
NATIONAL ACADEMY OF SCIENCES

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Irvine, CA 92717

NAS Colloquium on
Tempo and Mode in Evolution
27 - 29 January 1994
Beckman Center of the National Academies
Irvine, California

December 7, 1993

Name

Jonathan Eisen

We are pleased to inform you that you have been awarded a supplementary subsidy of \$ 175 for hotel expenses and \$ 100 for airfare to attend the NAS Colloquium on "Tempo and Mode in Evolution."

Awards will be **paid after** the Colloquium upon submitting by mail (no later than March 15, 1994) original or copy of paid hotel bill and/or airplane ticket.

The hotel supplementary subsidy is restricted to those staying at the Hyatt Regency Irvine.

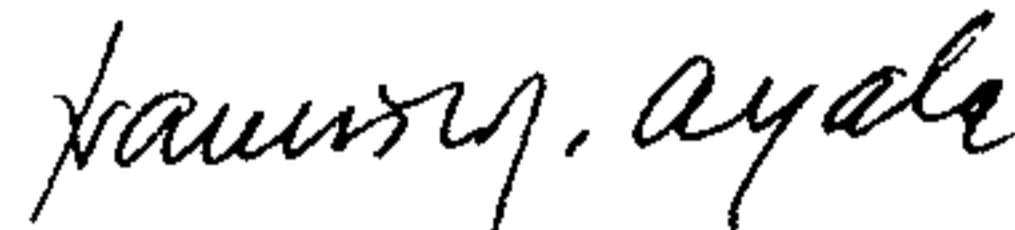
At a later date you will receive the final program, where the shuttle schedule between the Hyatt and the Beckman Center will be printed.

We look forward to your participation in the Colloquium.

Sincerely,



Walter M. Fitch, Co-chair
of the organizing committee



Francisco J. Ayala, Co-chair
of the organizing committee

February 22, 1994
Jonathan A. Eisen
Stanford Department of Biological Sciences
Stanford, CA 94305-5020
415-723-2425 (phone)
jeisen@kimura.stanford.edu

Walter M. Fitch
Department of Ecology and Evolution
University of California
Irvine, CA 92717

Dear Prof. Fitch

I was awarded a subsidy of \$100.00 for airfare to attend the Tempo and Mode in Evolution colloquium at the Beckman Center for the National Academies in January. I am enclosing copies of my boarding passes, flight itinerary, airline receipt, and award notification. The cost of my ticket was \$126.00 so I am requesting the full \$100.00 I was awarded. In addition I would like to thank you and Prof. Ayala for a great colloquium and the National Academy for the travel and hotel award. It was a great chance for many students like myself to get an overview as well as some history of the field in which we hope to be a part.

Thank you,

Jonathan A. Eisen

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Department of Ecology & Evolution
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NAS Colloquium on
Tempo and Mode in Evolution
27 - 29 January 1994
Beckman Center of the National Academies
Irvine, California

November 8, 1993

Dear Colleague:

This is to invite you to attend a colloquium on "Tempo and Mode in Evolution," sponsored by the National Academy of Sciences. The Colloquium will be 27-29 January 1994, at the Beckman Center of the National Academies of Sciences and Engineering in Irvine, California. A preliminary program is enclosed.

In 1944, George Gaylord Simpson published *Tempo and Mode of Evolution*, which extended the "modern evolutionary synthesis" to the fields of macroevolution and paleontology. The NAS Colloquium will commemorate the 50th anniversary of that classic with a broad-ranging examination of current evolutionary issues.

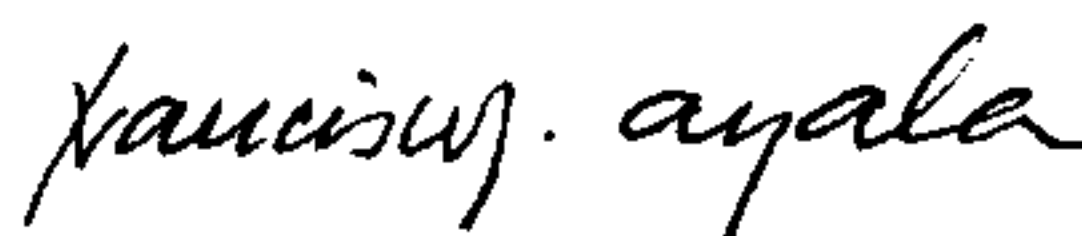
Attendance at the symposium is by invitation only and limited to 250 registered individuals. To facilitate the participation of younger scientists, we request that you extend this invitation to interested graduate students and postdocs (you may duplicate for this purpose the enclosed registration form). Moreover, the NAS has provided funds to make awards to supplement the expenses of participating graduate students and postdocs up to \$75 for hotel costs and \$100 for air travel. A maximum of 100 awards will be granted, with priority based exclusively on the order in which requests (accompanied by the registration fee of \$35) are received. (Notification of the award will be made shortly after receiving the application but the awards will be paid *after* the Colloquium, upon documentation of qualifying expenses.)

A registration form is enclosed. Registrations will be accepted only when the registration fee is included and in the order in which they are received. The cost of meals (including welcoming reception and banquet) is \$100, which will be waived for all those (not only graduate students and postdocs) whose registration is posted by **December 15**. A block of hotel rooms at a discount rate has been reserved at the Irvine Hyatt Regency. Transportation between the hotel and the Beckman Center will be provided free of charge at specified times.

For additional information write to Evolution Colloquium, Department of Ecology and Evolution, University of California, Irvine, California 92717. Fax (714) 725-2474; e-mail WMFITCH@UCI.EDU or FJAYALA@UCI.EDU.



Walter M. Fitch
Co-chair of the organizing committee



Francisco J. Ayala
Co-chair of the organizing committee

NATIONAL ACADEMY OF SCIENCES

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NAS Colloquium on
Tempo and Mode in Evolution
27 - 29 January 1994
Beckman Center of the National Academies
Irvine, California 92717

January 12, 1993

To: Registered Participants

Dear Colleague:

Enclosed please find the revised program for the Colloquium on *Tempo and Mode in Evolution*.

The response to the Colloquium announcement was overwhelming. We accepted the first 250 registrations and had to return many more. The resources of the Beckman Center (food services as well as auditorium seating) will be used to maximum capacity. Therefore, only registered participants will be allowed and **name badges will be required at all functions**. Your name badge will be available at the desk in the Atrium of the Beckman Center on the evening of Thursday, January 27 and on Friday, January 28.

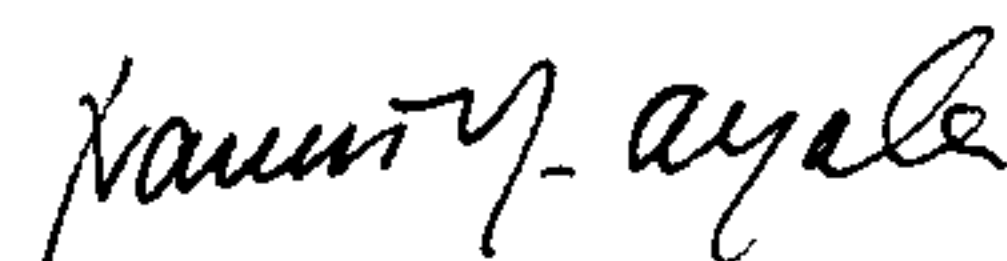
Complimentary van shuttle service will be available between the Irvine Hyatt and the Beckman Center on January 27, 28, and 29, but only at the times and places listed on the back of the enclosed program. Driving directions are also given for the convenience of those using their own car. There is an abundance of free parking available at the Beckman Center.

If you arrive at Orange County Airport on the evening of Thursday, January 27, you may choose to go directly to the Beckman Center where a coat and luggage closet is available. A taxi from the Airport to the Beckman Center will cost around \$10; from the Airport to the Irvine Hyatt, around \$8 (the Irvine Hyatt also runs a free shuttle van from the Airport to the Hotel). On Saturday afternoon there will be vans returning from the Beckman Center to the Hyatt and to Orange County Airport (see schedule).

Telephone and FAX numbers for the Irvine Hyatt and the Beckman Center are listed on the back of the program. If you need to contact us use: Fax (714) 725-2474; e-mail WMFITCH@UCI.EDU or FJAYALA@UCI.EDU.



Walter M. Fitch
Co-chair of the organizing committee



Francisco J. Ayala
Co-chair of the organizing committee

BOOK REVIEWS

Evolutionary Transitions

Tempo and Mode in Evolution. Genetics and Paleontology 50 Years after Simpson. WALTER M. FITCH and FRANCISCO J. AYALA, Eds. National Academy Press, Washington, DC, 1995. x, 325 pp., illus. \$49.95. From a colloquium, Irvine, CA, Jan. 1994.

In 1944, George Gaylord Simpson anticipated that readers of his new book, *Tempo and Mode in Evolution*, would find its attempted synthesis of paleontology and genetics "particularly surprising and possibly hazardous." Simpson's words describe what his own reaction might be at seeing the progression of this synthesis 50 years later, the subject of this volume. The surprise would be phenomenal new discoveries in both paleontology and genetics. Paleontologists have extended the known fossil record well into the Precambrian (Proterozoic eon), revealing enormous contrasts between the dominant evolutionary tempos and modes of the Proterozoic and subsequent Phanerozoic eons, and have established a far more significant role than Simpson envisioned for extinction in Phanerozoic evolution. The emergence of molecular evidence bearing on evolution and the use of bacterial chemostats as experimental systems for studying evolutionary tempo and mode are equally unanticipated genetic developments. The hazard is a tendency of this synthesis to downgrade Simpson's own field of paleontology by giving primacy to genetics.

Simpson highlighted tempo and mode because these are topics through which paleontology makes a unique contribution to evolutionary theory. Tempo encompasses evolutionary rates measured on a geological time scale, and mode constitutes the genetical and morphological means by which evolving lineages differentiate. Simpson identified three fundamental modes: speciation, the splitting of a population into separately evolving lineages; phyletic evolution, directional change evolving within species; and quantum evolution, rapid shift of a population between distinct adaptive zones through an unstable inadaptive phase. Traditional Darwinism emphasizes gradual change achieved through the phyletic mode. Gould presents here a macroevolutionary reconstruction of Darwinism that gives Simpson's other modes and extinction

increased significance, thereby restoring a central role for paleontology in evolutionary theory.

Recent paleontological studies document episodically increasing rates of speciation and extinction through time. Schopf describes Proterozoic life dominated by extremely slowly evolving prokaryotes, especially cyanobacteria. Established lineages exhibited large populations, ecological versatility, and long-term stasis. Extinction was rare, becoming a significant factor only late in the Precambrian, primarily among ecologically specialized eukaryotes. Likewise, Knoll's studies of single-celled eukaryotes show that Cambrian assemblages contained larger numbers of species that survived for shorter periods than their Proterozoic counterparts.

Phanerozoic evolution appears to have been dominated by high rates of speciation, ecological specialization, and extinction. Raup argues that extinction was not predominantly selective as Darwin envisioned it. Extinction of widespread species is rare except during episodes of mass extinction, when the killing event is beyond the experience of the species and outside the reach of natural selection. A series of mass extinctions produced major restructurings of the biosphere in which dominant groups were eliminated and formerly minor ones expanded and diversified.

The fossil record of the Hominidae has improved more than 100-fold since 1944. McHenry interprets this record as supporting punctuated equilibrium; major evolutionary trends result not from gradual phyletic change but from changes concentrated in discrete events of speciation. Morphological evolution was mosaic, with many apparent trends representing accumulation of rapid shifts between successive species that overlapped in geological time.

Paleontologists increasingly invoke properties of genetic systems to explain discontinuous evolutionary patterns. Knoll attributes a late Precambrian acceleration of

protistan evolution to genetic innovations including exon shuffling and sexual life cycles. Valentine attributes the explosive appearance of body plans in Cambrian bilaterians to regulatory genetic changes and associated developmental repatterning made possible by homeobox genes. The Cambrian explosion occurred largely or entirely within organisms having a single Hox/HOM cluster, but major increases in organismal complexity later in the Phanerozoic apparently involved duplications of this cluster.

Lenski and Travisano link genetic and paleontological phenomena using bacterial chemostats. Experimental lines demonstrate rapid change followed by stasis, replicating macroevolutionary dynamics. The crucial role of chance (historical accidents) in adaptive evolution is demonstrated by observing that replicate lines diversify in fitness even with controlled environments and very large populations. Sustained divergence among lines in mean fitness supports a Wrightian model in which replicate populations occupy different fitness peaks of unequal height in an adaptive landscape.

Doolittle and Brown divide molecular evolutionary tempo and mode into three historical stages: a pre-Darwinian period preceding origins of self-replicating informational molecules; a progressive Darwinian period between stage 1

and the first modern cells; and a postprogressive Darwinian period featuring evolutionary specialization but no general tendency for later forms to outperform earlier ones. Maizels and Weiner present a fascinating hypothesis for the second stage in which transfer RNAs evolved initially for replicational functions and later were co-opted for protein synthesis. Additional papers examine molecular evolution in the third phase, including studies of the molecular clock, properties of genetic systems, and molecular estimation of population genetic parameters.

This volume provides a dramatic illustration of how profoundly evolutionary practice and theory have advanced in the last 50 years, and of how important Simpson's themes of tempo and mode remain to the evolutionary synthesis of paleontology and genetics.

Allan Larson

Department of Biology,
Washington University,
St. Louis, MO 63130-4899, USA



George Gaylord Simpson, 1938. [Neg. no. 290411, photo by C. H. Coles; courtesy Department Library Services, American Museum of Natural History]

Will Molecular Data Set The Stage for a Synthesis?

Fifty years ago, the great evolutionary biologist George Gaylord Simpson, then at the American Museum of Natural History, published a classic volume called *Tempo and Mode of Evolution*. In that book, Simpson, a leader in what became known as the "modern synthesis" movement in evolution, attempted to combine the results of classical paleontology with those of the rapidly expanding field of genetics to give an overview of evolutionary theory. Fifty years later, 250 leading evolutionary theorists gathered in Irvine, California at a symposium in Simpson's honor.* Appropriately, the aim of the symposium was to provide a Simpsonian overview of the field, and the conclusion was that its tempo of change is rapid, and one of the main modes of change is the acquisition of new data from molecular biology.

As one presentation after another confirmed, molecular biology is offering researchers a multitude of new genetic clues about evolutionary change. "We have a tremendous explosion of discovery now," says Francisco Ayala, a molecular evolutionist at the University of California (UC), Irvine, who cochaired the meeting with UC Irvine's Walter Fitch. The challenge facing scientists in the field is to make sense of those discoveries, to fit diverse pieces of evidence into more comprehensive patterns. "We know we need the data from everyone else," says paleontologist William Schopf of the University of California, Los Angeles. "We know it's another arrow in our quivers."

This isn't an easy task, and often it raises questions as fast as it answers them. Ford Doolittle of Canada's Dalhousie University, who studies the genetics of primitive single-celled organisms called archaeobacteria, explained that molecular biology has reshaped his field in the last decade but that the new shape is hard to discern. In a talk called "The Root of Life," Doolittle said molecular comparisons of living organisms have rewritten the textbook story that the first cells were prokaryotes (cells without a nucleus), which in turn gave rise to nucleated eukaryotes.

The first deep wrinkle in this smooth fabric came more than a decade ago, Doolittle noted, when Carl Woese of the University of Illinois at Urbana-Champaign sequenced

RNA from the ribosomes of a variety of organisms (ribosomes being the cellular structures that make proteins). Comparisons of the ribosomal RNAs led Woese to divide prokaryotes into two groups—archaeobacteria and eubacteria—and to suggest that they are as distinct from each other as they are from eukaryotes.

More recently, said Doolittle, the popular notion that the three lineages diverged from a common ancestor, called a progenote, has been put on thin ice by studies of the distinctive genome organization in archaeobacteria. "Many of us have quietly been saying goodbye to the progenote concept," Doolittle said. "The root is back up in the air again." And with an upended root, it's anybody's guess as to how to draw these three branches on an evolutionary tree.

Molecular techniques are also raising new insights about where, exactly, humans fit on the evolutionary tree. UC's Ayala described how analyses of DNA from the human leukocyte antigen (HLA) are casting additional doubt on the disputed "mitochondrial Eve" theory of human origins, which, based on DNA analysis of mitochondria—cells' energy-producing organelles—holds that all humans today descended from a single lineage passed on by one woman some 200,000 years ago in Africa (*Science*, 7 February 1992, p. 686).

The "Eve" hypothesis came from the University of California, Berkeley's Rebecca Cann, a student of the late Allan Wilson, in 1987. HLA analysis, however, contradicts that tale. HLA is a key immune-system molecule that helps to distinguish between "self" and "nonself." DNA comparisons of HLA molecules reveal that some chimpanzee leukocyte antigens are actually closer to human sequences than some human antigens are to each other, indicating a tremendous diversity among human HLA alleles (slightly varying versions of the same gene). And in genetics, such diversity means the alleles have been in existence for a long time, since it takes millennia for genes to

diverge by accumulating mutations.

Using computer simulations that model human populations and their genes over time, Ayala finds that a population bottleneck, such as the one hypothesized in the Eve concept, is "outright impossible"—because an Eve-type genetic bottleneck would have eliminated the wide range of existing HLA alleles.

Not all questions are going unanswered, of course. The powerful tools of molecular biology have also been supplying the missing pieces of longstanding evolutionary puzzles. John Avise of the University of Georgia described at the meeting how he and

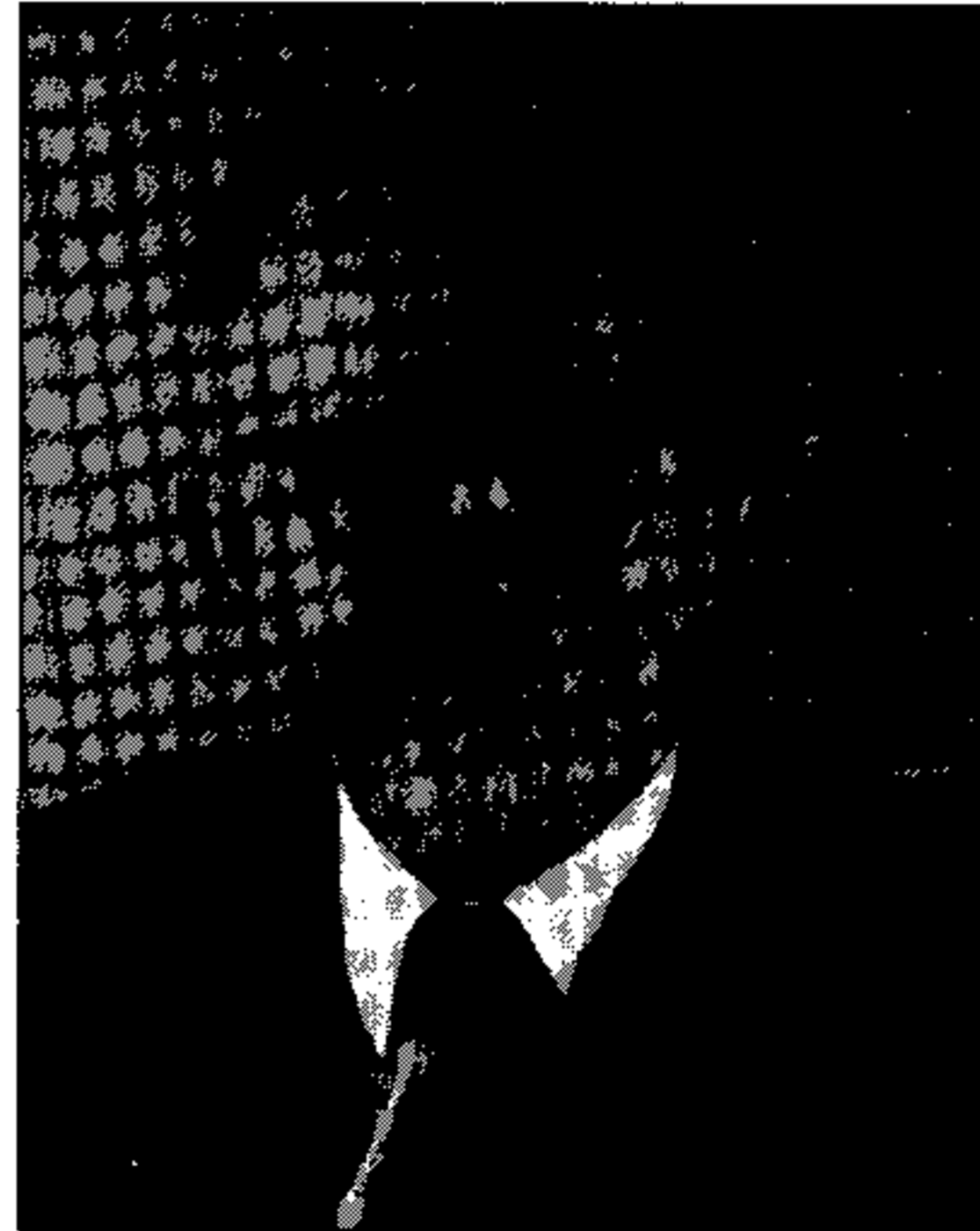
his former graduate student, Brian Bowen, are using genetic sequences to explore evolution within a single species.

In order to understand the dynamics of intraspecies evolution in the green turtle, researchers need to know whether mothers return to the rookeries where they were born to lay their eggs. Tagging the turtles, which was for a long time the only available technology for tracking the creatures, is an impractical way to answer this question, because it takes some 20 years before hatchlings return and nest.

Avise and Bowen exploited the fact that mitochondrial DNA (mtDNA) provides stable genetic markers that can link related animals together. The researchers, who began with a small sample of turtle colonies (*Science*, 11 May 1990, p. 724), have now expanded their sample by analyzing mtDNA patterns from more than 200 rookeries. The mtDNA patterns seem unique to each colony, indicating that females do seem impelled to return to their own natal sites for nesting. "This links mitochondrial genetics and population demography," said Avise. "And it can be applied to any creatures structured along maternal lines."

At the meeting, there were many other examples of the influx of molecular results into evolutionary theory. And the attendees were left with the feeling that the next task for the field is to integrate them into a synthesis of the kind Simpson tried to achieve. At the moment, however, that fusion seems far off. "Whether we'll have a synthesis of the magnitude seen in Simpson's era, I don't know," said Ayala at the meeting's end. Yet he argued that, as a result of the new findings, "the grounds are there."

—Jon Cohen



Search for a synthesis. George Gaylord Simpson argued in 1944 that evolutionary biology should draw from many diverse disciplines.

* 28-29 January, "Tempo and Mode in Evolution," sponsored by the National Academy of Sciences, Beckman Center, Irvine, California.

Name Badges will be required for all functions.
(Badges will be distributed at the desk in the Atrium of the Beckman Center)

Thursday, January 27

7:30 - 10:00 pm. Welcome Reception.

Friday, January 28

7:30 am. Buffet Breakfast in Refectory.

9:00 am. - 1:00 pm. **SESSION I. Early Evolution**

9:00 *Introduction and Chairperson*

Walter M. Fitch (UC Irvine)

9:10 **Phylogenies from Function:**

A Possible History of Replication

Nancy Maizels (Yale)

10:00 **The Root of Life**

Ford Doolittle (Dalhousie)

10:50 **Break**

11:10 **Proterozoic Eukaryotes:**

Evidence for Accelerating Rates of Evolution

Andrew Knoll (Harvard)

12:00 **The Earliest Life**

William Schopf (UC Los Angeles)

1:00 - 2:00 pm. Lunch in Refectory.

2:00 - 6:00 pm. **SESSION II. Microevolution**

Chairperson

John C. Avise (U of Georgia)

2:00 **Dynamics of Adaptation and Divergence
in Bacterial Populations**

Richard Lenski (Michigan State U)

2:50 **Genome Organization**

Daniel Hartl (Harvard)

3:40 **Break**

4:00 **DNA Polymorphism: Selection and Drift
Patterns of Chloroplast DNA Evolution**

*Richard R. Hudson (UC Irvine)
Michael Clegg (UC Riverside)*

Friday Evening

6:00 pm. Cocktails in the Atrium.

7:00 pm. Dinner in the Atrium.

8:15 pm. *Introduction: James W. Valentine (UC Berkeley)*

Banquet Lecture: Stephen Jay Gould (Harvard)

Pattern, Rate and Mode of Morphological Evolution

Saturday, January 29

7:00 am. Buffet Breakfast in Refectory.

8:30 am. - 12:30 pm. **SESSION III. Macroevolution**

Chairperson

Wyatt W. Anderson (U Georgia)

8:30 **On the Origin of Phyla**

James W. Valentine (Berkeley)

9:20 **Plants, Biomechanics, and the Invasion of Land**

Karl Niklas (Cornell)

10:10 **Break**

10:30 **Tempo and Mode in Human Evolution**

Henry McHenry (UC Davis)

11:20 **The Role of Extinction in Evolution**

David M. Raup (U Chicago)

12:30 - 1:30 pm. Lunch in Refectory.

1:30 - 5:30 pm. **SESSION IV. Patterns and Rates of Molecular Evolution**

Chairperson

Francisco J. Ayala (UC Irvine)

1:30 **Molecular Biogeography**

John C. Avise (Georgia)

2:20 **Molecular Genetics of Speciation**

Francisco J. Ayala (UC Irvine)

3:10 **Break**

3:30 **Molecular Clocks**

Walter M. Fitch (UC Irvine)

4:20 **Molecular Analysis of a Chromosomal
Phylogeny in Drosophila**

Wyatt W. Anderson (U Georgia)