SUMMARY REPORT

of the

Workshop on Evolutionary Biology

Held at the

American Museum of Natural History
New York City, NY

March 3-5, 1999

Editors

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         Development and differentiation

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         Internal interactions
         External interactions

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LIST OF ATTENDEES

Steve Arnold	Oregon State University
Maurice Averner	NASA Ames Research Center (ARC)
David Begun	University of Texas
Mary Berbee	University of British Columbia
Rita Briggs	Lockheed Martin Engineering & Sciences Co.
Colleen Cavanaugh	Harvard University
Russell Chapman	Louisiana State University
Cassie Conley	NASA Ames Research Center (ARC)
Greg Conway	NASA Ames Research Center (ARC)
Rob DeSalle	American Museum of Natural History (AMNH)
Darrel Frost	American Museum of Natural History (AMNH)
Gonzalo Giribet	American Museum of Natural History (AMNH)
Catherine Golden	NASA Headquarters (HQ)
Lisa Gugenheim	American Museum of Natural History (AMNH)
John Harshman	Lockheed Martin Engineering & Sciences Co.
Dan Janies	American Museum of Natural History (AMNH)
Diana Lipscomb	George Washington University
Bob MacElroy	NASA Ames Research Center (ARC)
Dan McShea	Duke University
Helen Matsos	American Museum of Natural History (AMNH)/ NASA Ames Research Center (ARC)
Michael Meyer	NASA Headquarters (HQ)
Rick Michod	University of Arizona
Cary Mitchell	NASA Ames Research Center (ARC)
Mark Norell	American Museum of Natural History (AMNH)
Michael Novacek	American Museum of Natural History (AMNH)
Ian Ross	University of California Santa Barbara
Lynn Rothschild	NASA Ames Research Center (ARC)
John Rummel	NASA Headquarters (HQ)
Neil Shubin	American Museum of Natural History (AMNH)
Joe Travis	Florida State University
Tyler Volk	New York University
John Wenzel	Ohio State University
Ward Wheeler	American Museum of Natural History (AMNH)

AGENDA

Wednesday, March 3

9:30 a.m.	*Breakfast*	*Shell Corridor*
10:00 a.m.	*Workshop begins*	*Kaufmann Theater*
10:00 a.m.	Welcome and Opening Remarks	Ward Wheeler (AMNH) Michael Novacek (Provost AMNH) Ellen Futter (President, AMNH)
10:15 a.m.	Evolutionary Biology and NASA	Mel Averner (ARC) Bob MacElroy (ARC)
10:30 a.m.	*Begin background talks in individual areas of Evolutionary Biology*	
10:30 a.m.	"NASA's Search for the Origins of Life"	Michael Meyer (NASA HQ)
11:00 a.m.	"The Fossil Record –What is it?"	Mark Norell (AMNH)
11:30 a.m.	"Process, Pattern, and Phylogeny"	Stevan Arnold (Oregon State)
12:00 p.m.	*Lunch*	*Curator's Lounge*
1:00 p.m.	*Reconvene for background talks on individual areas of evolutionary biology*	*Kaufmann Theater*
1:00 p.m.	"Challenges of Modern Systematics"	John Wenzel (Ohio State)
1:30 p.m.	"Development, Evolution, and Corroboration"	Rob Desalle (AMNH)
2:00 p.m.	"Current Horizons in Evolutionary Ecology"	Joe Travis (Florida State)
2:30 p.m.	Delivery of charges to participants and groups	Mel Averner (ARC)
2:45 p.m.	*Groups assemble, clarify charges, and begin discussion*	*Frick Building*
	Evolutionary Ecology	Colleen Cavanaugh (Harvard) Daniel Janies (AMNH)
	Comparative Biology	John Wenzel (Ohio State) John Harshman (ARC)
5:00 p.m.	*Museum Reception Dinner*	*Curator's Lounge*
7:00 p.m.	*Dinner*	*Astor Turret*
	After-dinner talk on Anthropology	Craig Morris (AMNH)

Thursday, March 4

8:00 a.m.	*Breakfast*	*Shell Corridor*
8:30 a.m.	Group Progress Presentations	Kaufmann Theater
	Evolutionary Ecology	Colleen Cavanaugh (Harvard) Daniel Janies (AMNH)
	Comparative Biology	John Wenzel (Ohio State) John Harshman (ARC)
9:00 a.m.	*Group discussions reconvene*	*Frick Building*
12:00 p.m.	*Lunch*	*Islamic Court*
	After lunch talk "How Evolution Works"	Niles Eldredge (AMNH)
1:20 p.m.	*Groups reconvene, discuss, and draft recommendations.*	*Frick Building*
5:00 p.m.	*Adjourn*	
7:00 p.m.	*Dinner*	*Hall of Human Biology*
	After dinner talk on Astronomy	Michael Shara (AMNH)

Friday, March 5

8:30 a.m.	*Breakfast*	*Shell Corridor*
9:00 a.m.	*Presentation of final group recommendations*	*Linder Theater*
	Evolutionary Ecology	Rick Michod (Arizona) Daniel Janies (AMNH)
	Comparative Biology	John Wenzel (Ohio State) John Harshman (ARC)
10:30 a.m.	Summary and discussion of future actions for evolutionary biology at NASA	Mel Averner (ARC) Bob MacElroy (ARC) Ward Wheeler (AMNH)
12:00 p.m.	*Adjourn*	

1.0 INTRODUCTION

The following pages summarize the commentary and the ideas generated by the participants at the *Workshop on Evolutionary Biology*, held at the American Museum of Natural History in New York City, on March 3 through March 5, 1999. The purpose of the workshop was to determine whether and how the discipline of <u>evolutionary</u> <u>biology</u> might contribute to two NASA science goals:

1. Understanding how life evolved on Earth and predicting the nature of extraterrestrial life.

2. Understanding the evolutionary responses of life to novel environments and the long-term consequences of carrying terrestrial life into space.

NASA, in its mission to explore the Universe, and in its search for evidence of past and present extraterrestrial life, recognizes that it is very important to understand the evolutionary paths that various forms of terrestrial life have followed. The Agency also appreciates that a principal determinant of evolutionary direction is the interaction of organisms with each other and with their environment. At this conference the participants discussed fundamental, shared features of organisms and ecosystems. The search for life in the universe demands knowledge and understanding of what evolved, what evolved repeatedly, and what did not evolve on Earth.

2.0 DEFINITIONS

For purposes of universal understanding of the topics discussed, some relevant terminology is briefly defined below.

Evolutionary Biology	The discipline of <u>evolutionary</u> <u>biology</u> centers on the study of processes that change the genetic makeup of populations of organisms and the study of historical patterns of organismal divergence and change.
Requirements for Evolution	The basic requirements for <u>evolution</u> are replication of individuals and heritable variation among individuals. <u>Natural selection</u>, the most important mechanism of evolution, further requires that individuals interact with their environments in ways that influence their success in reproduction, and that some fraction of the heritable variation creates differences in reproductive success among individuals. These requirements are likely to be universal because they are not dependent on any particular biochemistry of information storage, metabolism, or reproduction.
Natural Selection	<u>Natural</u> <u>selection</u> is the process of differential survival and reproduction of individuals with advantageous variations.

Mutation	Mutation is the alteration of genetic material in individuals, thus providing a source of heritable variation upon which natural selection can act.
Recombination	Recombination is rearrangement of existing genetic material, for example shuffling of genes by crossing over in meiosis (production of sex cells) or lateral gene transfer in bacteria. Rearrangements of genes also provide heritable variation upon which natural selection can act.
Genetic Drift	Genetic drift is the random change in the frequency of alleles (different forms of a gene) in a population. For example, a population can become homogeneous with respect to a certain gene if individuals carrying rare alleles, by chance, fail to reproduce.
Migration	Migrants from other populations can introduce new alleles into a population or change the frequency of alleles already present.
Systematics	Systematics is the discipline of evolutionary biology concerned with determining the historical relationships of organisms, i.e. with deriving and testing phylogenetic trees.
Comparative Biology	The goal of the discipline of comparative biology is first to reconstruct the history of past changes, and then to use the pattern of changes to infer the nature of the processes governing those changes. The raw materials of comparative studies are phylogenetic trees and comparative data.
Comparative Data	Comparative data are measurements or observations of the same set of varying biological characteristics for each species in the studied group. Comparative data are used both for construction of phylogenetic trees and for studies in comparative biology.
Phylogenetic Tree	A phylogenetic tree is a branching diagram, resulting from analysis of comparative data, that summarizes the evolutionary relationships among a group of species. Phylogenetic trees serve also as hierarchical maps of the evolution of characteristics within the group.
Convergence	The evolutionary principle of convergence states that similar selection pressures often lead to similar designs in organisms that may not be closely related.
Ecology	Ecology is the study of the interactions of organisms with their environment. The environment includes physical, chemical and biological parameters, the latter including organisms of the same or of other species.

3.0 POSSIBLE AREAS OF RESEARCH

The workshop identified several research areas that will aid the search for life in the universe. The workshop also suggested new techniques and tools needed to improve our abilities to perform research in the suggested areas. The areas of research and technology development that could be of possible interest to the NASA are discussed below.

3.1 Area 1:
Understanding how life evolved on Earth and predicting the nature of extraterrestrial life

NASA is interested in the evolution of life in the universe, especially complex life. Studies of terrestrial evolution can illuminate the conditions that have enabled or promoted the evolution of complexity and diversity. By examining the patterns of evolution in repeated, convergent events in the history of life (e.g., the evolution of multicellularity) using comparative methods, it may be possible to infer general rules of the evolutionary process. Conversely, widespread common features may be better understood by examining repeated, convergent exceptions. The comparative approach requires broad taxonomic surveys and carefully chosen data. The workshop identified (see below) a number of general topics that could be important for life in the universe and could be amenable to investigation.

Although each scientific question suggests its own appropriate study taxa, one group seems particularly important to many of the topics below. Protists are an assemblage of many groups of unicellular eukaryotes. The protists represent a vast, understudied range of biological organization and physiological adaptation. Comparative studies of their complexity and relationships to each other and to the various groups of multicellular organisms are needed. We expect that greater understanding of the phylogeny and diversity of protists will be important in addressing many of the questions of interest to NASA.

3.1.1 Evolution of organizational complexity

Formation of assemblages composed of subunits, and the differentiation of subunits within assemblages, are fundamental features of the evolution of complexity. Several topics are of interest in this broad area:

Association and Aggregation

Individuals form associations that may ultimately result in the appearance of higher-level individuals. This allows for specialization and differentiation of subunits, and the potential evolution of greater size or morphological complexity. The workshop identified five general types of associations:

1. organelles derived from within cells,
2. organelles derived by endosymbiosis,
3. multicellularity,
4. coloniality and sociality, and
5. mutualisms.

In addition to principles applying to individual origins of these five types of associations, there may be similar principles applying across types. For example, aggregations based on kinship (3 and 4) may in important ways be similar to each other but different from aggregations of unrelated individuals (2 and 5).

Development and Differentiation

Life on Earth displays a variety of mechanisms regulating the differentiation and growth of cells and tissues during the life cycle of an organism. Some of these mechanisms appear to be highly conserved between distant species while others appear to be very diverse. Currently scientists understand regulatory pathways in only a few regions of a handful of model organisms. Moreover, we know very little about the diversity of mechanisms of developmental regulation. Most of what we know concerns a handful of metazoans that are common laboratory organisms. The diversity of developmental and other genetic regulation in protists, fungi, and plants has not been examined. Understanding of life on Earth and the ability to predict what might exist elsewhere depend on comparative studies of the kinds of interactions between genes, gene products, and cells that have different morphogenetic results. Possible topics for comparative studies include studies of diversity and generality of many aspects of development, such as patterning genes and gene networks, cell-cell interactions, regulation of morphogenesis, and the consequences of increased size and cellular differentiation.

3.1.2 Evolution of function

Evolutionary adaptations, whose nature must depend on the combination of selective environment and any physical or genetic constraints on variation, are discussed in this section. The important question is to what extent similar conditions, both internal and external, will elicit similar adaptive evolutionary responses or constrain the evolutionary responses to other forces.

Internal Interactions

The relationship between biological complexity and the size and organization of genomes are poorly understood. The group suggested several features for exploration.

1. Gene packaging: the organization of genes relative to each other, their physical arrangements on chromosomes, separation into multiple genomes within the cell (e.g., nuclei, plastids, mitochondria), and so on, have consequences for gene expression and the processes of genomic evolution.

2. Ploidy and varying numbers of nuclei in cells influence expression in ways not obviously related to simple dosage compensation and differ from the influences of physical packaging. For example, autopolyploid plants are often substantially different in phenotype and more fecund than their diploid progenitor even though there is no new genetic information.

3. Recombination of genes is indisputably one of the primary forces of biological diversity, and the interactions of genes in various combinations is still poorly understood.

External Interactions

Interactions with the external environment generate the diversity of Earth's biota, and such interactions are expected to play a role of comparable importance in extraterrestrial forms. Certain categories of changes in interaction with the environment seem particularly important:

1. Modes of sensing the environment and the evolution of new senses are the starting point in organismal interactions with the environment.

2. Invasions of new habitats (e.g., land, hydrothermal vents, polar regions) are opportunities to learn generalities that would apply to evolution in alien or artificial environments, including those associated with space travel and extraterrestrial settlements.

3. Changes in resource dependency (e.g., transitions between heterotrophy and autotrophy) and changes in metabolic pathways are fundamental to the basic life processes that create and sustain order. A range of metabolic processes and pathways have evolved on Earth and further comparative analysis of metabolic interactions with the physico-chemical environment will better prepare us for understanding and dealing with extraterrestrial life.

4. Homeostasis, the various means by which life buffers the internal environment from changes in the external environment, may be important both for the invasion of new environments and for the evolution of complexity.

5. Processes of motility and dispersal represent another important commonality among terrestrial life that can be expected to be characteristic of extraterrestrial life.

3.1.3 Evolution of evolvability

We can define <u>evolvability</u> as evolutionary flexibility or the ability to generate taxonomic or morphological diversity. To study evolvability we need to investigate possible associations between the generation of diversity and various aspects of genetic and developmental organization. For example, one prediction has been that developmental programs of evolvable organisms will be organized as a number of (somewhat) independent modules. Any robust associations found may enable us to make predictions about the developmental organization of extraterrestrial organisms. Also of interest will be the question of whether evolutionary processes produce any long term tendency for evolvability to increase (or decrease).

3.2 <u>Area 2:</u>
 Understanding the evolutionary responses of life to novel environments and the long-term consequences of carrying terrestrial life into space

The following questions are fundamental to NASA's mission:

1. How can evolutionary biology aid in the search and identification of life in the universe?

2. What evolutionary trajectories and ecological interactions will occur among organisms that are carried from Earth into space?

Several areas of potential research have been identified to address these questions.

3.2.1 Identification of Life

The search for universally applied processes must be broad as life elsewhere may not be nucleic-acid-based, may not even be carbon-based, and may even use energy gradients that are not employed by terrestrial life. These studies may range from analysis of returned samples of a planet, potentially bearing anatomical fossils and traces of organic molecules, to remotely sensed features such as surface scans and atmospheric spectra.

3.2.2 The Study of ecological niches in which life has and has not evolved on Earth

Life on earth occurs in most physical habitats but uses only photo- or chemical-energy gradients. If a hierarchy of organizational complexity is tantamount to life, life should be recognizable through a deviation from randomness. Evolutionary mechanisms have produced organisms from organic molecules. Life can perhaps be recognized because molecules will be distributed far from thermodynamic equilibrium with the environment. Possible areas of inquiry include drilling for deep cores for microbial life and research on metabolism of deep-sea organisms.

3.2.3 Means to understand the potential of Earth life in space

Most organisms live in populations of breeding individuals distributed across patchy environments. However the reproductive isolation and colonization of novel niches of space will alter population-genetic structure of populations exposed to several generations of space travel. Moreover, microbiota may undergo many generations of evolution in a short period of time now occupied by space flight. As such space travel will have important effects on the evolutionary trajectory of many species, especially those with short life cycles. Possible research areas include the study of the evolution of human microbiota during space flight and plant pathogen interactions during space flight.

3.3 <u>Area 3:</u> Technology Development

To improve our ability to perform comparative studies, new methods of gathering and analyzing data are needed. We must develop analytical or observational tools that allow large amounts of data to be efficiently handled, or difficult taxa (or specimens) to be interpreted. Because these will be widely used, research that provides new applications and development of observational and analytical tools in the following areas is especially important.

3.3.1 Pattern recognition systems

We need better tools for discovering, interpreting, and analyzing patterns in biological data. Collaborations between biologists and computer scientists who specialize in pattern recognition are worth exploring.

Sequence Alignment Algorithms

We need more powerful methods for determining homologies of DNA and protein sequences.

Analysis of Stratigraphic Patterns

Drawing conclusions from the fossil record is difficult, because the stratigraphic records of species are biased and incomplete. Pattern recognition systems may help solve this problem. Stratigraphic incompleteness is a distinct problem from the incompleteness of many fossil specimens, discussed below under "Analysis of incomplete or noisy data."

Rapid Collection and Analysis of Gene Expression Data

Evolutionary biologists need technologies to rapidly collect spatio-temporal expression data for complete sets of genes involved in morphogenetic networks. Methods must be easily applied to a broad sample of species. Techniques must also be developed to analyze the expression data to identify and summarize differences across species, for use in comparative and phylogenetic analyses.

Phylogenetic Analysis

Current technology (software and hardware) for inferring phylogenetic trees is weak compared to the numerical complexity of the problem (see section 3.3.2). Support in this fundamental area will impact on many problems relevant to the understanding of life in the universe. Understanding the history of life on Earth and our ability to compare terrestrial life to life elsewhere will depend on phylogenetic algorithms that can accommodate large, diverse data sets.

Phylogenetic Patterns

We need more powerful tests for the recognition of patterns of evolutionary correlations among characters, conditions, diversity, and evolutionary rates.

Morphometric Analysis

Comparative biologists need improved methods to quantify differences and similarities in shape, and for the automated measurement of shape parameters.

3.3.2 Analysis of large data sets

Biologically interesting studies require large numbers of species and large and diverse data sets. New tools such as parallel algorithms and computing clusters are needed.

Collection of Comparative Morphological Data

We need to put advanced technology such as 3D digital imaging in the hands of morphologists. This will not only help scientists to see more in a specimen but will greatly improve the way information is presented and shared across networks.

Informatics

Biologists need new methods to compile, organize, and search for structure in large databases of comparative data. Efforts should include the creation of standardized relational databases, like NIH's Genbank, but inclusive of many types of data.

Tree Searches

In phylogenetic data sets with large numbers of taxa, the number of possible trees becomes astronomical, such that only a small proportion can be examined in a search. Systematists need algorithms that locate optimal trees more efficiently.

3.3.3 Analysis of incomplete or noisy data

Comparative biologists need improved methods for detecting patterns in comparative data and for finding trees in phylogenetic analyses, when some data are missing or unreliable. Phylogenetic analysis using fossils is an example of a situation in which data are expected to be incomplete.

3.3.4 Products of behavior

Organisms leave behind fossil evidence other than their bodies. Such evidence includes trace fossils, excreta, organic debris, and biominerals. Paleontologists need better means to identify the biological origins of these traces — ruling out inorganic phenomena — and means to identify them remotely, especially methods capable of being incorporated into unmanned space probes.

3.3.5 Microorganisms that are difficult to culture

The vast majority of microorganisms cannot yet be cultured. A comparative approach requires a broad sample, and scientists need techniques for genetic assays and characterization of protists and other microorganisms without the necessity to culture them first. Development of technology in this area is particularly important, because it is expected that it will be difficult to culture newly discovered life forms, either of extraterrestrial origin or new variants of terrestrial forms transported into space.

Appendix: Additional research approaches

Two further means of attacking the proposed areas of research (in addition to comparative studies) were not discussed extensively at the workshop but emerged when participants were asked to comment on a draft of the report. We include them here.

<u>Paleontological</u> <u>census</u> <u>methods</u> use counts of the numbers of species, or the distributions of species in morphologically-defined abstract spaces (morphospaces), censused during a series of time-periods (stratigraphic intervals), in order to investigate changes in these counts or distributions over long, evolutionary time-scales. This may help to infer general rules of evolution by searching for patterns of change (e.g., a linear trend, logistic curve, stasis) that repeat over time within groups. Patterns of change in diversity, speciation- or extinction-rate, disparity, morphologic covariance, complexity, or size that recur between mass extinctions, or in successive evolutionary faunas, would be candidates for general rules.

<u>Theoretical</u> <u>population</u> <u>genetics</u> is the application of mathematics to model and understand evolutionary processes. The effects on evolutionary outcomes of different models and of different parameter values within models can be explored by direct computation or computer simulation, and the results compared with observed data. This method can be used to attempt to deduce universal features from general principles. Modeling can help explain the results of comparative studies and produce new hypotheses to be tested by further comparative studies.