

**Syllabus for Honors Biology 159:  
An Introduction to Science & Biology**

**Instructor:** David L. Alles (If you wish to contact me, please do so by e-mail at < alles@biol.wvu.edu >.)

**Lecture / Discussion:** Tuesday and Thursday 2:00 pm to 4:20 pm

**Course Web Site:** <http://fire.biol.wvu.edu/trent/alles/159index.html>

**Grades:** Your grade for the course will be based on what you earn out of a total of 550 possible points. The points are divided as follows:

Class Discussions—450 points (18 discussions at 25 points each)

Final Exam—100 points

Your final grade for the course will be based on the following percentages of points earned.

A+	96-100%	(4.0)	
A	92-95%	(4.0)	A range 89-100%
A-	89-91%	(3.7)	
B+	86-88%	(3.3)	
B	82-85%	(3.0)	B range 79-88%
B-	79-81%	(2.7)	
C+	76-78%	(2.3)	
C	72-75%	(2.0)	C range 69-78%
C-	69-71%	(1.7)	
D+	66-68%	(1.3)	
D	63-65%	(1.0)	D range 60-68%
D-	60-62%	(0.7)	
F	0-59 %	(0.0)	Failing

**Course Policies:**

- Makeups assignments will only be accepted if arrangements are made prior to the assignment due date *and* approved by me.
- This applies as well if you are sick. If, however, your reason for missing a class discussion is sickness, you must, in addition to making prior arrangements, obtain a doctor's or health services' excuse.
- **Leaving a telephone message or sending an e-mail *does not* give you prior approval for missing a class discussion.**

- All makeup work or other assignments must be turned in *before* the last week of lectures to receive credit.
- The final test is cumulative. Test questions will come predominately from the material presented in lecture.
- **A note about electronic devices:** Manners and rules of decorum have not changed. Rude behavior is still just rude behavior. Therefore, do not use any electronic devices in the classroom, cell phones for instance, that may interrupt lectures or discussions.

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### Required Books for Honors Biology 159

Required books for the course are:

#### **The Pony Fish's Glow: And Other Clues to Plan and Purpose in Nature**

by George C. Williams

- **Paperback:** 192 pages
- **Publisher:** Basic Books; (April 1, 1998)
- **ISBN:** 0465072836

#### **Life on a Young Planet: The First Three Billion Years of Evolution on Earth**

by Andrew H. Knoll

- **Hardcover:** 277 pages
- **Publisher:** Princeton University Press; (April 1, 2003)
- **ISBN:** 0691009783

#### **Mapping Human History: Genes, Race, and Our Common Origins**

by Steve Olson

- **Paperback:** 304 pages
- **Publisher:** Mariner Books; 1st Marine edition (April 1, 2003)
- **ISBN:** 0618352104

On the following pages you will find an overall review of George C. Williams' work, a book review of Andrew Knoll's *Life on a Young Planet*, and a review of Steve Olson's book *Mapping Human History*, all from the journal *Science*.

# Stretching the Limits of Evolutionary Biology

In shaping current thinking about natural selection and adaptation, Williams's influence has spread beyond his field to encompass economics and medicine as well

**STONY BROOK, NEW YORK**—On a recent sunny Saturday, scientists from the United States, Canada, and Europe gathered at the State University of New York (SUNY), Stony Brook, to talk about their research. A geneticist from Harvard University spoke about preeclampsia, a potentially fatal condition during pregnancy. An ichthyologist described the loyalty—or lack thereof—that male fish show to the mothers of their offspring. Psychologists discussed economic decision-making. A psychiatrist reviewed some of the genes associated with clinical depression.

This lineup might seem like a random trawl through the sciences. But the researchers who assembled in the auditorium were there for a common purpose: to honor the lanky, white-bearded man who sat quietly in the fourth row, George C. Williams. He may not be as familiar as his peers Richard Dawkins or the late Stephen Jay Gould. But Williams, who spent 25 years at Stony Brook, is generally considered one of the major architects of the study of evolutionary biology, and the meeting's far-ranging talks reflected the scope of his influence.

“George Williams was instrumental in making natural selection an intellectually rigorous theory,” says Stephen Pinker of Harvard University, one admirer who wasn't at the meeting. “He forced people to think about how selection actually works and how we can see its fingerprints in the natural world.”

In the 1950s, when Williams was doing his graduate work at the University of California, Los Angeles, the science of evolutionary biology had just gone through two decades of spectacular advances. Ronald Fisher and Theodosius Dobzhansky, among others, had used the new science of genetics to work out some of the molecular underpinnings of evolution. Natural selection

was now recognized as a change in the frequency of genes in a population. Yet one important part still hadn't been nailed down: the nature of adaptations. It was clear that adaptations evolved, but few biologists had given serious thought to the rules that govern the process.

Williams was struck by the ad hoc way that even prominent biologists would explain an adaptation. They'd claim that it had evolved because it provided some benefit; often, an entire population or species supposedly benefited. Williams recalls a lecture he heard by Alfred Emerson, a zoologist at the University of Chicago, about why people age and die. “He said growing old and dying is a good thing,” Williams says. “We've evolved to do it so we get out of the way, so the young

people can go on maintaining the species.”

“I thought it was absolute nonsense,” says Williams. Whenever people like Emerson claimed that an adaptation was for the good of a species, they never offered an explanation of how, from one generation to another, that potential benefit produced real evolutionary change. Williams suspected that in most cases, no such explanation existed. For him, the primary engine of evolutionary change was the one Darwin had written about in the *Origin of Species*: competition among individuals

of the same species. Most biologists in the 1950s simply failed to think seriously enough about how natural selection could produce adaptations, he says.

Williams wrote a series of papers critiquing the notion that adaptations were generally good for a group or a species, rather than an individual. Ultimately, his work led to his classic 1966 book *Adaptation and Natural Selection*. In it, Williams explained that almost every aspect of biology, no matter how puzzling, was the

result of strict natural selection working on individuals.

Take a school of fish, for example. It seems as if every individual cooperates for the good of the group, working with others to avoid predators, even if it means that individual gets devoured in the process. Williams argued that the schooling behavior could instead be the product of individual fish trying to boost their personal chances of survival—by trying to get in the middle of the school and by watching other fish for signs of approaching predators.

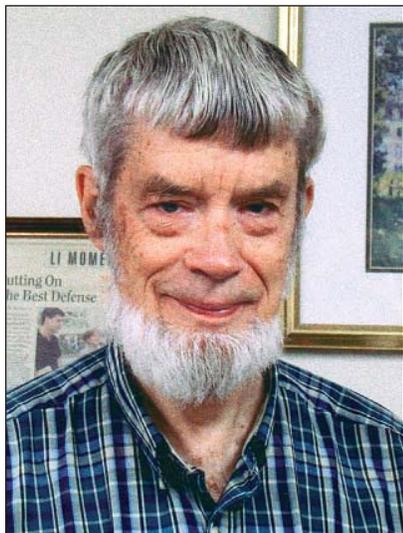
Williams's book had an immediate, profound effect. “It fundamentally changed how biologists think about how natural selection works,” says Randall Nesse, a psychiatrist at the University of Michigan, Ann Arbor, whose own studies of depression and other disorders are influenced by Williams.

One reason that the book was so effective was that Williams demonstrated how natural selection could influence the full course of a species' life history. It wasn't necessary to think of growing old as being for the good of the species, for example. Instead, Williams argued that the decline of old age could be caused by pleiotropy—in other words, the harmful side effects of genes selected for advantages they offered during youth. Just as long as the advantages of these genes outweighed the disadvantages, they would become widespread.

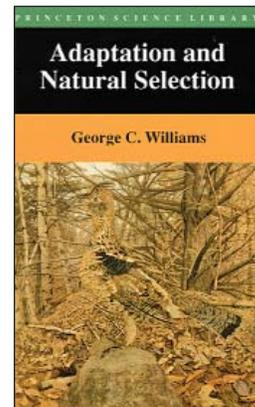
Ironically, cancer, declining stamina, deteriorating vision, and various diseases of old age could all be the result of natural selection, says Williams: “Pleiotropy is the ultimate reason for all these things.”

Williams argued that an organism faces these sorts of evolutionary tradeoffs throughout its lifetime: how much energy to invest in maturing before starting to reproduce, for example, or how much to invest in raising offspring before searching for another mate. Natural selection should find a balance between an animal's current investment in itself and its offspring and in potential future benefits. Williams speculated that animals could also keep track of how these factors change and adjust their behavior accordingly—like an investor deciding which stocks to keep or sell.

Researchers have now amassed a wealth



**Darwinian.** George Williams's dogged focus on natural selection has won both converts and skeptics.



of evidence showing that animals do alter their strategies in the face of changing conditions, as Williams proposed, investing more or less care in raising their young. Williams also suggested that his argument could apply to humans as well as animals, helping lay the groundwork for a Darwinian approach to human behavior (frequently referred to as evolutionary psychology).

“George was a supportive figure from the get-go,” said Martin Daly of McMaster University in Ontario, a leading evolutionary psychologist. At the meeting, Daly and his wife, psychologist Margo Wilson, illustrated Williams’s influence by describing an experiment they published in the 7 May issue of *Biology Letters*.

The experiments grew out of a well-known economic phenomenon called “future discounting.” People typically choose a small amount of money they can get today over a larger amount they will get in the distant future. Daly and Wilson proposed that the value people put on resources in the present and the future is influenced by natural selection: The better one’s prospects for reproductive success look in the near term, the more one will discount the future.

“We wanted to see if we could do an experiment that would manipulate people’s discount rate,” said Wilson. First, they ran a simple discounting experiment on a group of male subjects who, as expected, tended to choose small money now over bigger sums far in the future. Then they ran the experiment again, but after showing the men a picture of an attractive woman.

(They gave their subjects no explanation about the picture.) Daly and Wilson found that seeing that picture made the men even more likely to choose money in the short term. (Pictures of cars, by comparison, didn’t affect future discounting.)

Although Williams has convinced many people of the value of his ideas, the notion that human behavior can be broken down into such finely tuned reproduction-boosting adaptations is, to say the least, controversial. The late Stephen Jay Gould liked to call this approach “Darwinian fundamentalism,” and he credited Williams’s *Adaptation and Natural Selection* as “the founding document for this ultimate version of Darwinian reductionism.”

Likewise, Gould and others—such as Elliot Sober of the University of Wisconsin, Madison, and David Sloan Wilson of SUNY Stony Brook—have accused Williams’s followers of focusing obsessively on individuals and reflexively dismissing the possibility of group selection or species selection. Sober and Wilson, for example, argue that

cooperative behavior may have evolved in our own species because cooperative groups outcompeted uncooperative ones. It’s a testament to Williams’s stature that Sober is careful to distinguish between Williams and Williams’s followers. “Williams is less hostile to group selection than his followers are. It’s ironic that he’s become the icon for the anti-group selectionists.”

Although speakers at the meeting didn’t directly address these controversies, they did confront a major disappointment: the failure of Williams’s adaptationism to influence



**Tradeoffs.** Like investors deciding which stocks to keep or sell, animals may weigh how much to invest in current and future offspring.

medicine. Since the early 1990s, Williams has argued that because medicine compensates for the shortcomings of our adaptations, doctors should get a sound grounding in evolutionary biology. Exploring the evolutionary forces that have shaped our bodies could produce new hypotheses about the causes of diseases, he maintains, and point the way to more effective treatments.

At the meeting, evolutionary biologist David Haig of Harvard University offered an example of the insights that the Williams approach can offer to pregnancy. Haig pointed out that during a pregnancy, the evolutionary interests of mother and child overlap in some ways but conflict in others. The investment a mother puts into the child can potentially reduce the amount of energy she could put into future children. The child, on the other hand, benefits if its mother focuses all her attention on it.

Haig showed how this perspective on pregnancy can shed light on preeclampsia, a mysterious condition that causes dangerously high blood pressure in pregnant women.

Haig suggested that preeclampsia might be the result of a fetus trying to draw nutrients to the placenta. He proposed that, when in need, a fetus might release factors into the maternal bloodstream that damage the walls of the mother’s blood vessels, thereby raising the resistance of her circulatory system. Because the resistance in the vessels feeding the placenta would be lower, more blood would flow to the fetus.

At the Stony Brook meeting, Haig reported on recent research by Ananth Karumanchi of Harvard Medical School in Boston and his colleagues, who studied a curious protein released by the fetal placenta that blocks the repair of damaged blood vessels. Karumanchi and his co-workers found that levels of this substance—known as placental soluble Fms-like tyrosine kinase 1 (sFlt1)—rose significantly in women with preeclampsia just before the symptoms emerged, a finding that Haig cites as “evidence of the antagonistic relationship of fetal and maternal factors.”

“It’s an outstanding hypothesis,” Karumanchi says of Haig’s research. “It makes a lot of sense in my mind.” He points out that even in normal woman who do not experience preeclampsia, levels of sFlt1 rise toward the end of pregnancy. “As the fetus is growing, it needs to get more blood to itself, and so it secretes more of the protein,” he speculates.

Yet at the meeting, Haig readily admitted that this evolutionary approach has not yet penetrated the medical community. “Darwinian ideas are not making a big impact” on the way doctors think, said Haig, pointing out that at his own Harvard Medical School, students still get no training in evolutionary biology.

Karumanchi admits that he learned about Darwinian medicine only when Haig approached him recently. “I’d never thought that evolutionary biology was important before now,” he says. “There’s a big barrier between people like me who are physicians and people who are in biology departments. Those barriers need to be broken.”

Mart Gross, a biologist at the University of Toronto, agreed that Williams’s ideas have yet to produce as much impact outside of evolutionary biology as he and other followers believe they deserve. He, for one, puts an optimistic stamp on the situation. “It’s still very early on,” says Gross. “After all, think how long it took for Darwin’s ideas about natural selection to really take hold. I think Williams is at the same stage.” It is clear that just as Darwin remained controversial long after his death, the legacy of George Williams’s work will stimulate research for decades to come.

—CARL ZIMMER

Carl Zimmer is the author of *Soul Made Flesh: The Discovery of the Brain—and How it Changed the World*.

## PALEONTOLOGY

### The Crucial 80% of Life's Epic

Guy M. Narbonne

**T**he history of life on Earth, from its inception through its gradual development to the world we see around us, has captivated paleobiologists and has led, over the years, to several different but largely successful attempts to recreate the excitement of global evolution in book form. Andy Knoll's *Life on a Young Planet* stands apart from its predecessors in two fundamental respects. First, Knoll is perhaps the most qualified person to write such an epic: a renaissance man whose text is filled with insightful quotes from authors

**Life on a Young Planet: The First Three Billion Years of Evolution on Earth**  
by Andrew H. Knoll  
Princeton University Press, Princeton, NJ, 2003. 287 pp. \$29.95. ISBN 0-691-00978-3.

ranging from Darwin to Dickens to Dyson; a researcher who has worked for nearly three decades at the intersection of modern biology, paleobiology, Earth science, and chemistry; and a professor of geology and biology at Harvard University who was taught by, and in turn has taught and worked with, some of the greatest minds in Precambrian paleobiology. Second, in contrast with the usual historical recounting of the development of life—which Knoll amusingly characterizes as “the naturalist’s Generations of Abraham: bacteria begat protozoans, protozoans begat invertebrates, invertebrates begat fishes, and the like”—this book describes the coevolution of life and Earth as an integrated biochemical system that has profoundly and irrevocably changed over time.

Knoll begins at the time-honored starting point for books on the history of life, with the complex Cambrian fossils that define the base of the Phanerozoic eon. But, whereas most recountals then move forward in time to eventually culminate in our modern era, he instead steps backward to elucidate the 3 billion years of evolution that led to the Cambrian explosion of shells and brains. This immediately brings us to Darwin’s dilemma: the apparently abrupt appearance in the earliest Cambrian strata of abundant, morphologically complex fossils that encompass nearly every phylum of marine life.

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Knoll maintains that Darwin’s search image for Precambrian life was wrong. Over the next two chapters, he introduces readers to the cutting-edge techniques in biology and Earth science that provide the tools necessary to go beyond Darwin’s dilemma. Each ensuing chapter then documents a critical stage in the history of life based on a locality (ranging from southern Africa to western Australia to northern Siberia) that exemplifies the biota, rocks, and intellectual problems associated with the time period of interest.

Knoll is not afraid to wade into the major controversies, nor is he afraid to use words like “maybe” and “perhaps” where the evidence is not yet conclusive. He recommends caution in interpreting the earliest putative fossils, but believes that biomarkers for cyanobacteria and eukaryotes in rocks 2.7 billion years old and apparently modern carbon-isotopic ratios in even the oldest preserved sedimentary rocks (3.3 billion years old) imply that life originated very early in the history of our planet. He is unimpressed with the evidence for life in the Martian meteorite ALH 84001, but views the absence of such evidence as an urgent call to investigate its source planet directly, using the most modern methods and approaches. He is persuaded by evidence that the Neoproterozoic glaciations (between 770 and 600 million years ago) were the most extreme ice ages to have ever affected our planet (with ice sheets on every continent and reaching sea level in equatorial regions), but believes that the survival of diverse eukaryotic lineages imply that “snowball Earth” had a discontinuous ice cover with numerous marine refugia.

*Life on a Young Planet* includes three salient points that are absent from most or all previous syntheses of life through time. The first is Knoll’s contention that the world was and remains fundamentally prokaryotic, that eukaryotic food webs “form a crown—intricate and unnecessary—atop ecosystems fundamentally maintained by prokaryotic metabolism.” Such a world requires that the fossil evidence be continually integrated with the most up-to-date molecular studies to recreate the history of prokaryotic and early eukaryotic life. The second is the importance of ocean chemistry (specifically the formation and eventual breakdown of the

“Canfield ocean,” which was marked by moderate oxygen levels in surface waters and hydrogen sulfide at depth) as a fundamental control on the profound evolutionary changes that typified the first 3 billion years of life. This chemistry provides a unified explanation for such disparate problems as the disappearance of banded iron formation from the world’s oceans and then its brief reappearance nearly a billion years later, stratigraphically consistent changes in the growth form of Proterozoic stromatolites despite the fact that their prokaryotic constructors show little morphologic change over time, and the nearly 2-billion-year lull between the first appearance of eukaryotes in the Archean and the diversification of multi-



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**Signs of the times.** These mid-Proterozoic stromatolites (from 1.5-billion-year-old carbonates in northern Siberia) can easily be distinguished from forms that accumulated in similar coastal habitats in the early and late Proterozoic. Because the cyanobacteria that built them show evolutionary stasis, the morphological differences reflect environmental changes (in particular, changes in the carbonate chemistry of seawater).

cellular seaweeds and soft-bodied animals (the Ediacara biota) in the late Proterozoic. A third theme is Knoll’s concept of “permissive ecology,” the idea that these intervals of rapid environmental change caused temporary breakdowns of the established ecosystems with their harsh competition for resources and thereby permitted the new experiments in life that ultimately led to our modern world.

Near the book’s end, Knoll muses that, “If there is one lesson that paleontology offers to evolutionary biology, other than the documentation of biological history itself, it is that life’s opportunities and catastrophes are tied to Earth’s environmental history.” One can only hope that the elegance and success of *Life on a Young Planet* will encourage more interactions among the formerly disparate fields of paleontology, evolutionary biology, and Earth system science.

the interested lay reader, which is also a book that will further fascinate serious chronobiologists with the wonders of their subject. It is a reminder of the marvels of nature and of the critical role that endogenous biological timing plays in the life cycle of almost every organism.

## References

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## BOOKS: HUMAN GENETICS

## Moving and Mixing

Linda Vigilant

Among the first questions one asks a new acquaintance is “Where are you from?” This is not always as simple a question as it may seem. Living in Europe, I have tried to answer with just “the U.S.,” but this satisfies nearly no one. “But where in America?” The follow-up gives me pause. Is it New Jersey, where I spent my childhood? California or Pennsylvania, the places I lived as an adult? Which would I rather be linked with: Bruce Springsteen, the entertainment industry, or Three Mile Island? For we tend to use information about a person’s place of origin as a shortcut to knowing a whole range of things about them: likely educational background, religion, economic status, political views, and so on. Although I can edit my personal history at will, none of us can choose our ancestors.

The current boom in genealogical research suggests that I am in the minority in finding the history of long-dead ancestors irrelevant. The posting of information on the Internet allows one to ferret out of the names and birth dates of forebears without visits to obscure church registries, and if that information seems a bit dry, genetic analysis can help flesh out the story. There exist labs that are willing, for a fee, to analyze DNA from scraped-off cheek cells, report on the more or less likely geographic origin of the ancestral bearer of a miniscule fragment of the donor’s genome, and even

**Mapping Human History**  
**Discovering the Past Through Our Genes**  
*by Steve Olson*

Houghton Mifflin,  
 Boston, MA, 2002. 302  
 pp. \$25. ISBN 0-618-  
 09157-2.

provide a matching ancestral legend. Such entrepreneurial geneticists will hope that few read Steve Olson’s *Mapping Human History* and discover the truth that, due to the exponential growth in the number of our ancestors, we all are justified in claiming ancestry from say, Julius Caesar, Confucius, or (my personal favorite) Cleopatra.

Why, in an era of increasing mobility and mixture of individuals across traditional class and racial boundaries, are people increasingly fascinated with geographic (read: ethnic) origins? This is a conundrum raised by the book, yet ultimately outside its scope. In all respects, however, Olson does an admirable job of presenting an up-to-date, consensus view of what genetics tells us about who we are and how we got here as a species. The book’s central message concerns genetics and race: The classification of humans into racial categories ignores the biological reality of the overwhelming genetic similarity of outwardly different-seeming individuals. Somewhat breathless claims by the dust-jacket commentators notwithstanding, this is not a novel insight derived from the sequence of the human genome. Nonetheless, the author’s lucid explication of this theme is noteworthy and valuable, particularly for a general audience. Even some geneticists in the field would benefit from being reminded of the fundamentally misleading nature of population trees, which presuppose a sorting of individuals into neat categories. That populations are composed of individuals who move about is exactly what has made untangling the patterns of human dispersal challenging and interesting.

Olson duly presents the story of the origin of modern humans in Africa, with subsequent dispersal to the rest of the world. In a particularly effective approach, he then presents a series of chapters that focus on other geographic regions and the particular histories of populations found in each. Other books cover similar ground, but a notable advantage of *Mapping Human History* is the author’s background. He is a science writer with a broad knowledge of the literature, rather than a researcher who might have a vested interest in presenting a particular interpretation or even be tempted to engage in a bit of image-polishing.

Researchers’ voices are not absent, however, and comments from both major

**Image not available for online use.**

## A sample of human diversity in Hawaii.

and less-prominent geneticists enliven the presentation. Many express the hope that, among other things, the results of their work will serve to allay racial prejudices. Unfortunately, scientists can also be astonishingly unaware of potential negative implications and misconstructions of their work. This is all too apparent in the debacle of the Human Genome Diversity Project: The seemingly well-intentioned goal of cataloging worldwide variation in humans through a comprehensive genetic survey instead elicited distrust and hostility from the “native” peoples of interest. It remains to be seen how ably researchers interested in studying disease-associated genetic polymorphisms in particular groups of humans will manage similar challenges. Furthermore, while few would contest the justice of returning the remains of contemporary victims of scientific racism for burial in their native lands, other sets of remains—such as the case of the 9500-year-old Kennewick Man found in North America—pose a difficulty. Because we are all connected genetically a few thousand years back, who is entitled to claim ownership of a set of bones, or some artifacts, or a piece of land?

Looking toward the future, Olson is inspired by a visit to Hawaii to imagine “a world in which people are free to choose their ethnicity regardless of their ancestry.” Thus, in practical terms race will become divorced from genetics, in people’s minds as well as in biological reality. One could argue that it is clear that race has already become less meaningful today, to judge by the depressing extent of recent and ongoing armed conflict between physically indistinguishable groups. To whatever degree it may help, *Mapping Human History* lucidly conveys the utter senselessness of categorizing people in the face of the interconnectedness of all humanity.