



Valdosta State University, Department of Biology

BIOL 6010: Special Topics in Biology II: Macroevolution  
Prospective Syllabus 4 credit hours (with lab)

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Instructor: Dr. Joshua S. Reece

Classroom: (Lecture) BSC 2202 MW 2pm to 3:15pm; (Lab) BSC 3018 2pm-4:50pm

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Office hours: Wednesdays 12pm -1pm and 4-5pm, and by appointment

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## Course Overview

Welcome to BIOL 6010, special topics course in Macroevolution and Phylogenetics. We will explore major themes in evolutionary biology through the primary literature and learn how to generate phylogenetic trees from DNA sequence data. One of objectives of this course is to teach you how to read and assimilate primary literature quickly. Graduate students will read and be prepared to make a comment on each of the readings every week (undergraduates will each read a subset of the assigned readings). We will discuss the papers and then my lecture will synthesize the readings into the topic of discussion. The readings and lecture portion of this course will expose you to macroevolutionary principles and theory. The laboratory portion of the course will teach you the logistics of phylogenetic reconstruction and analysis. The course is literature intensive and will require extensive reading of primary literature. Assessments will include written essays of major themes and will enhance scientific writing as well as mastery of the course content. The laboratory section will complement the theory discussed in the lecture by teaching you both the basic theory behind phylogenetic reconstruction and how to use modern computer algorithms to create phylogenetic trees. The lecture will meet for two 1.5 hr sessions per week, and the lab will meet for one 3 hr session per week. This course will be taught jointly with undergraduate students as BIOL 4010.

## Course Objectives

This course will cover eight major topics in evolution. The course objectives are to be fluent in each of these topics. Additional objectives include the ability to read and assimilate primary literature and to write scientifically.

1. Darwinism and Macroevolution
2. Construction of Higher Taxa
3. Evolutionary Morphology
4. Species and Speciation
5. Tempo and Mode of Speciation and Morphological Evolution
6. Phylogenetic Reconstruction and Comparative Methods
7. Hierarchy of Sorting and Selection
8. Extinction

## Related Learning Objective for VSU Department of Biology

- To demonstrate competency in factual content and interpretation of the major biological concepts

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 3250. Students will be expected to read the literature assigned to them and come to class prepared to lead a discussion on those readings (each student will be graded on their personal contribution to the discussion). Course assessments will include a written midterm and final, and a class participation grade based on led discussions. Midterm and Final exams will consist of four synthetic and integrative questions related to topics discussed in class. Students will choose three of the four questions and write a five paragraph essay in response to each question. *This course will be co-offered with undergraduates at BIOL 4010. While undergraduate students will be expected each read a subset of the papers discussed in class, graduate students will be expected to read all papers. In addition, a more stringent rubric will be applied to graduate student Midterm and Final essay questions, and graduate student phylogenetic reconstructions will include larger datasets than will be expected of undergraduates.*

### **Course Credits**

BIOL 6010 is a four credit course to be taught during the Fall and Spring semesters.

### **Required Texts and Materials**

We will utilize peer reviewed literature for this course; there is no textbook. All readings will be made available through Blazeview. An excellent reference for students who need to familiarize themselves with basic evolutionary tenets is:

Futuyma, D. 2009. Evolution 2<sup>nd</sup> Edition. Sinauer Associates.

### **Basis for Final Grade**

<b>Assignment</b>	<b>% of final Grade</b>
Class participation during paper summaries and discussions*	20%
Department (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%
Phylogenetic Reconstruction Exercise #3	15%
<b>Total</b>	<b>100%</b>

**Students will have until the end of the following week to contest any grades; after that time grades are final. Any questions about grades must be made in writing through email.**

**Grade Scale:** 100-90% A; 80-89% B; 70-79% C; 60-69% D, 0-59% F

**Attendance Policy:** Students who miss two classes without an excuse cannot receive a lab grade above a “D” (60%).

## **Student Conduct**

You will be respectful of your classmates and your instructor. Cell phone use is not allowed during class.

## **Course Policies: Technology and Media**

**Email:** Please email me only from a VSU email account. I am unable to respond to emails from non-VSU accounts.

**Classroom Devices:** You may NOT use your cell phones in class under any circumstances. Computers and tablets are encouraged for note-taking and reference to papers. Internet will be disabled while in class. Use of internet during class will result in a zero participation grade for the course.

## **Accommodations Statement**

Students with disabilities who are experiencing barriers in this course may contact the Access Office for assistance in determining and implementing reasonable accommodations. The Access Office is located in Farber Hall. The phone numbers are 229-245-2498 (V), 229-375-5871 (Video Phone), and 229-219-1348 (TTY). For more information, please visit <http://www.valdosta.edu/student/disability> or email [access@valdosta.edu](mailto:access@valdosta.edu).

## **Academic Integrity**

***My Statement:*** You can probably get away with some cheating/plagiarism. But, if I catch you, I will do everything I can to kick you out of my class and impose all possible penalties. I have zero tolerance, so do not risk it.

***University Prepared Statement:*** Academic integrity is the responsibility of all VSU faculty and students. Students are responsible for knowing and abiding by the Academic Integrity Policy as set forth in the Student Code of Conduct and the syllabus. All students are expected to do their own work and to uphold a high standard of academic ethics. Cheating (including plagiarism) will not be tolerated. The instructor reserves the right to dismiss you from the course without credit if you are caught cheating. You will be respectful of your instructor and your fellow students at all times, or you will be dismissed from the class and potentially the course.

## Tentative Lecture Schedule, BIOL 6010

<b>Week</b>	<b>Topic:</b>	<b>Readings</b>
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 Queiroz 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

<b>Week</b>	<b>Topic:</b>	<b>Activities/Assignments</b>
<b>1</b>	Introduction to underlying theory of common descent and theory of Parsimony	Introductory Lecture and classroom relatedness exercise
<b>2</b>	Common descent, homoplasy, and homology	Classroom exercise (Lemke et al. 2012) and discussion
<b>3</b>	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
<b>4</b>	Marker choice, alignment and homology	GENEDOC and CLUSTAL- DNA sequence alignment- Assignment #1
<b>5</b>	Models of Evolution	Theory behind MODELTESTJ; classroom exercises
<b>6</b>	Using Genbank and forming phylogenetic questions and hypotheses	Form groups and propose projects, search databases to ensure that adequate data exist; download data
<b>7</b>	Forming alignments	CLUSTAL and GeneDoc- Assignment #1 due at end of class
<b>8</b>	Choosing a model of evolution	Assignment #2 due at end of class
<b>9</b>	Phylogenetic reconstruction I	Introduction to MEGA and BEAST*; Parsimony, Likelihood, and Bayesian methods
<b>10</b>	Phylogenetic reconstruction II	Setting parameters
<b>11</b>	Phylogenetic reconstruction III	Initiating first run(s)
<b>12</b>	Phylogenetic reconstruction IV	Compiling reconstructions, assessing parameter estimates, additional analyses
<b>13</b>	Testing hypotheses with Phylogenetic reconstruction	Assignment #3 due at end of class
<b>14</b>	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) - *addresses the need to establish an "extended evolutionary synthesis" to incorporate evolutionary morphology into the framework of the "modern synthesis" of the 1940s. 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. Some evolutionists have criticized Simpson's adaptationist focus, preferring the pluralism of the earlier 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) – *A good summary of the contributions of evolutionary developmental biology to an expanded evolutionary theory. Note specifically this author's emphasis on cis-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) – *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) – *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**

- Cracraft, J. (1990) - *Cracraft criticizes the concept of evolutionary innovation and the proposed roles of novel features in evolutionary diversification. He presents a protocol for comparative study of evolutionary novelties. Cracraft's critique warns evolutionists that origin of a novelty is not sufficient to predict high rates of speciation and ecological diversification in the subsequent evolution of a population. Many contemporary researchers overlook the messages of this paper, making arguments that await severe criticism when these lessons are fully acknowledged.*
- Wagner, G. P. and V. J. Lynch (2010) – *extends the arguments that the developmental genetic basis of the origins of morphological novelties is distinct from the genetic basis of other kinds of morphological evolution. If true, this would corroborate a major claim of Richard Goldschmidt in his opposition to genetic arguments in the modern evolutionary synthesis.*
- Galis, F. (2001) - *Here is a good review of uses of "key innovation" in evolution, including criticism of some widespread misuses.*
- Jablonski, D. (2005) - *influential work suggesting that evolutionary novelties associated with origins of higher taxa occur preferentially in highly disturbed environments in the marine fossil record. As a cladist, Cracraft is highly critical of these arguments, which utilize Simpsonian evolutionary taxonomy and its concept of nested adaptive zones*
- Larson, A. (2009) – *Note the important distinctions between adaptation, exaptation, nonadaptation, and disadaptation (primary and secondary). A critical message is that evaluating the evolutionary relationships between character origin and utility requires an explicitly historical context and robust hypotheses of homology. This author was my primary advisor in graduate school.*
- Gould, S. J. (1979) - *perhaps the most elegant criticism of just-so storytelling in science, and a highly cited criticism of the adaptationist regime.*
- Lewontin, R. (1977) - *a classic criticism of adaptationist studies, especially as used in sociobiology.*
- Ellstrand, N. E. (1983) - *an interesting critique of adaptationism from an unusual angle.*



- 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 "general lineage concept" in which species are 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 concepts, for example), although this distinction is debated. Some authors argue that Wiley's concept is 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 advisors in graduate school, and Dr. Anderson's advisor.*
- de Queiroz, K. (1999) - *an ambitious attempt to place all of the preceding concepts into a common conceptual framework recognizing important contributions from all of the concepts. Many recent papers invoke this concept as the basis for discussions of species and speciation. I interpret the argument basically as a statement that the ontological status of a species is a segment of a population lineage.*
- Kozak, K. H., D. W. Weisrock and A. Larson (2006) - *a quantification of rates of lineage accumulation across geographic space shows that vicariance and preemptive occupation of space can produce speciation rates that rival those of "adaptive radiations" without producing extensive ecological disparity among lineages.*

### **Tempo and Mode of Speciation and Morphological Evolution I**

- Gould, S. J. (2001) - *a good explanation of punctuated equilibrium by a strong advocate. Note how the explanations of punctuated equilibrium have changed during its first two decades.*
- Coyne, J. A. (2007) - *a good review of the empirical problems raised by the notion of sympatric speciation.*
- Gavrillets, S. (2004) - *An overview of modes of speciation as used in contemporary discussions.*

### **Tempo and Mode of Speciation and Morphological Evolution II**

- Templeton, A. R. (1996) - *an insightful review of experimental evidence testing predictions of founder-flush and genetic transience models of founder-induced speciation.*
- Jackson, J. B. C. and A. H. Cheetham (1999) - *A review of paleontological tests of punctuated equilibrium by authors whose work is considered the strongest empirical demonstration of punctuated equilibrium.*

### **Phylogenetic Reconstruction and Comparative Methods**

- Reece et al. (2010) - *a paper in which I utilized multiple phylogenetic reconstruction methods and a fossil clock calibration.*

- 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.*