# Valdosta State University, Department of Biology

BIOL 6010: Special Topics in Biology II: Macroevolution

areas of cell and molecular biology, genetics, organismal biology, and evolution and ecology. To demonstrate the ability to identify significant biological research questions, develop research protocols, and properly analyze research questions through the use of the scientific method.

# **Course Prerequisites and Expectations**

The course prerequisite is BIOL

Assignment	% of final Grade
Class participation during paper summaries and discussions*	20%
Deportment (This means behavior. Be courteous to your fellow students during discussions)	5%
Written Midterm	25%
Written Final	25%
Phylogenetic Reconstruction Alignment Exercise #1	5%
Phylogenetic Reconstruction Model Selection Exercise #2	5%

My Statement:

# **Tentative Lecture Schedule, BIOL 6010**

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Week	Topic:	Readings
1	Darwinism and Macroevolution	Mayr 1985, Gould 1995, Simpson 1944, Pigliucci 2008
2	Construction of Higher Taxa	Simpson 1953, Mayr 1982, de Queiroz 1988, Wagner 2007, Webster and Zelditch 2005
3	Evolutionary Morphology I	Pattee 1973, Hall 1998, Newman and Muller 2000, Wagner et al. 2007, Wagner 1988, Carroll 2008
4	Evolutionary Morphology II, Adaptation	Cracraft 1990, Wagner and Lynch 2010, Galis 2001, Jablonski 2005, Larson 2009; Gould 1979, Lewontin 1977, Ellstrand 1983, Brodie et al. 2004, Agosta and Dunham 2004
5	Species and Speciation	Mayr 1987, Cracraft 1989, Paterson 1985, Wiley 1981, Templeton 1989, de Quieroz 1999, Kozak et al. 2006
6	Review and Midterm	NA
7	Tempo and Mode of Speciation and Morphological Evolution I	Gould 2001, Coyne 2007, Gavrilets 2004
8	Tempo and Mode of Speciation and Morphological Evolution II	Templeton 1996, Jackson and Cheetham 1999
9	Phylogenetic Reconstruction and Comparative Methods	Reece et al. 2010, Reece et al. 2013
10	Hierarchy of Sorting and Selection I	Gould 1985, Vrba and Gould 1986, McCune et al. 1984
11	Hierarchy of Sorting and Selection II	Lieberman and Vrba 2005, Gould 2002
12	Extinction I	Gould 1991, Briggs et al. 1992, Briggs and Fortey 2005,
13	Extinction II	Jablonski 2005, Alvarez 1986, Van Valen 1973
14	Review and Final Exam	NA

# **Tentative Laboratory Schedule, BIOL 6010**

Week	Topic:	Activities/Assignments
1	Introduction to underlying theory of common descent and theory of Parsimony	Introductory Lecture and classroom relatedness exercise
2	Common descent, homoplasy, and homology	Classroom exercise (Lemke et al. 2012) and discussion
3	Introduction to different types of data used in phylogenetic reconstructions; generating DNA sequence data and downloading it online	Lecture and group exercises in Parsimony reconstructions of DNA sequence data
4	Marker choice, alignment and homology	GENEDOC and CLUSTAL- DNA sequence alignment- Assignment #1
5	Models of Evolution	Theory behind MODELTESTJ; classroom exercises
6	Using Genbank and forming phylogenetic questions and hypotheses	Form groups and propose projects, search databases to ensure that adequate data exist; download data
7	Forming alignments	CLUSTAL and GeneDoc- Assignment #1 due at end of class
8	Choosing a model of evolution	Assignment #2 due at end of class
9	Phylogenetic reconstruction I	Introduction to MEGA and BEAST*; Parsimony, Likelihood, and Bayesian methods
10	Phylogenetic reconstruction II	Setting parameters
11	Phylogenetic reconstruction III	Initiating first run(s)
12	Phylogenetic reconstruction IV	Compiling reconstructions, assessing parameter estimates, additional analyses
13	Testing hypotheses with Phylogenetic reconstruction	Assignment #3 due at end of class
14	Review and Final Exam	NA

## **Guide to Readings:**

#### **Darwinism and Macroevolution**

Mayr 1985: Read pages 755-772; the best summary that I know of the major components of Darwinian evolutionary theory as synthesized in the mid twentieth century by Mayr and others. This course emphasizes controversies concerning whether and how these principles provide a complete and satisfactory foundation for macroevolutionary phenomena.

Gould 1995: Read 125-134; argues that a hierarchically expanded evolutionary theory is needed to accommodate macroevolutionary phenomena. This theory is a direct challenge to the utility of gradualism and natural selection, although it accepts the other major components of Darwinism. Simpson, G. G. (1944) - excerpts from a classic work by the paleontologist credited with bringing paleontology and systematics into the Darwinian evolutionary synthesis, and discrediting formerly popular theories of orthogenesis and neo-Lamarckism. Stephen Jay Gould adopts Simpson's conceptual framework for the role of paleontology in evolutionary studies, but he challenges Simpson's substantive conclusions from it. Note especially Simpson's categorization of evolutionary modes and tempos, and how studies of fossils are intended to use measurements of tempo to infer mode.

Pigliucci, M. (2008) - address

The challenge from evolutionary developmental biology joins the challenge from evolutionary paleontology in claiming that traditional Darwinism is incomplete as a causal theory of macroevolution. Many specific topics of this article are covered in detail in later topics, and I do not expect you to understand all of the nuances of this paper at the start. Concentrate initially on why the Darwinian theory of the modern synthesis is perhaps inadequate to explain developmental and morphological evolution.

## **Construction of Higher Taxa**

Simpson, G. G. (1953) excerpts; note the emphasis on adaptationist principles in constructing higher taxonomic categories and evaluating their evolutionary origins, especially the concept of adaptive zone.

book. Simpson's "evolutionary taxonomy" as presented here remains the foundation for paleontological meta-analyses of macroevolution.

Mayr, E. (1982) - a concise summary and defense of evolutionary taxonomy following challenges by pheneticists and cladists. Note Mayr's defense of the important concept of "grade," an anathema to cladists.

de Queiroz, K. (1988) - a strong statement of the philosophical foundations of phylogenetic systematics (cladistics). Note especially the argument that the "evolutionary taxonomy" of Mayr and Simpson fails to serve Darwinian principles because it only puts an evolutionary veneer on an essentialistic taxonomic system.

### **Evolutionary Morphology I**

Wagner, G. P. (2007) - further exploration of the hierarchical structure of homology, including the relationship between morphological homology and the structures of genetic systems. Pay close attention to the meanings of character identity networks (ChINs) and gene regulatory networks (GRNs), and how systems of gene expression may correspond to morphological homologies.

Webster, M. and M. L. Zelditch (2005) - perhaps the finest-level separation of concepts pertaining to evolutionary changes to ontogeny and how they lead to ontogenetic repatterning. I find the authors arguments convincing, but the revised terminology is complex and probably will not gain widespread usage. This is a relatively tedious paper, but its insights reward careful reading.

Wagner, G. P. (1988) - the first paper to show that developmental constraints could enhance rather than just inhibit adaptive evolution by natural selection. This paper was critical in the synthesis of structuralist and functionalist approaches to the study of form, and made the concept of developmental constraint more accessible to hardcore Darwinians. Note the structure of the corridor models of

adaptation.

Carroll, S. B. (2008) ó A good summary of the contributions of evolutionary developmental biology to an -regulation at the level of

gene expression, a claim that has generated controversy. The author is a very influential evolutionary biologist and popular writer.

Pattee, H. H. (1973) - the work of a theoretical physicist who studies the origin of life and its hierarchical structure. It is an abstract paper with statements generalized to origins of individuality at any hierarchical interface. Evolution of new homologies through developmental synorganization is one example; evolution of new species through mate recognition systems is another one. Understanding this general model clarifies many macroevolutionary issues as instances of the origin of collective control constraints by a group of elements (cells, morphological structures, organisms). This is the general theory underlying evolution of individuality.

Hall, B. K. (1998) 6 Read pages 93-99, then 307-310. The first assigned part extends the notion of developmental constraint to the concept of a Bauplan, a highly controversial structuralist explanation of the morphological differences among higher taxa. The second chapter introduces the important concept of genetic assimilation, which illustrates the plasticity of the relationship between genotype and phenotype (explored in depth in the following topics).

Newman, S. A. and G. B. Müller (2000) - Genetic machinery is considered an evolved set of constraints on the realization of forms made possible by the intrinsic properties of biological materials. The causal connections between genotype and phenotype are elaborated and in some ways reversed from conventional treatments. This is one of the most challenging and perhaps useful modifications of evolutionary theory to emerge from evolutionary developmental biology.

Wagner, G. P., M. Pavlicev and J. M. Cheverud (2007) 6 A thoughtful and important coverage of the critical concept of modularity in evolution. Modularity is one of the key concepts underlying a proposed extended evolutionary synthesis to incorporate development and morphology into evolutionary theory.

#### **Evolutionary Morphology II, Adaptation**

Brodie, E. D. III, K. V. Young and E. D. Brodie Jr. (2004) - a response to the criticisms of Agosta and Dunham (2004).

Agosta, S. J. and A. E. Dunham (2004) - an interchange with the authors of Brodie et al. (2004) regarding use of phylogenetic criteria in adaptive interpretations.

### **Species and Speciation**

Mayr, E. (1987) - The philosophical question of whether species are classes, individuals or populations is an important one affecting all concepts of species and evolutionary theory in general (punctuated equilibrium and the hierarchical expansion of selection theory rely on the argument that species are individuals, for example). Mayr presents a clear coverage of this issue, and defends his biological species concept against criticism in this important paper. Ultimately, the issue was refined by the segments of population lineages.

Cracraft, J. (1989) - a concept designed to be optimal for reconstructing the phylogenetic history of life in the finest possible detail, especially with respect to biogeographical and conservational issues. This concept has gained numerous followers, who nonetheless have numerous disagreements among themselves regarding criteria of diagnosability. This paper is probably the most thorough general statement of the phylogenetic species concept.

Paterson, H. E. H. (1985) - a critique of the biological species concept emphasizing the species as a philosophical individual and important level of complexity in the genealogical hierarchy of life. This concept involves strong criticism of nonallopatric mechanisms for formation of species.

Wiley, E. O. (1981) - an update of Simpson's evolutionary species concept, which explicitly defines species as having a temporal dimension. It is often called a "lineage concept" of species to distinguish it from concepts that consider species only at a single moment in time (biological and recognition

equivalent to the general lineage concept, although this point is debatable.

Templeton, A. R. (1989) - a revision of the evolutionary species concept designed to make population genetic principles more explicit conceptually and to provide greater testability. Also one of my primary

Reece et al. (2013) - a paper in which I used the phylogeny from Reece et al. (2010) to execute phylogenetic comparative methods.

## Hierarchy of Sorting and Selection I

Gould, S. J. (1985) - an excellent paper arguing for the temporal discontinuity of evolutionary processes. I have problems with Gould's use of evolutionary progress, and I find his description of the evolutionary timescales a bit too rigid; however, it is still one of my favorite papers.

Vrba, E. S. and S. J. Gould (1986) - The distinction between sorting and selection is long overdue and extremely important. The structure of the hierarchically expanded theory of selection is covered thoroughly. An expanded concept of individuality is very important here. This is among the most important papers covered in the class.

McCune, A. R., K. S. Thomson and P. E. Olsen (1984) - This example is a favorite one illustrating opposition between evolutionary processes acting at different tiers of evolutionary time. The conflicts occur between what are essentially the second and third tiers, but the timescale involved is greatly compressed relative to the expected occurrence of species selection and catastrophic species selection.

### **Hierarchy of Sorting and Selection II**

Lieberman, B. S. and E. S. Vrba (2005) - an explanation of changing ideas on the contentious issue of species selection.

Gould, S. J. (2002) - This excerpt from Gould's 2002 book expands the general ideas presented in Vrba and Gould (1986) with a very helpful summary table. The concept of evolutionary drive is developed more explicitly here than in Gould's earlier writings on hierarchical expansion of evolutionary theory.

#### **Extinction I**

Gould, S. J. (1991) - Controversy over interpretation of the Burgess Shale arthropod fauna leads to an important distinction between morphological diversity and morphological disparity. The question of how to measure these factors is a highly debated topic and the subject of numerous recent papers.

Briggs, D. E. G., R. A. Fortey and M. A. Wills (1992) - These authors present an empirical refutation of Gould's interpretation of the Burgess Shale arthropod fauna using two different methods for quantifying morphospace. Are these authors successful in quantifying the relevant parameters and thereby refuting Gould's arguments?

Briggs, D. E. G. and R. A. Fortey (2005) - an update on the continuing problem of how to interpret the "Cambrian explosion."

#### **Extinction II**

Jablonski D. (2005) - an update on extinction peaks in evolution by a leading worker in this field. Alvarez, W. (1986) - This paper describes the author's highly influential work showing that asteroid impacts provide the best explanation for a mass extinction at the K-T boundary. It also discusses periodicity of mass extinctions and the associated "death star" hypothesis. This is the work that most directly inspired Gould to recognize tier 3 of evolutionary time as a source of novel selective processes. To date, the K-T boundary remains the only extinction peak well corroborated as coinciding with an impact crisis.

Van Valen, L. (1973) - Few papers have been both as influential and as controversial as this one has been. The methodology of this paper relies on evolutionary taxonomy and presents a discovery that would not have been made using cladistic taxonomy. Cladists almost universally discredit this work. It gave us the "Red Queen's hypothesis" of evolution, which has had pervasive influence. This paper launched a highly idiosyncratic evolutionary journal, dedicated to the primacy of content over display.