Science Bulletin 68 (2023) 2523–2526

Contents lists available at ScienceDirect

Science Bulletin

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

Perspective

The end-Paleozoic great warming

Haijun Song [a,*], Christopher R. Scotese [b]

[a] State Key Laboratory of Biogeology and Environmental Geology, School of Earth Sciences, China University of Geosciences, Wuhan 430074, China
[b] Department of Earth and Planetary Sciences, Northwestern University, Evanston IL 60208, USA

According to the recent global mean surface temperature curve [1], the temperature continued to rise over a period of 45 million years at the end of the Paleozoic. The global mean temperature increased from 11.7 °C at 295 Ma at the beginning of the Permian to 32.7 °C at 250 Ma at the beginning of the Triassic, a warming of 21 °C, one of the most dramatic warmings in the Phanerozoic (Fig. 1a), which is referred to in this paper as the end-Paleozoic great warming (EPGW). Another significant warming event occurred in the mid-Cretaceous, when the global average temperature rose by 8.8 °C in 8 million years, reaching 28.2 °C. The other two warming events of similar magnitude occurred after cooling events such as the Hirnantian Ice Age and the Cretaceous-Paleogene impact winter. Although the warming magnitudes were large, they mainly started from low points and did not exceed 25 °C after the warming events (Fig. 1a). Other warming events with much smaller magnitudes include the early Cambrian, early Silurian, mid-late Silurian, Emsian, mid-Devonian, Frasnian, Devonian-Carboniferous, early Pennsylvanian, Carnian, Norian, end-Triassic, Toarcian, Oxfordian, early Cretaceous, Albian, earliest Paleocene, Paleocene-Eocene, and Oligocene (Fig. 1b).

In addition to the great warming events, there have been several great cooling events, namely the early Paleozoic, late Paleozoic, and Cenozoic great cooling events. The duration of these major cooling events ranged from 36 to 78 million years, with global mean temperature decreases of 11.2–16.5 °C (Table 1). These three major cooling events led to three well-known ice ages in the Phanerozoic, i.e., the Hirnantian Ice Age, late Paleozoic Ice Age, and late Cenozoic Ice Age [2].

The end-Paleozoic great warming had a major impact on climate and terrestrial vegetation. Ice episodically covered the Gondwana during the late Carboniferous-early Permian, with land glaciers reaching as far as 30°S [2]. Subsequently, glaciers gradually disappeared as temperatures rose, resulting in an ice-free Earth by the end of the Guadalupian (Fig. 2b). The warming trend enhanced the aridity of the Pangaea supercontinent by altering ocean currents. In addition, the drift of northern Pangea towards the arid climate zone and the closure of Rheic contributed to the global aridification trend during this period [3]. Evaporite covered 20.9% of the world's land surface in the early Permian and reached 46.3% in the Early Triassic, more than twice as much as in the early Permian (Fig. 2b). With different degrees of land aridification in different regions, the vegetation underwent a major shift from wetland biomes to seasonally dry biomes [4]. Aridification has also led to a dramatic reduction in the geographic extent of tropical coal forests (Fig. 2b).

The end-Paleozoic great warming culminated in the Triassic hothouse. The Early Triassic was the hottest period of the Phanerozoic with global mean temperatures exceeding 30 °C [1]. During the Early Triassic, surface seawater temperatures near the paleoequator exceeded 40 °C [5]. The extremely hot climate was associated with long-term high CO_2 concentrations in the Early Triassic [6]. The lethally hot climate led to the end of the Paleozoic evolutionary fauna era, prompting Modern evolutionary fauna to dominate the oceans since the Early Triassic [7]. The Early Triassic was one of the most anomalous periods of the Phanerozoic environment, with remarkable fluctuations in carbon, nitrogen, sulfur, calcium, and mercury isotopes, accompanied by widespread abnormal sedimentary deposits such as microbialites and ooids (see Ref. [8] and references therein).

The end-Paleozoic great warming had a strong impact on the oceans. Sea level rise in the early-middle Permian may be related to the EPGW [9]. Continued warming led to a consistent decline in dissolved oxygen levels in seawater (Fig. 2a). At the same time, the EPGW caused a decrease in the temperature gradient between the equator and the poles, from 48.5 °C in the early Permian to 21.9 °C in the Early Triassic (Fig. 2b), which contributed to weaker ocean currents and reduced oceanic oxygenation of the deep ocean. The decrease in dissolved oxygen levels in surface seawater and the weakening of ocean currents may have been an important cause of ocean deoxygenation in the late Permian-Early Triassic oceans (Fig. 2). Evidence from several geological proxies suggests that oceanic anoxia was widespread in the Early Triassic (Table S2 online). Sediments in the superocean Panthalassa changed from middle Permian red oxic chert to late Permian gray anoxic chert, and to Changhsingian-Early Triassic claystone [10]. In addition, high water temperatures can increase the solubility and thus the toxicity of certain compounds, including heavy metals such as cadmium, zinc and lead [11].

The impact of the EPGW on marine life was dramatic. Two rapid warming events around the Guadalupian-Lopingian and Permian-Triassic boundaries were closely associated with two mass extinction events [12]. Long-term warming in the Permian and earliest Triassic also led to declines in diversity and extinctions of cli-

* Corresponding author.
E-mail address: haijunsong@cug.edu.cn (H. Song).

https://doi.org/10.1016/j.scib.2023.09.009
2095-9273/

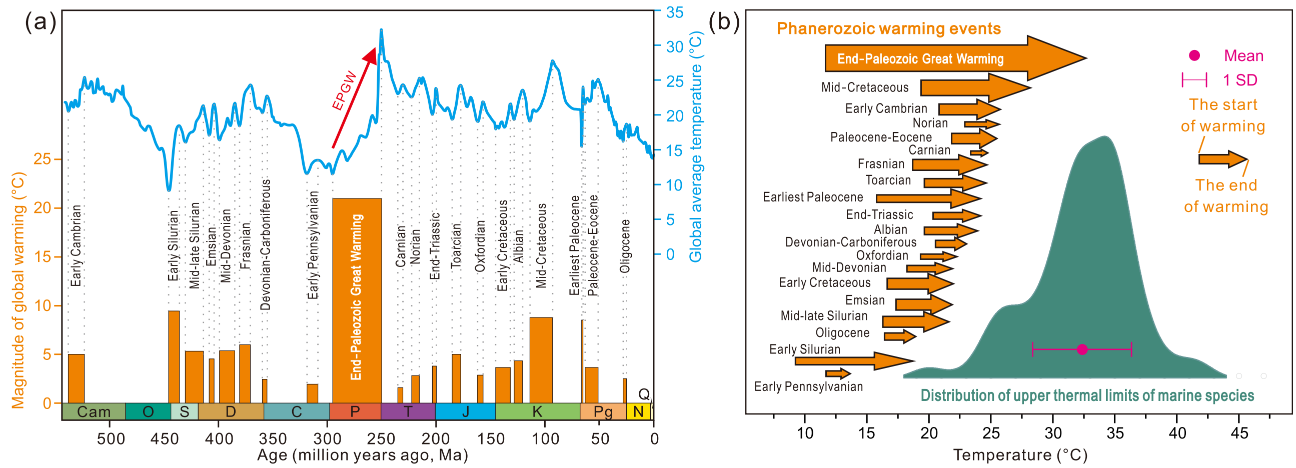

Fig. 1. Long-term global warming events in the Phanerozoic. (a) The curve of the global mean temperature and the magnitude of the warming events, data from Ref. [1]. (b) The start and end temperatures of warming events versus the distribution of upper thermal limits of modern marine species (data see Table S1 online).

Table 1
Major long-term climate events in the Phanerozoic. Paleotemperature data are from Ref. [1].[a)]

Major climate event	Start age (Ma)	End age (Ma)	Duration (Myr)	Magnitude (°C)
end-Paleozoic great warming	295	250	45	21.0
mid-Cretaceous great warming	114	93	21	8.8
early Paleozoic great cooling	522	444	78	−16.5
late Paleozoic great cooling	354	318	36	−11.2
Cenozoic great cooling	51	1	50	−11.5

a) Ma, million years ago; Myr, million years.

mate-sensitive clades such as rugose corals, fusulinoidean foraminifera, and gigantic bivalves (Fig. 2b). The body size of some marine animals, such as foraminifera, decreased with climate warming and ocean deoxygenation (Fig. 2b), as these two changes were more beneficial for smaller individuals. Evolutionary rates of marine invertebrates (extinction and origination rates) increased after the late-Paleozoic ice age (Fig. 2b). The synergistic effects associated with CO_2 release and warming, such as ocean hypoxia, ocean acidification, and sea level rise, may increase the extinction rate of marine species.

The greater the warming magnitude, the higher the peak temperature, and the greater the negative impact on organisms. Each species has an upper thermal limit. Once a species reaches its thermal limit, it can denature proteins (e.g., enzymes and carrier proteins), leading to cell death. The average upper thermal limit for modern marine animals is 32.4 ± 4 °C (Fig. 1b). Most warming events in the Phanerozoic reached the upper thermal limit for a number of marine species (Fig. 1b). Peak temperatures following the EPGW have exceeded the average upper thermal limit for modern marine species. The late Paleozoic ice age lasted for ∼50 million years [2] and organisms had adapted to this colder climate. Therefore, the warming that followed the late Paleozoic ice age would have had a greater negative impact on organisms. The magnitude and rate of warming exhibit variability across different intervals from the early Permian to the Early Triassic. It is therefore imperative to recognize the heterogeneity of environmental and ecological responses during this period.

The feedback of organisms to warming exacerbated ocean anoxia, which in turn amplified the negative effects of global warming. Warming can lead to increased photosynthetic rates, metabolic rates, and oxygen consumption rates of organisms. Early Triassic hothouse climate superimposed on nutrient inputs from enhanced terrestrial weathering improved the photosynthetic efficiency and productivity of marine producers, triggering red tides (algae bloom) and exacerbating ocean hypoxia. Increased metabolic rates place high oxygen demands on marine animals, further exacerbating the negative effects of hypoxia. In addition, the rapid warming around the Permian-Triassic boundary increased the efficiency of marine microbial metabolism, resulting in increased efficiency of particulate organic matter degradation and consumption of dissolved oxygen in deep waters, leading to the expansion of the oxygen minimum zone and euxinic conditions [13].

One of the most direct drivers of the EPGW was the rise in atmospheric CO_2 (Fig. 2). Atmospheric CO_2 rose slowly from ∼300 ppmv (1 ppmv = 10^{-6} m^3/m^3) in the early Permian to ∼800 ppmv in the late Permian, and increased rapidly to ∼2500 ppmv at the Permian-Triassic boundary interval (Fig. 2b). High CO_2 concentrations persisted for approximately five million years during the Early Triassic [6]. The driving mechanisms for the EPGW include at least the following potential contributors.

(i) Transition from Pangea B to Pangea A. In the Pangea B configuration, approximately 30% of the continental area of the equatorial humid belt was used for weathering (Table S2 online). In the middle Permian, the transition from Pangea B to A resulted in a northward drift of the equatorial humid belt into the tropical arid belt, leading to a decrease in continental area in the equatorial humid belt (Fig. 2b), a weakening of continental weathering, and an increase in atmospheric CO_2 concentration.

(ii) The lowering of the Hercynian mountains. During the assembly of the supercontinent Pangea, the uplift of the Hercynian mountains during the collision between Laurasia and Gondwana enhanced chemical weathering, reduced atmospheric CO_2 concentrations, and eventually led to the late Paleozoic ice age [14]. The lowering of the Hercynian moun-

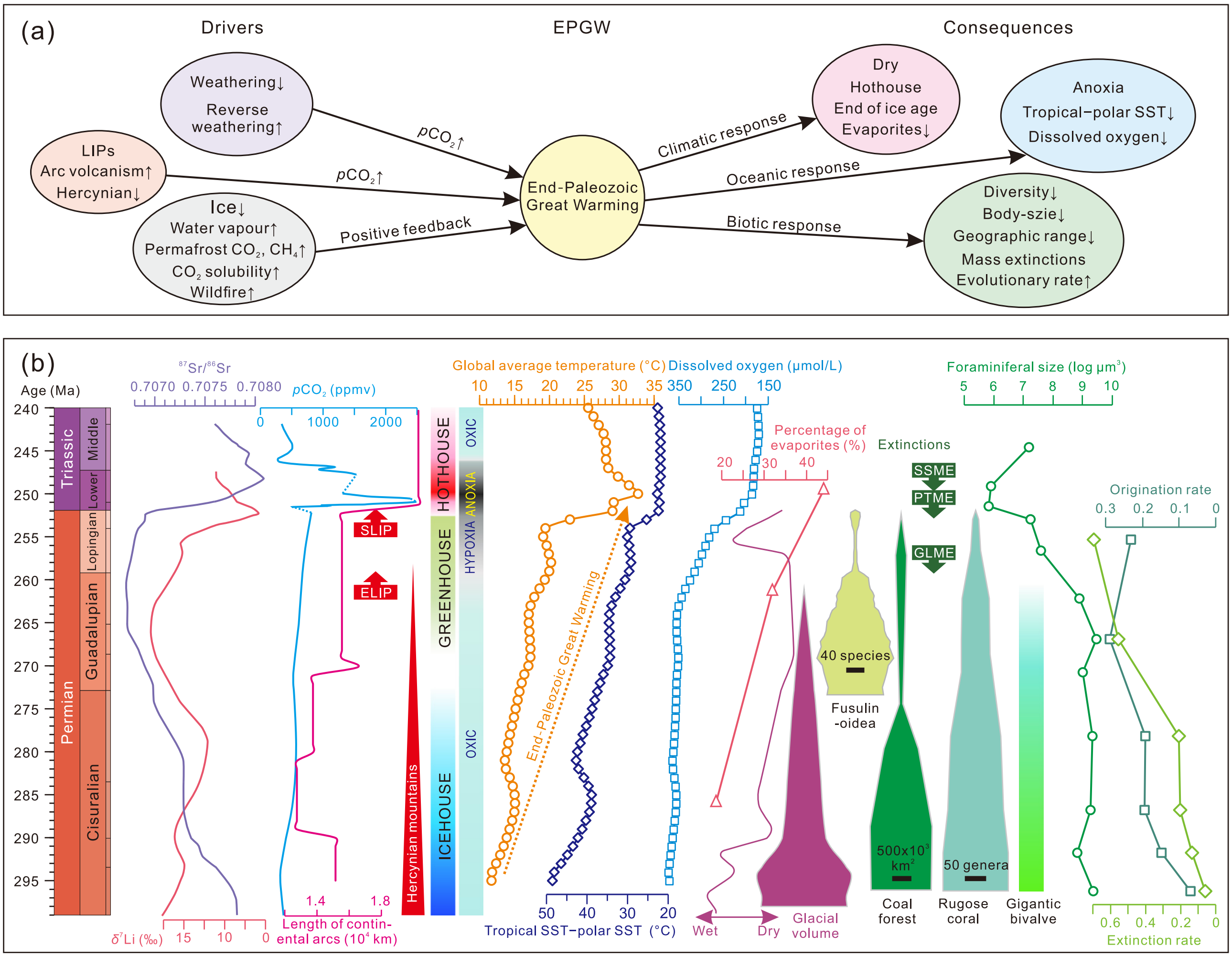

Fig. 2. End-Paleozoic great warming (EPGW) and its drivers and consequences. (a) The relationship between the EPGW and its drivers and consequences. (b) Geological, geochemical, sedimentary, and paleobiological records in the Permian-Triassic interval. SLIP, Siberian large igneous province; ELIP, Emeishan large igneous province; SST, sea surface temperature; SSME, Smithian-Spathian mass extinction; PTME, Permian-Triassic mass extinction; GLME, Guadalupian-Lopingian mass extinction. The area of Pangea is the continental surface area between 5°S and 5°N for Pangea A and Pangea B. The data sources are listed in Table S2 (online).

tains in the Permian would have had the opposite effect, weakening chemical weathering and increasing atmospheric CO_2, as supported by strontium isotopes and CO_2 records (Fig. 2b).

(iii) Continental arc volcanism. The length of continental arcs increased from 12,750 km in the early Permian to 20,300 km in the Early Triassic (Fig. 2b). Increased continental arc magmatism can release large amounts of CO_2 into the Earth's atmosphere during the early stages of continental arc development. In a striking contrast, continental arcs can also act as carbon sinks during their late stages. Therefore, the contribution of continental arcs to the end-Paleozoic great warming remains unclear and requires further study.

(iv) Large igneous provinces (LIPs). Two famous LIPs occurred at the Guadalupian-Lopingian and Permian-Triassic boundary intervals, i.e., the Emeishan Traps and Siberian traps (Fig. 2b). The lava volumes in the Emeishan and Siberian traps are approximately 1×10^6 and 3×10^6 km^3, respectively [15]. Such large lavas would have released large amounts of volcanic and thermogenic CO_2 (Table S2 online). In addition, a number of large igneous provinces were erupted during the early Permian, including the Tarim, Panjal, Skagerrak-Centered, and Barguzin-Vitim provinces ([15] and references therein), which have been identified as potential sources of CO_2 during the end-Paleozoic great warming.

(v) Enhanced reverse weathering. Lithium isotope data from bulk carbonates and brachiopod fossils suggest enhanced reverse weathering in the late Permian and Early Triassic, which could explain the persistently high atmospheric CO_2 in the Early Triassic (Fig. 2b).

Another important driver of the EPGW is the positive feedback of global warming. The reduction in ice cover area decreased the albedo and absorbed more solar energy. Warmer air can hold more water vapor. Water vapor is a greenhouse gas that can contribute to further warming. Warmer temperatures reduced the solubility of CO_2 in seawater, and oceanic CO_2 was released into the atmosphere. Warming also led to the release of CO_2 and CH_4 into the atmosphere as permafrost melted. Aridification led to a reduction in tropical forests, which in turn led to weaker weathering and less coal burial, which together contributed to warming. A warming climate and regional droughts increased the likelihood of wildfires, which released CO_2 into the atmosphere.

We are not in a position to comment on all the driving mechanisms and consequences of the end-Paleozoic great warming. Scientists are now more concerned with several rapid climatic events in the Permian to Triassic such as the Guadalupian-Lopingian warming, Permian-Triassic warming, and Carnian pluvial episode. The EPGW event is still in the early stages of research, and there are still vast areas to be explored. These include, but are not limited to: the complex interplay between tectonic movements and arc volcanism in relation to the EPGW; the impact of the EPGW on climate change; the impact of the EPGW on elemental cycling; the influence of the EPGW on changes in terrestrial and marine primary productivity; and the influence of the EPGW on the evolutionary trajectories of terrestrial and marine organisms.

Conflict of interest

The authors declare that they have no conflict of interest.

Acknowledgments

This work was supported by the National Natural Science Foundation of China (42325202 and 92155201).

Appendix A. Supplementary materials

Supplementary materials to this perspective can be found online at https://doi.org/10.1016/j.scib.2023.09.009.

References

[1] Scotese CR, Song H, Mills BJW, et al. Phanerozoic paleotemperatures: the Earth's changing climate during the last 540 million years. Earth Sci Rev 2021;215:103503.
[2] Crowley JK, Berner RA. CO_2 and climate change. Science 2001;292:870–2.
[3] Roscher M, Schneider JW. Permo-Carboniferous climate: early Pennsylvanian to late Permian climate development of central Europe in a regional and global context. Geol Soc Lond Spec Publ 2006;265:95–136.
[4] Montañez IP. A late Paleozoic climate window of opportunity. Proc Natl Acad Sci USA 2016;113:2334–6.
[5] Sun Y, Joachimski MM, Wignall PB, et al. Lethally hot temperatures during the Early Triassic greenhouse. Science 2012;338:366–70.
[6] Joachimski MM, Müller J, Gallagher TM, et al. Five million years of high atmospheric CO_2 in the aftermath of the Permian-Triassic mass extinction. Geology 2022;50:650–4.
[7] Dai X, Davies JHFL, Yuan Z, et al. A Mesozoic fossil lagerstätte from 250.8 million years ago shows a modern-type marine ecosystem. Science 2023;379:567–72.
[8] Dal Corso J, Song H, Callegaro S, et al. Environmental crises at the Permian-Triassic mass extinction. Nat Rev Earth Environ 2022;3:197–214.
[9] Haq BU, Schutter SR. A chronology of Paleozoic sea-level changes. Science 2008;322:64–8.
[10] Isozaki Y. Permo-Triassic boundary superanoxia and stratified superocean: records from lost deep sea. Science 1997;276:235–8.
[11] Wetzel RG. Limnology: lake and river ecosystems. San Diego: Academic Press; 2001.
[12] Chen B, Joachimski MM, Shen SZ, et al. Permian ice volume and palaeoclimate history: oxygen isotope proxies revisited. Gondwana Res 2013;24:77–89.
[13] Hülse D, Lau KV, van de Velde SJ, et al. End-Permian marine extinction due to temperature-driven nutrient recycling and euxinia. Nat Geosci 2021;14:862–7.
[14] Goddéris Y, Donnadieu Y, Carretier S, et al. Onset and ending of the late Palaeozoic ice age triggered by tectonically paced rock weathering. Nat Geosci 2017;10:382–6.
[15] Bond DP, Wignall PB. Large igneous provinces and mass extinctions: an update. Geol Soc Am Spec Pap 2014;505:29–55.

Haijun Song is a professor of paleontology and geobiology at China University of Geosciences (Wuhan). He received his Ph.D. degree in paleontology and stratigraphy in 2012. In 2016–2017, he worked as a Marie Curie Fellow at the University of Leeds. His research interest focuses on mass extinctions, macroevolution, and the application of big data and artificial intelligence in geobiology.