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Wake 2009

EVOLUTION

The First Four Billion Years

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THE BELKNAP PRESS OF
HARVARD UNIVERSITY PRESS

CAMBRIDGE, MASSACHUSETTS
LONDON, ENGLAND
2009

time. Having established the two events and their synchrony, they elaborated the ecological implications—that a large impact had caused a dust cloud to encircle the earth, cutting off photosynthesis and making it cold and dark for a sufficiently long period so that virtually all land animals over 50 pounds died, along with some 75% of marine organisms—and drew the inference that the impact had caused the extinction of a large fraction of species 65 million years ago, including the extinction of dinosaurs.

Alvarez's framing of the issues provided a broad basis for analysis in diverse fields. His original article has been cited thousands of times in hundreds of scientific journals from biology and geology to medicine and nuclear physics. The original hypothesis has been strengthened by further discoveries, most dramatically by direct evidence of the impact provided by the Chicxulub crater and its unique chemical signature. Further, the theory has captured the popular imagination, increasing interest in scientific investigation and promoting understanding of the unity of science. Alvarez has himself written a popular account of the discovery of the extraterrestrial impact and its implications for life on earth in *T. Rex and the Crater of Doom* (1997).

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—P.M.P.

Amphibians

Limbed vertebrates arose more than 375 million years ago in the Devonian period and they are generally called amphibians. This was a very diverse assemblage of aquatic and terrestrial animals, ranging from the size of a salamander to larger than an alligator. Some of them even became limbless. But by the end of the Paleozoic period and the great Permian extinction, about 300 million years ago, most of the lineages were extinct. A few thrived in the early Mesozoic period before they, too, disappeared. Recent amphibians and the amniotes represent the living descendants of this early radiation. There are three very different kinds of living amphibians. Perhaps the most familiar and certainly the most numerous and widespread are the frogs, which are found on every continent except Antarctica and even on a few oceanic islands (see figure). The salamanders are well known to inhabitants of the north temperate zone, but only one lineage has achieved any success in the tropics. In contrast, the relatively unfamiliar and secretive caecilians are restricted to tropical regions.

Recent amphibians differ dramatically from each other in structure and way of life. All have moist skins, however, and respiration is largely cutaneous.

The eastern spadefoot toad, *Scaphiopus holbrookii*, is a common but little-noticed inhabitant of the southeastern United States. Spadefoot toads breed explosively in the spring in ephemeral ponds after heavy rains; the tadpoles grow rapidly and metamorphose in about three weeks. The juveniles and adults feed on insects and other small animals in the litter layer of forests and burrow into sandy soil to await the next opportunity to emerge and breed. This species is part of an old lineage of frogs with representatives in the southwestern United States, whose tadpoles can complete development in ephemeral pools in the desert in as little as 10 days.

Most salamanders, a few frogs, and one caecilian lack lungs entirely. Although amphibians are associated with moist habitats, many species never enter water.

Frogs (Anura), with more than 5,500 species, have very short bodies, no tail, and well developed limbs, especially long hind limbs that have four main subdivisions. Many frogs are capable of prodigious leaps. Carnivorous as adults, they catch prey with projectile tongues. Frogs display diverse life histories, but the most general and familiar is one in which the sexes congregate in ponds in the spring, with females selecting males as mates based on the qualities of the male call. Mating involves external fertilization of eggs, which are generally laid in clusters or strings. Eggs develop into the distinctive tadpole, a larval form unique to frogs. Tadpoles typically live for one season, during which time they consume primary productivity in the form of algae or vegetation. However, there are many variations on this life history. Tadpoles may live more than one year before metamorphosing into froglets. Many frogs have no larval stage at all but lay large eggs in small numbers that develop directly into miniatures of the adult. Other frogs have tadpoles that may be brooded in special compartments that form in the skin of the back, in specialized pouches on the back, in the vocal sacs of males, or in diverse ecological settings such as arboreal bromeliads. A few frogs are viviparous, with eggs developing in the female reproductive tract, where they receive nourishment.

Salamanders (Caudata), with more than 560 species, resemble ancient amphibians more closely than do frogs or caecilians. They are generalized in structure, with a body of moderate length, a well-developed tail, and two pairs of limbs, with the hind limbs being only a little longer than the forelimbs. Heads of salamanders are relatively smaller than those of frogs, but both groups have well-developed eyes and excellent vision. Salamanders often gather in ponds to breed but males have no calls. Larvae are carnivorous rather than herbivorous, and metamorphosis is far less dramatic than in frogs. Some species remain in a permanently larval or semilarval state and some larvae become very large. Most clades of salamanders have some variation of the basic life history, but the most successful and numerous salamanders, in the family Plethodontidae, have direct development, and it is only these that have successfully invaded the tropics (restricted to tropical America). A few species of salamanders are viviparous.

Caecilians (Gymnophiona) are limbless and extremely elongate, with either a very short tail or no tail. The head is about the same diameter as the strongly segmented trunk, and the eyes are inconspicuous or invisible. A unique sensory organ, the tentacle, is formed from components of the nose and eye and provides environmental information to these mainly burrowing animals. Some caecilians have aquatic larvae but most have either direct development or are viviparous. Among the many viviparous species are forms that are exclusively aquatic. There are approximately 170 caecilian species.

Amphibians play important but generally underappreciated roles in ecosystems. Frogs are important predators as adults, but their larvae can be important consumers in aquatic systems. Removal of tadpoles from streams can quickly lead to overgrowths of algae and formation of large algal mats. Although salamanders are cryptic and less obvious than frogs, in some ecosystems they can be extremely numerous. As carnivores, they contribute to regulation of terrestrial food webs. Members of the soil community, caecilians are major consumers of earthworms, but their ecological role is less well understood than that of frogs and salamanders.

Amphibians have received attention because of concerns about evident declines and extinctions of populations as well as species throughout the world. A recent assessment of the status of amphibian species across the globe found that a higher proportion (more than one-third) were at risk of extinction than for any of the other vertebrate taxa. Especially troubling was the finding that a large percentage of the declines were from unknown causes. While most amphibian declines doubtless are related directly to habitat destruction and modification by humans, there are also other important factors. One infectious disease, a chytrid fungus that attacks the keratin of the skin and leads to dehydration, is responsible for well-documented declines in species living in protected areas in Central America, Australia, and California, where epidemics have been recorded. The disease spreads rapidly, and there is no known way to stop it. Global climate change also is implicated in the declines of many frogs in tropical montane forests. Other factors include effects of introduced species (e.g., for sport fishing), pollution from pesticides and fertilizers, and synergistic interactions of some of these factors and others such as ultraviolet radiation (UVB). However, in many parts of the planet amphibians remain abundant, adding to the puzzlement over the declines.

Today's living amphibians are remnants of a very ancient lineage; each major group can be traced back about 200 million years. Although many appear to be delicate, they were rugged survivors of many extinction events. It is troubling that amphibians that lived happily with the long-extinct dinosaurs should be facing extinction on our watch.

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—*D.B.W.*

Anderson, Edgar (1897–1969)

Edgar Anderson is regarded as one of the leading scientists of plant evolutionary biology during the twentieth century. A product of a number of diverse intellectual traditions, Anderson was able to synthesize newer developments in genetics and cytology to help address more traditional problems in plant systematics. He is best known for his inventive studies measuring variation in natural settings and for his articulation of the concept of introgressive hybridization, a process by which new genetic material is introduced through hybridization and backcrossing. Much of this work was formalized in 1949 with the publication of a small volume titled *Introgressive Hybridization*. The book was widely read and immediately recognized as an original contribution to plant genetics that could shed light on a general theory of evolution.

Anderson, born in Forestville, New York, was the son of an educational administrator and a pianist. His father became a professor of dairy science at the Michigan Agricultural College and moved his family to East Lansing when Anderson was three. From an early age, Anderson was fascinated by plants.

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West-Eberhard, M. J. 2003. *Developmental Plasticity and Evolution*. New York: Oxford University Press. —*J.T.*

Wade, Michael John (b. 1949)

Michael John Wade is an American evolutionary geneticist who used flour beetles of the genus *Tribolium,* as well as theoretical models, to investigate group (or interdemic) selection, kin selection, Sewall Wright's "shifting balance" theory, sexual selection, espistasis, maternal genetic effects, and speciation.

The oldest of eight children, Wade studied biology and mathematics at Boston College, graduating in 1971. Interested in combining mathematics and biology, Wade went to the University of Chicago's now-defunct Theoretical Biology program for graduate work. Coadvised by the population geneticist Montgomery Slatkin and the ecologist Thomas Park, Wade conducted the first experimental study of group selection by selecting flour beetles based not on individual characteristics of the beetles, but on aspects of the populations from which they arose. A strong response to selection was evident after only three generations of selection: populations in lines selected for high population size and those selected for low population size evolved substantial differences, showing that interdemic selection could be a powerful evolutionary force, at least under certain conditions.

From 1975 to 1998 Wade held a position at the University of Chicago, first in the Biology Department and culminating as chair of Ecology and Evolution (1991–1998). He moved to his present position at the University of Indiana in 1998. In 1980 Wade conducted the first experimental test of kin selection, observing that cannibalism in flour beetles evolved along different evolutionary trajectories depending on patterns of genetic relatedness determined by the mating system. Wade and his student Charles Goodnight used laboratory metapopulations to test the efficacy of Wright's "shifting balance" theory, a model of evolution that involves random genetic drift resulting in peak shifts in local subdivided populations and the spread of new, adaptive gene combinations across the larger population via migration and selection. They observed the largest response at intermediate levels of drift and interdemic selection.

Wade has made several important theoretical contributions. He was the first to show that allele frequency change under kin selection could be partitioned into separate components of change within and among kin groups. In sexual selection, he showed that there was a necessary relationship between the variance in reproductive success in males and that in females, explaining why selection acting on males was often many times greater than that acting on females. He showed that genes with maternal effects evolve much more readily in haplo-diploids than in diplo-diploids and, with his former student, Tim Linksvayer, argued that maternal effects theory provides a better account of the evolution of eusociality in the Hymenoptera than the haplo-diploidy hypothesis. His theoretical studies of gene interactions have shown how epistasis within populations can accelerate the adaptive divergence between isolated populations, contributing to speciation.

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Wake, David B. (b. 1936)

David Wake is one of America's leading evolutionary biologists. His numerous research contributions span many fields, including functional and comparative morphology, behavior, developmental biology and ontogeny, ecology, biogeography, population genetics, molecular evolution, taxonomy, systematics, and phylogeny. These studies have been motivated by a central and overarching interest in evolutionary patterns and the processes that produce them. Although the goal has been to identify and explore mechanisms of evolutionary diversification that are broadly applicable to all organisms, Wake's empirical work has focused almost exclusively on a single evolutionary lineage, the lungless salamanders of the family Plethodontidae. Largely through the efforts of Wake and his numerous students and collaborators over the nearly five decades that spanned the last half of the twentieth century and continue into the twenty-first, plethodontid salamanders are one of the most comprehensively investigated and fully documented instances of adaptive radiation in the history of evolutionary biology.

David Burton Wake was born on June 8, 1936, in Webster, South Dakota. Much of the Upper Midwest of North America had been extensively settled by Scandinavian immigrants in the late nineteenth and early twentieth centuries, and both of Wake's parents were of Norwegian descent. At the age of 17 Wake relocated with his immediate family to Tacoma, Washington, where he completed precollegiate education. As was typical of many children of Scandinavian immigrants living in the Pacific Northwest at the time, Wake enrolled at Pacific Lutheran College (now Pacific Lutheran University), where he completed his undergraduate degree in biology in 1958. From there he advanced to graduate school in biology at the University of Southern California (USC) in Los Angeles, where he worked under the supervision of Jay M. Savage for both master's (1960) and doctoral (1964) degrees. Savage, a leading tropical ecologist and biogeographer, was at that time launching a broad research effort on amphibians and reptiles of Central and South America, and he promoted Wake's interests in plethodontid salamanders, which have their principal species diversity in the neotropics. Savage's close association with the Los Angeles County Museum of Natural History also provided Wake with valuable experience with research collections in herpetology and facilitated his early studies in taxonomy and systematics.

Wake left USC in 1964 to assume his first full-time academic position, at the University of Chicago, where he remained for five years. In 1969 he returned to California to join the Zoology Department faculty at the University of California, Berkeley, and become curator of herpetology at Berkeley's Museum of Vertebrate Zoology (MVZ). This began a long and productive association with the MVZ, which Wake served as director for 27 years until 1998. Under Wake's direction the MVZ became one of the world's leading centers for research and teaching in evolutionary biology.

In purest terms Wake's research addresses a fundamental question in evolutionary biology: why are there so many different kinds of organisms? His work has been influential because it exemplifies a comprehensive approach to analysis of evolutionary diversification that evaluates the roles of both extrinsic and intrinsic factors and simultaneously considers a wide range of biological attributes, from molecules to organisms and their environments. The study of evolution since the modern synthesis has until recently focused largely on extrinsic factors as determinants of evolutionary change, such as the role of the external environment in mediating natural selection for adaptations. Wake's work has highlighted the need for complementary studies that evaluate the potential role of intrinsic factors, such as lineage-specific developmental traits or conserved anatomical features, which may both facilitate and constrain diversification in significant ways. A full understanding of the evolution of any taxon is likely to require such a holistic approach, which incorporates all relevant information.

Wake is the author of more than 250 peer-reviewed publications, as well as popular articles and books. He has received numerous honors and awards, including election to membership in the U.S. National Academy of Sciences in 1998.

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—*J.H.*

Wallace, Alfred Russel (1823–1913)

Alfred Russel Wallace was one of the most brilliant theoretical and field biologists of the nineteenth century. His fame in the history of evolution rests primarily upon his discovery, independently of Charles Darwin, of the theory of evolution by natural selection. Wallace was a meticulous field observer, a prolific generator of ideas on a broad range of issues ranging from evolutionary biology to social and political concerns, and a theoretician whose work laid some of the main foundations for the scientific study of modern zoology and botany.

By 1844 the 20-year-old Wallace had collected and analyzed an extensive array of local British plants. In 1844 he met Henry Walter Bates. An accomplished entomologist, Bates encouraged Wallace to move beyond the bounds of botany to a more general study of natural history. During the next few years Wallace read Charles Lyell's three-volume *Principles of Geology* (1830–1833), Robert Chambers's (then-anonymous) *Vestiges of the Natural History of Creation* (1844), William Lawrence's *Lectures on Comparative Anatomy, Physiology, Zoology, and the Natural History of Man* (1819), and Charles Darwin's *Voyage of the Beagle* (1839)—works that dealt, either explicitly or implicitly, with evolutionary speculations, the origin of species, the geographic distribution of animals and plants, and the difference between species and varieties. When Bates and Wallace met again in the summer of 1847, the two made the fateful decision to journey to the tropics. Wallace and Bates left England on April 26, 1848, destined for Pará (now Belém), Brazil. Thus began the first of the two tropical journeys that were to transform Wallace's life and the emerging science of evolutionary biology. After a four-year exploration of the Amazon basin of South America (1848–1852), Wallace returned to London. He published *A Narrative of Travels on the Amazon and Rio Negro* (1853), which established his reputation as the foremost analyst of the geographic distribution of animals and plants (biogeography). The recognition that the distribution of closely allied species was often marked by surprisingly precise and abrupt barriers was the most important scientific achievement of his Amazonian travels. However, although Wallace had been committed to some form of general evolutionary theory since 1845, he was not yet prepared to posit an explicit evolutionary mechanism in *A Narrative of Travels.*

Convinced that another voyage of exploration was the most certain means of providing the data required for the theoretical elucidation of what was termed *the species problem* (i.e., how new species originate from preexisting ones), Wallace decided on an expedition to the Malay Archipelago. He arrived in Singapore on April 24, 1854, to begin eight years of intensive travels in the islands of Java, Borneo, Celebes, New Guinea, and Bali and in many smaller islands in the archipelago. From 1854 to 1862 Wallace covered nearly 14,000 miles and collected the vast amount of 125,000 (primarily faunal) specimens. He encountered animals, birds, and insects in bewildering variety