Homework 2 Key

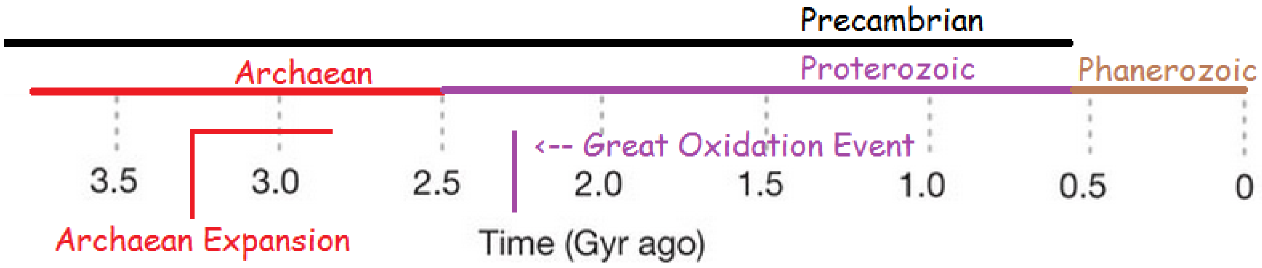
Part A:

The establishment of life on earth occurred roughly around 3.8 Gyr ago. Life has been constantly evolving since its emergence. A variety of biogeochemical factors have influenced the course of its diversification. Piecing together the history of life may provide details explaining how and why life is shaped the way we find it today.
In the paper, *Rapid evolutionary innovation during an Archaean genetic expansion*, the authors develop a phylogenomic method known as AnGST (analyzer of gene and species trees) to reconstruct the evolutionary history of 3,983 major gene families across the three domains of life onto a geological timeline.

Read the paper carefully and answer the following questions.
Read David and Alm (2011) Rapid evolutionary innovation during an Archaean genetic expansion. *Nature*. 469:93-96 carefully and answer the following questions.

1) In no more than 2 sentences and using your own words, what was the main finding of the paper? What's the broader perspective for this result? (4 points)
The authors find that a brief period of genetic innovation during the Archaean eon, which coincides with a rapid diversification of bacterial lineages, gave rise to 27% of major modern gene families that are found to be involved in electron-transport pathways. The use of these genes over time is consistent with an increasingly oxygenating biosphere.
(Can be obtained directly from the abstract. Guidelines for nature abstract: http://www.nature.com/nature/authors/gta/2c_Summary_para.pdf)

2) Draw a timeline like the one below and label the following periods or events: Archaean, Precambrian, Phanerozoic, Cambrian, Proterozoic, Archaean Expansion, and Great Oxidation Event. If any period is a subset of another, mention it in your answer. (6 points)



3) The authors developed a program AnGST which compares gene and species trees to determine the phylogenetic history. (6 points)
a. What are the differences between a gene tree and a species tree? (2 sentences maximum)
A species tree is a tree of a group of species that reflects the actual evolutionary pathways, whereas a gene tree is a tree of a group of homologous (orthologous) genes each sampled from a different species. A gene tree is a subset of a species tree such that a species tree may contain many different tangled gene trees that result from intra-species recombination and non-deleterious point mutations etc.

b. Under what circumstances would the pattern on the gene tree match the species tree?

(2 sentences maximum)
Under direct descent as in the case of higher organisms such as mammals where genetic recombination between different species is not possible, the gene and species trees will look the same. This way, when speciation occurs, genes from the ancestral species are split into two separate bundles and cannot interact with each other, resulting in branching of all gene trees where the species tree branches.

c. Define 2 evolutionary events that may result in observed differences between a gene tree and a species tree, and provide an example for how each evolutionary event can occur or where it occurs in nature. (4 sentences maximum)
Examples of possible answers:
Gene Duplication – Polyploid organisms such as certain plants like wheat
Gene Loss – Transposable genes
Speciation – Darwin's finches
Gene Birth – Chromosomal crossover/Genetic recombination during sexual reproduction
Genetic mutation, Polymorphism, etc.

4) What do the authors hypothesize were the evolutionary factors for the sudden increase in gene birth during the Archaean Expansion? What evidence do the authors provide to support their hypothesis? What evidence do they provide against it? (5 points) (4 sentences maximum)
The authors hypothesize that more efficient energy conservation pathways from the availability of certain metabolites during the Archaean Expansion resulted in a sudden increase in gene birth. Metabolites specific to the Archaean Expansion shown in figure 2, include Fe-S-binding, Fe-binding, and in particular, O2-binding gene families show most significant enrichment. Oxygen is a very good electron acceptor and aerobic processes can yield much more energy to the organism than anaerobic processes, and thus selective evolution of oxygen-using genes is very favorable. At the same time, oxygen-using genes were only enriched towards the end of the Archaean expansion.
5) Where do you think life existed during the time of the Archaean Expansion and for some time afterward? What evidence does the paper provide to support your guess? (3 points) (3 sentences maximum)
During the Archaean Expansion, life probably existed in water (or in the oceans). The authors show that increases in solubility of transition metals such as copper and molybdenum due to increasing oxygen levels resulted in corresponding increases in transition-metal-binding genes over time.

6) Refer to Figure 2 to answer the following questions. (5 points)
a. Give two possibilities that can account for the decrease in Mn-binding genes over time.
Possible answers:
1) Organisms with a greater number of Mn-binding genes were not as fit as organisms with fewer Mn-binding genes or with more diverse transition-metal-binding genes.
2) Increased availability of other transition metals in the ocean due to
3) Organisms have evolved to use other transition metals to replace Mn as a prosthetic group for super oxide dismutase.

4) Oxygen served as better terminal electron carrier than Mn, resulting in the loss of unused Mn genes and a corresponding increase in oxygen-binding genes.
5) The sharp decrease coincided with the large gene loss rate (figure 1), which may have eliminated many Mn-binding genes from the gene pool.
6) Evolution selecting against Mn-binding genes for other transition-metal-binding genes.

b. Many microbes use iron-binding proteins that serve important roles in metabolism. Given that iron must be obtained from the environment of the organism, the authors find the rise in Fe-binding genes contradictory because Fe became less soluble in the oceans over time. How can you explain this occurrence? (4 sentences maximum)
The confounding result may reflect evolutionary inertia, whereby microbes could have found more success in evolving a handful of metal-acquisition proteins rather than replacing a host of iron-binding proteins in the face of declining iron availability. Alternatively, the insolubility of iron in modern oceans may be offset by large organic pools of iron.

DO NOT WRITE BELOW THIS LINE

Part B:
In 1977, Carl Woese and George Fox published a brief paper in PNAS that established, for the first time, that the overall phylogenetic structure of the living world is tripartite. In *Phylogeny and beyond: Scientific, historical, and conceptual significance of the first tree of life*, Pace et al. describe the way in which this monumental discovery was made, its context within the historical development of evolutionary thought, and how it has impacted their understanding of the emergence of life and the characterization of the evolutionary process in its most general form.

Pace, NR *et al.* (2012) Phylogeny and beyond: Scientific, historical, and conceptual significance of the first tree of life *Proc Natl Acad Sci USA* 109:1011.

Additional suggested reading: *Phylogenetic structure of the prokaryotic domain: The primary kingdoms.* Woese and Fox. 1977. (http://www.pnas.org/content/74/11/5088.full.pdf)
Read the paper(s) carefully and answer the following questions.
Honoring the fact that this field is rife with controversy, and to promote the spirit of open discussion— these were leniently graded without much strict criteria. Guidelines are listed.

1) The theory of evolution as we know it today was neither spontaneously reasoned nor obvious. Rather, the theory has gone through numerous revisions by generations of evolution pioneers. (8 points)
a. Order the following pioneers mentioned in the paper, briefly describe their theories of evolution and biological classification.
Charles Darwin, Ernst Haeckel, Carl Linnaeus, Jean Baptiste de Lamarck,
Linnaeus, Lamarck, Darwin, Haeckel
b. Describe the discoveries that led the next person to modify the theory.
Linnaeus: classification, nested hierarchy system
Lamarck: organisms use adaptation, increase in complexity
Darwin: descent with modification through natural selection
Haeckel: developed important concepts related to speciation, coined Monera vs. Protista

2) Some questions remained after Woese and Fox (1977), but can now be answered (at least in part) today: (5 points)
a. Where was the root of the tree?
It is “deep” on the ends of the bacterial and archaeal lines. Also accept graphical representation.
b. Is there a hypothetical last universal common ancestor
In general, yes, but all plausible discussions were given credit. Because “explain” was not included in the question, the answer “Yes” had to be accepted.
c. Were two of the urkingdoms more closely related to one another than to the third urkingdom? Or did the three spring independently from some universal ancestor?
Bacteria diverged from the tree, followed by archaea. Eukaryotes are then more closely related to archaea than they are to bacteria.

3) Often, results of a controversial experiment are not widely accepted until they can be used to help predict or independently verify known relationships that previously lacked rhyme or reason, or answer classic questions by providing corroborating evidence on top of existing, widely accepted fundamental knowledge. The Fox and Woese paper published in 1977 experienced significant backlash. Name some key points of contention, and list some ways in which the findings of the paper were able to stand their own. (5 points) (6 sentences maximum)

Answers vary, but examples are:

contested idea of aboriginal lines of descent, bipartite scheme, rRNA not being a good marker

rRNA predictably conserved and distinct within each domain, archaea very distinct from bacteria, proved bacterial origin of chloroplasts

4) Describe, in your own words, the “fundamental breakthrough in biological science” that occurred in 1977. Discuss the ways that this paradigm shift influenced the fields of (a) microbiology and (b) evolutionary biology, giving specific examples. (5 points) (6 sentences maximum)

Answers giving a good overview were accepted (using new genetic technology to phylogenetically relate organisms, microbes as huge part and central to study of biosphere and evolution, redefined three-domain tree, etc).