Biology 4182 - Macroevolution
Spring 2012 - Allan Larson

Reading List and Syllabus

I. Epistemology

1. Mayr, E. 1982. *The Growth of Biological Thought.* Harvard Univ. Press. (Pp. 21-78)

2. Pattee, H. H. 1978. The complementarity principle in biological and social structures. *Journal of Social and Biological Structures* 1:191-200.

II. Darwinism and Macroevolution

3. Mayr, E. 1985. Darwin's five theories of evolution. Pp. 755-772 *in* D. Kohn (ed.) *The Darwinian Heritage.* Princeton Univ. Press, Princeton.

4. Gould, S. J. 1995. Tempo and mode in the macroevolutionary reconstruction of Darwinism. Pp. 125-144 *in* W. M. Fitch and F. J. Ayala (eds.) *Tempo and Mode in Evolution: Genetics and Paleontology 50 Years after Simpson.* National Academy Press, Washington. *(Assignment includes pages 125-134 only.)*

5. Simpson, G. G. 1944. *Tempo and Mode in Evolution.* Columbia Univ. Press, New York. (Pp. 197-217)

6. Pigliucci, M. 2008. Is evolvability evolvable? *Nature Reviews Genetics* 9:75-82.

III. Construction of Higher Taxa

A. Evolutionary Taxonomy

7. Simpson, G. G. 1953. *The Major Features of Evolution.* Columbia Univ. Press, New York. (Pp. 199-212; 338-359)

8. Mayr, E. 1982. *The Growth of Biological Thought.* Harvard Univ. Press, Cambridge. (Pp. 614-616; 233-235)

9. Miller, A. H. 1949. Some ecologic and morphologic considerations in the evolution of higher taxonomic categories. Pp. 84-88 *in* E. Mayr and E. Schuz (eds.) *Ornithologie als Biologische Wissenschaft.* Carl Winter/Universitätsverlag, Heidelberg.

B. Phenetic versus Cladistic Taxonomy

10. Kearney, M. 2007. Philosophy and phylogenetics: historical and current connections. Pp. 211-232 *in* D. L. Hull and M. Ruse (eds.) *The Cambridge Companion*

to the Philosophy of Biology. Cambridge University Press, Cambridge, UK.

11. Ereshefsky, M. 2008. Systematics and taxonomy. Pp. 99-118 *in* S. Sarkar and A. Plutynski (eds.) *A Companion to the Philosophy of Biology.* Blackwell Publishing. Malden, MA. *(Assignment includes pages 107-117 only.)*

12. Sneath, P. H. A. and R. R. Sokal. 1973. *Numerical Taxonomy.* W. H. Freeman and Co., San Francisco. (Pp. 5, 9-10, 27-30).

13. de Queiroz, K. 1988. Systematics and the Darwinian revolution. *Philosophy of Science* 55:238-259.

IV. Evolutionary Morphology

A. Taxic Homology

14. Patterson, C. 1982. Morphological characters and homology. Pp. 21-74 in K. A. Joysey and A. E. Friday (eds.) *Problems of Phylogenetic Reconstruction.* Academic Press, New York.

15. de Queiroz, K. 1985. The ontogenetic method for determining character polarity and its relevance to phylogenetic systematics. *Systematic Zoology* 34:280-299.

B. Transformational Homology

16. Kaplan, D. R. 1984. The concept of homology and its central role in the elucidation of plant systematic relationships. Pp. 51-70 *in* T. Duncan and T. F. Stuessy (eds.) *Cladistics: Perspectives on the Reconstruction of Evolutionary History*. Columbia Univ. Press, New York.

17. Wagner, G. P. 1989. The origin of morphological characters and the biological basis of homology. *Evolution* 43:1157-1171.

18. Roth, V. L. 1991. Homology and hierarchies: problems solved and unresolved. *Journal of Evolutionary Biology* 4:167-194.

19. Wagner, G. P. 2007. The developmental genetics of homology. *Nature Reviews Genetics* 8:473-479.

C. Heterochrony, Heterotopy and Ontogenetic Repatterning

20. Alberch, P., S. J. Gould, G. F. Oster and D. B. Wake. 1979. Size and shape in ontogeny and phylogeny. *Paleobiology* 5:296-317.

21. Raff, R. A. and G. A. Wray. 1989. Heterochrony: Developmental mechanisms and evolutionary results. *Journal of Evolutionary Biology* 2:409-434.

22. West-Eberhard, M. J. 2003. Heterotopy. Pp. 255-260 *in* West-Eberhard, M. J., *Developmental Plasticity and Evolution.* Oxford Univ. Press. Oxford, UK.

23. Webster, M. and M. L. Zelditch. 2005. Evolutionary modifications of ontogeny: Heterochrony and beyond. *Paleobiology* 31:354-372.

D. Developmental Constraints and Evolution

24. Pattee, H. H. 1973. The physical basis and origin of hierarchical control. Pp. 73-108 *in* H. H. Pattee (ed.) *Hierarchy Theory.* George Braziller, New York.

25. Alberch, P. 1989. The logic of monsters: evidence for internal constraint in development and evolution. *Geobios mémoire spécial n°* 12:21-57.

26. Wagner, G. P. 1988. The significance of developmental constraints for phenotypic evolution by natural selection. Pp. 222-229 *in* G. de Jong (ed.) *Population Genetics and Evolution,* Springer-Verlag, Berlin.

27. Hall, B. K. 1998. *Evolutionary Developmental Biology.* Chapman and Hall, London. (Pp. 93-99, 307-310)

E. Epigenetic Mechanisms, Modularity and Evolvability

28. Alberch, P. 1991. From genes to phenotype: dynamical systems and evolvability. *Genetica* 84:5-11.

29. Newman, S. A. and G. B. Müller. 2000. Epigenetic mechanisms of character origination. *Journal of Experimental Zoology* 288:304-317.

30. Preston, J. C., L. C. Hileman and P. Cubas. 2011. Reduce, reuse and recycle: Developmental evolution of trait diversification. American Journal of Botany 98:397-403.

31. Wagner, G. P., M. Pavlicev and J. M. Cheverud. 2007. The road to modularity. *Nature Reviews Genetics* 8:921-931.

32. Carroll, S. B. 2008. Evo-devo and an expanding evolutionary synthesis: a genetic theory of morphological evolution. *Cell* 134:25-36.

33. Pigliucci, M. 2010. Genotype-phenotype mapping and the end of the 'genes as blueprint' metaphor.

Philosophical Transactions of the Royal Society of London Series B 275:91-100.

F. Evolutionary Novelties: Origins and Evolutionary Consequences

34. Wagner, G. P. and V. J. Lynch. 2010. Evolutionary novelties. *Current Biology* 20:R48-R52.

35. Cracraft, J. 1990. The origin of evolutionary novelties: pattern and process at different hierarchical levels. Pp. 21-44 *in* M. H. Nitecki (ed.) *Evolutionary Innovations.* Univ. of Chicago Press, Chicago.

36. Galis, F. 2001. Key innovations and radiations. Pp. 581-605 *in* G. P. Wagner (ed.) *The Character Concept in Evolutionary Biology.* Academic Press, San Diego.

37. Fürsich, F. T. and D. Jablonski. 1984. Late Triassic naticid drillholes: Carnivorous gastropods gain a major adaptation but fail to radiate. *Science* 224:78-80.

38. Jablonski, D. 2005. Evolutionary innovations in the fossil record: The intersection of ecology, development and macroevolution. *Journal of Experimental Zoology* 304B:504-519.

G. Evolution of Adaptation

39. Lewontin, R. 1977. Adaptation. Pp. 65-84 *in* R. Levins and R. Lewontin (1985) *The Dialectical Biologist.* Harvard Univ. Press, Cambridge.

40. Ellstrand, N. E. 1983. Why are juveniles smaller than their parents? *Evolution* 37:1091-1094.

41. Larson, A. 2009. Adaptation. Pp. 93-100 *in* S. A. Levin (ed.) *The Princeton Guide to Ecology.* Princeton University Press. Princeton, NJ.

42. Agosta, S. J. and A. E. Dunham. 2004. Comment on "How the lizard got its horns." *Science* 306:230.

43. Brodie, E. D. III, K. V. Young and E. D. Brodie Jr. 2004. Response to comment on "How the Lizard got its horns." *Science* 306:230.

H. Alternative Adaptations

44. West-Eberhard, M. J. 1986. Alternative adaptations, speciation and phylogeny (a review). *Proceedings of the National Academy of Sciences USA* 83:1388-1392.

45. Liem, K. F. and L. S. Kaufman. 1984. Intraspecific macroevolution: functional biology of the polymorphic cichlid species, *Cichlasoma minckleyi.* Pp. 203-215 *in* A. A. Echelle and I. Kornfield (eds.) *Evolution of Fish Species Flocks.* Univ. of Maine Press. Orono, ME.

46. Sinervo, B. and E. I. Svensson. 2004. The origin of novel phenotypes: Correlational selection, epistasis, and speciation. Pp. 171-194 *in* Hall, B. K., Pearson, R. D. and G. B. Müller (eds.) Environment, Development, and Evolution: Toward a synthesis. MIT Press. Cambridge, MA.

47. West-Eberhard, M. J. 2005. Phenotypic accommodation: Adaptive innovation due to developmental plasticity. *Journal of Experimental Zoology* 304B:610-618.

V. Species and Speciation

A. Essentialism, Typology and the Biological Species Concept

48. Mayr, E. 1987. The ontological status of species: scientific progress and philosophical terminology. *Biology and Philosophy* 2:145-166.

B. The Recognition Concept of Species

49. Paterson, H. E. H. 1985. The recognition concept of species. *Transvaal Museum Monograph* 4:21-29.

C. The Evolutionary Species Concept

50. Wiley, E. O. 1981. *Phylogenetics.* Wiley & sons, New York. (Pp. 24-34)

D. The Cohesion Concept of Species

51. Templeton, A. R. 1989. The meaning of species and speciation - a genetic perspective. Pp. 3-27 *in* D. Otte and J. A. Endler (eds.) *Speciation and its Consequences.* Sinauer Assoc., Sunderland.

E. The Phylogenetic Concept of Species

52. Cracraft, J. 1989. Speciation and its ontology: The empirical consequences of alternative species concepts for understanding patterns and processes of differentiation. Pp. 28-59 *in* D. Otte and J. A. Endler (eds.) *Speciation and its Consequences.* Sinauer Assoc., Sunderland.

F. The Genetic Concept of Species

53. Baker, R. J. and R. D. Bradley. 2006. Speciation in mammals and the genetic species concept. *Journal of Mammalogy* 87:643-662.

G. The General Lineage Concept of Species

54. de Queiroz, K. 1999. The general lineage concept of species and the defining properties of the species category. Pp. 49-89 *in* R. A. Wilson (eds.) *Species: New Interdisciplinary Essays.* MIT Press, Cambridge, MA.

H. Spatial Dynamics of Speciation

55. Cracraft, J. 1983. Cladistic analysis and vicariance biogeography. *American Scientist* 71:273-281.

56. Dillon, S. and J. Fjeldså. 2005. The implications of different species concepts for describing biodiversity patterns and assessing conservation needs for African birds. *Ecography* 28:682-692.

57. Heaney L. R. 2007. Is a new paradigm emerging for oceanic island biogeography? *Journal of Biogeography* 34:753-757.

58. Genner, M. J., P. Nichols, G. Carvalho, R. L. Robinson, P. W. Shaw, A. Smith, and G. F. Turner. 2007. Evolution of a cichlid fish in a Lake Malawi satellite lake. *Proceedings of the Royal Society of London series B* 274: 2249-2257.

59. Kozak, K. H., D. W. Weisrock and A. Larson. 2006. Rapid lineage accumulation in a non-adaptive radiation: Phylogeographic analysis of diversification rates in eastern North American woodland salamanders (Plethodontidae: *Plethodon*). *Proceedings of the Royal Society of London Series B* 273:539-546.

I. Modes of Speciation

60. Gavrilets, S. 2004. Introduction to *Fitness Landscapes and the Origin of Species*. Princeton Univ. Press. Princeton, NJ. (Pp. 1-18)

61. Paterson, H. E. H. 1981. The continuing search for the unknown and unknowable: a critique of contemporary ideas on speciation. *South African Journal of Science* 77:113-119.

62. Templeton, A. 1981. Mechanisms of speciation - a population genetic approach. *Annual Review of Ecology and Systematics* 12:23-48.

63. Coyne, J. A. 2007. Sympatric speciation. *Current Biology* 17:787-788.

J. Adaptive Landscapes and Speciation

64. Carson, H. L. and A. R. Templeton. 1984. Genetic revolutions in relation to speciation phenomena: the founding of new populations. *Annual Review of Ecology and Systematics* 15:97-131.

65. Templeton, A. R. 1996. Experimental evidence for the genetic transilience model of speciation. *Evolution* 50:909-915.

66. Gavrilets, S. 2010. High-dimensional fitness landscapes and the origins of biodiversity. Pp. 45-80 *in* M. Pigliucci and G. Muller (eds), *Toward an Extended Evolutionary Synthesis.* Cambridge, MA: MIT Press. *(Assignment includes pages 45-64 only.)*

VI. Tempo and Mode of Speciation and Morphological Evolution – Punctuated Equilibrium versus Phyletic Evolution

67. Gould, S. J. 2001. The interrelationship of speciation and punctuated equilibrium. Pp. 196-217 *in* J. B. C. Jackson, S. Lidgard and F. K. McKinney (eds.) *Evolutionary Patterns: Growth, Form and Tempo in the Fossil Record.* University of Chicago Press, Chicago.

68. Turner, J. R. G. 1988. The evolution of mimicry: a solution to the problem of punctuational evolution. *American Naturalist* 131:S42-S66.

69. Jackson, J. B. C. and A. H. Cheetham. 1999. Tempo and mode of speciation in the sea. *Trends in Ecology & Evolution* 14:72-77.

70. Eldredge N., J. N. Thompson, P. M. Brakefield, S. Gavrilets, D. Jablonski, J. B. C. Jackson, R. E. Lenski, B. S. Lieberman, M. A. McPeek and W. Miller, III. 2005. The dynamics of evolutionary stasis. *Paleobiology* 31:S133-145.

VII. Hierarchy of Sorting and Selection

A. General Theory

71. Gould, S. J. 1985. The paradox of the first tier: an agenda for paleobiology. *Paleobiology* 11:2-12.

72. Vrba, E. S. and S. J. Gould. 1986. The hierarchical expansion of sorting and selection: sorting and selection cannot be equated. *Paleobiology* 12:217-228.

73. Lieberman, B. S. and E. S. Vrba. 2005. Stephen Jay Gould on species selection: 30 years of insight. *Paleobiology* 31:S113-121.

74. (same as #4). Gould, S. J. 1995. Tempo and mode in the macroevolutionary reconstruction of Darwinism. Pp. 125-144 *in* W. M. Fitch and F. J. Ayala (eds.) *Tempo and Mode in Evolution: Genetics and Paleontology 50 Years after Simpson.* National Academy Press, Washington. *(Assignment includes pages 134-144, following the material assigned in #4.)*

75. Gould, S. J. 2002. The grand analogy: A speciational basis for macroevolution. Pp. 714-744 *in* Gould, S. J. *The Structure of Evolutionary Theory.* Harvard Univ. Press. Cambridge, MA.

B. Challenges to the Paradox of the First Tier

76. Kitchell, J. A. 1990. The reciprocal interaction of organism and effective environment: Learning more about "and." Pp. 151-169 *in* R. M. Ross and W. D. Allmon (eds.) *Causes of Evolution: A Paleontological Perspective.* Univ. of Chicago Press, Chicago.

77. Jackson, J. B. C. and F. McKinney. 1990. Ecological processes and progressive macroevolution of marine clonal benthos. Pp. 173-209 *in* R. M. Ross and W. D. Allmon (eds.) *Causes of Evolution: A Paleontological Perspective.* Univ. of Chicago Press, Chicago.

78. McCune, A. R., K. S. Thomson and P. E. Olsen. 1984. Semionotid fishes from the mesozoic great lakes of North America. Pp. 27-44 *in* A. A. Echelle and I. Kornfield (eds.) *Evolution of Fish Species Flocks.* Univ. of Maine Press, Orono.

79. Lieberman, B. S. 1995. Phylogenetic trends and speciation: Analyzing macroevolutionary processes and levels of selection. Pp. 316-337 *in* D. H. Erwin and R. L. Anstey (eds.) *New Approaches to Speciation in the Fossil Record.* Columbia Univ. Press, New York.

VIII. Extinction

A. Taxonomic Survivorship Curves

80. Van Valen, L. 1973. A new evolutionary law. *Evolutionary Theory* 1:1-30.

81. McCune, A. R. 1982. On the fallacy of constant extinction rates. *Evolution* 36:610-614.

82. Foote, M. 2001. Evolutionary rates and the age distributions of living and extinct taxa. Pp. 245-294 *in* J. B. C. Jackson, S. Lidgard and F. K. McKinney (eds.) *Evolutionary Patterns: Growth, Form and Tempo in the Fossil Record.* University of Chicago Press, Chicago.

83. Roy, K., G. Hunt, and D. Jablonski, 2009. Phylogenetic conservatism of extinctions in marine bivalves. Science 325:733-737.

84. Krug, A. Z., D. Jablonski, and J. W. Valentine, 2009. Signature of the end-Cretaceous mass extinction in the modern biota. Science 323:767-771.

B. Periodicity of Extinction

85. Raup, D. M. and J. J. Sepkoski, Jr. 1984. Periodicity of extinctions in the geologic past. *Proc. Natl. Acad. Sci. USA* 81:801-805.

86. Patterson, C. and A. B. Smith. 1987. Is periodicity of mass extinctions a taxonomic artefact? *Nature* 330:248-251.

87. Sepkoski, J. J., Jr. and D. C. Kendrick. 1993. Numerical experiments with model monophyletic and paraphyletic taxa. *Paleobiology* 19:168-184.

C. Evolutionary Consequences of Episodic Extinction Peaks

88. Alvarez, W. 1986. Toward a theory of impact crises. *Eos* 67:649-658.

89. Raup, D. M. 1995. The role of extinction in evolution. Pp. 109-124 *in* W. M. Fitch and F. J. Ayala (eds.) *Tempo and Mode in Evolution: Genetics and Paleontology 50 Years after Simpson.* National Academy Press, Washington.

90. Jablonski D. 2005. Mass extinctions and macroevolution. Paleobiology 31S:192-210.

IX. Diversity Through Time

A. Taxonomic Diversity Versus Disparity

91. Gould, S. J. 1991. The disparity of the Burgess Shale arthropod fauna and the limits of cladistic analysis: why we must strive to quantify morphospace. *Paleobiology* 17:411-423.

92. Briggs, D. E. G., R. A. Fortey and M. A. Wills. 1992. Morphological disparity in the Cambrian. *Science* 256:1670-1673.

93. Briggs, D. E. G. and R. A. Fortey. 2005. Wonderful strife: Systematics, stem groups, and the phylogenetic signal of the Cambrian radiation. *Paleobiology* 31:S94-112.

94. Foote, M. 1993. Discordance and concordance between morphological and taxonomic diversity. *Paleobiology* 19:185-204.

B. Phanerozoic Diversity

95. Sepkoski, J. J., Jr. 1981. A factor analytic description of the Phanerozoic marine fossil record. *Paleobiology* 7:36-53.

96. Alroy, J., M. Aberhan, D. Bottjer, M. Foote, F. Fursich, P. J. Harries et al. 2008. Phanerozoic trends in the global diversity of marine invertebrates. *Science* 321:97-100.

All readings are available on the library's electronic reserve: *http://ares.wustl.edu/ares/ares.dll?SessionID=S154501520U&Action=22&Type=10&ItemID=78384*

Geological time:
http://www.ucmp.berkeley.edu/help/timeform.html

Tentative Schedule: Reading Assignments (as numbered above)

1. January 17: 1
2. January 19: 2-3
3. January 24: 4-6
4. January 26: 7-9
5. January 31: 10-13
6. February 2: 14-15
7. February 7: 16-17
8. February 9: 18-19
9. February 14: 20-23
10. February 16: 24-27
11. February 21: 28-29
12. February 23: 30-34
13. February 28: 35-38
14. March 1: 39-43
15. March 6: 44-47
16. March 8: 48-50
17. March 20: 51-54
18. March 22: 55-59
19. March 27: 60-63
20. March 29: 64-66
21. April 3: 67-70
22. April 5: 71-75
23. April 10: 76-79
24. April 12: 80-84
25. April 17: 85-87
26. April 19: 88-90
27. April 24: 91-94
28. April 26: 95-96

Exam format and schedule - Exams will be 4 take-home questions to be answered in essay format. Graduate students answer all 4 questions; undergraduates answer any 3 of the four questions.

Exam	Readings	Questions Distributed	Exam Due
1	1-27	February 16	March 1
2	28-66	March 29	April 12
3	67-98	April 26	May 8

Macroevolution:

- Evolutionary change on a grand scale, encompassing the origin of novel designs, evolutionary trends, adaptive radiation and mass extinction. (Neil A. Campbell, *Biology)*

- A large evolutionary pattern usually viewed through the perspective of geologic time, such as the evolution of the horse from *Eohippus* to *Equus.* The evolutionary changes in taxonomic categories above the species level, and the evolutionary changes that bring about the origin of a new higher taxon. (Robert C. King and William D. Stansfield, *A Dictionary of Genetics)*

Office Hours are immediately after class or by appointment.

Reading Guide to Papers

I. Epistemology

1. Mayr, E. (1982) - *the philosophical foundations of biological science discussed by a major contributor to the evolutionary synthesis. Mayr's emphasis on quality of concepts and theory as the measure of a science is central to this course. This assignment introduces hypothetico-deductivism, comparative methodology, essentialism versus populational thinking, hierarchy, and reductionism, all of which are major themes of macroevolution. This is the best concise coverage of these issues that I know.*

2. Pattee, H. H. (1978) - *an important statement on the epistemology of complex systems, arguing that knowledge requires simultaneous but distinct structural versus functional and objective versus subjective descriptions. The complementarity principle is derived from quantum mechanics, and that perspective is evident in this article. Failure to understand this principle almost certainly delayed the synthesis of developmental biology and population genetics for at least several decades. Failure to identify both the*

subjective and objective components of research is a general problem in biology.

II. Darwinism and Macroevolution

3. Mayr, E. (1985) - *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.*

4. Gould, S. J. (1995) - *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 as presented in reading #3, although it accepts the other major components of Darwinism. Does traditional Darwinism or a hierarchically expanded theory as advocated here provide the best guide for macroevolutionary research?*

5. 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.*

6. 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.*

III. Construction of Higher Taxa

A. Evolutionary Taxonomy

7. Simpson, G. G. (1953) - *excerpts from an updated, expanded and retitled version of the book from reading #5. 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. Cladistic criticism of it is severe, as subsequent readings show.

8. 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.*

9. Miller, A. H. (1949) - *an excellent example of evolutionary analysis of the origin of a higher taxonomic category (genus) using Simpsonian principles. This is perhaps the first use of the term "key innovation" (also termed key adaptation, key invention, and key character by various authors), which remains influential and appears in later topics. This kind of study later would be severely criticized by cladistic systematists.*

B. Phenetic versus Cladistic Taxonomy

10. Kearney, M. (2007) - *This historical summary of the evolutionary, phenetic and cladistic schools of taxonomy shows how taxonomists struggled with the roles of subjectivity versus objectivity in developing a useful taxonomic system. This article plus reading #11 together give a good summary of the clash of major taxonomic theories. Maureen Kearney is currently a program officer in the NSF systematics program.*

11. Ereshefsky, M. (2008) - *a summary of phenetic and cladistic taxonomic principles presented in the context of a philosophical criticism of Linnaean taxonomy.*

12. Sneath, P. H. A. and R. R. Sokal (1973) - *excerpts from the classic work (updated version) of phenetic taxonomy, a modernist challenge to Simpsonian principles. Quantitative measurement and computation are given priority over evolutionary principles in constructing higher taxa. These excerpts give excellent definitions of important terms and the main arguments for a taxonomic system that is now largely discredited. It is perhaps the best example of how emphasis on "practicality," quantification and computation without conceptual integrity produces unsatisfactory science.*

13. 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. Cladistic critics (especially Michael Ghiselin) use this argument to call Mayr an essentialist, knowing how much this claim upset him (compare these statements to Mayr's comments on essentialism in reading #1).

IV. Evolutionary Morphology

A. Taxic Homology

14. Patterson, C. (1982) - *This is the most influential writing on the subject of taxic homology since a rebirth of interest in morphological characters and homology in the early 1980s. Patterson's review of the three tests of homology and how they distinguish homology from alternative relationships among characters is extensively used and cited. His decision to equate homology with synapomorphy remains controversial. The important theme of ontogeny and phylogeny as introduced here is central to the course. This paper is also an argument for a taxonomic philosophy called "pattern cladism," which denies an evolutionary basis for phylogenetic systematics. Patterson builds his argument for pattern cladism from Karl Popper's philosophical principles of hypothetico-deductivism, which he abuses (see reading #15). This paper and the next one are probably the most tedious ones in the course; working through them is useful, however, for getting a thorough understanding of morphological homology. Patterson's tests are also the basis for distinguishing different kinds of molecular homology (covered in Bio 4183).*

15. de Queiroz, K. (1985) - *a critique of pattern cladism showing the conceptual problems of Patterson's scheme. I agree with this criticism and with the argument that phylogenetic systematics should be based explicitly on Darwin's theory of common descent. The novel character concept presented here is insightful, although few morphological systematists have implemented it (not even the author). This paper, like #14, is tedious reading but provides a thorough understanding of morphological characters in systematics and the relationship between ontogeny and phylogeny. Its insights reward a careful reading. I disagree with the author's nonstandard use of "homology."*

B. Transformational Homology

16. Kaplan, D. R. (1984) - *an excellent illustration of using ontogenetic and temporal series to test hypotheses of homology among characters. It counters Patterson's argument that transformational concepts of homology are untestable. It can be viewed as an elaboration of methods for implementing Patterson's "similarity test." The formal terminology proposed*

regarding homology and related concepts is highly nonstandard and should be disregarded.

17. Wagner, G. P. (1989) - *Wagner's writings on homology are critical in forming a synthesis of developmental biology and evolutionary biology. Of his various papers on homology, this one is still my favorite general overview. Pay close attention to the three fundamental properties of biological homology. How does Wagner's approach to homology differ from Patterson's?*

18. Roth, V. L. (1991) - *my favorite paper on the hierarchical expansion of the concept of homology. It shows to my satisfaction how a character can be a valid homology in theory but still fail Patterson's congruence test. This is the phenomenon recognized in molecular evolution as "lineage sorting," derived here in a more general context. "Genetic piracy" of homologies is another important concept central to understanding the relationship between ontogeny and phylogeny.*

19. 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.*

C. Heterochrony, Heterotopy and Ontogenetic Repatterning

20. Alberch, P., S. J. Gould, G. F. Oster and D. B. Wake (1979) - *a classic paper giving formal definitions of the standard patterns and processes of heterochrony, especially as relevant to changes occurring relatively late in ontogeny (retroactively termed "de Beerian heterochrony" by many authors). This is the standard scheme against which all others are compared.*

21. Raff, R. A. and G. A. Wray (1989) - *an important paper showing that the standard categorization of heterochronic patterns and processes (reading #20) is difficult to apply to early ontogeny and/or between hierarchical levels (organismal morphology versus gene expression).*

22. West-Eberhard, M. J. (2003) - *Heterotopy, including the phenomenon of homoeosis, received less general discussion in the evolutionary literature than did heterochrony in the early history of evolutionary developmental biology, although it has now acquired equal or greater importance in explaining origins of new characters. This is a good explanation of the most common usage of heterotopy and how it contrasts with heterochrony.*

23. 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.*

D. Developmental Constraints and Evolution

24. 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.*

25. Alberch, P. (1989) - *a relatively late but well illustrated paper in Alberch's structurtalist/internalist critique of Darwinian evolutionary theory. His main goal is to understand how properties of development bias the production of variation and thereby channel the directions of morphological evolution. Attention to "developmental constraint" in evolution originated in these writings.*

26. 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.*

27. Hall, B. K. (1998) - *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). Note that the electronic reserve includes two complete chapters but that only parts of these chapters are assigned.*

E. Epigenetic Mechanisms, Modularity and Evolvability

28. Alberch, P (1991) – *The conceptual transition from developmental constraint to evolvability is the main reason for assigning this paper.*

29. 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.*

30. Preston, J. C., L. C. Hileman and P. Cubas (2011) – *a nice summary of the applications of evolutionary developmental genetics to botany. The relationships between genotype and phenotype, modularity, and concept of developmental genetic toolkits are well illustrated with botanical case studies.*

31. 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.*

32. 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 a former Washington University undergraduate.*

33. Pigliucci, M. (2010) – *The critical concepts of evolvability and robustness, and their relationships to each other at different hierarchical levels, are explored precisely and critically.*

F. Evolutionary Novelties: Origins and Evolutionary Consequences

34. Wagner, G. P. and V. J. Lynch (2010) – extends the arguments of reading #19 to argue 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.

35. 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. Useful comparisons can be made between this paper and reading #9. 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.*

36. Galis, F. (2001) - *Here is a good review of uses of "key innovation" in evolution, including criticism of some widespread misuses.*

37. Fürsich, F. T. and D. Jablonski (1984) - *In the spirit of readings #35-36, this paper shows that a "key innovation" does not inevitably lead to adaptive diversification, evolutionary success or extensive speciation. Does this paper effectively answer the criticism that a key innovation can be identified only in the context of adaptive diversification and not independently?*

38. 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 (see reading #35) is highly critical of these arguments, which utilize Simpsonian evolutionary taxonomy and its concept of nested adaptive zones.*

G. Evolution of Adaptation

39. Lewontin, R. (1977) - *a classic criticism of adaptationist studies, especially as used in sociobiology.*

40. Ellstrand, N. E. (1983) - *an interesting critique of adaptationism from an unusual angle, and one of my favorites.*

41. Larson, A. (2009) – *Note the important distinctions between adaptation, exaptation, nonaptation, and disaptation (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. I use more microevolutionary examples than I did in earlier writings on adaptation because the paper was written for an ecological volume, but the historical contingency of adaptation and alternative concepts is the same in both microevolutionary and macroevolutionary studies.*

42. Agosta, S. J. and A. E. Dunham (2004) - *an interchange with the authors of reading #43 regarding use of phylogenetic criteria in adaptive interpretations.*

43. Brodie, E. D. III, K. V. Young and E. D. Brodie Jr. (2004) - *a response to the criticisms of reading #42.*

H. Alternative Adaptations

44. West-Eberhard, M. J. (1986) - *an often ignored but important hypothesis that evolutionary divergence between alternative characters often precedes rather than follows evolutionary divergence of the populations containing those characters. Evolutionary theory is generally constructed with the opposite assumption, and this paper at least makes us acknowledge that assumption. This thesis was expanded into a book-length treatment of evolutionary plasticity by the author in 2003 (source of reading #22). This is a saltational hypothesis and inconsistent with traditional Darwinian gradualism.*

45. Liem, K. F. and L. S. Kaufman (1984) - *one of the best examples meeting the criteria of West-Eberhard's "alternative adaptations," and a dramatic case of a population maintaining polymorphism for alternative characters whose divergence approaches macroevolutionary proportions.*

46. Sinervo, B. and E. I. Svensson (2004) - *This paper presents a nice, concise synthesis of the phenomenon of "alternative adaptations," morphological novelty, and speciation, although it does not cite West-Eberhard's work directly.*

47. West-Eberhard, M. J. (2005) - *a reassessment of the role of phenotypic plasticity in adaptive evolution. Have the concepts developed by evolutionary developmental biologists following her earlier paper (reading #43) caused important changes in her thinking on this issue?*

V. Species and Speciation

A. Essentialism, Typology and the Biological Species Concept

48. 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 (reading #54)

B. The Recognition Concept of Species

49. 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.*

C. The Evolutionary Species Concept

50. 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 (see #54 below). Some authors argue that Wiley's concept is equivalent to the general lineage concept of #54, although this point is debatable.*

D. The Cohesion Concept of Species

51. 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.*

E. The Phylogenetic Concept of Species

52. 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.*

F. The Genetic Concept of Species

53. Baker, R. J. and R. D. Bradley (2006) - *a concept that preserves many goals of the phylogenetic species concept but which explicitly acknowledges population genetic studies of haplotype variation for multiple loci.*

G. The General Lineage Concept of Species

54. 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.

H. Spatial Dynamics of Speciation

55. Cracraft, J. (1983) - *For a concise statement of the principles of vicariance biogeography, this paper remains my favorite. It clearly shows the importance of using a phylogenetic species concept for understanding the biogeographic history of a group. Empirical data collected by Cracraft and many others eventually rejected the utility of general area cladograms and therefore of the vicariance biogeographic paradigm, although vicariance as a process remains critically important in historical biogeography.*

56. Dillon, S. and J. Fjeldså (2005) - *a comparative study of the utilities of the biological and phylogenetic species concepts for assessing spatial patterns of differentiation in birds, which are the best-characterized animal taxon.*

57. Heaney, L. R. (2007) - *synthesizes new findings that many vertebrate groups comprise cryptic species lineages that replace each other geographically. Continental and island forms are more similar in their overall patterns of spatial fragmentation than formerly suspected.*

58. Genner, M. J., P. Nichols, G. Carvalho, R. L. Robinson, P. W. Shaw, A. Smith, and G. F. Turner (2007) - a study illustrating the traditional "peripatric" speciation mode of Mayr, which inspired the theory of punctuated equilibrium. This paper is important for several issues covered in the next topic, "modes of speciation."

59. 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. Compare this approach to the criticisms of reading #35.*

I. Modes of Speciation

60. Gavrilets, S. (2004) - *An overview of modes of speciation as used in contemporary discussions. This system of geographic modes is an old one criticized in reading #62, but it continues to dominate discussions of speciation despite those criticisms.*

61. Paterson, H. E. H. (1981) - *The title is pessimistic, but the paper makes a compelling argument that allopatric*

speciation is the only geographic mode for which evidence is convincing. Have the past 29 years of research in this area refuted Paterson's major claims? (compare to reading #63)

62. Templeton, A. (1981) - *categorizes modes of speciation explicitly on population-genetic criteria rather than geographic ones. This scheme has not replaced use of geographic categories to describe modes of speciation, but it makes important conceptual distinctions that are overlooked by the standard geographic categorizations.*

63. Coyne, J. A. (2007) - *a good review of the empirical problems raised by the notion of sympatric speciation. Compare this discussion to the results of reading #59.*

J. Adaptive Landscapes and Speciation

64. Carson, H. L. and A. R. Templeton (1984) - *after many years, still my favorite paper on the issue of founder-induced speciation as a population genetic process.*

65. Templeton, A. R. (1996) - *an insightful review of experimental evidence testing predictions of founder-flush and genetic transilience models of founder-induced speciation.*

66. Gavrilets, S. (2010) - *a reassessment of multidimensional adaptive landscapes arguing that populations do not need to pass through unstable nonadaptive conditions to make transitions between alternative fitness peaks. This is a clearly argued and influential criticism of evolution by shifting balance or founder-induced speciation. Nonetheless, I disagree with Gavrilets. His major mistake is to assume that evolution by shifting balance or by founder-induced speciation are* de novo *deductions from mathematical theory, whereas they are actually attempts to explain empirical observations mathematically. I accept the empirical evidence as more definitive than Gavrilets' theoretical deductions.*

VI. Tempo and Mode of Speciation and Morphological Evolution – Punctuated Equilibrium versus Phyletic Evolution

67. 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.*

68. Turner, J. R. G. (1988) - *an important critique of punctuated equilibrium that accepts some but not all of its claims. He argues for "punctuated phyletic evolution," an alternative to the contrasting hypotheses of phyletic gradualism and punctuated equilibrium. His arguments are addressed in #67, but I do not find Gould's refutation of this criticism convincing.*

69. 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.*

70. Eldredge N., J. N. Thompson, P. M. Brakefield, S. Gavrilets, D. Jablonski, J. B. C. Jackson, R. E. Lenski, B. S. Lieberman, M. A. McPeek and W. Miller, III (2005) - *An assessment of the mechanistic basis of species stasis as formulated by the theory of punctuated equilibrium.*

VII. Hierarchy of Sorting and Selection

A. General Theory

71. 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.*

72. 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. Like #71, this is among the most important papers covered in the class.*

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

74. Gould, S. J. (1995) - *We now complete the article assigned originally as #4 to understand the hierarchically expanded Darwinian theory of evolution. Gould's 2002 book (excerpted in #75) is devoted to this issue.*

75. Gould, S. J. (2002) - *This excerpt from Gould's 2002 book expands the general ideas presented in #72-74, 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.*

B. Challenges to the Paradox of the First Tier

76. Kitchell, J. A. (1990) - *a sophisticated attempt to evaluate evolutionary trends in predator/prey coevolution using coupled differential equations. The hypothesis that directional trends are predicted from Darwinian natural selection is strongly attacked. If she is correct, Gould's argument that first-tier processes predict progress is refuted. Do Kitchell's mathematical models lead us to greater understanding or to scientific paralysis?*

77. Jackson, J. B. C. and F. McKinney (1990) - *Can second-tier processes be a source of progressive macroevolutionary trends? What are the implications of such findings for the arguments of readings #73 and 78?*

78. 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 discussed in paper 71, but the timescale involved is greatly compressed relative to the expected occurrence of species selection and catastrophic species selection.*

79. Lieberman, B. S. (1995) - *Here is some empirical work testing hypotheses of hierarchical evolutionary processes.*

VIII. Extinction

A. Taxonomic Survivorship Curves

80. 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.*

81. McCune, A. R. (1982) - *This paper notes important ambiguities in the interpretation of reading #80 and discusses the importance of these results for hierarchical selection theory. Is the Red Queen's hypothesis actually supported by these results?*

82. Foote, M. (2001) - *I consider this paper the most thorough explanation of Van Valen's results and their real message for macroevolution.*

83. Roy, K., G. Hunt, and D. Jablonski (2009) – *Using methods other than taxonomic survivorship curves, these authors seek to quantify rates of extinction of taxonomic families and to ask whether phylogenetic affinity influences these rates. It thus tests Van Valen's "new evolutionary law."*

84. Krug, A. Z., D. Jablonski, and J. W. Valentine, 2009 – *Taxonomic survivorship curves serve to quantify the mark of the end-Cretaceous mass extinction on the biogeographic structure of modern biota.*

B. Periodicity of Extinction

85. Raup, D. M. and J. J. Sepkoski, Jr. (1984) - *In the Simpsonian tradition, statistical studies of taxic diversity in the post-Paleozoic marine fossil record suggest a periodicity of mass extinctions. This paper is a classic and one generally disliked by cladistic systematists (#86). The claim for periodicity of extinction peaks is largely dismissed today, but the issues resulting from this analysis have important implications for the more general issue of using Simpsonian higher taxa as units of analysis in studies of extinction and biodiversity (see readings 86 and 87).*

86. Patterson, C. and A. B. Smith (1987) - *presents the major cladistic arguments against the claims of #85.*

87. Sepkoski, J. J., Jr. and D. C. Kendrick (1993) - *Numerical methods indicate that Simpsonian higher taxa may serve as valid sampling units for measuring extinction rates of species lineages in the fossil record. Does this result confirm the validity of Simpsonian evolutionary taxonomy?*

C. Evolutionary Consequences of Episodic Extinction Peaks

88. 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 (#85) 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.*

89. Raup, D. M. (1995) - *This influential paleontologist argues that our current knowledge of extinction gives it an important role in evolution not anticipated by Darwin and Simpson. Incorporation of this extinction theory is one of the most important revisions of Darwinian evolutionary theory. Demonstration of episodic extinction peaks using the "kill curve" is more widely accepted than the argument for periodicity of extinctions argued in reading #84.*

90. Jablonski D. (2005) - *an update on extinction peaks in evolution by a leading worker in this field.*

IX. Diversity Through Time

A. Taxonomic Diversity Versus Disparity

91. 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.

92. 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?*

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

94. Foote, M. (1993) - *A classic paper showing a methodology for comparing taxonomic diversity versus disparity through time and thereby testing hierarchical evolutionary. Many studies conducted in this manner have followed.*

B. Phanerozoic Diversity

95. Sepkoski, J. J., Jr. (1981) - *a classic paper of evolutionary paleontology, implementing Simpson's taxic approach to examine biological diversity through time in the marine fossil record. The three great faunas identified by Sepkoski's factor analysis are a major concept of evolutionary paleontology. It is one of the most influential macroevolutionary meta-analyses.*

96. Alroy, J., M. Aberhan, D. Bottjer, M. Foote, F. Fursich, P. J. Harries et al. 2008 - *a thorough evaluation of historical changes in marine invertebrate faunal diversity throughout the Phanerozoic. The authorship comprises members a study group at the National Center for Ecological Analysis and Synthesis in Santa Barbara, California. Ecological meta-analyses of this kind are the focal work of that center.*