Evolving Large and Complex Brains

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with clouds, heat transport between the atmosphere and the Earth's surface, radiation and turbulence, that have a spatial scale smaller than the resolution of the model grid. There are important differences between the parameterizations used by various climate modeling groups. To evaluate these differences, the authors used two different climate models: the Canadian Middle Atmosphere Model (CMAM) and the National Center for Atmospheric Research/Community Atmospheric Model (CAM3). To investigate the possible impact of the ocean and sea ice, the researchers performed separate model runs in which the sea surface temperature and sea ice concentrations were either specified or allowed to vary with time through coupling with the atmosphere. All model experiments produced similar results, including increased summer precipitation in the subtropics that is very similar to the observed precipitation trend. The results indicate a lack of sensitivity to different climate models, and a limited role for the coupling of the atmosphere with the oceans and sea ice.

Kang *et al*. also addressed the question of what physical mechanism links ozone depletion with changes in tropical precipitation. Their model calculations show that the ozone decline is associated with a poleward expansion of the Hadley cell (a tropical circulation pattern characterized by air masses that rise near the equator, flow poleward in the upper troposphere, then descend in the subtropics and flow back toward the equator in the lower troposphere). What process drives the Hadley cell expansion? Previous studies have shown that an important driver of the Hadley cell is the momentum flux associated with synoptic-scale waves (the atmospheric waves that correspond to day-to-day weather) (*10*, *11*); indeed, Kang *et al*. find that the Hadley cell changes are linked to changes in wave momentum flux. This relationship between ozone depletion and wave momentum flux is tied to a fundamental question: What is the physical mechanism that connects wind and temperature change in the lower stratosphere to changes in these and other variables in the troposphere? This is an open question, and a number of researchers are actively pursuing an answer. One common factor underlying most proposed mechanisms involves changes to synoptic- and planetary-scale waves, particularly their instability (linear and nonlinear), propagation, breaking, and feedback features (*12*–*16*), all of which influence the wave momentum flux. Additional diagnostics studies with observational and model data could go a long way toward enhancing our understanding of both stratosphere/troposphere interaction in general and the linkage between the Antarctic ozone hole and tropical precipitation in particular.

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PALEONTOLOGY

Evolving Large and Complex Brains

X-ray studies of two Early Jurassic fossils offer insight into the evolution of mammalian brains.

R. Glenn Northcutt

During the Mesozoic (~250 million to 65 million years ago), two distantly related groups of reptiles—the cynodont (or mammal-like) reptiles and the coelurosaurian theropod dinosaurs—gave rise to mammals and birds, respectively. Both mammals and birds evolved brains some 10 times as large, relative to a given body weight, as those of their ancestors (*1*). In both groups, these brains contributed to the evolution of the ability to control body temperature (endothermy) and complex social interactions, including parental care and a reliance on learning that even involves tool use (*2*, *3*). The size of most parts of the brain increased in birds and mammals, but the cerebral hemispheres and cerebellum, both of which are involved in sensory and motor integration, underwent particularly spectacular development (see the figure). Although mammals and birds evolved from distantly related groups of reptiles, the higher integrative centers and circuitry of their cerebral hemispheres are very similar, and comparative neurobiologists continue to vigorously debate whether these centers evolved from the same ancestral neural centers (*4*, *5*) or from different ones (*6*–*8*). Speculation about the evolutionary steps leading to large and complex mammalian and avian brains is equally contentious and unresolved, in part because of the rarity of fossil skulls and, until recently, the need to destroy such skulls in order to expose the endocasts (casts molded by the cranial cavity). Typically, endocasts are the only record of the brain's outward appearance in a transitional form, because brains themselves are rarely fossilized.

On page 955 of this issue, Rowe *et al*. (*9*) offer new insights into the early evolution of mammalian brains. Using high-resolution x-ray computed tomography, they reconstructed the endocasts of *Morganucodon* and *Hadrocodium*, two basal mammaliaforms from the Early Jurassic (~199 million to 175 million years ago). These data allow the authors to postulate that the evolution of these large and complex brains occurred in three major steps.

Triassic cynodont reptiles appear to have had relatively poor olfaction and vision, insensitive hearing, and a lack of fine motor coordination (*9*, *10*). Their brains were characterized by small olfactory bulbs, narrow and tubular cerebral hemispheres (exceeded in width by the cerebellum), and a dorsally exposed midbrain. The *Morganucodon* endocast reconstructed by Rowe *et al*. indicates that the brain was almost 50% larger than that of the earlier Triassic cynodonts, with the olfactory bulbs and cerebral hemispheres showing the greatest expansion, and the cerebral hemispheres now wider than the cerebellum and covering the midbrain. It is also likely that *Morganucodon* had body hair. The

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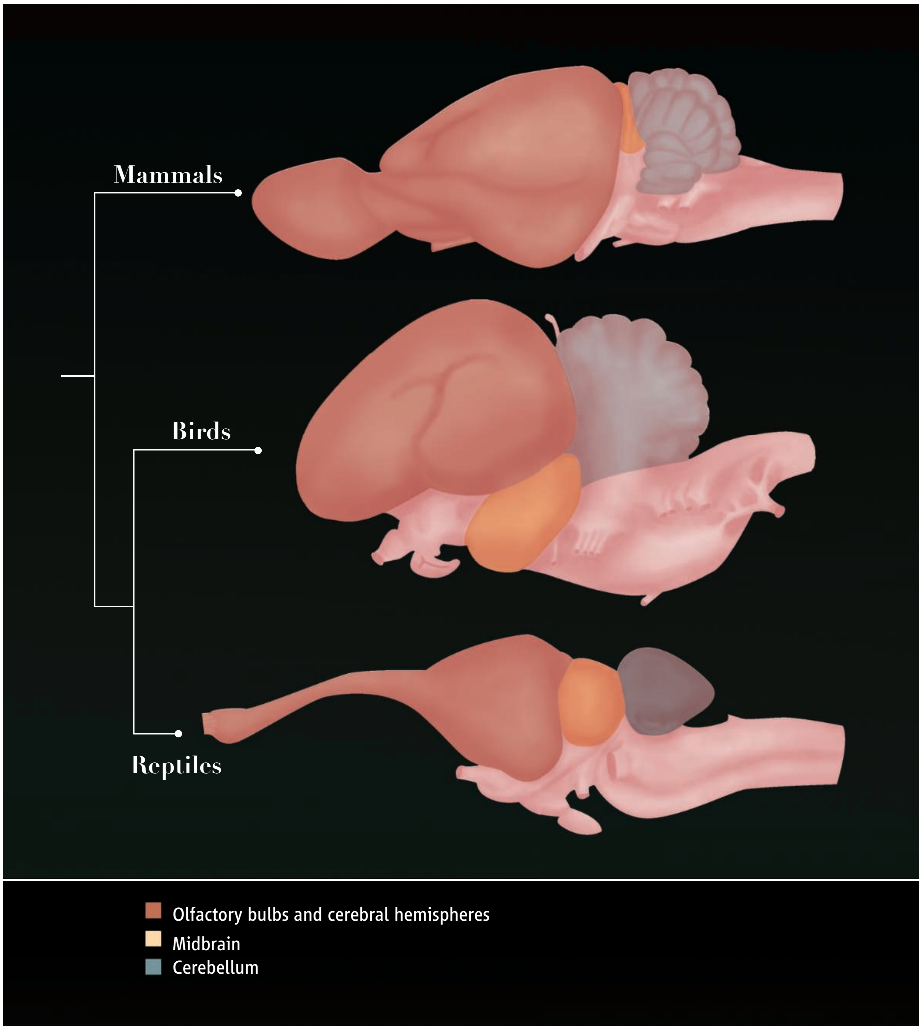
characteristics of its pelt are unknown, but the pelt of a closely related basal mammaliaform, *Castorocauda*, comprised guard hairs and an underfur. An initial phase in the evolution of mammalian brains was therefore characterized by an enlargement of the olfactory bulb, cerebral hemispheres, and cerebellum, suggesting increased olfactory sensitivity and neuromuscular coordination. The presence of body hair also indicates tactile sensitivity and suggests that endothermy and parental care likely occurred at this stage as well.

The reconstructed endocast of *Hadrocodium*, the closest known fossil relative of living mammals, indicates that a second phase in mammalian brain evolution occurred, with brain size again increasing by almost 50%, bringing it within the range of relative brain size in living mammals, with the olfactory bulbs and cerebral hemispheres accounting for most of the increase. In *Hadrocodium*, the relative size of the cerebellum had also increased, which suggests that sensory-motor integration as well as olfactory enhancement characterized this second phase in mammalian brain evolution.

Rowe *et al*. note that the origin of living mammals was apparently accompanied by a third phase in their brain evolution, marked by an increase in olfactory elaboration. The olfactory epithelium expanded by a factor of 10 and was supported by newly evolved nasal bones. The expanded epithelium was also apparently accompanied by a vast increase in odorant receptor genes and by the presence of different types of olfactory receptors, resulting in the high-resolution olfaction that is unique to mammals.



Bigger brains. In terrestrial vertebrates, large brains evolved, independently, twice. Relative brain size in living mammals and birds has increased by at least a factor of 10 over that in living reptiles. Pictured brains show the relative dimensions of the olfactory bulbs and cerebral hemispheres, the midbrain, the cerebellum, and the medulla. In birds, the midbrain lobes have been displaced laterally and ventrally by the expansion of the cerebral hemispheres, and the expansion of the cerebellum in both mammals and birds has resulted in pronounced foliation (folding) of the cerebellum.

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The endocasts of *Morganucodon* and *Hadrocodium* provide the first solid evidence of the stages in mammalian brain evolution. Unfortunately, far less is known about the emergence of the brains of living birds. The endocast of the oldest known Late Jurassic bird, *Archaeopteryx*, reveals reduced olfactory bulbs, large cerebral hemispheres that are in contact with an expanded cerebellum, and lateroventrally displaced midbrain lobes (*11*). All of these neural traits also characterize living birds, and, not surprisingly, the relative size of the brain of *Archaeopteryx* appears to have been intermediate between that of living reptiles and that of living birds (*11*, *12*). All these derived neural traits, plus its skeletal characteristics, suggest that *Archaeopteryx* was capable of flight. The missing part of this story is the appearance of the brain in the coelurosaurian theropod dinosaurs that gave rise to birds. The endocasts of these dinosaurs have not been described, but the endocast of an oviraptorid theropod, *Conchoraptor*, revealed reduced olfactory bulbs, enlarged cerebral hemispheres, displaced midbrain lobes, and an enlarged cerebellum (*13*), as in living birds. Furthermore, the relative brain size in *Conchoraptor* was similar to that in *Archaeopteryx*. This suggests that the neural traits of *Conchoraptor* may have evolved parallel to those of avian theropods, but it is also possible that these neural traits were widely distributed among theropods. If so, many "avian" neural traits may have already been present in coelurosaurian theropods and were co-opted for flight.

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