

BZ 520 ADVANCED SYSTEMATICS
Spring 2013

Instructors: Boris C. Kondratieff, Mark P. Simmons

Office: Boris: 012 Laurel Hall; phone: 491-7314; e-mail: Boris.Kondratieff@Colostate.edu

Mark: E212B Anatomy / Zoology Building; phone 491-2154; e-mail: psimmons@lamar.colostate.edu

Office hours: Mark: Monday 12:00 – 1:00 PM, Thursday 2:00 – 3:00 PM

Lecture: Monday / Wednesday / Friday 3:10 – 4 PM

Objectives:

Students will be able to conduct a phylogenetic analysis using both morphological and molecular characters. Students will be able to select appropriate loci for the desired level of phylogenetic analysis, align the sequences, code the characters, obtain the most parsimonious tree(s) and branch-support values, and infer the evolutionary patterns of characters and taxa using the trees. Students will be able to critically evaluate the methods used and the support for conclusions reached in the phylogenetic literature.

Grading:

Exam #1:	30%
Exam #2:	30%
Cumulative final	40%

Course web site: <https://ramct.colostate.edu/>

- Course number: BZ520 Advanced Systematics
- Instructor: Mark P. Simmons

Exam information:

- sample tests will be provided
- a review session will be scheduled before each test
- the final exam is cumulative, but will emphasize material not covered on the earlier tests
- be parsimonious in your answers to test questions. If you answer a question correctly, but provide additional information that is incorrect, points will be taken off for the incorrect part(s).

Readings:

- references in regular font = suggested readings
- italicized references = secondary readings
- references preceded by @ = available from library website in pdf format
- references preceded by * = available in books from library
- references preceded by # = available as individual articles from course website
- references not otherwise indicated = available from library shelves as hard copies

Reference books:

- Felsenstein, J. 2004. *Inferring phylogenies*. Sunderland, Mass., Sinauer Associates, Inc.
- Hall, B. G. 2001. *Phylogenetic trees made easy a how-to manual for molecular biologists*. Sunderland, Mass.: Sinauer Associates. [NOTE: THIS IS A HOW-TO BOOK FOR PEOPLE WHO HAVE NO IDEA WHAT THEY ARE DOING AND WANT EASY ANSWERS; DON'T SIMPLY ACCEPT HALL'S SUGGESTIONS]
- Hillis, D. M., C. Moritz and B. K. Mable, eds. 1996. *Molecular systematics*. Sunderland, Mass.: Sinauer Associates.
- Kitching, I. J., P. L. Forey, C. J. Humphries and D. M. Williams. 1998. *Cladistics: the theory and practice of parsimony analysis*. Oxford: Oxford University Press.
- Li, W.-H., Ed. 1997. *Molecular evolution*. Sunderland, Mass.: Sinauer Associates.
- Schuh, R. T. 2000. *Biological systematics*. Comstock Publishing Associates, Ithaca.
- Soltis, P. S., D. E. Soltis and J. J. Doyle, eds. 1992. *Molecular systematics of plants*. New York: Chapman and Hall.

- Soltis, D. E., P. S. Soltis and J. J. Doyle, Eds. 1998. *Molecular systematics of plants II DNA sequencing*. Boston: Kluwer Academic Publishers.
- Williams, D. M. and M. C. Ebach. 2008. *Foundations of systematics and biogeography*. New York, Springer.
- Yang, Z. 2006. *Computational molecular evolution*. Oxford, Oxford University Press.

Useful web sites:

- Society of Systematic Biologists (*Systematic Biology*): <http://systbiol.org/>
- Willi Hennig Society (*Cladistics*): <http://www.cladistics.org/>
- TreeBase (catalog of data matrices and trees from empirical studies): <http://www.treebase.org/treebase/>
- Tree of Life: <http://tolweb.org/tree/phylogeny.html>
- PAUP* homepage (tree construction using distance, maximum likelihood, parsimony): <http://paup.csit.fsu.edu/>
- MacClade homepage (data matrix viewing and manipulation): <http://macclade.org/>
- Download ClustalX (progressive pairwise alignment): <http://www-igbmc.u-strasbg.fr/BioInfo/ClustalX/>
- Download MEGA (tree construction using distance and parsimony, data manipulation): <http://www.megasoftware.net/>
- Download Mesquite (various modules for tree construction and simulations): <http://mesquiteproject.org/mesquite/mesquite.html>
- Download Modeltest (model selection for parametric tree-construction methods): <http://darwin.uvigo.es/software/modeltest.html>
- Download MrBayes (Bayesian MCMC tree construction): <http://mrbayes.csit.fsu.edu/>
- Download Muscle (progressive pairwise alignment): <http://www.drive5.com/muscle/>
- Download Phylip (tree construction using many different methods): <http://evolution.genetics.washington.edu/phylip.html>
- Download SeqState (code gap characters): <http://www.nees.uni-bonn.de/downloads/SeqState/index.htm>
- Download WinClada (data manipulation), NONA (tree construction using parsimony), and TNT (Tree analysis using New Technology): <http://www.cladistics.com/>

WEEK 1: January 23-25 (BORIS)

The scope of systematics:

History of taxonomy (Mayr, E and P. D. Ashlock. 1991. *Principles of Systematic Zoology*, 2nd Ed., McGraw-Hill).

The three school of Systematics: Phenetics, Cladistics, Evolutionary Classifications.

(Duncan, T. and T. F. Stuessy (eds.). 1984. *Cladistics*. Columbia University Press); Sneath, P. H. A. 1995. *Thirty Years of Numerical Taxonomy*. Syst. Biol. 44: 281-298; Quick, D. L. J. 1993. *Principles and Techniques of Contemporary Taxonomy*. Blackie Academic and Professional, London).

WEEK 2: January 28 – February 1

Taxonomic Monographs: Strategy of Publishing

Review of selected sources for nomenclature and systematics; review of publications in systematic zoology and botany.

WEEK 3: February 4 – February 8

Evolution of the theory of Nomenclature.

International Code of Zoological Nomenclature. 1999. (4th edition)

WEEK 4: February 11 – 15

Species, subspecies, and variety concepts. (Mallet, J. 1995. *A species definition for the modern synthesis*. Trends Ecol. Evol. 10: 294-299; handouts).

WEEK 5: February 18 – 22 (MARK)

■ Monday: phylogenetic analysis

Gaffney, E. S. 1979. An introduction to the logic of phylogeny reconstruction. In J. Cracraft and N. Eldredge [eds.], *Phylogenetic analysis and paleontology*, pp. 79-111. Columbia University Press, New York.

@ Penny, D., M. D. Hendy and M. A. Steel. 1992. *Progress with methods for constructing evolutionary trees. Trends in Ecology and Evolution* 7: 73-79.

@ Platnick, N. I. 1979. *Philosophy and the transformation of cladistics. Systematic Zoology* 28: 537-546.

■ Wednesday: parsimony

@ Bergsten, J. 2005. A review of long-branch attraction. *Cladistics* 21: 163-193.

@ Farris, J. S. 1979. *The information content of the phylogenetic system. Systematic Zoology* 28: 483-519.

Farris, J. S. 1983. The logical basis of phylogenetic analysis. In N. I. Platnick and V. A. Funk [eds.], *Advances in Cladistics, Volume 2: Proceedings of the Second Meeting of the Willi Hennig Society*, pp. 1-36. Columbia University Press, New York.

Felsenstein, J. 1978. Cases in which parsimony or compatibility methods will be positively misleading. *Systematic Zoology* 27: 401-410.

■ Friday: catch-up day

WEEK 6: February 25 – March 1

■ Monday: background information on trees

■ HANDOUT – BASIC TERMS

■ monophyletic, paraphyletic, and polyphyletic groups

Farris, J. S. 1974. Formal definitions of parafyly and polyphyly. *Systematic Zoology* 23: 548-554.

@ Platnick, N. I. 1977. *Paraphyletic and polyphyletic groups. Systematic Zoology* 26: 195-200.

■ formal definitions of symplesiomorphy, synapomorphy, autapomorphy

Hennig, W. 1966. *Phylogenetic systematics. University of Illinois Press, Urbana.*

■ tree statistics

Farris, J. S. 1989. *The retention index and the rescaled consistency index. Cladistics* 5: 417-419.

@ Kluge, A. G. and J. S. Farris. 1969. *Quantitative phyletics and the evolution of Anurans. Systematic Zoology* 18: 1-32.

Sanderson, M. J. and M. J. Donoghue 1989. Patterns of variation in levels of homoplasy. *Evolution* 43: 1781-1795.

■ Wednesday: character coding for morphology and characters of special interest

■ characters of special interest

Coddington, J. A. 1988. *Cladistic tests of adaptational hypotheses. Cladistics* 4: 3-22.

de Queiroz, K. 2000. *Logical problems associated with including and excluding characters during tree reconstruction and their implications for the study of morphological character evolution. In J. J. Wiens [eds.], Phylogenetic analysis of morphological data, pp. 192-212. Smithsonian Institution Press, Washington, D.C.*

Luckow, M. and A. Bruneau. 1997. Circularity and independence in phylogenetic tests of ecological hypotheses. *Cladistics* 13: 145-152.

Wenzel, J. W. 1997. *When is a phylogenetic test good enough? In P. Grandcolas [ed.], The origin of biodiversity in insects: phylogenetic tests of evolutionary scenarios, pp. 31-45. Museum National d'Histoire Naturelle, Paris.*

Wenzel, J. W. and J. M. Carpenter. 1994. *Comparing methods: adaptive traits and tests of adaptation. In P. Eggleton and R. I. Vane-Wright [eds.], Phylogenetics and ecology, pp. 79-101. Academic Press, London.*

■ character coding for morphology

Pimentel, R. A. and R. Riggins. 1987. The nature of cladistic data. *Cladistics* 3: 201-209.

@ Wilkinson, M. 1995. *A comparison of two methods of character construction. Cladistics* 11: 297-308.

■ Friday: ***FIRST IN-CLASS EXAM***

WEEK 7: March 4 - 8

■ Monday: optimization and polymorphism / missing data / inapplicable data

■ HANDOUT – FITCH OPTIMIZATION

■ optimization

@ Farris, J. S. 1970. *Methods for computing Wagner trees. Systematic Zoology* 19: 83-92.

@ Fitch, W. M. 1971. *Toward defining the course of evolution: minimum change for a specific tree topology.* *Systematic Zoology* 20: 406-416.

■ polymorphism / missing data / inapplicable data

Maddison, W. P. 1993. Missing data versus missing characters in phylogenetic analysis. *Systematic Biology* 42: 576-581.

Nixon, K. C. and J. I. Davis. 1991. Polymorphic taxa, missing values and cladistic analysis. *Cladistics* 7: 233-241.

Strong, E. E. and D. Lipscomb. 1999. Character coding and inapplicable data. *Cladistics* 15: 363-372.

@ Wiens, J. J. 1998. *Does adding characters with missing data increase or decrease phylogenetic accuracy.* *Systematic Biology* 47: 625-640.

■ Wednesday: testing hypotheses of homology

de Pinna, M. C. C. 1991. Concepts and tests of homology in the cladistic paradigm. *Cladistics* 7: 367-394.

Doyle, J. J. and J. I. Davis. 1998. *Homology in molecular phylogenetics: a parsimony perspective.* In D. E. Soltis, P. S. Soltis and J. J. Doyle [eds.], *Molecular Systematics of Plants II DNA Sequencing*, pp. 101-131. Kluwer Academic Publishers, Boston.

@ Janies, D. and R. DeSalle. 1999. *Development, evolution, and corroboration.* *The Anatomical Record* 257: 6-14.

Patterson, C. 1982. *Morphological characters and homology.* In K. A. Joysey and A. E. Friday [eds.], *Problems of Phylogenetic Reconstruction*, pp. 21-74. Academic Press, London.

@ Wake, D. B., M. H. Wake and C. D. Specht. 2011. *Homoplasy: from detecting pattern to determining process and mechanism of evolution.* *Science* 331: 1032-1035.

Wray, G. A. 1999. *Evolutionary dissociations between homologous genes and homologous structures.* In G. R. Bock and G. Cardew [eds.], *Homology*, pp. 189-206. John Wiley & Sons, Chichester.

■ Friday: catch-up day

WEEK 8: March 11 – 15

■ Monday: maximum likelihood

Felsenstein, J. 1973. Maximum likelihood and minimum-steps methods for estimating evolutionary trees from data on discrete characters. *Systematic Zoology* 22: 240-249.

* Lewis, P. O. 1998. *Maximum likelihood as an alternative to parsimony for inferring phylogeny using nucleotide sequence data.* In D. E. Soltis, P. S. Soltis and J. J. Doyle [eds.], *Molecular Systematics of Plants II DNA Sequencing*, pp. 132-163. Kluwer Academic Publishers, Boston.

@ Posada, D. and K. A. Crandall. 1998. *MODELTEST: testing the model of DNA substitution.* *Bioinformatics* 14: 817-818.

■ Wednesday: maximum likelihood vs. parsimony

Sanderson, M. J. and J. Kim. 2000. Parametric phylogenetics? *Systematic Biology* 49: 817-829.

@ Siddall, M. E. and M. F. Whiting. 1999. *Long-branch abstractions.* *Cladistics* 15: 9-24.

@ Steel, M. and D. Penny. 2000. *Parsimony, likelihood, and the role of models in molecular phylogenetics.* *Molecular Biology and Evolution* 17: 839-850.

Tuffley, C. and M. Steel. 1997. *Links between maximum likelihood and maximum parsimony under a simple model of site substitution.* *Bulletin of Mathematical Biology* 59: 581-607.

■ Friday (potential reading if we're not behind schedule):

Posada, D. and K. A. Crandall. 2001. Selecting models of nucleotide substitution: an application to human immunodeficiency virus 1 (HIV-1). *Molecular Biology and Evolution* 18:897-906.

WEEK 9: March 25 – 29

■ Monday: rooting and consensus trees

■ rooting

Nixon, K. C. and J. M. Carpenter. 1993. On outgroups. *Cladistics* 9: 413-426.

Wheeler, W. C. 1990. *Nucleic acid sequence phylogeny and random outgroups.* *Cladistics* 6: 363-367.

■ consensus trees

- @ Adams, E. N. 1972. *Consensus techniques and the comparison of taxonomic trees. Systematic Zoology* 21: 390-397.
- # Bremer, K. 1990. Combinable component consensus. *Cladistics* 6: 369-372.
- # Nixon, K. C. and J. M. Carpenter. 1996. On consensus, collapsibility, and clade concordance. *Cladistics* 12: 305-321.

■ Wednesday: branch support

- # Bremer, K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution* 42: 795-803.
- @ Davis, J. I. 1993. *Character removal as a means for assessing stability of clades. Cladistics* 9: 201-210.
- @ Davis, J. I., M. P. Simmons, D. W. Stevenson and J. F. Wendel. 1998. *Data decisiveness, data quality, and incongruence in phylogenetic analysis: an example from the monocotyledons using mitochondrial atpA sequences. Systematic Biology* 47: 282-310.
- @ Farris, J. S., V. A. Albert, M. Källersjö, D. Lipscomb and A. G. Kluge. 1996. *Parsimony jackknifing outperforms neighbor-joining. Cladistics* 12: 99-124.
- # Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783-791.
- @ Gatesy, J., P. O'Grady and R. H. Baker. 1999. *Corroboration among data sets in simultaneous analysis: hidden support for phylogenetic relationships among higher level artiodactyl taxa. Cladistics* 15: 271-313.

■ Friday: catch-up day

WEEK 10: April 1 – 5

■ Monday: phylogenetic signal and tree searches

■ tree searches

- @ Farris, J. S. 1970. *Methods for computing Wagner trees. Systematic Zoology* 19: 83-92.
- @ Felsenstein, J. 1978. *The number of evolutionary trees. Systematic Zoology* 27: 27-33.
- @ Goloboff, P. A. 1999. *Analyzing large data sets in reasonable times: solutions for composite optima. Cladistics* 15: 415-428.
- # Maddison, D. R. 1991. The discovery and importance of multiple islands of most-parsimonious trees. *Systematic Zoology* 40: 315-328.

■ phylogenetic signal

- # Hillis, D. M. 1991. *Discriminating between phylogenetic signal and random noise in DNA sequences. In M. M. Miyamoto and J. Cracraft [eds.], Phylogenetic analysis of DNA sequences, pp. 278-294. Oxford University Press, Oxford.*
- # Hillis, D. M. 1996. Inferring complex phylogenies. *Nature* 383: 130-131.
- # Källersjö, M., J. S. Farris, A. G. Kluge and C. Bult. 1992. *Skewness and permutation. Cladistics* 8: 275-287.
- # Meyer, A. 1994. *Shortcomings of the cytochrome b gene as a molecular marker. Trends in Ecology and Evolution* 9: 278-280.
- @ Ortí, G. and A. Meyer. 1996. *Molecular evidence of ependymin and the phylogenetic resolution of early divergences among euteleost fishes. Molecular Biology and Evolution* 13: 556-573.
- # Wenzel, J. W. and M. E. Siddall. 1999. Noise. *Cladistics* 15: 51-64.

■ Wednesday: alignment

- @ Gatesy, J., R. DeSalle and W. Wheeler. 1993. *Alignment-ambiguous nucleotide sites and the exclusion of systematic data. Molecular Phylogenetics and Evolution* 2: 152-157.
- @ Lake, J. A. 1991. *The order of sequence alignment can bias the selection of tree topology. Molecular Biology and Evolution* 8: 378-385.
- # Phillips, A., D. Janies and W. Wheeler. 2000. Multiple sequence alignment in phylogenetic analysis. *Molecular Phylogenetics and Evolution* 16: 317-330.
- @ Wheeler, W. C., J. Gatesy and R. DeSalle. 1995. *Elision: a method for accommodating multiple molecular sequence alignments with alignment-ambiguous sites. Molecular Phylogenetics and Evolution* 4: 1-9.
- @ Wheeler, W. 1996. *Optimization alignment: the end of multiple sequence alignment in phylogenetics? Cladistics* 12: 1-10.

- Friday: catch-up day

WEEK 11: April 8 – 12

- Monday: character coding for genes and gap characters
 - nucleotides, amino acids
 - # Simmons, M. P. 2000. A fundamental problem with amino-acid-sequence characters for phylogenetic analyses. *Cladistics* 16: 274-282.
 - # Simmons, M. P. and J. V. Freudenstein. 2002. Artifacts of coding amino acids and other composite characters for phylogenetic analysis. *Cladistics* 18: 354-365.
 - gap characters
 - @ Giribet, G. and W. C. Wheeler. 1999. On gaps. *Molecular Phylogenetics and Evolution* 13: 132-143.
 - # Simmons, M. P. and H. Ochoterena. 2000. Gaps as characters in sequence-based phylogenetic analyses. *Systematic Biology* 49: 369-381.
 - # Simmons, M. P., H. Ochoterena, and T. G. Carr.. 2001. Incorporation, relative homoplasy, and effect of gap characters in sequence-based phylogenetic analyses. *Systematic Biology* 50: 454-462.
- Wednesday: lineage sorting, paralogy, introgression
 - @ Bradley, R. D. and D. M. Hillis. 1997. Recombinant DNA sequences generated by PCR amplification. *Molecular Biology and Evolution*. 14: 592-593.
 - # Doyle, J. J. 1992. Gene trees and species trees: molecular systematics as one-character taxonomy. *Systematic Botany* 17: 144-163.
 - * Doyle, J. J. 1996. Homoplasy connections and disconnections: genes and species, molecules and morphology. In M. J. Sanderson and L. Hufford [eds.], *Homoplasy: The Recurrence of Similarity in Evolution*, pp. 37-66. Academic Press, San Diego.
 - * Rieseberg, L. H. and S. J. Brunnsfield. 1992. Molecular evidence and plant introgression. In P. S. Soltis, D. E. Soltis and J. J. Doyle [eds.], *Molecular systematics of plants*, pp. 151-176. Chapman and Hall, New York.
 - @ Sanderson, M. J. and J. J. Doyle. 1992. Reconstruction of organismal and gene phylogenies from data on multigene families: concerted evolution, homoplasy, and confidence. *Systematic Biology* 41: 4-17.
 - @ Simmons, M. P. and J. V. Freudenstein. 2002. Uninode coding vs. gene-tree parsimony for phylogenetic reconstruction using duplicate genes. *Molecular Phylogenetics and Evolution* 23: 481-498.
 - @ Slowinski, J. B. and R. D. M. Page. 1999. How should species phylogenies be inferred from sequence data? *Systematic Biology* 48: 814-825.
 - # Wendel, J. F. and J. J. Doyle. 1998. Phylogenetic incongruence: window into genome history and molecular evolution. In D. E. Soltis, P. S. Soltis and J. J. Doyle [eds.], *Molecular Systematics of Plants II DNA Sequencing*, pp. 265-296. Kluwer Academic Publishers, Boston.

- Friday: ***SECOND IN-CLASS EXAM***

WEEK 12: April 15 – 19

- Monday: lineage sorting, paralogy, introgression (continued)
- Wednesday: simultaneous analysis
 - @ Barrett, M., M. J. Donoghue and E. Sober. 1991. Against consensus. *Systematic Zoology* 40: 486-493.
 - @ Gatesy, J. and R. H. Baker. 2005. Hidden likelihood support in genomic data: can forty-five wrongs make a right? *Systematic Biology* 54: 483-392.
 - @ Kluge, A. G. 1989. A concern for evidence and a phylogenetic hypothesis for relationships among *Epicrates* (*Boidae*, *Serpentes*). *Systematic Zoology* 38: 7-25.
 - @ Kluge, A. G. and A. J. Wolf. 1993. *Cladistics: what's in a word?* *Cladistics* 9: 183-199.
 - @ Miyamoto, M. M. and W. M. Fitch. 1995. Testing species phylogenies and phylogenetic methods with congruence. *Systematic Biology* 44: 64-76.
 - # Nixon, K. C. and J. M. Carpenter. 1996a. On simultaneous analysis. *Cladistics* 12: 221-242.
 - # Sullivan, J. 1996. Combining data with different distributions of among-site variation. *Systematic Biology* 45: 375-380.
- Friday: catch-up day

WEEK 13: April 22 – 26

■ Monday: organellar genomes

■ mitochondrial genome

- @ Adams, K. L. and J. D. Palmer. 2003. Evolution of mitochondrial gene content: gene loss and transfer to the nucleus. *Molecular Phylogenetics and Evolution* 29: 380-395.
- @ Bergthorsson, U., K. L. Adams, B. Thomason and J. D. Palmer. 2003. Widespread horizontal transfer of mitochondrial genes in flowering plants. *Nature* 424: 197-201.
- @ Bergthorsson, U., A. O. Richardson, G. J. Young, L. R. Goertzen and J. D. Palmer. 2004. Massive horizontal transfer of mitochondrial genes from diverse land plant donors to the basal angiosperm *Amborella*. *Proceedings of the National Academy of Sciences of the U.S.A.* 101: 17747-17752.
- @ Gray, M. W., B. F. Lang, R. Cedergren, G. B. Golding, C. Lemieux, D. Sankoff, M. Turmel, N. Brossard, E. Delage, T. G. Littlejohn, I. Plante, P. Rioux, D. Saint-Louis, Y. Zhu and G. Burger. 1998. Genome structure and gene content in protist mitochondrial DNAs. *Nucleic Acids Research* 26: 865-878.
- * Palmer, J. D. 1992. Mitochondrial DNA in plant systematics: applications and limitations. In P. S. Soltis, D. E. Soltis and J. J. Doyle [eds.], *Molecular Systematics of Plants*, pp. 36-49. Chapman and Hall, New York.

■ plastid genome

- @ Clegg, M. T., B. S. Gaut, G. H. Learn and B. R. Morton. 1994. Rates and patterns of chloroplast DNA evolution. *Proceedings of the National Academy of Sciences of the USA* 91: 6795-6801.
- * Clegg, M. T. and G. Zurawski. 1992. Chloroplast DNA and the study of plant phylogeny: present status and future prospects. In P. S. Soltis, D. E. Soltis and J. J. Doyle [eds.], *Molecular Systematics of Plants*, pp. 1-13. Chapman and Hall, New York.
- @ Lavin, M., J. J. Doyle, et al. 1990. Evolutionary significance of the loss of the chloroplast-DNA inverted repeat in the Leguminosae subfamily Papilionoideae. *Evolution* 44: 390-402.
- @ Olmstead, R. G. and J. D. Palmer. 1994. Chloroplast DNA systematics: a review of methods and data analysis. *American Journal of Botany* 81: 1205-1224.
- * Palmer, J. D. and C. F. Delwiche. 1998. The origin and evolution of plastids and their genomes. In D. E. Soltis, P. S. Soltis and J. J. Doyle [eds.], *Molecular systematics of plants II DNA sequencing*, pp. 375-409. Kluwer Academic Publishers, Boston.
- Sugiura, M. 1992. The chloroplast genome. *Plant Molecular Biology* 19: 149-168.

■ Wednesday: nuclear genes

■ nuclear ribosomal DNA

- # Baldwin, B. G., M. J. Sanderson, J. M. Porter, M. F. Wojciechowski, C. S. Campbell and M. J. Donoghue. 1995. The ITS region of nuclear ribosomal DNA: a valuable source of evidence on angiosperm phylogeny. *Annals of the Missouri Botanical Garden* 82: 247-277.
- * Hamby, R. K. and E. A. Zimmer. 1992. Ribosomal RNA as a phylogenetic tool in plant systematics. In P. S. Soltis, D. E. Soltis and J. J. Doyle [eds.], *Molecular systematics of plants*, pp. 50-91. Chapman and Hall, New York.
- @ Kjer, K. M. 1995. Use of rRNA secondary structure in phylogenetic studies to identify homologous positions: an example of alignment and data presentation from the frogs. *Molecular Phylogenetics and Evolution* 43: 314-330.
- * Kuzoff, R. K., J. A. Sweere, D. E. Soltis, P. S. Soltis and E. A. Zimmer. 1998. The phylogenetic potential of entire 26S rDNA sequences in plants. *Molecular Biology and Evolution* 15: 251-263.
- Rogers, S. O. and A. J. Bendich. 1987. Ribosomal RNA genes in plants: variability in copy number and in the intergenic spacer. *Plant Molecular Biology* 9: 509-520.
- @ Wheeler, W. C. and R. L. Honeycutt. 1988. Paired sequence difference in ribosomal RNAs: evolutionary and phylogenetic implications. *Molecular Biology and Evolution* 5: 90-96.

■ “single copy” nuclear genes

- # Clegg, M. T., M. P. Cummings and M. L. Durbin. 1997. The evolution of plant nuclear genes. *Proceedings of the National Academy of Sciences of the USA* 94: 7791-7798.

■ Friday: catch-up day

WEEK 14: April 29 – May 3

- Monday: computer alignment
 - Databases (GenBank, EMBL, SwissProt, TreeBASE)
 - MAFFT
 - # *Zurawski, G. and M. T. Clegg. 1987. Evolution of higher-plant chloroplast DNA-encoded genes: implications for structure-function and phylogenetic studies. Annual Review of Plant Physiology 38: 391-418.*

■ Wednesday: catch-up day

■ Friday: catch-up day

WEEK 15: May 6 – May 10 (BORIS)

- Monday: PAUP – parsimony tree searches
 - constraints, negative constraints
- Wednesday: MacClade – tree viewing and manipulation
- Friday (potential reading if we're not behind schedule):
 - # *Simmons, M. P., H. Ochoterena and J. V. Freudenstein. 2002a. Amino acid vs. nucleotide characters: challenging preconceived notions. Molecular Phylogenetics and Evolution 24:78-90.*
 - # *Simmons, M. P., H. Ochoterena and J. V. Freudenstein. 2002b. Conflict between amino acid and nucleotide characters. Cladistics 18:200-206.*

FINAL EXAM:

- May 15 (Wednesday) 4:10 PM – 6:10 PM in our regular classroom (Clark C364)

ADDITIONAL TOPICS NOT HAVE TIME FOR IN CLASS

- Popper:
 - # *Popper, K. R. 1994. The myth of the framework. Routledge, London. [chapter four]*
 - @ *Siddall, M. E. and A. G. Kluge. 1997. Probabilism and phylogenetic inference. Cladistics 13: 313-336.*
 - @ *Wiley, E. O. 1975. Karl R. Popper, systematics, and classification: a reply to Walter Bock and other evolutionary taxonomists. Systematic Zoology 24: 233-243.*
- quantitative characters:
 - @ *Stevens, P. F. 1991. Character states, morphological variation, and phylogenetic analysis: a review. Systematic Botany 16: 553-583.*
 - @ *Thiele, K. 1993. The holy grail of the perfect character: the cladistic treatment of morphometric data. Cladistics 9: 275-304.*
- character and taxon sampling:
 - character sampling:
 - @ *Cummings, M. P., S. P. Otto, and J. Wakeley. 1995. Sampling properties of DNA sequence data in phylogenetic analysis. Molecular Biology and Evolution 12: 814-822.*
 - taxon sampling:
 - most stable hierarchy if include every species in group rather than representative species or composite higher-level taxa
 - assume that all terminals monophyletic when above species level
 - danger of compartmentalization (Maddison et al., 1984) in that not applying global parsimony
 - # *Graur, D., L. Durent and M. Gouy. 1996. Phylogenetic position of the order Lagomorpha (rabbits, hares and allies). Nature 379: 333-335.*
 - @ *Hillis, D. M. 1998. Taxonomic sampling, phylogenetic accuracy, and investigator bias. Systematic Biology 47: 3-8.*
 - @ *Kim, J. 1996. General inconsistency conditions for maximum parsimony: effects of branch lengths and increasing numbers of taxa. Systematic Biology 45: 363-374.*
 - @ *Graybeal, A. 1998. Is it better to add taxa or characters to a difficult phylogenetic problem? Systematic Biology 47: 9-17.*

- @ Lecointre, G., H. Philippe, H. L. Van Le and H. Le Guyader. 1993. Species sampling has a major impact on phylogenetic inference. *Molecular Phylogenetics and Evolution* 2: 205-224.
- step matrices:
 - @ Wheeler, W. C. 1993. The triangle inequality and character analysis. *Molecular Biology and Evolution* 10: 707-712.
 - # Williams, P. L. and W. M. Fitch. 1989. Finding the minimal change in a given tree. In B. Fernholm, K. Bremer and H. Jörnvall [eds.], *The hierarchy of life*, pp. 453-470. Elsevier Science Publishers B. V., Amsterdam.
 - weighting
 - a priori weighting
 - slippery slope as can get any tree you want to support your preconceived notions
 - @ Albert, V. A., M. W. Chase and B. D. Mishler. 1993. *Character-state weighting for cladistic analysis of protein-coding DNA sequences*. *Annals of the Missouri Botanical Garden* 80: 752-766.
 - # Irwin, D. M., T. D. Kocher and A. C. Wilson. 1991. *Evolution of the cytochrome b gene of mammals*. *Journal of Molecular Evolution* 32: 128-144.
 - # Källersjö, M., V. A. Albert and J. S. Farris. 1999. Homoplasy increases phylogenetic structure. *Cladistics* 15: 91-93.
 - # Naylor, G. J. P., T. M. Collins and W. M. Brown. 1995. Hydrophobicity and phylogeny. *Nature* 373: 565-566.
 - * Olmstead, R. G., P. A. Reeves and A. C. Yen. 1998. *Patterns of sequence evolution and implications for parsimony analysis of chloroplast DNA*. In D. S. Soltis, P. S. Soltis and J. J. Doyle [eds.], *Molecular Systematics of Plants II DNA Sequencing*, pp. 164-187. Kluwer Academic Publishers, Boston.
 - a posteriori weighting
 - # Carpenter, J. M. 1988. *Choosing among multiple equally parsimonious cladograms*. *Cladistics* 4: 291-296.
 - @ Farris, J. S. 1969. *A successive approximations approach to character weighting*. *Systematic Zoology* 18: 374-385.
 - # Kluge, A. G. 1998. *Sophisticated falsification and research cycles: consequences for differential character weighting in phylogenetic systematics*. *Zoologica Scripta* 26: 349-360.
 - # Goloboff, P. A. 1993. Estimating character weights during tree search. *Cladistics* 9: 83-91.
 - @ Siddall, M. E. and A. G. Kluge. 1997. *Probabilism and phylogenetic inference*. *Cladistics* 13: 313-336.
 - biogeography and cospeciation:
 - Humphries, C. J. and L. R. Parenti. 1999. Cladistic biogeography second edition: interpreting patterns of plant and animal distributions. Oxford University Press, Oxford.*
 - @ Page, R. D. M. 1994. Maps between trees and cladistic analysis of historical associations among genes, organisms and areas. *Systematic Biology* 43: 58-77.
 - @ Platnick, N. I. and G. Nelson. 1978. A method of analysis for historical biogeography. *Systematic Zoology* 27: 1-16.
 - alternative molecular characters – rare genomic changes:
 - # Rokas, A. and P. W. H. Holland. 2000. Rare genomic changes as a tool for phylogenetics. *Trends in Ecology and Evolution* 15:454-459.
 - SINES (short interspersed elements):
 - @ Hillis, D. M. 1999. *SINEs of the perfect character*. *Proceedings of the National Academy of Sciences of the USA* 96:9979-9981.
 - @ Nikaido, M., A. P. Rooney and N. Okada. 1999. *Phylogenetic relationships among cetartiodactyls based on insertions of short and long interspersed elements: Hippopotamuses are the closest extant relatives of whales*. *Proceedings of the National Academy of Sciences of the USA* 96:10261-10266.
 - gene order – inversions and transpositions:
 - @ Blanchette, M., T. Kunisawa, and D. Sankoff. 1999. *Gene order breakpoint evidence in animal mitochondrial phylogeny*. *Journal of Molecular Evolution* 49: 193-203.
 - Cosner, M. E., R. K. Jansen, J. D. Palmer, and S. R. Downie. 1997. The highly rearranged chloroplast genome of Trachelium caeruleum Campanulaceae: multiple inversions, inverted repeat expansion and contraction, transposition, insertions/deletions, and several repeat families. Current Genetics 31: 419-429.*
 - @ Sankoff, D., G. Leduc, N. Antoine, B. Paquin, B. F. Lang and R. Cedergren. 1992. Gene order comparisons for phylogenetic inference: evolution of the mitochondrial genome. *Proceedings of the National Academy of Sciences of the USA* 89:6575-6579.
 - deletions:
 - losses of introns:

- @ Bailey, C. D. and J. J. Doyle. 1997. *The chloroplast rpl2 intron and ORF184 as phylogenetic markers in the legume tribe Desmodieae. Systematic Botany 22: 133-138.*
- @ Downie, S. R., E. Llanas and D. S. Katz-Downie. 1996. *Multiple independent losses of the rpoC1 intron in angiosperm chloroplast DNAs. Systematic Botany 21: 135-151.*
- losses of chloroplast inverted repeats:
 - how assayed (Lavin et al., 1990: 391-392)
 - @ Lavin, M., J. J. Doyle, et al. 1990. Evolutionary significance of the loss of the chloroplast-DNA inverted repeat in the Leguminosae subfamily Papilionoideae. *Evolution 44: 390-402.*
- alternative molecular characters – restriction sites, AFLPs, RAPDs:
 - restriction sites:
 - need to map restriction sites, not just count presence or absence of individual fragments (due to independence problem)
 - pain to combine data sets because need to totally reassess homology; most people never even try (in contrast to sequence data)
 - * Dowling, T. E., C. Moritz and J. D. Palmer. 1990. *Nucleic acids II: restriction site analysis. In D. M. Hillis and C. Moritz [eds.], Molecular Systematics, pp. 250-316. Sinauer Associates, Inc., Sunderland, Massachusetts.*
 - # Holsinger, K. E. and R. K. Jansen. 1993. Phylogenetic analysis of restriction site data. *Methods in Enzymology: Molecular Evolution: Producing the Biochemical Data 224: 439-455.*
 - AFLPs:
 - @ Roa, A. C., M. M. Maya, M. C. Duque, J. Tohme, A. C. Allem and M. W. Bonierbale. 1997. *AFLP analysis of relationships among cassava and other Manihot species. Theoretical and Applied Genetics 95: 741-750.*
 - @ Sharma, S. K., M. R. Knox and T. H. N. Ellis. 1996. *AFLP analysis of the diversity and phylogeny of Lens and its comparison with RAPD analysis. Theoretical and Applied Genetics 93: 751-758.*
 - @ Vos, P., R. Hogers, M. Bleeker, M. Reijans, T. van de Lee, M. Hornes, A. Frijters, J. Pot, J. Poleman, M. Kuiper and M. Zabeau. 1995. AFLP: a new technique for DNA fingerprinting. *Nucleic Acids Research 23: 4407-4414.*
 - @ Waugh, R., N. Bonar, E. Baird, B. Thomas, A. Graner, P. Hayes and W. Powell. 1997. *Homology of AFLP products in three mapping populations of barley. Molecular and General Genetics 255: 311-321.*
 - RAPDs:
 - problem with reproducibility
 - markers dominant, not codominant
 - # Black, W. C. 1993. PCR with arbitrary primers: approach with care. *Insect Molecular Biology 2: 1-6.*
- hybridization and polyploidy:
 - hybridization:
 - Rieseberg, L. H., S. J. E. Baird and K. A. Gardner. 2000. Hybridization, introgression, and linkage evolution. *In J. J. Doyle and B. S. Gaut [eds.], Plant molecular evolution, pp. 205-224. Kluwer Academic Publishers, Dordrecht.*
 - @ Rieseberg, L. H., B. Sinervo, C. R. Linder, M. C. Ungerer, and D. M. Arias. 1996. *Role of gene interactions in hybrid speciation: evidence from ancient and experimental hybrids. Science 272: 741-745.*
 - polyploidy:
 - * Soltis, P. S., J. J. Doyle and D. E. Soltis. 1992. *Molecular data and polyploid evolution in plants. In P. S. Soltis, D. E. Soltis and J. J. Doyle [eds.], Molecular systematics of plants, pp. 177-201. Chapman and Hall, New York.*
 - @ Wendel, J. F., A. Schnabel and T. Seelanan. 1995. *Bidirectional interlocus concerted evolution following allopolyploid speciation in cotton (Gossypium). Proceedings of the National Academy of Sciences of the USA 92: 280-284.*
 - Wendel, J. F. 2000. Genome evolution in polyploids. *In J. J. Doyle and B. S. Gaut [eds.], Plant molecular evolution, pp. 225-249. Kluwer Academic Publishers, Dordrecht.*
- incongruence
 - # Bull, J. J., J. P. Huelsenbeck, C. W. Cunningham, D. L. Swofford and P. J. Waddell. 1993. Partitioning and combining data in phylogenetic analysis. *Systematic Biology 42: 384-397.*
 - # Farris, J. S., M. Källersjö, A. G. Kluge and C. Bult. 1995. Testing significance of incongruence. *Cladistics 10: 315-319.*
 - # Goloboff, P. A. 1991. *Homoplasy and the choice among cladograms. Cladistics 7: 215-232.*

* Johnson, L. A. and D. E. Soltis. 1998. *Assessing congruence: empirical examples from molecular data*. In D. E. Soltis, P. S. Soltis and J. J. Doyle [eds.], *Molecular Systematics of Plants II DNA sequencing*, pp. 297-348. Kluwer Academic Publishers, Boston.

@ Micevich, M. F. and J. S. Farris. 1981. *The implications of congruence in Menidia*. *Systematic Zoology* 30: 351-370.

■ DNA preservation and PCR amplification:

■ DNA preservation:

■ need little DNA for PCR, but need lots (and fresh) DNA for restriction-site study & Southern blots

■ almost all fossil DNA studies from mid-1990s entirely refuted

Chase, M. W. and H. H. Hills 1991. *Silica gel: an ideal material for field preservation of leaf samples for DNA studies*. *Taxon* 40: 215-220.

Rogstad, S. H. 1992. *Saturated NaCl-CTAB solution as a means of field preservation of leaves for DNA analyses*. *Taxon* 41: 701-708.

Sytsma, K. J., T. J. Givnish, J. F. Smith, and W. J. Hahn. 1993. *Collection and storage of land plant samples for macromolecular comparisons*. *Methods in Enzymology* 224: 23-37.

■ PCR amplification:

■ PCR selection – compensate by changing reaction conditions

■ PCR drift – compensate by doing several PCR runs

■ problem in that not sample all of paralogs and/or alleles

■ genomics:

Freudenstein, J. V., K. M. Pickett, M. P. Simmons and J. W. Wenzel. Submitted. *Whither phenotypic characters in the age of genomics*. *Cladistics*.

@ Naylor, G. J. P. and W. M. Brown. 1998. *Amphioxus mitochondrial DNA, chordate phylogeny, and the limits of inference based on comparison of sequences*. *Systematic Biology* 47: 61-76.

■ supertrees:

@ Gatesy, J., C. Matthee, R. DeSalle and C. Hayashi. 2002. *Resolution of a supertree/supermatrix paradox*. *Systematic Biology* 51:652-664.

Sanderson, M., A. Purvis, and C. Henze. 1998. *Phylogenetic supertrees: assembling the trees of life*. *Trends in Ecology and Evolution* 13:105-109.

■ Bayesian MCMC:

Holder, M. and P. O. Lewis. 2003. *Phylogeny estimation: traditional and Bayesian approaches*. *Nature Reviews Genetics* 4:275-284.

@ Huelsenbeck, J. P., B. Larget, R. E. Miller and F. Ronquist. 2002. *Potential applications and pitfalls of Bayesian inference of phylogeny*. *Systematic Biology* 51:673-688.

Lewis, P. O. 2001. *Phylogenetic systematics turns over a new leaf*. *Trends in Ecology and Evolution* 16:30-37.