Earth-Science Reviews 224 (2022) 103886

Contents lists available at ScienceDirect

Earth-Science Reviews

journal homepage: www.elsevier.com/locate/earscirev

Review Article

Tetrapod turnover during the Permo-Triassic transition explained by temperature change

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ARTICLE INFO

Keywords:
P/Tr
Permo-Triassic extinction
Tetrapoda
Lystrosaurus
Dicynodontia
Climate change

ABSTRACT

Global temperatures significantly changed from the late Permian to the Early Triassic: the Earth transformed from a cool world to a hothouse climate. This transition undoubtedly had a strong impact on tetrapod physiology and distribution. During the global cooling, tetrapods generally increased their size; and the currently recognized late Permian tetrapod extinction, exemplified by the record preserved in the South African Karoo Basin, occurred in the late stage of cooling. Rapid warming in the Early Triassic is predicted to have resulted in extinctions and/or local extirpation of low latitude tetrapods, but the very limited fossil record from this region makes testing this hypothesis difficult. Warming is predicted to have had less negative impacts on the tetrapod diversity of mid-latitudes, and promoted the success of tetrapods in the high latitudes. Based on the known fossil record, a tetrapod gap could have existed in central Pangea between ~30°N and ~ 40°S, and lasting from the Induan to the early Spathian. However, the exact boundaries of this gap likely varied over time, and it could have encompassed a larger area during the hottest phases (Griesbachian and near the Smithian–Spathain boundary).

1. Introduction

One of the great ecosystem transitions of Earth history occurred 251.9 million years ago, at the boundary between the Permian and Triassic periods. Initially, evidence for an end-Permian mass extinction was detected mainly from the marine fossil record (e.g., Schindewolf, 1954; Newell, 1956; Raup and Sepkoski, 1982; Erwin, 1993; Fan et al., 2020), and there was debate over whether a comparable extinction occurred among tetrapods (e.g., Romer, 1945; Newell, 1967; Colbert, 1973; Pitrat, 1973; Olson, 1982, 1989; Benton, 1989; King, 1991; Maxwell, 1992). Extensive research over the past three decades (see Angielczyk, 2014; Botha et al., 2020; Lucas, 2017; Gastaldo et al., 2019; Roopnarine et al., 2019; Smith and Botha-Brink, 2014; and references therein) has led to the general consensus that the end-Permian extinction strongly affected terrestrial tetrapod communities (e.g., Viglietti et al., 2021), with a loss of nearly 90% of known tetrapod genera (Benton et al., 2013; but see Lucas, 2021).

Beyond the overall loss of species diversity, the extinction also affected the macroevolutionary trajectories of many tetrapod clades. For example, among the three major herbivore lineages of the Lopingian, dicynodonts, pareiasaurs, and captorhinids, only a few dicynodont lineages survived into the Triassic, of which one (the kannemeyeriiforms) rediversified to become important herbivores of the Middle and Late Triassic (Fröbisch, 2008; Sues and Fraser, 2010; Ruta et al., 2013a; Bernardi et al., 2017; Romano et al., 2020). Although the diversification of cynodonts was already underway in the Lopingian, the group radiated rapidly in the aftermath of the extinction, including the emergence of the Gomphodontia, which became another major herbivorous therapsid clade in the Triassic (Abdala and Ribeiro, 2010; Ruta et al., 2013b; Abdala and Gaetano, 2018; Lukic-Walther et al., 2019; Abdala et al., 2020). Procolophonids diversified as small herbivores from the Induan, although diversity trends for parareptiles as a whole suggest that the

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https://doi.org/10.1016/j.earscirev.2021.103886
Received 25 August 2021; Received in revised form 29 November 2021; Accepted 30 November 2021
Available online 4 December 2021

clade may have been a 'dead clade walking' following the extinction (Cisneros, 2008; Ruta et al., 2011; MacDougall et al., 2019; Pinheiro et al., 2021). Finally, stereospondyls diversified to become major aquatic predators in the aftermath of the extinction (Eltink et al., 2019), and archosauriforms appeared as top predators during the Triassic and began their rapid rise to dominance of Mesozoic terrestrial ecosystems (Nesbitt et al., 2010, 2017; Ezcurra and Butler, 2018).

Many disruptive mechanisms have been proposed to explain the end-Permian mass extinction in the marine and terrestrial realms, with much attention concentrated on the biotic effects of rapid temperature rise (Sun et al., 2012; Benton, 2018; Bernardi et al., 2018; Penn et al., 2018; Allen et al., 2020). This raises the question of how such environmental changes affected tetrapod diversity during the Permo-Triassic transition. In the modern world, the spatial distributions of amphibians and reptiles are strongly controlled by the physical environment, especially temperature and precipitation. In a recent work, we showed that tetrapod distributions during the Permo-Triassic transition were strongly correlated with estimates of paleoclimate (Liu et al., 2021). Here, we explore how tetrapod distribution patterns and extinctions were influenced by climate changes, especially the latest Permian interval of global cooling that preceded the rapid warming of the Early Triassic.

2. Background and methods

Temperature fluctuations are greater on land than in marine environments. Climate models facilitate investigation of the responses of different regions in global warming and cooling scenarios (Roscher et al., 2011), and they predict a stronger overall impact of global cooling, whereas, global warming may have a greater impact on the biological diversity of tropics (Deutsch et al., 2008). A bimodal latitudinal diversity gradient (LDG) was suggested for terrestrial tetrapods during the late Permian – Middle Triassic (Allen et al., 2020), but that pattern could stem from spatial biases (Jones et al., 2021). In contrast, a unimodal LDG was recovered for marine invertebrates during the late Permian and Middle Triassic, and a flat LDG has been hypothesized for the Early Triassic (Song et al., 2020).

Extant tetrapod distributions fall within the range of their critical thermal minimum (CT_{min}) and maximum (CT_{max}), which generally spans −1–37 °C for modern amphibians and 4–44 °C for modern reptiles (Bennett et al., 2018). We predicted preferred climates (temperature and precipitation) for major tetrapod groups from the Lopingian to the Early Triassic based on their observed geographic distributions and paleoenvironmental data (Liu et al., 2021). Tetrapod species would shift their geographic ranges to climates they can tolerate or become extinct in the face of rapid changes that exceed their limits. During global cooling, low temperatures at mid-high latitudes could fall below 0 °C, leading to the disappearance of many tetrapod species in those areas. Likewise, during global warming, hyperthermal conditions should lead to the local extirpation of many tetrapod species in low latitude regions.

We compiled data on tetrapod fossil occurrences from the Lopingian to the Olenekian using the Paleobiology Database (PBDB, https://paleobiodb.org, downloaded 18 May 2021). We checked our dataset against the most recent literature, especially two comprehensive review papers (Bernardi et al., 2017; Romano et al., 2020). Missing records were added (Table S1), and we produced a global correlation chart (Fig. S1). The PBDB includes two sets of paleogeographic coordinates for localities that are derived from different sources (PBDB FAQ; accessed 6/11/2021). The relative accuracy of these reconstructions is beyond the scope of this paper, but the tetrapod distribution patterns under different paleogeographic hypotheses have different implications for the paleoclimate. Today, the Global Average Temperature (GAT) is ~14 °C, and the boundaries of the warm temperate belt are ~50°N and ~ 50°S. The reconstruction of Scotese (2014) indicates a higher Global Average Temperature during late Permian than that of Torsvik and Cocks (2016) because the more poleward distribution of areas bearing tetrapod fossils.

We also compiled size and abundance data for dicynodont therapsids during the time interval of interest. For species i, N_i = number of specimens; L_i = skull maximum length; average dicynodont skull length = $\Sigma N_i{*}L_i/\Sigma N_i$ ($i = 1$, n). Abundance data for the *Tropidostoma – Gorgonops* Subzone (SZ) of the *Endothiodon* Assemblage Zone (AZ)(see Day and Smith, 2020 for recent proposal of the subzone) and the *Cistecephalus* AZ are revised from Smith et al. (2012); abundance data for the two subzones of the *Daptocephalus* AZ are from Viglietti et al. (2016) (Table S2).

3. Lopingian cooling and its effect on tetrapods

During the early Wuchiapingian, there was a warm period whose temperature was close to that of the end-Permian interval (Ts, mean tropical seawater surface temperature, >30 °C), that was followed by climatic cooling of ~9 °C that lasted until the late Changhsingian, indicated by oxygen isotope ratios measured on conodont apatite (Chen et al., 2013). The Changhsingian cooling has been documented at the Meishan GSSP section (paleolatitude: 18°N) (Chen et al., 2016), but not at the equator (Chen et al., 2020). A warming climate was suggested for Changhsingian times based on brachiopod data from the Xiakou section (paleolatitude: 13°N) (Wang et al., 2020), but their samples may be too sparse to capture the details of the cooling event. A stronger cooling signal was recorded in Changhsingian carbonates from the East European Platform (Davydov et al., 2020), whereas a cooling of 10 ± 6 °C was documented from tetrapod apatite from South African faunas (Rey et al., 2016), located at ~50/65°S at the time. The overall effect of the cooling would be to move the boundary of the cool temperate zones towards the equator.

During the warm phase of the Wuchiapingian, temnospondyls spread south to the Sydney Basin (Warren, 1997), and captorhinids, which preferred warm climates (Bernardi et al., 2017; Liu et al., 2021), reached the margin of the south warm temperate zone (Modesto and Smith, 2001). In the Karoo Basin, the climate was dry and warm, with faunas of the *Tropidostoma – Gorgonops* SZ of the *Endothiodon* AZ dominated by small-sized dicynodonts such as *Diictodon* (comprising more than two-thirds of known specimens of the former *Tropidostoma* AZ) (Smith et al., 2012; Day and Smith, 2020). During the succeeding *Cistecephalus* AZ (27 °C < Ts < 30 °C), the Karoo Basin assemblage reached its highest recorded diversity of the late Permian and Early Triassic (Fig. 1, TableS3). Finally, during the *Dicynodon – Theriognathus* SZ of the *Daptocephalus* AZ (23 °C < Ts < 27 °C), tetrapods were still diverse but species richness began to decrease in the Ripplemead Member, near the top of this subzone (Viglietti et al., 2021).

When ambient temperatures fell below 20 °C, photosynthesis would be expected to decrease (Berry and Björkman, 1980), reducing plant biomass available to herbivores, ultimately affecting energy transfer to carnivores. The number of fossils gradually decreased in the *Lystrosaurus maccaigi – Moschorhinus* (L-M) SZ (Viglietti, 2020), the latest Permian faunal assemblage from the Karoo, where only dicynodonts display a relatively high taxonomic diversity (Viglietti et al., 2021). If not a taphonomic artifact, this could be evidence of decreasing population sizes and diversity in response to decreased levels of productivity in the Karoo Basin. *Lystrosaurus* gradually increased in abundance within the L-M SZ, reflecting its hypothesized lower Tp than other dicynodonts and better adaptation for a cooler climate (Liu et al., 2021).

By ~252.3 Ma, the coldest phase of the Lopingian was reached, and Ts could be lower than 21 °C at paleolatitude 17°N (Chen et al., 2016). Using the radiometric date of Gastaldo et al. (2020) for the lower Katberg Formation, this would be near the boundary of the *Daptocephalus* AZ and *Lystrosaurus declivis* AZ in the Karoo Basin. At this time, the Karoo Basin is predicted to have a winter with sub-freezing temperatures in which the ambient temperatures were lower than CT_{min} of all tetrapods. Survival under these conditions would require a means to moderate the effects of cold temperatures, such as by burrowing behavior in *Lystrosaurus* (Botha-Brink, 2017) and other species (Damiani et al., 2003; Fernandez et al., 2013). Because plants survived here (Gastaldo et al., 2005, 2015, 2017; Botha et al., 2020), daily temperatures should

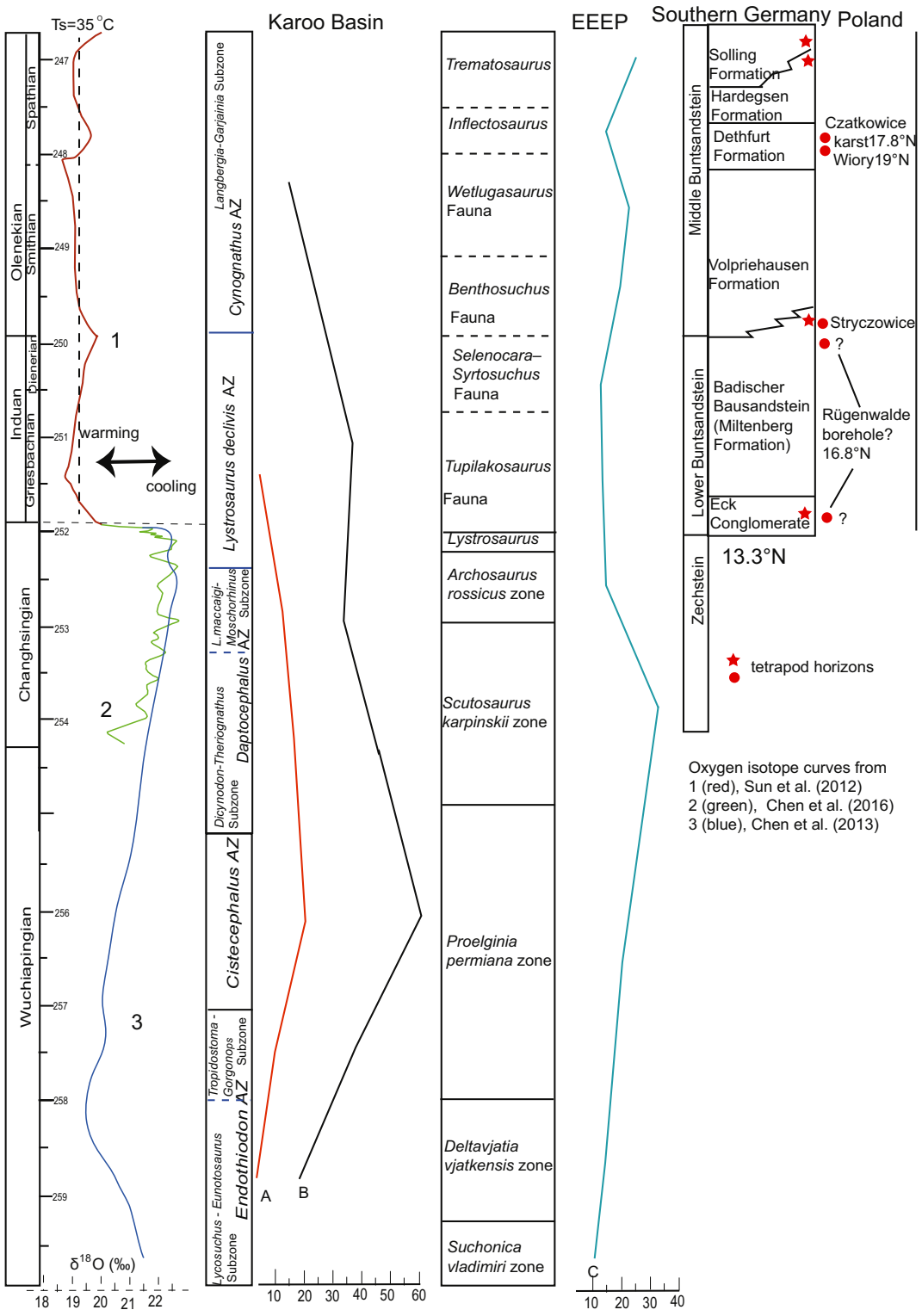

Fig. 1. Relationship between global temperature proxies and tetrapod diversity in the Karoo Basin, East European Platform and PreUrals (EEPP), and central Europe. Taxonomic diversity is shown for: A, Karoo Basin dicynodonts (red); B, Karoo Basin tetrapods (black); and C, EEPP tetrapods (blue). Karoo assemblage zones from Smith et al. (2020), EEPP tetrapod zones are from Sennikov and Golubev (2017) and Novikov (2018); southern Germany data from Schoch (2011); Poland data from Brusatte et al. (2011) and von Huene (1942). Timescale based on Henderson et al. (2020) and Ogg et al. (2020). Abbreviation: AZ, Assemblage Zone. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

have been higher than 10 °C for at least four months per year, so local annual mean temperature (Ta) > 5 °C. Meanwhile, farther south, an end-Permian extinction among plants is documented in the cooler Sydney Basin (Fielding et al., 2019), the so-called end-Permian terrestrial ecological disturbance (Kaiho et al., 2020). During the following short warming in the latest Changhsingian, only *Saurodektes* (Procolophonoidea), *Proterosuchus*, *Prolacerta* (Archosauromorpha) and three new therocephalian genera appeared (Viglietti et al., 2021).

Although dicynodonts diverged by the Guadalupian, they achieved their highest diversity in southern Pangea during the Lopingian cool phase (*Cistecephalus* and *Daptocephalus* AZs) (Fröbisch, 2008; Ruta et al., 2013a), reflecting a hypothesized preference for cooler temperatures (Liu et al., 2021). Average sizes of dicynodont species also increased across this interval, with the most abundant species changing from small-sized *Diictodon* to larger-sized *Oudenodon* or *Lystrosaurus* (Smith et al., 2012; Viglietti et al., 2016), consistent with a Bergmann's rule-like response to global cooling (Chen et al., 2013; Chen et al., 2020; Davydov et al., 2020; Rey et al., 2016) (Fig. 2). A similar trend of increasing average size of species also occurred in therocephalians and cynodonts of the Karoo Basin (Huttenlocker, 2014: Fig. 1). It may have occurred in gorgonopsians of the Karoo Basin as well: Rubidgeinae, which includes the largest species of the group, diversified in *Cistecephalus* AZ and *Daptocephalus* AZ (Smith et al., 2012; Kammerer, 2016).

Diictodon feliceps was the most successful dicynodont species in the Karoo Basin, having the longest stratigraphic range (*Tapinocephalus* AZ to *Daptocephalus* AZ), and usually at comparatively high abundance (Fig. 2). However, it decreased in abundance during the *Lystrosaurus maccaigi – Moschorhinus* SZ of the *Daptocephalus* AZ, finally disappearing from the Karoo Basin along with many other dicynodonts during the latest Changhsingian coldest phase (Viglietti et al., 2016, 2021).

A comparable tetrapod fauna comes from Xinjiang, China (TableS3, FigS2), located in the northern hemisphere warm temperate zone during the Changhsingian (Scotese, 2014; Huang et al., 2018). *Lystrosaurus* appeared in the upper part of the Guodikeng Formation (= upper Wutonggou low order cycle of Yang et al., 2021) and soon became the dominant tetrapod. Three other dicynodont genera, *Turfanodon, Jimusaria,* and *Diictodon*, are rare and did not persist to the upper boundary of the Guodikeng Formation, when the mean annual temperature fell below 10 °C (Thomas et al., 2011). *Lystrosaurus* is highly abundant in the overlying Lower Triassic Jiucaiyuan Formation. *Proterosuchus yuani* appears at the base of the Jiucaiyuan Formation, and lasted for more than half the thickness of the formation (Zhao, 1980), a much longer lithostratigraphic range than *Proterosuchus fergusi* in the Karoo Basin (Viglietti et al., 2021). Although the Xinjiang tetrapod fossil record is less extensive than that of the Karoo, a similar overall pattern of tetrapod turnover to the Karoo is observed, with *Lystrosaurus* becoming abundant and other dicynodonts disappearing during the latest Changhsingian cool phase.

In the East European Platform and PreUrals (EEPP) (middle latitude arid zone), the Lopingian cooling is detected from lacustrine and pedogenic carbonate isotope curves (Davydov et al., 2020), but its impact on tetrapods is hard to quantify due to small sample sizes. During

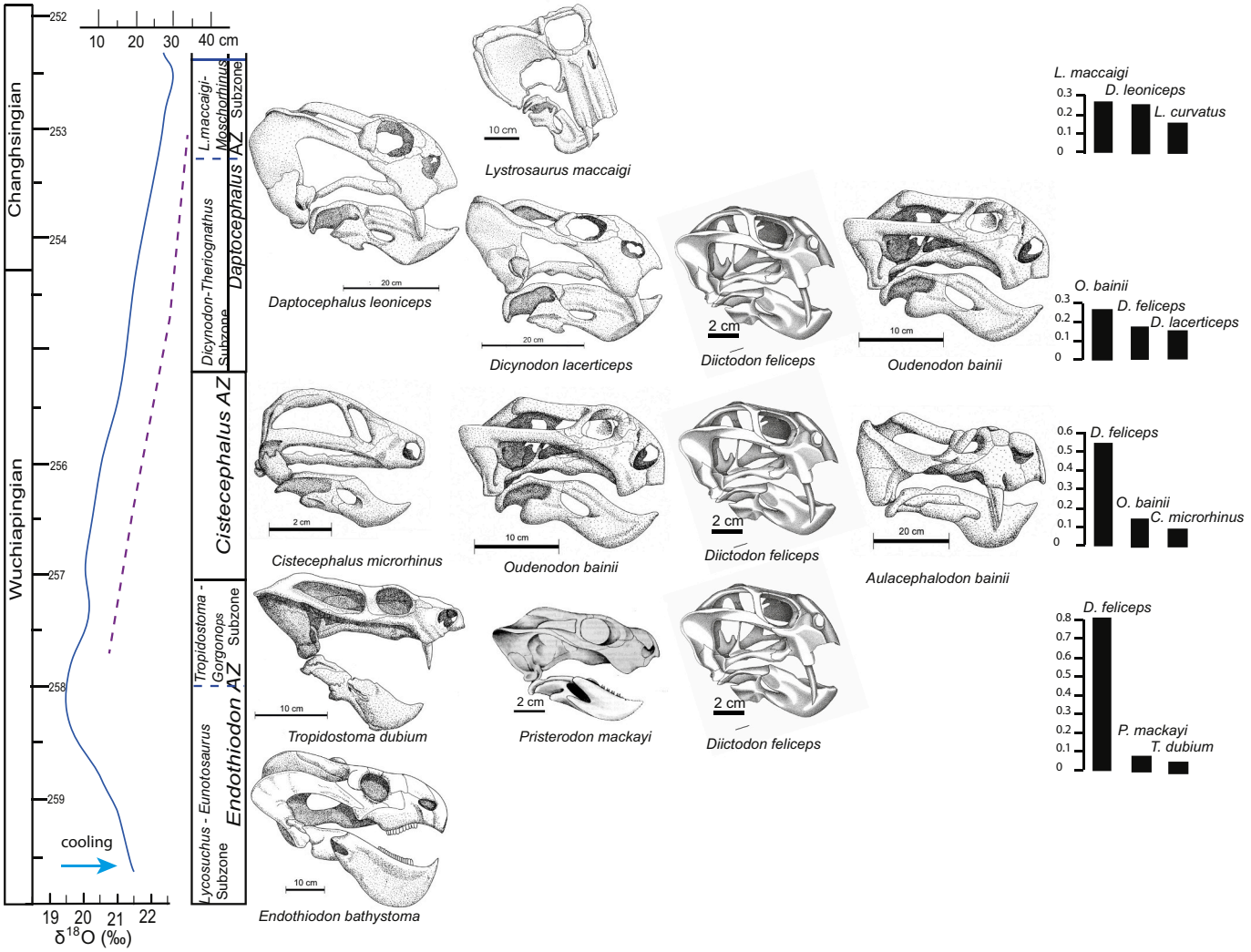

Fig. 2. The Lopingian tetrapod assemblages in the Karoo Basin, showing the most abundant dicynodont species of each assemblage zone and the changes in average skull size (dotted line), compared to a global temperature proxy (tropical seawater oxygen isotope curves from Chen et al., 2013). The bar charts show the relative abundance of species (number of specimens vs. total dicynodont specimens) in a given (sub)zone. Skull drawings from Sullivan et al. (2003), Day and Smith (2020), and Smith (2020).

the Lopingian to Early Triassic interval, tetrapod diversity was highest in the Sokolki Fauna (*Scutosaurus karpinskii* Zone), with 34 species, six of which are dicynodonts (Fig. 1, Table S3). Only undiagnostic dicynodont specimens were discovered in the succeeding *Archosaurus rossicus* Zone and a few *Lystrosaurus* specimens are from the Astashikha Fauna, which is regarded as latest Permian (Davydov et al., 2020).

Lystrosaurus was absent in the Ordos and surrounding basins of North China, which were located in the low latitude arid zone in the Lopingian (Huang et al., 2018). A biostratigraphic correlation between Chinese late Permian faunas is provided by the dicynodonts *Jimusaria* and *Turfanodon,* which coexisted in North China and Xinjiang (Liu, 2019, 2021). No change in tetrapod faunal composition is currently apparent within the Naobaogou Formation (a fauna also dominated by dicynodonts; Liu, 2019, 2021), which has the only continuous late Permian tetrapod record of the North China Block (Liu, 2021).

Tetrapod-bearing strata of Lopingian age are also known from Niger, Morocco, Tanzania, and Zambia and span arid to warm temperate climatic zones (Fig. S1; Liu et al., 2021: Fig. 2). The former two areas host atypical late Permian assemblages including large captorhinids, pareiasaurs, and relict temnospondyls (Bernardi et al., 2017), but their precise age has been difficult to determine due to a lack of biostratigraphically relevant taxa or radiometric dates (Hmich et al., 2006; Sidor et al., 2005). Nevertheless, they demonstrate a restricted set of tetrapods inhabiting arid to hyper-arid environments at low paleolatitudes near the center of Pangea (Smith et al., 2015). Basins in Tanzania and Zambia preserve Wuchiapingian (*Cistecephalus* and likely lower *Daptocephalus* AZ-equivalent; Angielczyk et al., 2014; Angielczyk and Kammerer, 2017) rocks that contain tetrapods mostly similar to those seen in the Karoo Basin of South Africa, which is not surprising as they fall within the same climatic zone (Liu et al., 2021: Fig. 2). None of these areas has yielded Lower Triassic tetrapod fossils, although putative Lower Triassic tetrapods, including fragmentary *Lystrosaurus*-like specimens were recently reported from the neighboring Metangula Graben of Mozambique (Araújo et al., 2020).

4. Early Triassic hothouse and its effect on tetrapods

At the end of the Permian, a rapid seawater temperature rise of 6–10 °C associated with an abrupt extinction was documented from many tropical marine sections (Joachimski et al., 2019). Ts reached as high as ~32 °C at the Permian-Triassic boundary (Sun et al., 2012). In the earliest Triassic, temperatures increased further, reaching a temperature maximum (36 °C) within the Griesbachian, followed by some degree of cooling in the Dienerian. A second rise to high temperatures (>38 °C) is seen in the late Smithian, followed by relatively stable temperatures in the Spathian, cooling at the end of this stage, and stabilization by early Anisian times (Sun et al., 2012).

In the tropical zone, diurnal temperature ranges are narrow. Even though the magnitude of predicted warming is less than at higher latitudes, increasing temperatures can cause extinction among terrestrial ectotherms in the tropics because they typically live very close to their optimal temperature (Deutsch et al., 2008). The Lopingian tropical zone included Cimmeria, Indochina and South China (Boucot et al., 2013; Nowak et al., 2020). There is only one known Permian tetrapod horizon, the Purple Claystone Formation of the Luang Prabang Basin, Laos, within this zone (Arbez et al., 2018; Olivier et al., 2019), and the Lower Triassic is missing (Rossignol et al., 2016). Therefore the impact of warming climates on Permo-Triassic tetrapods in the tropics is currently unknown.

In the low latitude arid zone, daily temperature variation is expected to be high. In the modern world, a 30 °C annual mean temperature marks the boundary of this arid zone, which brings a few hot months with monthly mean maximum temperature > 42 °C. During the Early Triassic, this area should have been much warmer (Ta > > 30 °C) based on hypothesized seawater temperatures. Under such extreme temperatures, only a few plants and reptiles can survive (Bennett et al., 2018). Although tetrapod thermal safety margins and CT_{max} are relatively wide in this zone (Clusella-Trullas et al., 2011), we predict that tetrapods would shift their geographic ranges towards higher latitudes in the face of rapid warming.

Most modern fish and amphibians cannot survive water temperatures above 37 °C (Bennett et al., 2018), and typically their temperature limit is Ta > 35 °C near the equator. If Permo-Triassic temnospondyls had temperature tolerances similar to modern amphibians, some species could survive in areas with Ta < 35 °C, such as the low latitudes of the early Induan. So, at this time, in low latitudinal arid areas where Ta > 30 °C, some aquatic forms (e.g., temnospondyls) could survive in lakes, even if terrestrial tetrapods were largely absent; e.g., the Nagold Valley of Germany (paleolatitude 13.2/21.0°N) (Schoch, 2011). However, terrestrial species could survive in somewhat higher latitudes with Ta < 30 °C, e.g., Rügenwalde (Darłowo) borehole of Poland (paleolatitude 16.8/28.6°N) (von Huene, 1942) (Fig. 3).

After the rapid warming, many species that originated at lower latitudes disappeared from their areas of origin, but some species appear to have survived in cooler, higher latitude areas, e.g., *Proterosuchus yuani* in Xinjiang (Young, 1936) and *Prolacerta broomi* in Antarctica (Spiekman, 2018). Indeed, Early Triassic warming likely made the mid-high latitudes more inhabitable for tetrapods, with higher-latitudes areas such as Australia and Antarctica potentially serving as refugia for taxa formerly found at lower latitudes (Cosgriff et al., 1982; Fröbisch et al., 2010; Romano et al., 2020; Whitney and Sidor, 2020). During the cooler phases of the Early Triassic, the low latitudes were likely more amenable, and locally extirpated tetrapods could migrate back, as evidenced by the Olenekian footprints from Italy and Poland (Brusatte et al., 2011; Petti et al., 2020). So, changes in low-mid latitude tetrapod faunas could mirror temperature fluctuations.

5. Tetrapod gap: duration and geographic extent

A gap in the record of tetrapods in equatorial Pangea between the paleolatitudes of 30°N and 40°S was proposed as the consequence of rapid warming in the Early Triassic (Sun et al., 2012). Recently, the gap was disputed or suggested to be restricted to palaeolatitudes between 15°N and ~ 31°S (Bernardi et al., 2018; Allen et al., 2020; Petti et al., 2020; Romano et al., 2020). Here we will review the relevant fossil record and compare it to expected tetrapod distributions under hyperthermal conditions to discuss if the tetrapod gap existed, and its potential duration and geographic extent.

Tetrapod records are absent from equatorial Pangea during the Induan (Figs. 3, S1). In the southern hemisphere, the Early Triassic South American records were located at 30°/40°S, and the most northern Induan records include *Kenyasaurus mariakaniensis* from Kenya (paleolatitude: 42°/32°S) and *Aphaneramma kokeni* from Pakistan (paleolatitude: 41°/35°S) (Harris and Carroll, 1977; von Huene, 1920). In the northern hemisphere, the southernmost Induan tetrapod fossils are known from Germany (paleolatitude: 13.2°/21°N) and Poland (paleolatitude: 16.8°/29°N) (Schoch, 2011; von Huene, 1942) (Figs. 3, S1, Table S1).

If an arid zone existed in equatorial Pangea during the early Induan, a tetrapod gap separating the two hemispheres should be present when Ta > 35 °C. Based on climate models, the southern low latitudinal arid zone could have included regions with Ta > > 35 °C, a reasonable estimation based on high pCO2 values during the Permo–Triassic mass extinction (2507 + 4764/−1193 ppmv) (Winguth et al., 2015; Wu et al., 2021). This may have acted as a barrier for the exchange of tetrapods between two hemispheres for most of the Early Triassic (Liu et al., 2021).

However, this scenario would change if the local climates were humid. If equatorial areas had a tropical wet climate, even Ta = 36 °C would be not lethal for tetrapods because their highest temperature ≤ 40 °C and some modern tetrapods such as squamates can survive in such conditions (Clusella-Trullas et al., 2011). Some low latitudinal areas

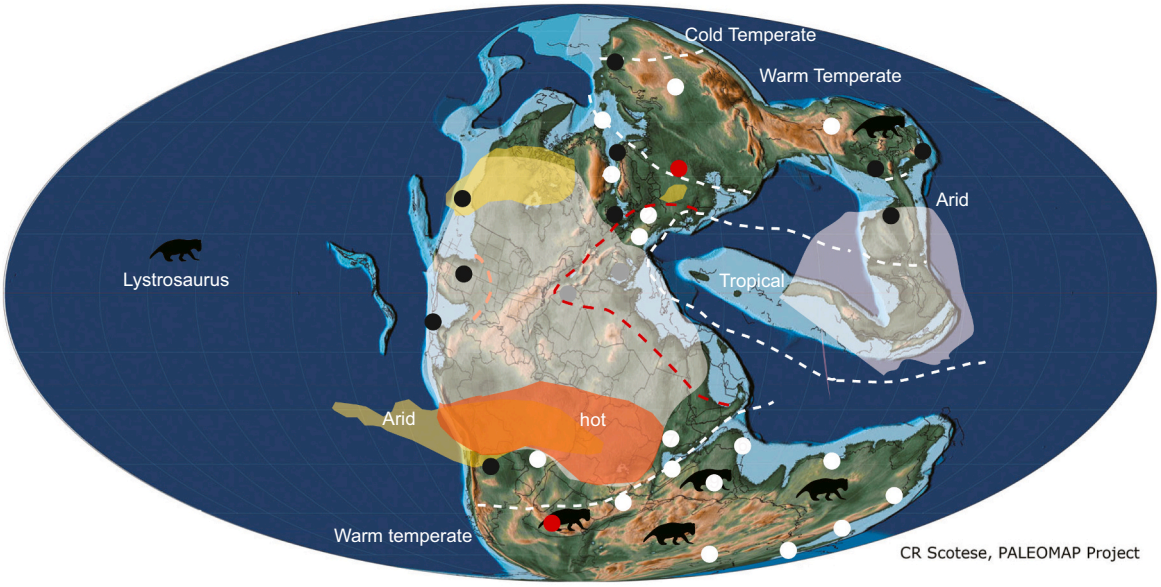

Fig. 3. The distribution of major Early Triassic tetrapod localities on a palaeogeographic reconstruction from Scotese (2014), showing the possible extent of the tetrapod gap (white shading). Yellow shading, arid; red shading, hottest area in Induan; estimated by Winguth et al. (2015). White dots, Induan; black dots, Olenekian (mostly Spathian); red dots, Induan and Olenekian. (Modified from Liu et al., 2021). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

must have transitioned from arid to wet during the early Spathian, because tetrapods, especially archosauriforms, were widely distributed in the late Olenekian (Spathian) and the tetrapod gap was refilled (Bernardi et al., 2018), as evidenced by the shared genera *Garjainia* and *Parotosuchus* in the EEPP and the Karoo Basin (Hancox et al., 2020; Shishkin et al., 2000). These changes in low-latitude precipitation may have prompted allopatric speciation in these areas (Saupe et al., 2019), driving the high biodiversity of the late Olenekian.

Based on the current fossil record, the tetrapod gap covers a wide area between ~30°N and ~ 40°S (white shading in Fig. 3), and lasted from the Induan to early Spathian. However, this range could be the result of preservation bias. The real geographic extent of the tetrapod gap likely varied at different temperatures. During the 'cool' phases, this geographic range could be a reasonable estimation based on the climate data and models, although the real range could be smaller. Additional fossil discoveries in low latitude regions could help to refine the boundaries of the gap, and offer a test of its hypothesized existence. During the hot phases (Griesbachian and near the Smithian/Spathain boundary, when Ts > 35 °C), the geographic extent of the gap could have expanded to a larger area, as exemplified by the fossil gaps within the Buntsandstein from central Europe (Brusatte et al., 2011; Romano et al., 2020; Schoch, 2011) (Figs. 1, 3).

The tetrapod gap should have existed in South China and Indochina during part of the Early Triassic. These areas were located in the tropical (wet) zone, and global warming is predicted to have had a strong impact here, as demonstrated in the marine record and by fossil plants (Feng et al., 2020; Sun et al., 2012). The close relationship between Lopingian tetrapods from Laos and North China, shown by dicynodonts and chroniosuchians, implies the existence of tetrapods in South China during the Lopingian (Liu, 2020; Liu and Chen, 2021; Liu et al., 2020; Angielczyk et al., 2021). Triassic tetrapods (marine reptiles) first appear in this area in the Spathian (Jiang et al., 2016); terrestrial tetrapods only appeared in the Anisian (Hu et al., 2011; Xing et al., 2013).

Based on this model, tetrapod diversity should have declined in North China after the rapid warming, but some species could have survived through the entire Early Triassic because North China was relatively wet and never too hot during this interval (Boucot et al., 2013; Roscher et al., 2011; Winguth et al., 2015). This inference contrasts with the absence of tetrapod fossils from the Liujiagou and Laowopu formations, although this could be partially due to their coarse lithology. Further work is needed to test this hypothesis.

6. Faunal changes during the early Triassic

Following the Early Triassic warming, the climate conditions for tetrapods were worse in the low latitudes, similar in the mid-latitudes, and better in the high latitudes. So tetrapods flourished in the mid-high latitudes, although their total diversity compared with the late Permian was decreased.

The Buntsandstein of central Europe documents low latitude tetrapod fossils, and it is among the most intensively investigated terrestrial strata of Early Triassic age (Romano et al., 2020). The fossiliferous horizons in Germany and Poland can be correlated to the cool phases of the Early Triassic (Fig. 1), and fit the previous gap model.

The EEPP and the Karoo Basin were both located near the boundary between the arid and warm temperate zones, the former dominated by aquatic taxa, the latter by terrestrial taxa. Russia lacks a good tetrapod record from latest Permian (Astashikha Member) (Davydov et al., 2020; Table S1), but preserves the most continuous tetrapod record of the Early Triassic, which can be divided into five or six assemblage zones (Davydov et al., 2020; Novikov, 2018).

In the Karoo Basin, tetrapod diversity slightly increased across the Permian-Triassic boundary (Fig. 1), particularly after the warming event (Viglietti et al., 2021). Several tetrapod clades show evidence of shortened life spans and smaller sizes in the Early Triassic (Huttenlocker and Botha-Brink, 2014; Canoville and Chinsamy, 2015; McHugh, 2015; Botha-Brink et al., 2016), with recent work attributing the small sizes of Triassic *Lystrosaurus* to high juvenile excess mortality (Botha, 2020). Tetrapod diversity decreased in the *Langbergia – Garjainia* SZ of *Cynognathus* AZ (Hancox et al., 2020), perhaps related to a warm climate phase. Even though the paleolatitude of the Karoo Basin was south of 47°S, the Early Triassic summer is predicted to be hot and dry, and many species show evidence of burrowing activity (Abdala et al., 2006; Bordy et al., 2011; Damiani et al., 2003; Fernandez et al., 2013; Groenewald, 1991). Indeed, burrowing behaviors evolved to be more complicated during the *Cynognathus* AZ (Groenewald et al., 2001).

Although also in the warm temperate zone, the Junggar and Turpan-Hami basins of Xinjiang were cooler than the Karoo Basin based on

climate modeling (Winguth et al., 2015), and the absence of tetrapod burrows perhaps reflects this difference. The known tetrapod record from this area is not as rich as that of the Karoo Basin, but species diversity increased from the Guodikeng Formation to the Jiucaiyuan Formation (Table S3, FigS2), and sedimentological and paleobotanical data suggest that environmental change across the Permo-Triassic boundary was less severe than in the Karoo (Yang et al., 2021). Histological data for Chinese specimens of *Lystrosaurus* show life history patterns broadly similar to species from South Africa, with evidence of rapid growth and lack of osteological maturity (Han et al., 2021). However, more frequent pauses in growth and larger body sizes in the Chinese populations suggest that although these individuals faced periodic environmental disruptions, these events did not cause juvenile mortality at the same scale as observed in South Africa (Botha, 2020; Kulik et al., 2021). Therefore, although *Lystrosaurus* was successful in the Early Triassic of South Africa, populations there may have been more stressed than in regions where more favorable conditions persisted such as Xinjiang. The longer survival of *Proterosuchus yuani* in China compared to *Proterosuchus fergusi* in South Africa also is consistent with cooler conditions in the Early Triassic of Xinjiang, assuming the climate preferences hypothesized for *Proterosuchus* by Liu et al. (2021) are correct.

During the Triassic, Antarctica and Australia (Tasmania and Sydney basins) changed from lands seemingly devoid of tetrapods to regions with tolerable winters, and tetrapods began to migrate into these areas. The Australian tetrapod fauna was dominated by temnospondyls (Cosgriff, 1984), representing littoral zone-estuarine habitats, although rare dicynodont records are also known (Thulborn, 1983; King, 1983; Rozefelds et al., 2011). The Antarctic fauna was dominated by terrestrial tetrapods, including relatively terrestrial temnospondyls (Peecook et al., 2018; Gee and Sidor, 2021), representing more inland conditions.

7. Conclusions

(1) The currently recognized late Permian tetrapod extinction occurred during a period of global cooling, and likely occurred before and/or over a longer time interval than the marine end-Permian mass extinction.
(2) Rapid warming in the Early Triassic is predicted to have resulted in extinctions and/or local extirpation of low latitude tetrapods, but the very limited fossil record from this region makes testing this hypothesis difficult. Warming is predicted to have had less negative impacts on the tetrapod diversity of the mid-latitudes, and promoted the success of tetrapods in high latitude regions.
(3) Based on the known fossil record, a tetrapod gap existed in central Pangea between ~30°N and ~ 40°S, lasting from the Induan to the early Spathian. Variations in the geographic extent of the gap likely coincided with climate fluctuations, with the gap covering a larger area during the hottest phases (Griesbachian and near the Smithian/Spathain boundary).
(4) A bimodal LDG existed for Early Triassic tetrapods, but the pattern is less certain for the late Permian because of the poor fossil record (sampling) at low latitudes.

Declaration of Competing Interest

The authors acclaim no conflict of interest.

Acknowledgements

We are grateful to ZHAO Qi and Michael Benton for initial discussion on this topic, TIAN Li and FENG Zhuo provided helpful literature. This work was supported by the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB26000000 to J.L.), the International Partnership Program of Chinese Academy of Sciences (132311KYSB20190010), and the U.S. National Science Foundation (EAR-1714829 to K.D.A.; EAR-1713787 to C.A.S.). CONICET (Argentina), the National Research Foundation (South Africa) and the DSI/NRF Centre of Excellence for Palaeosciences supported F.A.'s research.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.earscirev.2021.103886.

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