Macroevolution: Evolution above the Species Level

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Speakers at the "Macroevolution: Evolution above the Species Level" symposium, held at the National Association of Biology Teachers annual meeting last October, focused on macroevolutionary processes, the evolution of key innovations and major lineages of organisms, and the evidence for these processes.

The American Institute of Biological Sciences (AIBS) and its cosponsors, the Biological Sciences Curriculum Study (BSCS) and the National Evolutionary Synthesis Center (NESCent), hosted the third special symposium on evolution at the annual conference of the National Association of Biology Teachers. About 200 educators attended the day-long symposium on macroevolution, held on 14 October 2006 in Albuquerque, New Mexico.

The most obvious difference between macroevolution and microevolution is one of scale. Macroevolutionary processes, such as origins, diversifications, and extinctions, happen on a grand scale and take time—geologic time. To understand such processes requires historical evidence, for example, fossils dating back hundreds of millions of years, or slowly evolving molecular sequences. To tell us anything, geological data must persist for eons. "Some in the antievolution community assert that microevolution happens but not macroevolution," Gordon Uno, chair of the AIBS education committee, pointed out in his opening remarks, "because they believe there is no evidence for it."

Origins and body plans

Nicole King, from the University of California–Berkeley, spoke first on the origin of animals and the transition from unicellularity to multicellularity, which represents a pivotal event in the history of life on Earth. The origins of the vast diversity of animal life we currently see can be traced back over a billion years, to a time for which there is no real fossil record. Given this limitation, which living organisms will best help us identify what the first organisms were like?

King thinks the answer may be revealed in the study of choanoflagellates. King is confident that the simple protozoa are the closest living relatives of animals. They can be found in almost any body of water and are easy to culture in the lab. Her work has already provided evidence for the expression in choanoflagellates of protein families required for animal cell signaling and adhesion. Genes shared by choanoflagellates and animals were most likely present in their common ancestor and may shed light on the transition to multicellularity.

King's lab is developing techniques for manipulating gene activity of choanoflagellates in vivo, establishing a reference point for studies of gene family evolution in animals. "Multicellularity evolved many times over," said King. "Animals, fungi, plants, and other multicellular lineages evolved multicellularity separately, and each lineage has a different common ancestor. Which means that the mechanism by which multicellularity developed [in each lineage] is evolutionarily different and unique." This raises interesting questions. For example, were unicellular organisms preadapted for multicellularity? In other words, were sequences that served certain biological functions in the unicellular ancestor coopted for new roles in a multicellular organism? Or were key innovations, novel sequences leading to entirely new functions, necessary for the leap?

Nipam Patel, also of the University of California–Berkeley, talked about the evolution of development mechanisms, in particular the development and evolution of animal body plans. "Macroevolution," he explained, "is the change in development over large spans of time, that is, millions of years. If we want to understand evolution, we need to understand development in a sophisticated way, at a molecular and genetic level. If we

know that, we can ask how developmental changes actually allowed organisms to generate new morphologies."

Scientists are just beginning now to understand the genetic basis for morphological macroevolution. The fruit fly, *Drosophila*, has a short life cycle and complex body plan, so it makes an ideal model organism for studying development. "We can use forward genetics," says Patel. "That is, we can randomly mutate or disable genes and ask what goes wrong with the embryo, with an eye towards finding mutations which change the body plan." In one groundbreaking experiment, the antennae of the fly were transformed into legs. In another, a mutation transformed the thoracic area of a fly, producing two pairs of wings instead of one. These particular transformations were caused by mutations in what are called the homeotic genes.

Homeotic genes are present in all animals. In *Drosophila*, there are eight of these genes, clustered together and expressed along the anterior to posterior length of the body axis. All these genes are closely related and encode transcription factors that turn many other genes on or off, making them master regulatory genes. One of the most stunning discoveries in developmental biology is how well conserved homeotic genes are in other organisms. Just as in flies, the human body plan is controlled by anterior–posterior expression of homeotic genes that control regionalization.

More recently, changes have been identified in the homeotic genes that alter the spatial expression of these genes, and appear to be responsible for some of the evolutionary changes in body plans between organisms. For example, changes in the anterior expression boundary of one of these genes appear to be responsible for the evolutionary changes in the number, position, and morphology of feeding appendages in crustaceans. Similarly, shifts in homeotic gene expression also explain the differences in the types of vertebrae in the backbones of different vertebrate species.

Radiation and extinction

Jeffrey S. Levinton, of the State University of New York at Stony Brook, focused on diversification in his presentation. Levinton's research looks at the Cambrian explosion of animal life, dating the radiation of the animal phyla by means of molecular divergence estimates. The fossils generally point to a sudden occurrence near the beginning of the Cambrian, whereas the molecular clock evidence points to an earlier divergence.

Pictured above are five of the six symposium speakers. They are, from left to right, Jeffrey S. Levinton, David Jablonski, Scott Hodges, Nipam Patel, and Philip Gingerich. The sixth speaker was Nicole King. Photograph: Jory Weintraub.

"Evidence serves only to test hypotheses," said Levinton. "Much of what we know about the Cambrian explosion hypothesis is an issue of timing—the idea of something happening so rapidly in a short time, perhaps in less than 30 million years. The Cambrian explosion is when most major groups of animals with bilaterally symmetrical body plans first appear in the fossil record. Many of the appearances of developmental novelties in this period are very important in the rise and diversification of animal body plans."

The idea of a sudden rise of animal life was mentioned by Darwin, who thought that there must have been a long period of time during which modern animal groups diverged. With the discovery of the Burgess Shale in the Canadian Rockies and more recent discoveries from the Early Cambrian, scientists have ample fossils to assemble evolutionary trees of the bilaterian animal phyla. Evidence of the radiation continues to be found, and techniques such as radiometric dating help to test hypotheses of the timing of the radiation. There is clear documentation, said Levinton, that the history of life is not one of "a steady increase in numbers or a simple linear trajectory towards the modern world. Instead, the story is one of rapid radiations, fluctuations in biodiversity, and mass extinctions. The Cambrian explosion marks the appearance of most bilaterian multicellular animal designs, but the actual divergence of these groups may have occurred many millions of years before the Cambrian."

Extinction was also discussed at the symposium, in a presentation by David Jablonski, of the University of Chicago. He examines living and fossil organisms to determine their environmental histories and the evolutionary significance of extinction events.

"The fossil record is punctuated by extinction events at all scales," Jablonski said, "and at least 95 percent of the species that have ever lived are extinct." The "Big Five" mass extinctions, though global in scale, were geologically brief events—less than a million years—that are estimated to have removed "more than 50 percent of living species and affect[ed] a broad spectrum of organisms."

Mass extinctions are important in macroevolution because they change the rules of survival, eliminating the dominant groups of the time and allowing adaptations to hitchhike on traits, such as geographic range size, that determine

Teachers work through activities in a workshop conducted by the Biological Sciences Curriculum Study. Photograph: Jory Weintraub.

survivorship during extinction episodes. Mass extinctions homogenize the biota, and they encourage postextinction evolutionary bursts. Recoveries, on the other hand, are slow in human timescales, and they are unpredictable.

Whale fossils and nectar spurs

Philip Gingerich, of the University of Michigan–Ann Arbor, has been a "fossil hunter" in several parts of the world, Egypt and Pakistan among them. His team was the first to find whales with feet, and the first to find skeletons that linked carnivorous whales to ancient artiodactyl land mammals, which were plant eaters. In his presentation, he talked about the fossil evidence for the origin of whales.

"The process of evolution is so fast," said Gingerich, "and life goes back so far, that the history of life is almost entirely a reflection of environmental perturbations in Earth's history. The process is continuous even if the resulting pattern is punctuated." The fossil record for whales is particularly interesting because it shows that whales returned to an aquatic life after spending time on land.

The oldest whale fossil, *Himalayacetus*, was found in marine strata that indicated it was about 53 million years old. Other whale fossils from the early Eocene, such as the riverine *Pakicetus*, show that all of the earliest whales that we know about so far were semiaquatic. Nearly complete skeletons of *Rodhocetus* and *Artiocetus* represent foot-powered swimmers with large webbed feet. But by the middle to late Eocene, ancient whales such as the *Dorudon* were swimming like the whales of today, using their tail—a transition from land to sea once thought inexplicable in terms of evolution.

Scott Hodges, from the University of California–Santa Barbara, described his findings on the genetic structure of plant adaptation, diversity, and reproduction. He investigates questions about plant diversity, inquiring whether particular traits make a plant group more prolific than others. He also wants to understand more generally how we identify significant patterns and test for underlying mechanisms.

One macroevolutionary pattern of interest is that some groups of organisms are represented by very many species, while one or only a few species represent others. Are there biological processes or features responsible for these differences? One way to test whether a trait has affected species diversity is to make multiple sister-group comparisons. Sister groups are the same age and thus have had equal amounts of time to diversify.

There are about 20 different groups of plants that independently evolved what are known as nectar spurs. In these plants, one part of the flower extends into a tube filled with nectar, and pollinators must probe down the tube to get at the sweetness, and in so doing pollinate the flower. After identifying sister-group relationships, Hodges discovered that there are significantly more species in the groups with spurs than in the nonspur sister groups.

"Finding this association," he said, "suggests that nectar spurs affect the process of speciation or extinction." Hodges hypothesized that spurs cause animals to visit the flowers in a specific way and attract one pollinator to the exclusion of another, so that reproduction is isolated and speciation is promoted. His experiments have shown that simple differences such as color, length, and orien-

Visitors to the exhibit hall learned how to use the CD that supplements the symposium from Kristin Jenkins, of the National Evolutionary Synthesis Center (NESCent). AIBS shared the exhibit booth with NESCent. Photograph: Jory Weintraub.

tation of nectar spurs strongly affect pollinator visitation and thus reproductive isolation.

Curricular materials and other resources

In addition to the talks by evolutionary biologists, the symposium offered classroom activities from BSCS that use the "5E" model: engage, explore, explain, elaborate, and evaluate. The 5E model, based on a constructivist approach to teaching, encourages students to take an active role in learning. Project directors and science educators Mark Bloom and Anne Westbrook led two workshops. In one, participants explored the concept of species from a variety of biological perspectives. Biological examples were presented that illustrate the difficulty in using a simple definition for species. In the other, participants acted as scientists trying to decide whether different populations of salamanders living in California constitute different species or subspecies. Participants received a CD, produced by NESCent, to supplement the presentations and workshops (a Web-based version is available at *www.nescent.org/eog/NABT/*).

In her closing remarks, Kathleen Smith, director of NESCent and professor of biology at Duke University in Durham, North Carolina, summed up the salient points of the symposium:

> The genetic toolkit is important in the study of macroevolution. The same sets of genes are used again and again, so that major evolutionary change does not necessarily require major genetic changes.
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> There is complexity in the tempo and mode of evolution. There are many different patterns in macroevolutionary events.
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> Many macroevolutionary changes depend on significant changes in the environment, some of which have led to large extinction events.
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> The processes of microevolution and macroevolution are continuous.

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Slides and audio recordings from the symposium presentations will be available on the AIBS Web site, www.aibs.org. *Presentations from the 2005 symposium are now online at* www.aibs.org/special-symposia/2005-NABT.html.