

**Some Like It Hot**

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EVOLUTION

Some Like It Hot

Felisa A. Smith

Body size matters. It sets the energetic demands of organisms, regulates the rates of physiological processes, and influences population densities and other key characteristics of animal communities and populations (1). Thus, it is no surprise that most animals have a characteristic (2) and highly heritable size (3). Yet the body sizes of mammal lineages have varied greatly over evolutionary history. The demise of dinosaurs ~65.5 million years ago marked the onset of rapid morphological and ecological diversification in terrestrial mammals that ultimately led to size increases of more than four orders of magnitude. On page 959 of this issue, Secord *et al.* (4) illustrate the critical role of temperature in driving body size evolution between ~55.5 and 54.5 million years ago.

According to Bergmann's rule, within a broadly distributed genus, species of larger size are found in colder environments, and species of smaller size are found in warmer areas (5). Some researchers argue that the rule arises as a result of the need for heat conservation or loss; others attribute it to ecosystem properties such as productivity (6). Regardless, Bergmann's rule holds for more than 70% of modern endotherms (animals that maintain a constant internal body temperature) (6). Moreover, it has been documented over historical and microevolutionary time (6, 7); recent work even suggests that temperature constrained the maximum size that mammals could attain in the course of evolution (8). Thus, temperature may be expected to influence body size evolution within lineages.

The early Cenozoic is an interesting chapter in Earth history. Not only does its onset ~65.5 million years ago mark the end of dinosaurs and the beginning of the radiation of mammals, but it was also a time of rapid fluctuation of climate. The most severe hot episode was the Paleocene-Eocene Thermal Maximum (PETM), which occurred ~55



Early horses. This painting by the German artist Heinrich Harder (1858–1935) was part of a series of collector cards illustrating prehistoric animals commissioned by the Reichardt Cocoa Company. It depicts an early species of *Sifrhippus* (*Hyracotherium*) that first appeared about 55 million years ago. Secord *et al.* show that the body size of *Sifrhippus* changed in response to temperature fluctuations between ~55.5 and 54.5 million years ago.

million years ago (9). During the PETM, sea surfaces warmed by more than 5°C (9, 10), causing changes in aquatic and terrestrial ecosystems, including substantial changes in mammalian diversity (11). In particular, the immigration of modern ungulate taxa (Perissodactyla and Artiodactyla) into North America profoundly and permanently altered ecosystems on the continent (11, 12). Dwarfing of numerous archaic and modern lineages during the PETM has been reported (13), but a quantitative assessment of how the PETM influenced mammalian body size evolution has been lacking.

Secord *et al.* examine the consequences of climatic shifts on the body size of the small early horse *Sifrhippus* (also known as *Hyracotherium*), which first appeared in North America during the PETM. They test the two main causal mechanisms underlying Bergmann's rule: temperature and productivity.

The authors build on previous work in the Clarks Fork Basin of northwestern Wyoming, a site rich in mammal fossils with a continuous stratigraphic section between ~60 and 53 million years in age (13). They estimate body mass for ~44 adult horses by measuring the area of the first molar. Using $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ signatures recorded in the tooth enamel of more than 150 mammalian fossils collected at Cabin Fork, Wyoming, they develop a highly resolved local paleoclimatic record spanning

A study of horse evolution illustrates the connection between environmental temperature and mammal body size.

the PETM. The carbon signature mirrors the abrupt negative carbon excursion associated with the PETM in other locations (9), whereas the oxygen isotopes yield estimates of changes in air temperature. As expected on the basis of Bergmann's rule, the authors find that changes in $\delta^{18}\text{O}$ were significantly related to body size changes in *Sifrhippus*. The size shifts were substantial: Body size decreased by ~30% at the start of the PETM, and increased abruptly by more than 75% at its end.

But was temperature the ultimate driver behind the body size shifts? Or were they caused by changes in productivity? Barring unusual instances of exceptional preservation,

direct estimation of vegetation structure or local productivity in the fossil record has been problematic. Secord *et al.* take a clever approach by comparing oxygen isotopes in fossil teeth of mammal taxa that varied in their affinity for aquatic environments. Oxygen isotopes in herbivores largely reflect the composition of local surface and plant water. Isotopic enrichment occurs in species that occupy drier habitats with little surface water. For such evaporation-sensitive species, enrichment tends to be positively related to habitat aridity (14). By comparing the evaporation-sensitive *Sifrhippus* with *Coryphodon*, an archaic herbivorous ungulate generally considered to be associated with aquatic habitats, Secord *et al.* develop a proxy for "aridity." This, they argue, is inversely related to productivity.

The correspondence between this metric and mean annual precipitation estimated from analysis of nearby soil sediments of the same age is quite high, suggesting that Secord *et al.* have captured something akin to productivity. However, they find no correlation between productivity and body size. In fact, the opposite trend is evident: a decrease in body size during wetter conditions. Thus, body size evolution over the PETM appears to have been driven by temperature fluctuations, consistent with the original characterization of Bergmann's rule (5).

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At the start of the Cenozoic, mammals rapidly increased in size across the globe, probably as a result of ecological release and the occupation of newly vacated niches (8). Ten million years later, the upper boundary of mammalian size was still increasing, but Secord *et al.* also demonstrate the operation of opposing selective forces at this time. Their highly resolved and local paleotemperature and productivity proxy, tested against a single, well-resolved sequence of mammalian fossils, allows a mechanistic and quantitative examination of the processes influencing body size over time.

The findings of Secord *et al.* underscore the importance of the fossil record for examining how future environmental changes may influence life on Earth. Recent climate warming has already led to changes in the phenology, distribution, and morphology of species (15). However, it remains unclear how rapidly animals may adapt. Pat-

terns such as Bergmann's rule demonstrate the ability of species to adapt to fluctuating abiotic conditions, and highlight the strong selection imposed on organisms by their environment.

However, some caution is warranted when extrapolating from the past to the future. The extreme change in Earth's surface conditions during the PETM is not unlike that expected to occur in the future, but the time frame was considerably longer. There may be more appropriate analogies for anthropogenic warming in the fossil record, such as the Younger Dryas, when large abrupt temperature shifts took only decades. As we increasingly turn from explaining the present to anticipating the future (16), an understanding of evolutionary history becomes imperative for untangling biological complexity. Nowhere is such a deep-time perspective more important than in studies of anthropogenic warming.

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ATMOSPHERIC SCIENCE

Frictional Dissipation— Blame It on the Rain

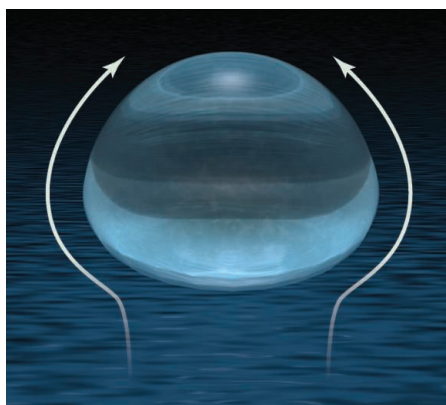
Dargan M. W. Frierson

Frictional dissipation in a turbulent flow occurs when kinetic energy is transferred to smaller and smaller scales until it is eventually removed by molecular diffusion. In addition to this turbulent dissipation, kinetic energy in Earth's atmosphere is also removed in the shear zones surrounding falling raindrops and ice particles. On page 953 of this issue, Pauluis and Dias (1) provide the first observational estimate of the precipitation-induced dissipation and show that its magnitude is comparable to that of turbulent dissipation in air.

As raindrops or other hydrometeors fall downward, shear zones around the particles develop, providing frictional deceleration and causing the hydrometeor to fall at a terminal velocity (see the figure). Although it is clear that dissipation occurs around any given hydrometeor, the substantial contribution of hydrometeors to the global mean dissipation is disproportionate to the small total mass of these particles. After all, water

vapor makes up only around 1% of the mass of the atmosphere, and liquid and ice water are orders of magnitude smaller in atmospheric concentration.

Pauluis and Dias used a precipitation radar for their calculation of the dissipation



Frictional dissipation around a falling raindrop. Drag forces around falling raindrops deform and decelerate the droplets, causing them to fall at a terminal velocity. There is also kinetic energy dissipation associated with the drag, and this precipitation-induced dissipation makes up an appreciable fraction of the total frictional dissipation on Earth.

Satellite observations reveal the extent to which rainfall removes kinetic energy from the atmosphere, and thus its impact on circulation.

induced by falling hydrometeors. Instead of the traditional ground-based radars used by TV meteorologists to warn viewers of the location of severe weather bands, the first spaceborne precipitation radar (PR) is used, from the Tropical Rainfall Measuring Mission (TRMM), which launched in 1997. The TRMM PR uses 13.8 GHz radio wave pulses to detect falling hydrometeors throughout the tropics.

The TRMM PR measures radar reflectivity and translates this into fall speeds relative to the surrounding air. Because the frictional dissipation surrounding hydrometeors is proportional to the terminal velocity relative to air, the precipitation rate can be translated into a dissipation rate. Thus, Pauluis and Dias calculate a tropically averaged dissipation rate of 1.8 W m^{-2} , a value that is consistent with previous theoretical estimates (2).

Pauluis and Dias also show the structure of precipitation-induced dissipation as a function of latitude and longitude. The dissipation field is similar to that of precipitation itself, but can be appreciably larger over continental areas where rain falls into drier air below. If reevaporation of rain occurs in a column,

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