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Permo-Triassic tetrapods and their climate implications

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ABSTRACT

The narrow active temperature ranges of ectothermic tetrapods can be used as proxies for reconstructing paleoclimates. Here we deduce the climatic preferences of major Permo-Triassic tetrapod groups based on their known geographic distributions, the critical thermal limits of living tetrapods, and paleoclimate information from other sources. The resulting preferred temperature sequence of amniotes places most Triassic archosauromorphs at the high end of the spectrum, with preferred temperatures over 32 °C in some cases, followed by captorhinids, pareiasaurs, procolophonids, cynognathian cynodonts, dicynodonts (excluding *Lystrosaurus*), *Proterosuchus fergusi,* and finally *Lystrosaurus* at the lowest preferred temperature. The poleward distribution of Permian *Lystrosaurus* marks the border of cool temperate climates, whereas Triassic *Lystrosaurus* delineates the border of the arid zone. Most temnospondyls indicate the availability of perennial water sources. Captorhinids and pareiasaurs preferred dry climates, whereas dicynodonts preferred wetter conditions. Based on current evidence, central Pangea transitioned from an arid zone to a tropical zone during the late Olenekian.

1. Introduction

The spatial distribution of modern amphibians and reptiles is controlled by the physical environment, especially temperature and precipitation. These tetrapods are active in the typically narrow temperature range between their critical thermal minimum and maximum, and prefer habitats with ambient temperatures close to their preferred temperature (Vitt and Caldwell, 2014). The availability of food sources is also important; thus herbivore distributions are strongly influenced by plants, whose ranges are also controlled by temperature and precipitation. Therefore, the record of ectothermic tetrapods has the potential to serve as a climate proxy. Assuming the thermal tolerances of fossil amphibians and reptiles were similar to those of their living relatives, their distributions can be used as indicators of paleoclimate. For example, fossil crocodilian distributions have been used as an important indicator of the boundaries of the warm temperate zone, by analogy with the range of the extant American alligator (Boucot et al., 2013; Markwick, 1994).

To be a paleoclimate indicator, the ambient temperature and/or moisture requirements of a specific fossil tetrapod need to be inferred. From the late Permian to the Early Triassic, the Earth changed from a cool world to a hothouse (Chen et al., 2013; Chen et al., 2016; Chen et al., 2020; Joachimski et al., 2019; Sun et al., 2012); concomitantly, tetrapod faunal assemblages underwent dramatic changes (Bernardi et al., 2018; Bernardi et al., 2017; Romano et al., 2020). After the abrupt warming of the latest Permian, tropical temperatures surpassed the critical thermal maximum of most tetrapods, and the low latitudes switched from areas of high biodiversity to one essentially barren of tetrapods (Romano et al., 2020; Sun et al., 2012). In contrast, the high latitudes, where the lowest temperatures in the late Permian were below the critical thermal minimums of most tetrapods, hosted diverse Early Triassic tetrapod assemblages, and may have served as a refuge from higher temperatures elsewhere (Fröbisch et al., 2010; Romano et al., 2020; Whitney and Sidor, 2020). Considering the profound alteration of global temperature and latitudinal climate gradients during the Permo-Triassic transition, comparison of Permian and Triassic tetrapod distributions can potentially provide important climate information. Therefore, we seek to deduce the climate preferences of the Permo-Triassic

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tetrapods from their geographic distributions and other sources of paleoclimate data.

Abbreviations: AZ, Assemblage Zone; CT_{max}, critical thermal maximum; CT_{min}, critical thermal minimum; MAP, mean annual precipitation (mm y^{-1}); MAT, mean annual air temperature (°C); T_{cold}, temperature of coolest month; T_{amb}, ambient temperature, T_{hot}, temperature of warmest month; T_{max}, maximum temperature; T_{min}, minimum temperature; T_{pref}, preferred temperature, T_{sea}, annual mean seawater surface temperature.

2. Background and methods

Boucot et al. (2013) reconstructed Permian and Triassic "paleo"–Köppen Climate Belts using lithologic indicators of climate such as coal, evaporite, and glacial deposits. Their reconstruction has the arid zone spanning all of central Pangea, in contrast to wetter tropical conditions for western Pangea (mostly USA today) proposed by others (e.g., Roscher et al., 2011; Nowak et al., 2020). In the recent modified version of Köppen Climate Belts, the criteria for the arid zone are: if more than 70% of precipitation falls in the summer half of the year and MAP<20MAT + 280, or more than 70% of precipitation falls in the winter half of the year and MAT<20MAT, or neither half of the year has 70% or more of precipitation and MAP<20MAT + 140. The tropical zone is characterized by $T_{cold} \geq 18$ °C, the temperate zone is characterized by $0 < T_{cold} < 18$ °C & $T_{hot} > 10$ °C, the cold zone is characterized by $T_{hot} > 10$ °C & $T_{cold} \leq 0$ °C, and the polar zone is characterized by $T_{hot} \leq 10$ °C (Beck et al., 2018).

Nowak et al. (2020) recently reconstructed Wuchiapingian to Ladinian vegetational biomes based on paleofloras. They utilized ten biomes of Ziegler (1990), with the warm temperate biome defined by the daily minimum temperature of the coolest month above freezing, the cool temperate climate defined as having at least four months with an average daily temperature above 10 °C, and the cold temperate climate defined as having at least one month with an average daily temperature above 10 °C.

Both climate zonation schemes provide the general climate framework we used to reconstruct the climate preferences of the fossil tetrapods, although we also made a small number of additional modifications. Boucot et al. (2013) provided an Artinskian–Lopingian paleoclimate map in which the climate zone of the North China Block is ambiguous because of indicators for both humid and dry conditions. Checking their original data, evaporites existed in the Lopingian of the North China Block, indicating arid climates; accordingly the North China Block is here considered as an arid zone during the Lopingian. To obtain estimates of climate on more local scales during the Permian and Triassic, we also compiled oxygen isotope data from conodont apatite, brachiopod calcite, carbonates and vertebrate apatite (Arefiev et al., 2015; Chen et al., 2013; Chen et al., 2016; Chen et al., 2020; Gastaldo et al., 2020a; Gastaldo et al., 2020c; Rey et al., 2016; Sun et al., 2012). We estimated local mean annual precipitation using $\delta^{13}C$ values from the calcite and organic matter in paleosols (Gastaldo et al., 2020a; Gastaldo et al., 2020b; Tabor et al., 2017).

The critical thermal minimum of modern amphibians is generally 0–5 °C, and 5–10 °C for modern reptiles, whereas the critical thermal maximum is 33–37 °C for modern amphibians and 40–44 °C for modern reptiles (Bennett et al., 2018) (Fig. S1). Because the critical thermal minimum is usually higher than 0 °C for ectothermic tetrapods, their distribution indicates the spread of the warm temperate zone. The absence of fossil tetrapods in Early Triassic low latitudes (Allen et al., 2020) may be the result of sampling bias (Benson and Upchurch, 2013; although see Brocklehurst et al., 2017), but it could also indicate that the extreme high temperature surpassed the critical thermal maximum of tetrapods here.

However, modern ectothermic tetrapods can avoid harsh surface air temperatures (hot or cold) by seeking refuge underground or in water. Therefore, they can survive in areas where the extreme temperatures greatly exceed their critical thermal limits; e.g., *Rana amurensis* occurs in the Arctic Circle (Vitt and Caldwell, 2014). Permo-Triassic tetrapods are known to have made burrows, a behavior which is often interpreted as contingent for survival in harsh climate regimes (Botha-Brink, 2017; Krummeck and Bordy, 2017; Liu and Li, 2013; Sidor et al., 2008; Whitney and Sidor, 2020; Smith et al., 2021) . This kind of behavior may decrease our ability to judge the temperature range based on tetrapod distributions, but the abundance of burrows also may be a good indicator of a harsh climate, especially when associated with distinctive lithofacies that suggest a similar interpretation (Smith et al., 2021).

3. Results and discussion

During the Lopingian and Early Triassic, the major tetrapod groups include Temnospondyli, Captorhinidae, Pareisauria, Procolophonidae, Archosauromorpha, and Therapsida (Dicynodontia, Gorgonopsia, Therocephalia, Cynodontia). Their temporal ranges within this period and those of some major subclades are plotted in Fig. 1.

3.1. Temnospondyls

Modern amphibians have lower critical thermal minimums than modern reptiles, so currently amphibians have ranges that extend farther poleward than reptiles, although both groups reach their highest diversity levels in the tropics (Fritz and Rahbek, 2012; Roll et al., 2017). The Sydney Basin of Australia has produced lower Wuchiapingian or Capitanian temnospondyl fossils, and is the highest latitudinal late Permian tetrapod occurrence currently known (Warren, 1997) (Fig. 2, Locality 1). These fossils show that temnospondyls had more poleward distributions than other tetrapods, suggesting that Permian amphibians

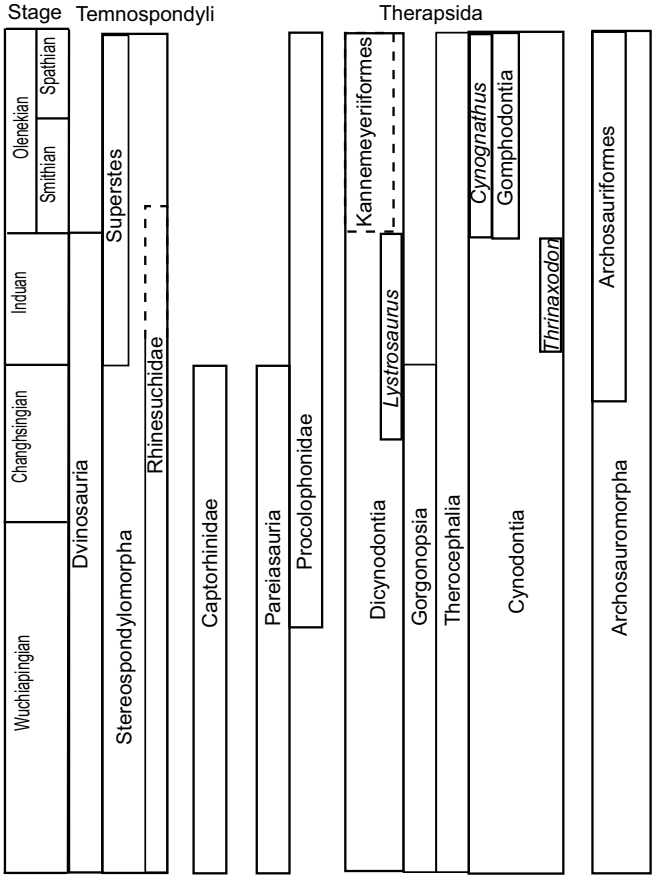

Fig. 1. Temporal range chart of major tetrapod clades from Lopingian to Early Triassic.

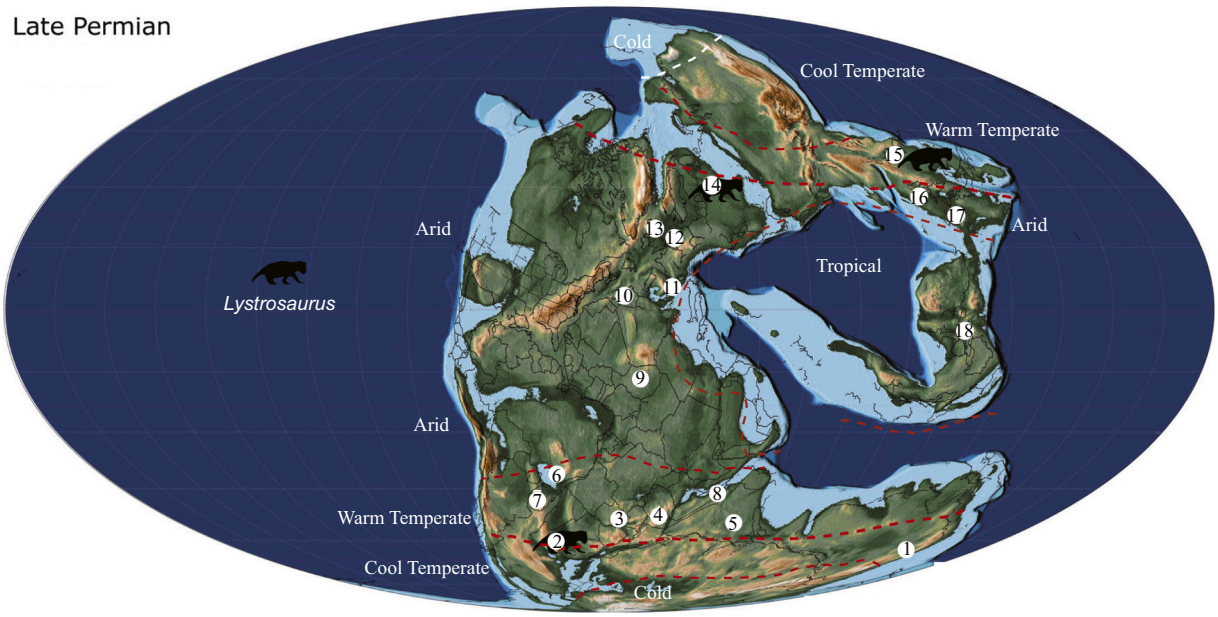

Fig. 2. Major Lopingian tetrapod localities and the paleoclimate zones projected on a palaeogeographic reconstruction from Scotese (2014). Localities: 1, Sydney Basin, Australia; 2, Karoo Basin, South Africa; 3, Zambia & Zimbabwe; 4, Malawi & Tanzania; 5, Pranhita-Godavari and Satpura basins, India; 6, Paraná Basin, Brazil; 7, Uruguay; 8, Madagascar; 9, Niger; 10, Morocco; 11, Italy; 12, Germany & Poland; 13, Scotland; 14, Urals, Russia; 15, Junggar Basin, China; 16, Alxa Block, China; 17, Ordos Basin, China; 18, Laos.

also had a lower critical thermal minimum than contemporary amniotes. Some fossil temnospondyls have been found in burrow structures (Fernandez et al., 2013; Hembree et al., 2004), suggesting they may have used such shelters to survive in areas with temperatures below 0 °C. However, the Permian temnospondyls from the Sydney Basin existed during the Permian warm phase (Chen et al., 2013), so this basin could have been closer to, or even within, the warm temperate zone at that time.

Because large bodies of water have lower temperatures than land at the same latitude, fossil tetrapods from the hottest areas during the Induan and Smithian (early Olenekian) are mostly aquatic tetrapods, especially temnospondyls, e.g., in the region between 41 and 46°S

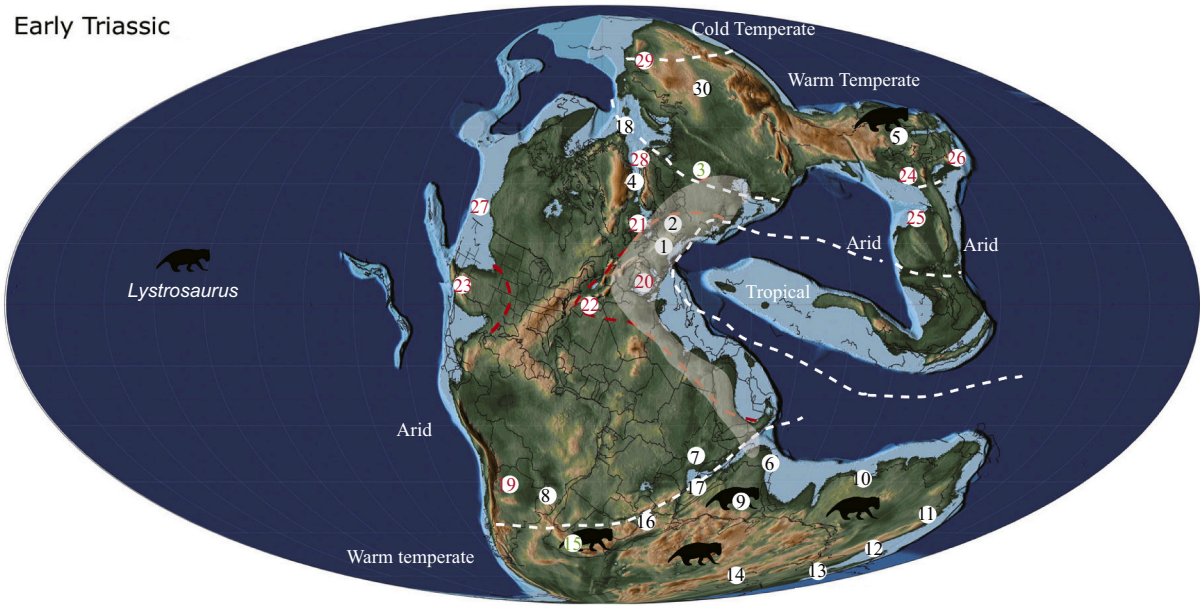

Fig. 3. Major Early Triassic tetrapod localities and the paleoclimate zones projected on a palaeogeographic reconstruction from Scotese (2014). White lines are the borders of different climate zones during Induan & Smithian, red lines are the inferred expansion of tropical climate during the Spathian. Grey shading indicates possible route for tetrapod migration. 1, southern Germany; 2, Poland; 3, Urals, Russia; 4, Greenland; 5, Junggar Basin, China; 6, Pakistan; 7, Kenya; 8, Paraná Basin, Brazil; 9, India; 10, Western Australia; 11, Queensland, Australia; 12, Sydney Basin, Australia; 13, Tasmania; 14, Antarctica; 15, Karoo Basin, South Africa; 16, Mozambique; 17, Madagascar; 18, Svalbard; 19. La Rioja, Argentina; 20, Italy; 21, UK; 22, Morocco; 23, western USA; 24, North China; 25, South China; 26, Japan; 27, British Columbia, Canada; 28, Norway; 29, Sakha, Russia; 30, Evenk, Russia. Numbers in black, Induan; in red, Olenekian; in green, Induan & Olenekian. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Western Australia, Madagascar, Kenya, Pakistan), between 13 and 31°N (central Europe, South Urals, and Greenland) (Fig. 3). Because of the dominance of temnospondyls and the diversity of reptiles in these areas, water temperatures most likely remained below 35 °C and maximum air temperature should have been less than 40 °C; so MAT should be less than 30 °C based on modern climate data for arid regions (Harris et al., 2014). This estimation may be applied to the cases of Lopingian low latitude tetrapod faunas, e.g., those in Morocco and Niger.

Although some temnospondyls could survive in cool climates, some if not most temnospondyls probably preferred a warm environment (higher T_{pref}), especially members of Dvinosauria and Superstes based on their distribution (Eltink et al., 2019; Marsicano et al., 2021). Stereospondylomorpha is known almost exclusively from low latitudes in the Permian, with the exception of Rhinesuchidae, which originated in the tropics (Cisneros et al., 2015), but dispersed to high latitudes in the Captitanian, a relatively warm period (Marsicano et al., 2017). Two proximal outgroups of Superstes existed in the warm temperate zone of Gondwana, but during the warm early Wuchiapingian (Eltink et al., 2019). So their preferred temperatures are suggested as ~20 °C.

3.2. Amniotes

Three major herbivorous tetrapod groups (captorhinids, pareiasaurs, and dicynodonts) lived during the Lopingian. Three herbivorous clades dominated in the Early Triassic as well: the dicynodont *Lystrosaurus*, procolophonids, and the gomphodont *Langbergia*.

Captorhinids preferred hot and dry climates, based on their occurrence primarily in the low-latitude arid zone (MAT>20 °C)(Bernardi et al., 2017), with a few exceptions from the Kundaram Formation of India (Kutty, 1972), the Madumabisa Mudstone formations of Zimbabwe (Gaffney and McKenna, 1979) and Zambia (Gow, 2000), and the *Tropidostoma* – *Gorgonops* Subzone of the *Endothiodon* AZ of the Karoo Basin (Modesto and Smith, 2001; Day and Smith, 2020). Most of these exceptions are early–middle Wuchiapingian in age (Bandyopadhyay and Ray, 2020; Sidor et al., 2014; Day and Smith, 2020), a warm period of the Permian (Chen et al., 2013), and it is noteworthy that they are rare components of the fauna in each case. Their preferred temperatures should be higher than 20 °C. The distribution of captorhinids also indicates a relatively high CT_{min}, corresponding to difficulty in surviving in a cool climate.

Pareiasaurs had a wider distribution than the captorhinids. They were relatively abundant in the arid zone (including the Urals, the Ordos Basin, and Morocco, less so in Scotland), present as a subordinate faunal component in the south warm temperate zone (South Africa and Brazil), and absent in the north warm temperate zone and tropical wet zone. Their distribution generally correlates with the distribution of conifer and ginkgophyte woodlands (Bernardi et al., 2017), and they may have preferred a hot and dry climate. This interpretation contrasts with some previous suggestions that pareisaurs were semi-aquatic (e.g., Ivakhnenko, 1987, 2001; Gubin, 1989; Kriloff et al., 2008), but it is consistent with geochemical indicators of habitat preference (Canoville et al., 2014; Rey et al., 2020), aspects of skeletal morphology like the relatively upright limb posture of *Bunostegos* (Turner et al., 2015), and taphonomic evidence of preservation in terrestrial conditions (Benton et al., 2012).

The procolophonids were important primary consumers in Gondwana in the Early Triassic. This clade originated in the Wuchiapingian and diversified in Changhsingan (Cisneros, 2008), as confirmed by the Lopingian age of *Pintosaurus* (Ernesto et al., 2020), and it spread to both hemispheres by the end of the Permian. Their existence in Antarctica during the Induan indicates the lineage could live in both the arid and warm temperate zones (MAT>10 °C). However, their activity range may be narrower because some widespread species made burrows (Groenewald, 1991), an adaptation that can mediate the impact of extreme climate.

The abundance of dicynodonts in the Lopingian was linked to the flourishing of ferns and sphenophytes (Bernardi et al., 2017), which indicated a locally wet environment, even in arid zones. Dicynodonts can be abundant in the arid zone (e.g., the Ordos Basin), where ferns and sphenophytes were present (Nowak et al., 2020), but they were less diverse than in the warm temperate zone (Liu, 2019; Sennikov and Golubev, 2017). Considering this, we infer that they had lower T_{pref} and CT_{min} (~5 °C) and higher water requirements than the pareiasaurs and the captorhinids. We estimate their MAT as ~10–20 °C. Most dicynodont species disappeared in the Karoo Basin, one of the coolest tetrapod-bearing regions in the late Permian, by the top of the *Daptocephalus* AZ (Viglietti et al., 2021). An estimated MAT of 10 ± 4 °C for the upper *Daptocephalus* AZ (Gastaldo et al., 2020c) fits this scenario and indicates that the Karoo Basin could have occasionally shifted into a cool temperate zone during the late Changhsingian. This is further confirmed by the coexistence of Changhsingian fossil plants indicative of warm and cool temperate biomes in the Balfour Formation of the Karoo Basin (Gastaldo et al., 2015; Nowak et al., 2020).

Permian *Lystrosaurus* had a similar geographic range to that of Dicynodontia as a whole, ranging from the Karroo Basin to the Junggar Basin, but fossils are extremely rare in the low latitudes (Bernardi et al., 2017; Fröbisch, 2009). Only a few specimens from eastern Europe establish the presence of *Lystrosaurus* in the Permian arid zone (Surkov et al., 2005; Davydov et al., 2020) (Fig. 2, locality 14), and the genus is unknown from the tropics. This pattern suggests that *Lystrosaurus* should have a lower T_{pref} than other dicynodonts. Another line of evidence supporting this is the burrowing behavior proposed for *Lystrosaurus* (Bordy et al., 2011; Botha-Brink, 2017) because in modern squamates, burrowing species have a mean T_{pref} that is 5 °C lower than non-burrowing species from the same habitats (Clusella-Trullas et al., 2011).

During the upper *Daptocephalus* AZ, *Lystrosaurus* survived longer than other dicynodonts under cool conditions at the end Permian of the Karoo. Although the minimum temperature excursion on the curve is not dramatically lower than the temperatures when dicynodonts were more diverse, *Lystrosaurus* is the only dicynodont to persist throughout the cool interval (Viglietti et al., 2021) (Fig. 4). This resilience can be explained by a lower CT_{min} and/or burrowing or hibernation behavior of *Lystrosaurus* (Bordy et al., 2011; Botha-Brink, 2017; Whitney and Sidor, 2020). In the Early Triassic, *Lystrosaurus* is frequently said to have a global distribution, but in reality it has been discovered only within the warm temperate zone south of 55°S and north of 40°N (Fröbisch, 2009; Romano et al., 2020) (Fig. 3), a pattern that has been extended recently by the identification of *Lystrosaurus*-like fossils in Mozambique (Araujo et al., 2020). This Triassic distribution corroborates the hypothesis that *Lystrosaurus* had a low preferred temperature.

The geographic distribution of *Lystrosaurus* also supports the hypothesis that it was ectothermic (Benton, 2020), rather than endothermic as suggested by apatite oxygen isotope values (Rey et al., 2017). The lower boundary of the thermal neutral zone of endotherms is generally high (>20 °C) (Bennett et al., 2018), which would have provided better tolerance to higher temperatures in lower latitude regions of Pangea. The near-complete absence of *Lystrosaurus* from this region is suggestive of a physiology attuned to more moderate temperatures, although other factors, such as the absence of preferred food sources, may also be at play.

Based on its occurrences in both the northern and southern hemispheres, *Lystrosaurus* dispersed across the equator in the Permian. There was a wetter zone along the east coast of Pangea (Boucot et al., 2013), where ferns and sphenophytes grew (Nowak et al., 2020), and this may have served as a possible dispersal corridor for many Permian tetrapods, including *Lystrosaurus*. Because T_{sea} at the equator is estimated to be ~25 °C (Chen et al., 2020), the highest temperature along this dispersal corridor is estimated as ~30 °C; so the CT_{max} of *Lystrosaurus* should not be much above 30 °C, and less than 38 °C (based on values for burrowing squamates). This estimate is consistent with its absence in the hot and dry region of southern Brazil during the Early Triassic, where *Procolophon trigoniceps* dominated (Dias-da-Silva et al., 2017; Silva-Neves et al.,

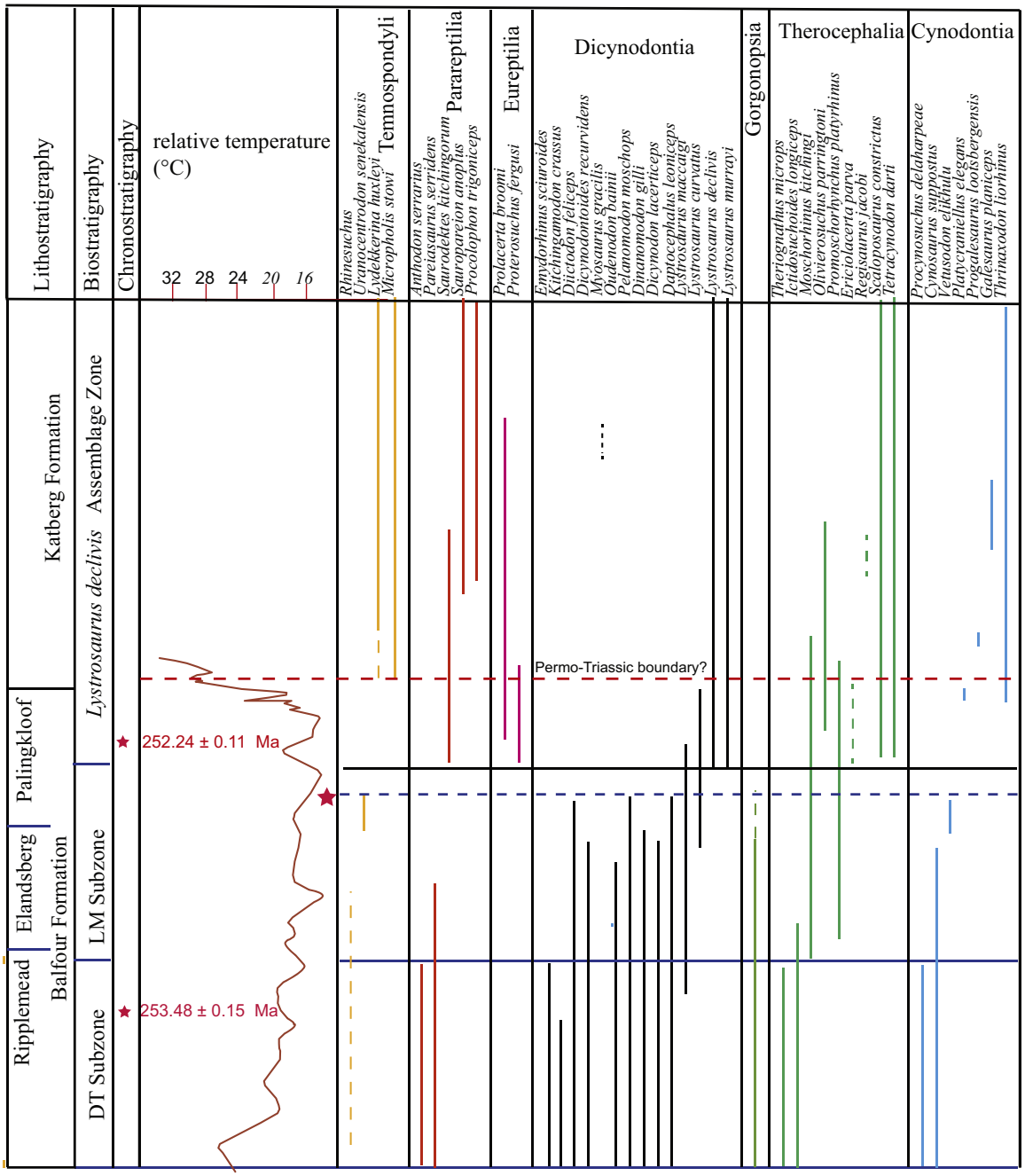

Fig. 4. Chart showing a composite section for part of the Balfour and Katberg formations, the stratigraphic position of two absolute dates (Gastaldo et al., 2015; Gastaldo et al., 2020b), a paleotemperature curve from $\delta^{18}O$ apatite records from Meishan, China (Chen et al., 2016), and the stratigraphic distribution of tetrapods from the upper part of the *Dicynodon–Theriognathus* Subzone to lower part of the *Lystrosaurus declivis* Assemblage Zone (Botha et al., 2020; Botha and Smith, 2020; Viglietti, 2020; Viglietti et al., 2021). Solid lines indicate reliable stratigraphic and temporal ranges; broken lines indicate uncertain ranges. The large red star indicates the upper boundary of the *Daptocephalus* AZ proposed by Viglietti et al. (2016). The position of the Permian-Triassic boundary follows Gastaldo et al. (2020b). Abbreviations: DT, *Dicynodon–Theriognathus*; LM, *Lystrosaurus maccaigi-Moschorhinus*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2018). Increasing temperatures and aridity in low latitude Pangea during the Early Triassic likely cut off this dispersal corridor, and we predict that there was no exchange of *Lystrosaurus* between the two hemispheres in the Early Triassic.

During the Early Triassic, warming in the Karoo Basin is predicted to have been greater than the 6–10 °C estimated for the tropics (Roscher et al., 2011), and was proposed to be 17 ± 5 °C based on isotopic records from tetrapod apatite (Rey et al., 2016), so the MAT≈18–36 °C using MAT = 10 ± 4 °C from the upper *Daptocephalus* AZ. If correct, the Karoo Basin would no longer fall in the temperate zone, but it is important to note that the upper end of this range (36 °C) is much higher than the estimated temperatures from Karoo calcite nodules (maximum mean temperatures between 15 °C and 20 °C) (Viglietti et al., 2013). Based on the above data and the tetrapod fauna, MAT would have been about 20 °C in the Karoo Basin during the early Induan. Accordingly this basin would have been situated near the equator-ward border of the temperate zone, as corroborated by other data sources (Boucot et al., 2013; Nowak et al., 2020). The mean daily maximum temperature may have been higher than 35 °C in the Karoo Basin, but *Lystrosaurus* and coeval tetrapods could have avoided these harsh conditions by sheltering

underground, as evidenced by abundant Early Triassic tetrapod burrow casts (Bordy et al., 2011; Damiani et al., 2003; Groenewald, 1991).

Late Permian carnivore guilds were dominated by theriodont therapsids (i.e., gorgonopsians, therocephalians, and cynodonts), although theriodonts may have been less successful at low latitudes, and our picture of the composition of carnivore guilds may be biased by not considering ichnofossils (Bernardi et al., 2017). Among the carnivorous therapsids, therocephalians thrived in both arid and warm temperate zones of the late Permian (Huttenlocker, 2014; Liu and Abdala, 2020; Sennikov and Golubev, 2017), but only a few therocephalians survived until the end-Permian (Sennikov and Golubev, 2017; Viglietti et al., 2021) (Figs. 4, 5). Most Early Triassic therocephalians had short temporal ranges and included three medium-sized akidnognathids (*Moschorhinus*, *Olivierosuchus*, *Promoschorhynchus*); only the small baurid *Scaloposaurus* and possibly *Tetracynodon* lasted longer in the *Lystrosaurus declivis* AZ (Botha and Smith, 2020; Viglietti et al., 2021) (Fig. 4). Thus, late Permian therocephalians seem to have been adapted to or preferred cooler climates. Their noteworthy decline in diversity and abundance in the earliest Triassic of the Karoo Basin may have been triggered by competition with successful cynodonts such as *Thrinaxodon*, a small-sized, burrowing faunivore with a similar ecological niche, in the unfavorable hot and dry Early Triassic climate. Indeed, Roopnarine and Angielczyk (2012) predicted that the high relative diversity of small faunivores in the Early Triassic Karoo likely resulted in intense interspecific competition for food resources and increased vulnerability to extinction. Therocephalians may have fared better in Antarctica (Huttenlocker and Sidor, 2012), consistent with their predicted preference for cooler climates.

Late Permian cynodonts appear to have preferred the warm temperate zone. This helps to explain the temporary absence of cynodonts from the Karoo Basin during the coolest phase of the Changhsingian, when the Karoo likely shifted to cool temperate zone climates (Fig. 4). The abrupt appearance of several cynodonts (i.e., *Progalesaurus, Galesaurus, Thrinaxodon, Platycraniellus*) in the *Lystrosaurus declivis* AZ indicates a rapid return as climates warmed, suggesting a migration from Changhsingian warmer regions.

Body sizes of eutheriodont therapsids significantly decreased during the Induan, a proposed example of the Lilliput effect (Huttenlocker, 2014). The decrease in size, which is observed in most faunal components of the *Lystrosaurus declivis* AZ, could be the result of high temperatures, low productivity ecosystems, and/or demographic pressures like high juvenile mortality causing changes in growth/life history (Botha-Brink et al., 2016).

Phylogenetic relationships imply that Cynognathia originated in Gondwana near the Permo-Triassic boundary (Lukic-Walther et al., 2019). Therefore, early diverging taxa like *Cynognathus* likely evolved in the warm climate of the Olenekian-Anisian (Hancox et al., 2020, Lukic-Walther et al., 2019; Liu et al., 2018; but see Ottone et al., 2014). *Cynognathus* shows evidence of a faster growth rate and higher energy demands (Botha and Chinsamy, 2000), suggesting that it had a relatively high T_{pref}. The oldest fossils of Diademodontidae are from the Anisian (Abdala, 2021; Hancox et al., 2020), but the clade is predicted to have originated in the Olenekian, as the earliest record of Neogomphodontia, the sister clade of diademodontids, is late Olenekian (Hendrickx et al., 2020). However, *Diademodon* was restricted to Gondwana and did not spread to Laurasia during the Anisian. This absence may stem from the absence of its preferred plants in Laurasia. For example, the *Dicroidium* flora was almost endemic to Gondwana (Abu Hamad et al., 2008; Anderson et al., 1999), and if an association existed between this flora and *Diademodon*, it could help explain the latter taxon's distribution. *Diademodon* apparently did not compete with kannemeyeriiform dicynodonts because they successfully coexisted for an extended time interval in Gondwana (Hancox et al., 2020; Singh et al., 2021). Furthermore, it is interesting to note that the most prevalent eutheriodont primary consumer lineages differed between Laurasia and Gondwana in the Anisian (Liu and Abdala, 2015). In Russia and China that role was dominated by bauriid therocephalians, whereas the early record of gomphodont cynodonts constitutes one of the major successes in the history of this lineage in Gondwana. This pattern suggests persistent differences in warm temperate faunas from both hemispheres.

Triassic tetrapod faunas were characterized by the presence of archosauriforms as apex predators (Sennikov, 1996; Sues and Fraser, 2010). Lopingian footprint records suggest that many Permian archosauromorph species lived at low latitudes (e.g., central Europe,

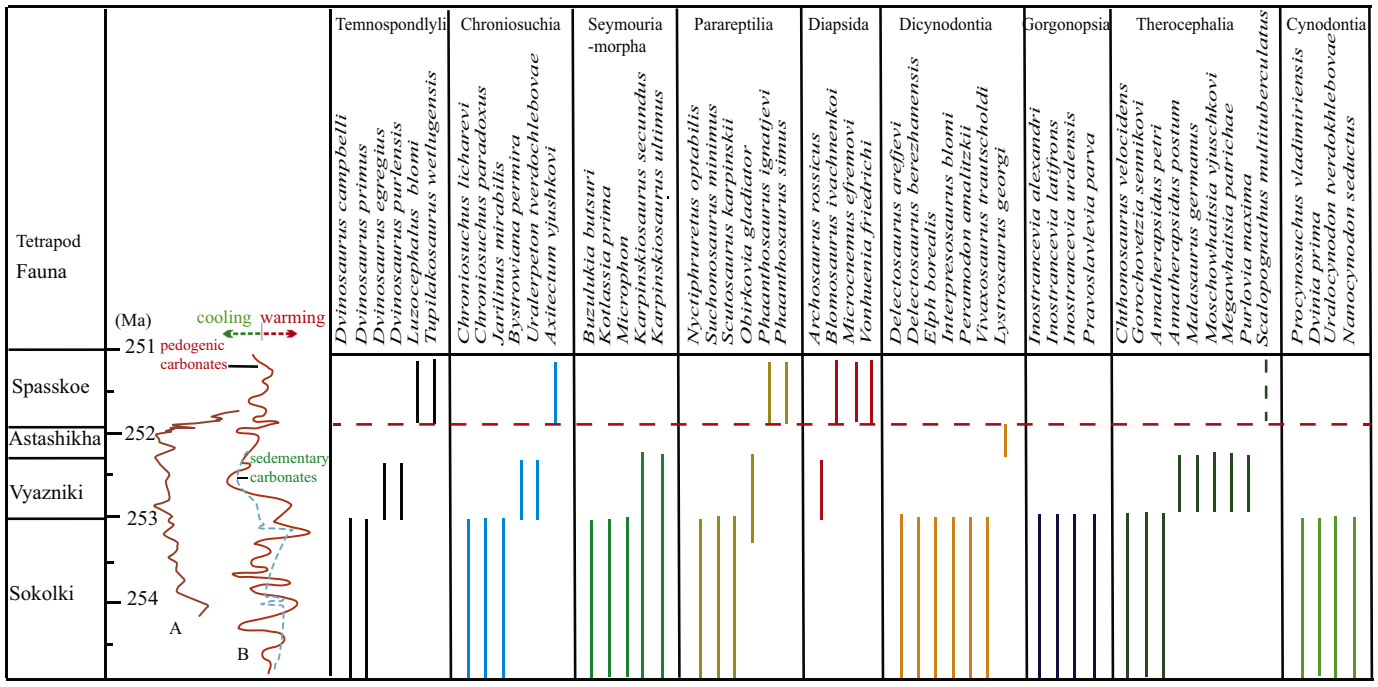

Fig. 5. Chart showing Changhsingian to Induan tetrapod faunas from eastern Europe, modified from Sennikov and Golubev (2017) and Davydov et al. (2020), with oxygen isotopic curves from tropical conodont apatite (A, Chen et al., 2016) and from carbonates of the Moscow Syncline (B, Arefiev et al., 2015).

Morocco) (Bernardi et al., 2017). In this arid region, MAT should have been higher than T_{sea} at the equator (MAT >25 °C). However, this clade displays evidence of wide temperature tolerances: species present in the cool phase of the Karoo Basin (Fig. 4) experienced conditions where T_{min} would have been low (~5 °C), whereas species in the low latitude arid zone would have experienced quite high temperatures ($T_{max} \approx 40$ °C). Some may have evolved higher metabolic rates (e.g., *Prolacerta broomi*, Legendre et al., 2016) and higher T_{pref}, allowing them to maintain higher activity levels in cooler areas such as the Karoo Basin, at the cost of requiring more food to survive. Their higher T_{pref} and reduced reliance on the external environment for thermoregulation could have given them a survival advantage as climates warmed in the Early Triassic. By contrast, some species, such as *Proterosuchus fergusi*, may have evolved to have a low T_{pref}, similar to that of *Lystrosaurus*. This was suitable for cool climates in the latest Permian but not for Early Triassic warmer climates. In the Karoo Basin, *Proterosuchus fergusi* went extinct soon after the rapid Early Triassic warming, wheras *Prolacerta broomi* thrived for a longer time (Botha and Smith, 2020; Viglietti et al., 2021). Many archosauromorph species also lived in higher latitudes during the Induan, such as *Prolacertoides jimusarensis*, and *'Chasmatosaurus' yuani* in Xinjiang (Young, 1936; Young, 1973), and *Prolacerta broomi* in Antarctica (Spiekman, 2018), potentially utilizing these regions as refuges from extreme temperatures at low latitudes, or expanding their ranges as conditions became more favorable at higher latitudes. The Antarctic individuals of *P. broomi* were larger than those from South Africa, as predicted by Bergmann's rule (Spiekman, 2018). A geographic range expansion towards lower latitudes is also apparent during the cool phase of the Induan/Smithian, evidenced by the Stryczowice tracksite of Poland (Brusatte et al., 2011; Ezcurra and Butler, 2018).

The more crownward clade Archosauriformes diversified and flourished from the late Olenekian onwards, with a distribution initially centered near the equator (Bernardi et al., 2018). To be successful in hothouse climates, archosauriforms would be required to alter their thermal tolerances towards a higher CT_{max} and T_{pref}. During the late Olenekian, 32 °C < T_{sea} < 36 °C (Sun et al., 2012), with MAT > 32 °C in low latitudes, some archosauriforms likely evolved T_{pref} > 32 °C, a comparatively high preferred temperature. As they spread to cooler areas, some species may have decreased their T_{pref}, but some likely increased their metabolic rate to maintain high body temperatures.

If central Pangea was positioned in the arid zone during the Early Triassic, wide daily tempertature fluctuations would be expected as in modern tropical deserts (>35 °C), with the highest temperatures near the equator reaching beyond the CT_{max} of tetrapods (>50 °C). In this scenario, there would be no available dispersal routes between the northern and southern hemispheres. However, some low latitude areas of central Pangea were sufficiently humid to support fossil plants (Nowak et al., 2020), and the tropical/arid border shifted westward during this period (Fig. 3), permitting dispersal. Gomphodont cynodonts probably migrated to Laurasia during the late Olenekian, where they are represented by the Chinese trirachodontids *Beishanodon* and *Sinognathus* (Abdala, 2021; Gao et al., 2010). In addition, Russia and South Africa share two late Olenekian genera: the archosauriform *Garjainia* and the temnospondyl *Parotosuchus*, the latter also known in Antarctica (Gower et al., 2014; Hancox et al., 2020; Novikov, 2018; Sidor et al., 2007). Both cases demonstrate that a dispersal corridor across central Pangaea existed in the Early Triassic.

During the late Spathian (~247.3 Ma), Triassic marine reptiles appeared in Chaohu, South China (~15°N) and soon spread worldwide (localities 23–28 in Fig. 3). Their major food source was fish and they were able to survive the heat of the Spathian, as seawater temperature in Chaohu is predicted to have been lower than 35 °C based on the CT_{max} values for fish (Bennett et al., 2018). This matches the temperature tolerances in modern aquatic reptiles, which have the highest T_{pref} (≈36 °C) (Clusella-Trullas et al., 2011).

An important caveat for our study is the fact that our results are based on a literal reading of the fossil record. However, geographic sampling of the Permo-Triassic fossil record is not even (e.g., Benson and Upchurch, 2013; Brocklehurst et al., 2017; Bernardi et al., 2018; Allen et al., 2020); higher latitude regions are more densely sampled than tropical and subtropical areas through most of this interval and some large geographic areas, such as North America in the Lopingian, have little to no known tetrapod fossil record. Therefore, it is possible that improved sampling would reveal records that would change our picture of the thermal tolerances of the Permo-Triassic tetrapods we considered. This potential bias is difficult to mitigate in our study because we are not concerned with the species richness of different geographic areas, which can be corrected using various sample standardization methods, but instead focus on the specific identities of the taxa that are present in different regions. More detailed considerations of the specific lithologies in which tetrapod fossils are preserved in different areas also might allow refinement of predicted environmental preferences (e.g., the identification of taxa that lived near water bodies in otherwise dry habitats), and is an area worthy of additional attention. Nevertheless, even at the relatively coarse scale of this study, our reconstructed thermal preferences yield interesting insights, such as the hypothesis that *Lystrosaurus* dispersal between the northern and southern hemisphere most likely occurred only in the Permian. This aspect of physiology deserves further attention when considering the impacts of environmental change on tetrapods during the Permo-Triassic extinction and subsequent recovery.

4. Conclusions

We investigated the preferred temperatures of major tetrapod groups from the Lopingian to the Early Triassic, using their observed geographic distributions and comparison with modern taxa. Some clades have narrow ambient ranges and can be used as climate indicators.

1. Temnospondyls likely tolerated lower temperatures than other tetrapods, and their distribution records should indicate the existence of perennial water sources.
2. We predict a spectrum of preferred temperatures for Permo-Triassic amniotes, with most Triassic archosauromorphs at the high end, followed by captorhinids, pareiasaurs, procolophonids, cynognathian cynodonts, dicynodonts (excluding *Lystrosaurus*), *Proterosuchus fergusi,* and finally *Lystrosaurus* at the low end of the spectrum.
3. Captorhinids and pareiasaurs preferred dry and warm climates, and captorhinids may have had a relatively high CT_{min}. Procolophonids had a wide active temperature range.
4. Dicynodonts lived in local humid conditions, with a lower critical thermal CT_{min} than pareiasaurs. *Lystrosaurus* may have had a lower CT_{min} and CT_{max} than other dicynodonts, which could have contributed to its survival during the latest Permian cold period.
5. The geographic distribution of *Lystrosaurus* was confined mostly to warm temperate climatic belts, although rare records (e.g., Russia) suggest that it may have had some presence in arid zones in the Permian.
6. Some archosauromorph species (e.g., *Proterosuchus fergusi*) may have evolved low CT_{min} (~5 °C) and low T_{pref}, whereas more crownward species appear to have preferred higher temperatures (T_{pref} > 32 °C).
7. East central Pangea appears to have had a wetter tropical, rather than arid climate during the late Olenekian, and likely served as a dispersal corridor for tetrapods during the Early Triassic.

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Declaration of Competing Interest

The authors declare no conflict of Interest.

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