Fossils of Morganucodon—an extinct genus from the Mesozoic—revealed a major step in brain evolution in mammaliaform animals.

PALEONTOLOGY

The road to a larger brain

Ecological opportunities in the early Cenozoic favored larger, not smarter, mammals

By **Felisa A. Smith**

Modern mammals have the largest brains relative to their body size among vertebrates (*1*, *2*). Because brain size is correlated with cognitive ability, complex behavior, and puzzle-solving abilities, this suggests that mammals are better able than other animals to interface with their environment (*3*, *4*). But how and why did mammals evolve large brain sizes relative to their body mass? The question of whether the rapid morphological evolution of mammals after the Cretaceous-Paleogene extinction was accompanied by equally rapid changes in brain size speaks to the role of ecology in macroevolution. On page 80 of this issue, Bertrand *et al*. (*5*) address the idea of "brawn before brain" by characterizing the timing and pattern of mammal brain development across the Early Jurassic to the middle Cenozoic (~200 million to 30 million years ago).

The phylogenetic encephalization quotient (PEQ) is a measure of relative brain size: the ratio of actual to expected brain volume for a given body size and phylogeny. Encephalization refers to an increase in this ratio. Although the mammal lineage experienced several sudden increases in encephalization during the Mesozoic—perhaps driven by selection for enhanced hearing, smell, taste, and feeding abilities—the range of body mass and PEQ was relatively limited compared with that of modern mammals (*6*–*10*). This changed with the extinction of nonavian dinosaurs at the Cretaceous-Paleogene boundary (66 million years ago) as surviving mammals rapidly diversified to occupy newly vacated ecological niches (*10*, *11*). But was this rapid increase in body mass accompanied by an equally rapid and proportional increase in brain size (*8*)? Or did encephalization occur at a different pace? That is, did mammals first become "smarter" then larger, or larger then smarter?

Across contemporary mammals, there is a highly nonlinear scaling of body and brain size, with a strong phylogenetic signal (*2*, *4*). Slopes and intercepts vary substantially among mammalian orders, with groups such as carnivores exhibiting steeper slopes than those of ungulates (*2*, *4*). Recent work demonstrates that the allometric scaling of brain to body size appears to have been repatterned multiple times during the Cenozoic, especially near the Cretaceous-Paleogene and Paleogene-Neogene boundaries (~23 million years ago), when changing environmental conditions may have precipitated evolutionary innovations and ecological radiations (*4*). However, it is difficult to determine how and when mammals encephalized to near-modern levels because well-preserved skulls dating to the Mesozoic and early Cenozoic are fairly rare. Moreover, investigating brain development is complicated because relative or absolute brain size may

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not be the best measure of cognition (*4*). Ideally, studies should examine brain complexity and the relative proportions of different brain regions—the volume of brain devoted to higher cognition versus mediating basic autonomic and sensory functions (*4*).

Bertrand *et al.* combined previously reported endocranial data with high-resolution computed tomography (CT) images of newly discovered early Cenozoic mammal skulls. Not only did they measure brain size, they also characterized the individual sensory components for many fossils. These included the neocortex, which is related to higher-order brain functions such as sensory perception and cognition; the olfactory bulbs, which are related to smell; and the cerebellar petrosal lobules, which are related to eye movement. The authors examined 124 extinct species dating from early in mammal evolution to the middle Cenozoic. Their study was particularly data-rich for the crucial period immediately after the Cretaceous-Paleogene extinction, which marked the onset of rapid morphological and ecological diversification in terrestrial mammals and an expansion in mass of more than four orders of magnitude (*10*). They found that immediately after that extinction, mammals were actually less encephalized than earlier, or later, in their evolutionary history. Mammals expanded in body size much faster than brain size as they diversified after the end-Cretaceous extinction—favoring "brawn" before "brain" (*8*). The reduction in PEQ was relatively short-lived, however. By the early Eocene (~50 million years ago), relative brain size had substantially expanded in all clades, although more so in crown orders (earliest members of extant placental orders) than in stem taxa (archaic placentals). The rate of encephalization slowed by 40 million years ago, about when morphological diversification plateaued (*10*).

Notably, changes in relative brain volume over the Cenozoic were not uniform across the different sensory regions; larger brains were not simply scaled-up versions of smaller brains (*4*). Rather, there was a large increase in the neocortex, whereas the proportion of the brain devoted to olfaction decreased. And after an initial decrease in the relative size of the petrosal lobules after the Cretaceous-Paleogene, they too increased over time. These changes in brain composition were more marked in crown orders than in stem taxa, supporting the idea that differences contributed to the eventual decline and extinction of the latter. Overall, encephalization after the initial drop in the Paleocene was driven by the expansion of brain regions mediating balance, vision and eye movement, head control, and sensory integration, rather than olfaction.

Brains are energetically expensive, using almost an order of magnitude more energy per gram than that of other body tissues (*12*). Evolving a larger brain relative to body size can necessitate higher basal metabolic rates and/or reduced allocation to other essential physiological processes (*12–14*), although trade-offs remain unclear (*2*, *4*). Given this cost, why have mammals undergone such remarkable encephalization over the Cenozoic? Although numerous hypotheses have been proposed—including selection related to sociality, improved hearing, feeding, taste, olfaction, miniaturization, parental care, endothermy, and nocturnality [for example, (*6*, *8*)], the ecological niche is likely important (*2*, *4*, *15*). Bertrand *et al.* posit that as mammals evolved larger sizes and ecosystems began saturating, interspecific competition intensified selection for larger relative brains. For example, predators developed substantially larger PEQ than that of prey groups by the Eocene. Earlier work reported a transition between the growth and saturating phase of body size evolution at this time, which is consistent with the saturation of ecological niches (*10*).

Understanding the trade-offs between the high energetic demands of brain tissue and the potential value of increased brain size for survival and reproductive success remains a challenge. Studies such as Bertrand *et al.* highlight the utility of the fossil record for disentangling fundamental allometric scaling among contemporary mammals, as well as highlighting the central role of ecology in mammal macroevolution. ■

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PHOTOVOLTAICS

Perovskite solar cells can take the heat

Layered surface structure adds durability to packaged perovskite cells

By **Joseph M. Luther** *and* **Laura T. Schelhas**

Solar panels must endure extreme conditions during their service lifetime. There are few other products, let alone pristine semiconductor electronics, that are manufactured today and expected to withstand decades of abuse from full exposure to outdoor elements, including harsh ultraviolet sunlight, rain and hail, and daily and seasonal thermal cycles. Over the past decade, a new class of semiconductors, known as metal halide perovskites, has emerged, which constitutes the light-absorbing material in solar panels and has made incredible advancements, potentially taking photovoltaics in new directions. Perovskite materials have been touted as a potential game changer for solar energy production (*1*). On page 73 of this issue, Azmi *et al.* (*2*) present a reproducible layered surface structure of the perovskite for improved durability. The resulting perovskite cells can maintain performance under high heat and humidity.

Perovskite solar panels promise an efficient, low-cost, and simple-to-manufacture solution that is on the cusp of commercialization, as either a stand-alone technology or an add-on to silicon in a tandem configuration. However, naysayers of perovskite's future potential often point to the lack of studies demonstrating durability in packaged cells and modules. In a commercial product, arrays of solar cells are packaged to create a solar module. Packaging is used to contain the cells and can protect them from the environment. Commercial solar panels are often subjected to accelerated stress testing to quickly assess their durability in the field. When developing new technologies, researchers cannot simply place panels outside and wait multiple decades to assess stability; rather, they are forced to develop accelerated test procedures and protocols (*3*, *4*).

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