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Cold climate after the end-Permian crisis as implied by the aftermath vegetation*

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Abstract The flora after the end-Permian mass extinction is characterized by the presence of conifers and lycopod, e.g., Pleuromeia. It resembles modern boreal forest in community structure and may represent similar climatic conditions. The needle-shaped leaves of the Pleuromeia and its companion by conifer indicate it is adapted to cold climate, instead of hot dry climate. The replacement of the flourishing tropical-subtropical floras of the Latest Permian by the aftermath flora like modern boreal forest should be caused by a substantial climate cooling. The universal distribution of this flora indicates that there was no climate zonation after the mass extinction and the whole Earth was a "cooling ball".

Keywords: end-Permian, mass extinction, flora, climate, boreal forest

1 The aftermath flora and its paleoecology

During the Late Permian Changhsingian Stage, the terrestrial plants were very flourishing. They differentiated into 4 floral kingdoms: the Angara kingdom, Atlantic kingdom, Cathaysian kingdom and Gondwana Kingdom (Dobruskina, 1987), representing North Temperate mid-latitude climates, palaeo-equator and lower latitude climate, paleo-equator and low latitude climate, and South Temperate to Cold high latitude climate, respectively. The crisis at the close of the Permian totally destroyed the four floras, leaving only a few refugees including a few conifers, some *Glossopteris*, and some lycopods.

The aftermath flora of the early Griesbachian was very monotonous in composition. It contained some conifers, such as *Voltzia*, some seed fern, such as *Glossopteris*, and some lycopods, such as *Pleuromeia*. Though its simple composition, this flora had worldwide distribution (Meyen, 1973; Dobruskina, 1987). The conifer *Voltzia* and seed fern *Dicriodium* occurred at almost all paleo-latitudes (Dobruskina, 1987; Veevers et al., 1994; Retallack, 1995) and *Pleuromeia* was encountered in virtually all coastal habitats (Wang, 1996). It accommodated only a few large animals, but with abundant insects.

Mainly adapted to cool to cold climates, modern conifers are mainly distributed in the frigid zone, temperate zone, variable zone, as well as the high mountains in the torrid zone. The conifer of the aftermath flora such as *Voltzia* should be adapted to similar climatic conditions. Modern lycopods are distributed to every parts of the Earth, including the torrid zone, subtropics, temperate zone, variable zone, as well as frigid zone, indicating they are climatically eurytopic. The needle-shaped leaves of *Pleuromeia* have been regarded to be adapted to arid climate. But knowledge from modern botany tells us that needle-shaped leaves can be an adaptation to cold climate, an adaptation to the physiological drought resultant from cold climate (Wu et al., 1983). Since they were associated with conifers, the needle-shaped leaves of *Pleuromeia* were adapted to cold climate, instead of hot dry conditions. As a whole, the aftermath flora characterized by conifers and lycopods was adapted to cold climate.

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2 Comparison to modern floras

Modern terrestrial plants are divided as 6 floral kingdoms: the tundra, the boreal forest, the temperate deciduous forest, the tropical rain-forest, the grassland, and the desert (Emberlin, 1983).

The tundra occupies the zone between latitude 57 degrees north and the polar regions and has no growing season. It contains low weeds including heaths, grasses, sedges, mosses and lichens, lacking any trees. The tundra communities lack substantial layering and the overall species diversity is low. Most of the species, however, have wide distributions.

The boreal forest occupies the zone from the edge of the tundra to about 800 km southwards. Containing a few dominant trees, some shrub and a few herbaceous plants, the communities are homogeneous, lacking diversity and layering. Most of the trees have wide distributions. For example, species of pine, spruce and fir are found throughout. Some large animals and many insects dwell in this flora.

The temperate deciduous forests contain diverse species of tree, with 12~60 dominant, and prolific undergrowth. The vegetation structure may have several layers. The animals inhabit the flora are diverse and abundant. The tropical rain-forests are dominated by broad-leafed evergreen trees and are extremely diverse, highly stratified, inhabited by diverse and abundant animals. The temperate grasslands are dominated by Gramineae. The deserts contain few plants or animals.

The aftermath flora differed from the tundra and grasslands in that the latter has no trees. It was different from modern temperate deciduous forests and tropical rain-forests in the development of broad-leafed trees and other tall broad-leafed plants in the latter. Its difference from modern deserts lies in the absence of conifers in the latter.

In terms of total appearance and community structure, the aftermath flora was very similar to modern boreal forest. The similarities between them lie in: (1) both are homogeneous in species composition, (2) both are composed of a few species of conifers, lycopods, and some others, (3) both are dominated by the plants of needle-shaped leaves, (4) though homogeneous, most species are cosmopolitan in distribution, encountered throughout; (5) both lack layering of communities; (6) both are inhabited by a few large animals but relatively abundant insects. Because of their similarity, the aftermath flora should be adapted to the climate conditions similar to those of modern boreal forest. The climate of modern boreal forest is characterized by the annually average temperatures of below 0 ºC, the common temperatures of 0~18ºC during the warmest months (2~4 months per year), and the short growth season of 3-4 month annually.

The replacement of the flourishing tropical to subtropical floras of the Latest Permian by the aftermath flora of cold climate was one of the key aspects of the end-Permian mass extinction. It should be caused by a drastic climatic cooling event, in the order of a decrease in temperature by 10~20ºC. Such a cooling not only totally destroyed the terrestrial ecosystems but also the diverse marine ecosystems.

Since the aftermath flora was cosmopolitan in distribution, the aftermath Earth was speculated to have no climatic zonation. That is, the whole Earth was a “cooling ball”.

In Chinese:

二叠纪末大绝灭后的寒冷气候：来自植被面貌的信息

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摘 要 晚二叠世十分繁盛的高大造煤植物在二叠纪末全部绝灭了。大绝灭后的陆生植物群由针叶的松杉类、石松和少数草本植物组成，属种单调，却有世界性的分布。对比发现，大绝灭后的陆生植物群与现代北方针叶林的面貌十分相似，因此推测它们代表相同或相似的古气候条件。由于这种大绝灭后植物群具有全球性分布，所以推测当时没有气候分带；全球为一个凉球。

关键词 二叠纪末；集群绝灭；古气候；植物群；北方针叶林

1．引言

发生在二叠纪末的生物集群绝灭是显生宙最大的生物绝灭事件之一。对其特征和成因的研究仍然是地质学界的重大课题之一。这次大绝灭事件不仅彻底摧毁了晚二叠世曾经丰富多样、生机勃勃的海洋生态系，而且对陆地生态系也给予毁灭性的打击。深入研究这次大绝灭对陆地生态系的影响方式是通向大绝灭的成因和机制的途径之一。这次大绝灭究竟如何影响了陆生生态系？哪些生物绝灭了？哪些生物残留了？绝灭的生物与残留的生物在生态特点上有何种差异？本文试图根据现有的文献资料对这些问题作初步探讨。

2．晚二叠世的陆生植物群面貌

晚二叠世是显生宙的主要造煤期之一，植物群不仅十分繁茂，而且有明显的地理分区。晚二叠世全球有四大植物区系：安加拉植物群，大西洋植物群，华夏植物群和冈瓦纳植物群（Dobruskina, 1987）。安加拉植物群分布在西伯利亚，代表中纬度北温带气候。大西洋植物群分布在北美和乌拉尔，代表古赤道和低纬度气候。华夏植物群分布在中国、印度和苏门答腊南部，也代表古赤道和低纬度气候。冈瓦纳植物群分布在冈瓦纳大陆，代表南温带到高纬度的凉-冷气候。

3．二叠纪末陆生植物的选择性绝灭

在二叠纪末的大灾变中，这四大植物群的分子几乎全部绝灭，只有少数舌羊齿和极少的其它植物幸免于难。舌羊齿是晚二叠世冈瓦纳植物群的核心分子，但它的分布不限于冈瓦纳植物群；它还出现在凉温带、暖温带、中纬度沙漠、北极区、冷温带中，表明它有宽广的温度或气候适应范围（Asama, 1985; Meyen, 1987; Archangelsky, 1990）。也许正是得益于其温度广适性，在大多数舌羊齿绝灭的情况下，有少数舌羊齿逃过了二叠纪末的大劫难（Pantt, 1987; Pant & Pant, 1987）。其它逃过二叠纪末大劫难的植物是一些松杉类、一些草本的水韭和种子蕨（如 *Dicroidium*）（Retallack, 1995）。

4．大绝灭后的陆生植物群面貌及类群生态特点

大绝灭后的早格柔斯巴赫期的植物群面貌极其单调，主要由针叶松杉类，如 *Voltzia*（伏脂杉），并有一些种子蕨，如舌羊齿，以及一些石松类，如 *Pleuromeia*（肋木）。这个植物群尽管组成单调，却有世界性的广布（Meyen, 1973; Dobruskina, 1987）。*Voltzia* 和 *Dicriodium* 出现在所有纬度（Dobruskina, 1987；Veevers et al., 1994; Retallack, 1995）；*Pleuromeia* 则出现在几乎所有的滨海环境（Wang, 1996）。在这个植物群中只有极少的大型动物，但却有比较丰富的昆虫。

现代松杉类多分布在寒带、温带以及热带的高山上，说明是耐寒冷的植物。舌羊齿是二叠纪冈瓦纳植物群的核心分子，能够适应温带-凉冷-寒冷气候。现代石松类的分布遍及全世界，包括热带、亚热带、温带和寒带地区。大绝灭后的 *Pleuromeia* 具有适应干旱气候的典型形态特征。

5．大绝灭后的陆生植物群与现代陆生植物群的对比

现代的植物群主要包括：苔原，北方针叶林，温带落叶林，热带雨林，草地，沙漠（Emberlin, 1983）。苔原位于北极到北纬 57 度之间。这里没有生长季节，植物群由低矮的草本组成，缺乏树木。这里的植物群落物种反映度分异度极低，没有分层结构。但种的分布却很广。

现代的北方针叶林位于苔原南缘到其南约 800 公里处。这里的植物群主要由少数木本及少数灌木和草本组成。群落组成单调，缺少分异度和分层结构。这里的树木主要是针叶的松杉类。它们的分布极广，在全区内几乎无处不见。该植物群内只有少数大型动物，但昆虫却颇为丰富。

现代北方针叶林树木的叶缩小成针状，并具有各种抗寒抗旱的结构，是对生长季短和低温引起的生理性干旱的一种适应（武吉华等，1983）。极地针叶林中的草本植物有苔藓、石松和矮小灌木。

现代温带落叶林分布于温带区，由丰富多样的木本组成，通常有 12~60 个优势种，并有丰富茂盛的低层植物。这里的群落具有分层结构，栖居的动物也丰富多样。热带雨林主要由常绿阔叶树组成，物种分异度高，群落分层多，栖居的动物丰富多样。温带草地主要由禾本科草本组成。沙漠中的动植物都十分稀少。

大绝灭后的陆生植物群与现代苔原、草地的区别是后者根本没有木本植物；与现代温带落叶林和热带雨林的区别是后二者中阔叶树的发育。与现代荒漠的区别是后者根本不会有松杉类的分子。

就总体特征和群落结构而言，大绝灭后的陆生植物群与现代的北方针叶林很相似。两者的相似性在于：（1）物种组成都很单调，（2）都以少数针叶的木本为优势种，兼有一些灌木和草本；（3）其木本分子都是松杉类，草本分子中都有石松类；（4）作为对寒冷气候的生理性干旱的适应，树叶的形态都呈针状，（5）尽管物种单调，但它们的分布却十分广泛，几种主要的种类几乎无处不见；（5）群落都没有分层性；（6）其中栖居的都只有少数大型动物，但却有较为丰富的昆虫。

由于它们的相似性，所以推测大绝灭后的陆生植物群生活于与现代北方针叶林相似的气候条件。现代北方针叶林区全年大多数月份气温在 0 度以下，最暖月份（2~4 个月）的气温仅在 0~18 度，可生长月份为 3-4 个月。

由于晚二叠世代表温暖气候环境的高大植物全部绝灭，而大绝灭后的陆生植物群是适应寒冷气候的，所以推测二叠纪末的陆生生物大绝灭是由气候变冷引起的。由于大绝灭后的植物群具有世界性的分布，尤其是分布到当时的低纬度区，所以推测当时没有气候分带，全球为一“凉球”。

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