We study the sedimentary record to gain perspective on the range of environmental conditions through Earth’s history. Lithology, internal organization, fossil content and composition are used to reconstruct depositional environments, guided by a uniformitarian-approach: physical laws that command Earth systems today have not changed through time. Most Phanerozoic continental sediments indicate surface conditions within the range of modern Earth. This is intuitively obvious, for the fossil record documents vertebrate and plant life on land at least since the Silurian (ca. 440 Ma), and environmental conditions never went outside the limits where these can survive. Occasionally the sedimentary record preserves evidence for conditions too extreme for complex life, outside the modern range. Extraordinarily harsh climatic conditions are documented by Zambito and Bennison (2013, p. 587 in this issue of Geology), who use fluid inclusion homogenization temperatures ($T_h$) in uppermost Lower Permian (ca. 270 Ma) halite beds of the Nippewalla Group (Kansas, United States) as proxies for surface air temperatures. The region was then in the tropics. Average $T_h$ values rise from those typical for the modern tropics ($\sim 26 ^\circ C$) near the base of the Nippewalla Group, to $\sim 40$–$45 ^\circ C$ in its lower and middle parts, then return to typical values of 21–33 $^\circ C$ toward its top. The zone of peak average $T_h$ includes maximum values of $>70 ^\circ C$, and diurnal variability of $>30 ^\circ C$, both more extreme than recorded on Earth today. Evidence for extremely high surface temperatures during deposition of the Nippewalla Group provides a better understanding of some of the peculiar aspects of the Permian terrestrial record in western tropical Pangea, but also presents paradoxic paleoclimate problems, which can be appreciated only within the broader context of Permian–Carboniferous (P–C) sediments, soils, and plant and animal fossil assemblages.

During the late Paleozoic, the continents were grouped into two large landmasses: Laurasia, moving southward on the Northern Hemisphere, and Gondwana, moving northward on the Southern Hemisphere. At $\sim 340$–$320$ Ma (Early Carboniferous), they collided near the equator to form Pangea (Scotese et al., 1979). Around this time, climate cooled, with continental ice-sheet development documented by proxies collected at high paleolatitudes (near-field) and low paleolatitudes (far-field). There may have been multiple centers of ice-sheet growth, and retreats of variable extent and duration (Isbell et al., 2012). Beginning in the mid-Carboniferous (ca. 327 Ma), ice sheets grew from small centers, reached their maximum extent and duration (Isbell et al., 2012). Warming across the P–C boundary may have affected fossil flora in tropical western Euramerica (DiMichele et al., 2006).

Long-term floral change in western tropical Euramerica records a prolonged, stepped, trend: (1) Late Mississippian through Middle Pennsylvanian coal swamps were dominated by lycopods, pteridosperms, and tree ferns, forming wetland ecosystems; (2) in the Late Pennsylvanian (ca. 306–304 Ma), opportunistic tree ferns and pteridosperms became dominant in response to intensified seasonality (DiMichele et al., 2010); (3) the wetland biome was intercalated with a biome dominated by conifers, callipterids, and other seed plants resistant to prolonged periods of dryness during glacial-interglacial cycles (DiMichele et al., 2006); (4) the seasonally dry biome became dominant near the P–C boundary, but cyclic alternation of wet-dry biomes continued through the Lower Permian, with progressively more drought-tolerant assemblages; (5) a macrofloral hiatus in upper Lower Permian strata is coeval with sedimentary indicators of aridity; and (6) a depauperate, drought-resistant and conifer-dominated flora appeared above this hiatus, with its elements otherwise known only from the Late Permian and Mesozoic of Europe (DiMichele et al., 2001).

Pennsylvanian–Early Permian terrestrial tetrapods are best known from western tropical Euramerica. After the Carboniferous rainforests collapsed, endemism and increased tetrapod diversity developed during the Late Pennsylvanian and Early Permian (Saehney et al., 2010). Tetrapod diversity remained high up to the late Early Permian, but a tetrapod record is essentially absent in younger strata of western tropical Euramerica, after a major collapse of amphibians and basal synapsids in the tropics which has been named “Olson’s extinction” (Benton, 2012). Thereafter, tetrapods in mid- to high-paleolatitude basins in South Africa and Russia are dominated by therapsids. There is no marine extinction corresponding to Olson’s extinction and the Early Permian tropical terrestrial biome collapse.

Permian amphibians were likely ectothermal, but it is unclear whether Permian synapsids were endothermic or ectothermic (Ruben, 1995). Modern large ectotherms (crocodilians, varanids) do not survive sustained temperatures in excess of 40–45 $^\circ C$ (Spellerberg, 1972). Terrestrial endotherms (birds and mammals) experience facultative hyperthermia and death at sustained temperatures of 41–46 $^\circ C$ (e.g., Adolph, 1947). At
temperatures above 35–40 °C, most modern plants experience protein denaturation, malformed cellular membranes, and greatly diminished CO₂ uptake (Daniell et al., 1969). Woody C₃ plants such as the xeromorphic Permian floras in the western tropics (Montañez et al., 2007) are especially sensitive to the effects of diminished CO₂ uptake at high temperatures (Berry and Downton, 1982). Seedlings of the most drought-tolerant conifers have threshold temperatures (~63 °C; Kolb and Robberecht, 1996) that could not survive the temperatures implied by the Tₑ values in Zambito and Benison (2013).

In conclusion, lithological, paleopedogenic, and paleontological data define a P-C trend toward increased aridity, completed by late Early Permian, with conditions exceedingly unfavorable for complex life in terrestrial basins of western tropical Euramerica during the latest Early Permian. Zambito and Benison show exceedingly high temperatures may have been part of these conditions, and lethal temperatures are particularly useful in framing the significance of their high Tₑ values. Precise chronometric correlation among the terrestrial basins of western tropical Pangea is not yet possible, and it is unclear whether the extreme Tₑ values reported by Zambito and Benison reflect regional surface temperatures. However, extremely high surface air temperatures over the western tropical basins of Euramerica would provide environmental forcing for the observed collapse of the seasonally dry plant biome and extirpation/extinction of amphibians and synapsids near the end of the Early Permian.

Zambito and Benison provide ancient climate dynamics that are typically neither captured by other proxies (e.g., Tabor and Poulsen, 2008) nor considered at such time scales (e.g., Peyser and Poulsen, 2008). If the Tₑ values correspond to seasonal high temperatures, the results have important implications for the Permian “ice house.” Surface air temperatures of ~40–45 °C in the area of deposition of the Nippewalla Group halite at a paleolatitude of ~10° would correspond to seasonal temperatures well above freezing at the Permian poles. Either the Permian equator-to-pole temperature gradient was significantly larger than the modern gradient of ~0.4 °C per degree of latitude, or there were distinct non-glacial episodes during the Early Permian (Isbell et al., 2012).

The mechanisms responsible for such high surface air temperatures in the low-latitude tropics are not known, but the paleoclimatic pattern is similar to that modeled in Early Permian general circulation models, including a substantial rise in atmospheric CO₂ (Peyser and Poulsen, 2008; Poulsen et al., 2007). Those scenarios indicate that the western tropics should have become increasingly dry and arid in response to higher atmospheric CO₂; an intriguing twist offered by Zambito and Benison is that the arid tropics were at times very wet (albeit saline).

REFERENCES CITED

Printed in USA