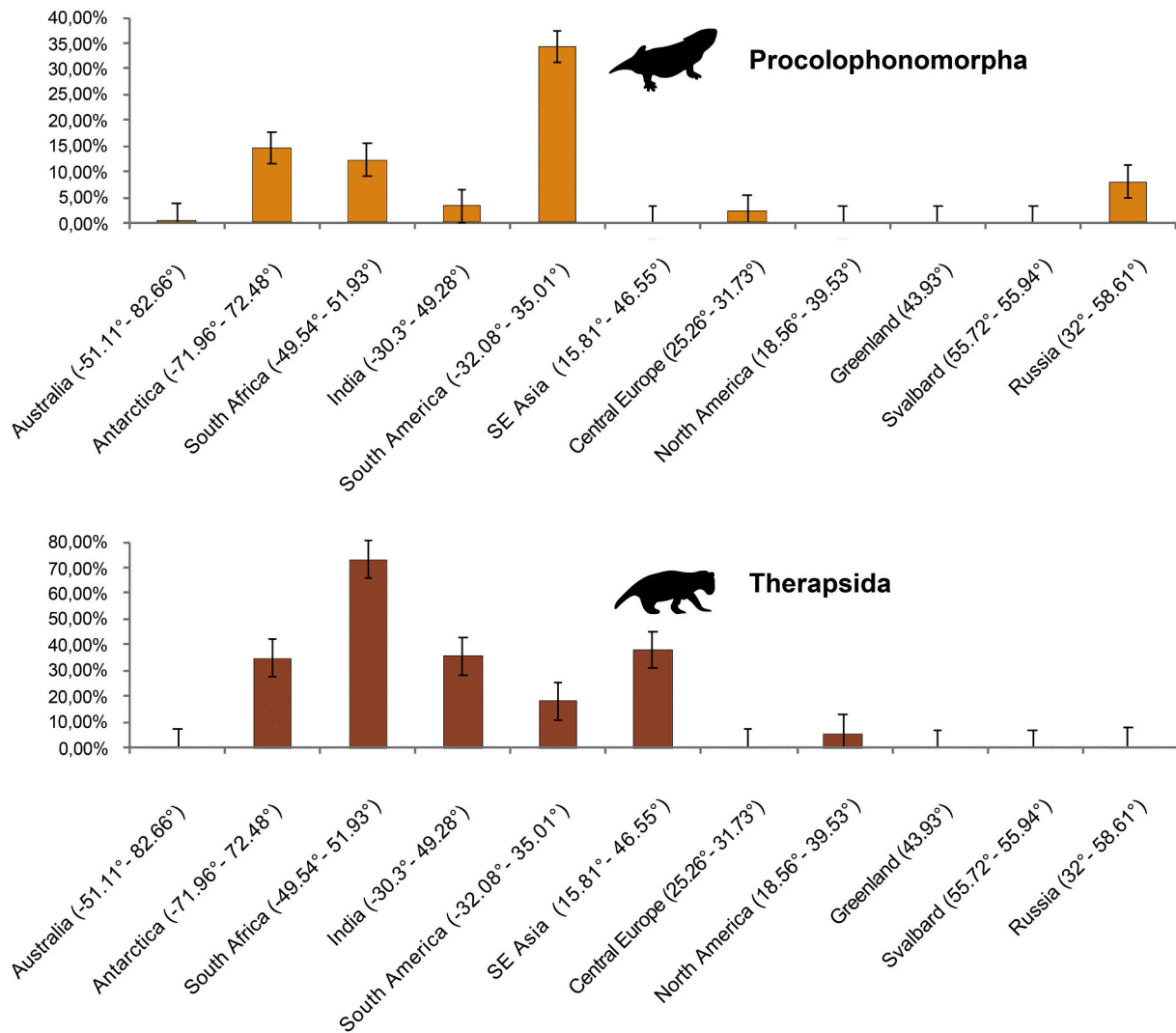


Fig. 16. Procolophonomorpha (orange) and Therapsida (light brown) relative abundance (percentage with standard error bars) in relation to the selected paleolatitudes. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Fernandez et al., 2013; Iqbal, 2015; Jasinowski and Abdala, 2017; Butler et al., 2019), that likely enabled terrestrial tetrapods to survive the Early Triassic aridification in southern Gondwana. As noted above, this behaviour may also have been associated with an ability to tolerate high carbon dioxide and low oxygen levels.

This review shows that Temnospondyli differed from the amniote clades in being excluded from the equatorial belt (Figs. 15, 16). According to Sun et al. (2012), the lethally hot temperatures in the Early Triassic Greenhouse drove most animals and plants out of equatorial terrestrial ecosystems, which caused the end-Smithian crisis. Benton and Newell (2014) also stressed how the extreme warming in the Early Triassic caused a substantial northward and southward expansion of low-latitude arid belts in the formerly humid basins of European Russia and the South African Karoo (Chumakov and Zharkov, 2003; Royer et al., 2004).

Drought tolerance by the amniotes may have been important, as stressed by Botha and Smith (2006). Extant reptiles are characterized by low ventilation rates, water-resistant integuments, solute-linked water reabsorption mechanisms, excretion of quite dry faecal pellets, and rarely drinking of water, taking it directly from their food (Withers, 1992; Pough et al., 1996). All these physiological adaptations make the extant reptiles, and probably also the Early Triassic Archosauromorpha, Lepidosauromorpha and Procolophonomorpha, well adapted to conserving water and to environments characterized by severe aridity and

drought.

The equatorial belt was not entirely devoid of life, however. Temperatures at the Equator have been estimated at 32–35 °C in the earliest Triassic (Joachimski et al., 2012), and up to 40 °C at the Smithian–Spathian boundary (Sun et al., 2012), so they were periodically inimical to life. Our results, however, do not entirely confirm the equatorial ‘tetrapod gap’, as we note terrestrial tetrapods from Southeast Asia in a palaeolatitudinal belt between 15.81° and 46.55° N, and tetrapods from South America between 32.08° and 35.01° South. Our evidence suggests that the inferred “death belt” of terrestrial life in the Early Triassic is narrower and is restricted to a palaeolatitudinal belt between 15° N and about 31° S, providing support to a previous, though independent from this analysis, finding by Bernardi et al. (2018).

Another effect of the extreme heating in the Early Triassic was cosmopolitanism. By inhibiting the radiation of many taxonomic groups, the Early Triassic was a time of remarkable global uniformity of faunas and floras (Hallam and Wignall, 1997; Grauvogel-Stamm and Ash, 2005; Brayard et al., 2006; Preto et al., 2010). However, we have demonstrated marked regionalisation of Early Triassic tetrapods, with variations in taxonomic composition and relative abundance in relation to palaeolatitudinal belt.

The evidence for regionalisation and against cosmopolitanism, was confirmed by the cluster analysis, with a clustering consistent with the palaeobiogeography of the Early Triassic (Fig. 17). It demonstrates that

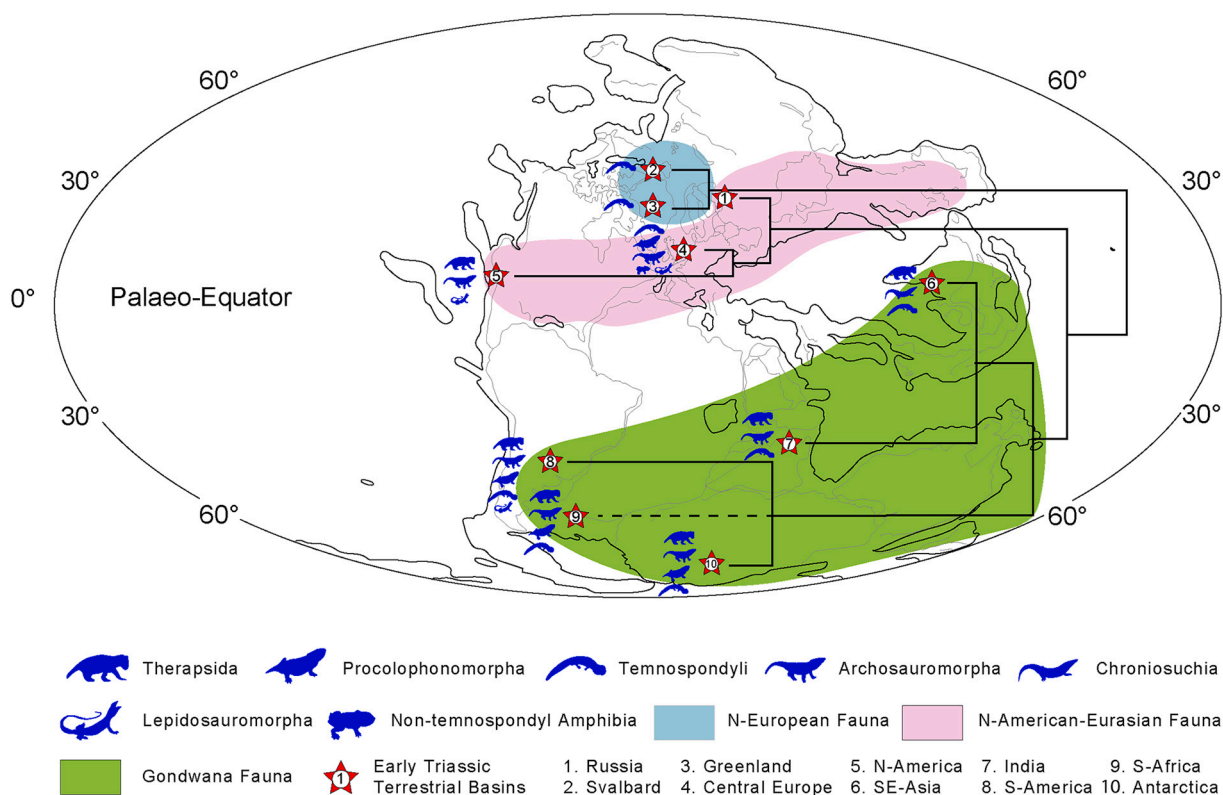


Fig. 17. Result of the cluster analysis based on the faunal list and relative abundance of different taxa plotted against Early Triassic paleobiogeography. The detected affinities indicate three major clusters for Early Triassic Tetrapoda fully coherent with tetrapod occurrences and palaeoclimatic distribution.

there was some provincialism after the PTME, reflected in the composition of terrestrial tetrapod faunas. The general pattern in the Early Triassic largely reflects that found for the Late Permian by Bernardi et al. (Bernardi et al., 2017, Fig. 7, p. 34) using similar semi-quantitative methods and abundance matrixes. The results indicate that even after the extreme PTME bottleneck, the Early Triassic recovery faunas show an “inherited” imprint when the general composition of terrestrial tetrapod faunas is taken into consideration.

9. Conclusions

The PTME was one of the most severe biotic crises of the Phanerozoic, eliminating > 90% of marine and terrestrial species. Such a major crisis was followed by a long period of recovery in the Early and Middle Triassic which revolutionised the structure of both marine and terrestrial ecosystems, greatly influencing the course of tetrapod evolution in the remainder of the Mesozoic and Cenozoic eras. In particular, entire new clades emerged after the mass extinction, including decapods and marine reptiles in the oceans and new tetrapods on land. In both marine and terrestrial ecosystems, the recovery was stepwise and slow, from a combination of continuing environmental perturbations and complex multilevel interaction between species in the new environments. The Early Triassic experienced extreme climate perturbations, with severe anoxic and alkaline conditions in the oceans, and the expansion of deserts and migration of warm temperatures to high southern hemisphere latitudes. Levels of O_2 substantially decreased and CO_2 increased; repeated greenhouse crises led to very harsh environmental conditions, which had a major influence on the tempo and mode of biotic recovery.

In marine ecosystems a full recovery is detected about 8–9 Myr after the mass extinction (middle to late Anisian), and a similar pattern has been inferred also for recovery in terrestrial communities. The recovered terrestrial faunas included ancestors of most key modern

groups such as crocodiles, frogs, lizards, turtles and mammals, and the first dinosaurs. The crisis on land led to the collapse and disappearance of well-structured latest Permian ecosystems including carnivorous gorgonopsian therapsids and herbivorous parietosaurs and dicynodonts, replaced by an Early Triassic unbalanced ‘disaster fauna’, which lacked top predators as well as diverse herbivores, and was dominated by very abundant specimens of the dicynodont *Lystrosaurus*.

In the present contribution, we have reviewed Early Triassic fossiliferous formations and their tetrapod faunas, which enabled a semi-quantitative analysis of faunal compositions and provincialism, based on a dataset of Early Triassic terrestrial tetrapods. We presented data on 11 regions, namely Russia, Svalbard, Greenland, North America, Central Europe, South America, India, Southeast Asia, South Africa, Antarctica and Australia. The semi-quantitative analysis suggests the following general conclusions:

- 1) Marked regionalisation of Early Triassic terrestrial tetrapods is detected, with different faunas changing in both taxonomic composition and relative abundance in relation to palaeolatitudinal belt. We therefore reject the alleged uniformity of faunas (cosmopolitanism) all around Pangaea suggested as a result of a greenhouse climate driving a very low equator-to-pole temperature gradient, and general uniformity worldwide in floras and faunas.
- 2) The inferred “death belt” of terrestrial life in the Early Triassic can be restricted to a paleolatitudinal belt between 15° N and about 31° S, based on the occurrence of terrestrial tetrapods from Southeast Asia in a palaeolatitudinal belt between 15.81° and 46.55° N, and tetrapods from South America between 32.08° and 35.01° South. Therefore, the wide ‘tetrapod gap’, with a total absence of tetrapod taxa between 30° N and 40° S, and linked to Early Triassic critically high temperatures, must be narrowed according to our results.
- 3) Early Triassic Temnospondyli are concentrated mostly at high latitudes in both the north and south, and are absent in the tropical belt.

This can be explained by the dependence of temnospondyls on stable bodies of water for their survival. In light of the hot climate and arid environments of the Early Triassic, it is assumed that high southern and northern latitudes operated as refuges, retaining stable freshwater tables with temperate conditions.

- 4) Archosauromorpha, Lepidosauromorpha and Procolophonomorpha are characterized by greater abundance at low-middle palaeolatitudes, when compared to Temnospondyli. This reflects their likely adaptations to drought tolerance. In particular, Archosauromorpha, Lepidosauromorpha and Procolophonomorpha were pre-adapted to a hot and arid environment, by likely having adaptations to conserve water in arid and drought-affected regions. Archosauromorpha also occur at high northern and southern palaeolatitudes, and this might presage their rising dominance as the major terrestrial tetrapod clade of the Mesozoic.
- 5) Therapsida during the Early Triassic were concentrated in the southern hemisphere, especially between 30° and 72° South palaeolatitudes. Their substantial presence between medium and high southern palaeolatitudes can also be linked to their environmental tolerance. In particular, *Lystrosaurus* was likely pre-adapted to extreme climatic conditions of the Early Triassic by being able to burrow. Similarly, the therocephalian *Tetracynodon* and the cynodonts *Thrinaxodon*, *Galesaurus* and *Progalesaurus* were characterized by a fossorial lifestyle which, very likely, enabled them to survive the Early Triassic aridification in southern Gondwana. It has also been suggested that the surviving therapsids also had tolerance to low oxygen conditions.
- 6) The cluster analysis of faunal lists and relative abundances provided results consistent with Early Triassic palaeobiogeography, and demonstrates fairly strong provincialism even so soon after the PTME. There are three regional clusters, in Greenland-Svalbard, North America-Eurasia, and south China-Gondwana. The overall pattern in the Early Triassic largely mirrors that in the Late Permian (see Bernardi et al., 2017). Evidently, faunas recovered and retained a pre-extinction palaeogeographic imprint.

Declaration of Competing Interest

None.

Acknowledgements

Kenneth D. Angielczyk and Pia Viglietti are warmly thanked for their useful comments and suggestions that improved an early version of the manuscript. Two anonymous reviewers and the Editor Alessandra Negri are thanked for their comments and suggestions that have improved the text. The study is part of the project 'The end-Permian mass extinction in the Southern and Eastern Alps: extinction rates vs. taphonomic biases in different depositional environments' financed by the Euregio Science Fund (call 2014, IPN16) of the Europaregion Euregio. MB is grateful to the 'Gino Zobebe Fund for Research' and Giovanna Zobebe Lipparini for their generous support. This work was supported by the Palaeontological Scientific Trust (PAST) and its Scatterlings of Africa programmes, and DSI/NRF Centre of Excellence in Palaeosciences. MJB is grateful for funding by NERC BETR grant NE/P013724/1, Natural Environment Research Council (UK), grant NE/I027630/1 and ERC Advanced Grant 788203 (Innovation).

Declaration of Competing Interest

None.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://>

doi.org/10.1016/j.earscirev.2020.103331.

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