BiSci 6216: Morphological Systematics

3 hrs. lecture, 2 hr. lab
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Office hours: Wed 11-12A, Lisner 346

SUMMARY

This course surveys methods of studying organismal morphology as a means of inferring phylogeny and studying evolution, emphasizing the concept of homology. Students will read a variety of papers chosen for either their historical influence, broad overview of a topic, or cogent arguments. Each class session will begin with a lecture on the topic followed by a discussion of the papers by the students.

LECTURES

Part I - The first set of lectures and discussions outline the history and logical foundations of homology, as similarities shared by organisms due to a common evolutionary heritage. The hierarchical organization of homologies is the primary evidence for evolutionary relationships, and the goal of phylogenetic systematics is to reconstruct these relationships based upon the simplest explanation of the pattern of shared similarity. Analyses of morphological similarity by definition concern shape, and topological correspondence is therefore the most important criterion for recognizing shared similarities. The information content of shared similarities for phylogenetic inference is codified into states of a character that are hypothesized to be transformations of one another, and methods of coding characters therefore receive particular attention.

Part II - The second set of lectures and discussions concern the transformation of morphology during ontogeny, and the use of ontogenetic data in inferring phylogeny. Special attention is given to whether ontogenetic transformation provides a means of inferring relationships (sequence and direction) among character states. Historical views of recapitulation are reviewed, and current attempts to integrate hypotheses of developmental processes with evolutionary hypotheses are discussed.

Part III - The third set of lectures and discussions concern the interpretation of fossils. The difficulties and advantages of studying fossils are considered, including sampling biases of the sedimentologic record, problems of missing data, whether ancestors can be recognized, and comparisons of inferred relationships with the stratigraphic record of taxa.

Part IV - The last section covers morphometric approaches to the comparison of morphological similarity among organisms and the comparison of size and shape. Quantitative methods offer more precision than qualitative comparisons by providing an objective basis for evaluating when features of organisms are similar and when they are not, but methods founded upon degrees of difference are problematic indicators of phylogeny. Geometric morphometrics will be the main focus of this section.

LABORATORIES
Laboratories include a variety of topics complementing those presented in the lectures, including methods of observing morphology and capturing it digitally, methods of preparing fossils, methods for coding characters, and morphometric methods. A field trip in the spring will visit a local fossil site, the Calvert Cliffs.

LEARNING GOALS: Students will learn the principles and methods of phylogenetic analysis of organismal morphology. This mainly involves interpreting variability within and between taxa and codifying it in a matrix for phylogenetic analysis. Students should understand how to analyze ontogenetic changes and the relevance of the age of fossils to phylogenetic analysis. Students should understand how to quantify morphological comparisons, and the importance of size in these comparisons.

LEARNING OBJECTIVES: Students should acquire skills in coding morphological characters, analyzing allometry, interpreting fossils, and studying developmental sequences. These will be sufficient for students to publish research in comparative morphology and systematics, and to interpret the results of work published in journals such as *Systematic Biology, Evolution,* and *Cladistics*.

COURSE PREREQUISITES
BiSc 210 (Phylogenetic Systematics) or equivalent course.

STUDENT EVALUATION
Two closed book written exams will be given, on part I and on parts II-IV, and one paper. They will all have equal weight (33%) in the final grade.

READINGS: PDFs of papers will be distributed. The section on morphometrics draws mainly on one book that the students may want to purchase:

> Zelditch, M.L., D.L. Swiderski, H.D. Sheets, and W.L. Fink. 2004. Geometric morphometrics for biologists – A primer. Elsevier, NY.

LECTURE READINGS

PART I Homology and Character Delimitation

LECTURE 1: Historical foundations of morphological analysis

Aristotle (D'Arcy Thompson, translator) 1910. The Works of Aristotle, Volume IV: Historia Animalium. Clarendon Press, Oxford. (Selections).

Darwin, C. 1859. Mutual affinities of organic beings: morphology: embryology: rudimentary organs. Chapter 14 in The Origin of Species.

Rupke, N.A. 1993. Richard Owen's vertebrate archetype. Isis 84: 231-251.

LECTURE 2: Similarity and primary homology statements

Rieppel, O. and M. Kearney. 2002. Similarity. Biological Journal of the Linnean Society. 75(1): 59-82.

Hawkins, J.A. 2000. A survey of primary homology assessment: different botanists perceive and define characters in different ways. Pp. 22-53 in: Scotland, R. and Pennington, R.T., eds., Homology and Systematics. Taylor and Francis, London.

LECTURE 3: Character state coding

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

Hawkins, J.A., C.E. Hughes, and R.W. Scotland. 1997. Primary homology assessment, characters and character states. Cladistics 13:275-283.

LECTURE 4: Character correlation

Kangas, A. T., A. R. Evans, I. Thesleff and J. Jernvall. 2004. Non-independence of mammalian dental characters. Nature 432: 211-214.

Maddison, W. 1990. A method for testing the correlated evolution of two binary characters: are gains or losses concentrated on certain branches of a phylogenetic tree? Evolution 44: 539-557.

Sadleir, R. and P. Makovicky 2008. Cranial shape and correlated characters in crocodilian evolution. Journal of Evolutionary Biology 21: 1578-1596.

LECTURE 5: Morphological ontologies and databasing

Dahdul et al., 2010. The teleost anatomy ontology: Anatomical representation for the genomics age. Systematic Biology 59(4): 369-383.

LECTURE 6: Polymorphic characters
Mabee, P.M. and J. Humphries. 1993. Coding polymorphic data: examples from allozymes and ontogeny. Systematic Biology 42:166-181.

Wiens, J. 2000. Coding morphological variation within species and higher taxa for phylogenetic analysis. Pp. 115-145 in: J. Wiens, ed., Phylogenetic Analysis of Morphological Data. Washington, DC, Smithsonian Press.

LECTURE 7: Continuous variables I
Thiele, K. 1993. The holy grail of the perfect character: the cladistic treatment of morphometric data. Cladistics 9:275-304.

Garcia-Cruz, J. and V. Sosa. 2006. Coding quantitative character data for phylogenetic analysis: A comparison of five methods. Systematic Biology 31: 302-309.

LECTURE 8: Continuous variables II
Strait, D., M.A. Moniz, and P. T. Strait 1996. Finite mixture coding: A new approach to coding continuous characters. Systematic Biology 45:67-78.

Goloboff, P.A., C.I. Mattoni and A.S. Quinteros. 2006. Continuous characters analyzed as such. Cladistics 22: 589-601.

LECTURE 9: Uncertainty in primary homology statements
Ramirez, M.J. 2007. Homology as a parsimony problem: a dynamic homology approach for morphological data. Cladistics 23: 588-612.

Agnarsson, I. and J. Coddington. 2008. Quantitative tests of primary homology. Cladistics 24: 51-61.

LECTURE 10: Likelihood and Bayesian analysis of morphology
Lewis, P. O. 2001. A likelihood approach to estimating phylogeny from discrete morphological character data. Systematic Biology 50:913-925.

Nylander J.A., F. Ronquist, J.P. Huelsenbeck and J.L. Nieves-Aldrey. 2004. Bayesian phylogenetic analysis of combined data. Systematic Biology 53(1):47-67.

LECTURE 11: Adaptation and phylogeny
Gould, S. J., and R. C. Lewontin. 1979. The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. Proceedings of the Royal Society of London, B205:581-598.

Coddington, J.A. 1988. Cladistic tests of adaptational hypotheses. Cladistics 4:1-20

LECTURE 12: MID-TERM TEST

PART II Ontogeny

LECTURE 13: Ontogeny and phylogeny
Alberch, P., S.J. Gould, S.J., G.F. Oster, and D.B. Wake 1979. Size and shape in ontogeny and phylogeny. Paleobiology **5**: 296-317.

Fink, W.L. 1982. The conceptual relationship between ontogeny and phylogeny. Paleobiology 8:254-264.

Dayrat, B. 2003. The roots of phylogeny: How did Haeckel build his trees? Systematic Biology 52: 515-527.

LECTURE 14: Does the ontogenetic sequence of characters have phylogenetic information?
Nelson, G. 1978 Ontogeny, phylogeny, paleontology, and the biogenetic law. Systematic Zoology 27:324-345.

Kluge, A.G. and R.E. Strauss 1985 Ontogeny and systematics. Annual Reviews in Ecology and Systematics 16:247-268.

De Pinna, M.C.C. 1994 Ontogeny, rooting, and polarity. Pp. 157-172 in Models in Phylogeny Reconstruction, R.W. Scotland, D.J. Siebert, and D.M. Williams eds. Clarendon Press, Oxford.

LECTURE 15: Empirical tests of the "ontogeny criterion"
Mabee, P.M. 2000 The usefulness of ontogeny in interpreting morphological characters. Pp. 84-114 in: J. Wiens, ed., Phylogenetic Analysis of Morphological Data. Washington, DC, Smithsonian Press.

LECTURE 16: Developmental sequence analysis
Maxwell, E.E. and L.B. Harrison. 2009. Methods for the analysis of developmental sequence data. Evolution and Development 11: 109-119.

Schulmeister, S. and W.C. Wheeler 2004. Comparative and phylogenetic analysis of developmental sequences. Evolution & Development 6:50–57.

LECTURE 17: Developmental genetics and homology

Hall, B.K. 2005. Homoplasy and homology: Dichotomy or continuum? Journal of Human Evolution 52: 473-479.

Shubin, N., C. Tabin and S. Carroll. 2009. Deep homology and the origins of evolutionary novelty. Nature 457: 818-823.

Bang, R., T. Schultz, and R. DeSalle. 2002. Development, homology, and systematics. Pp. 175-186 in: R. DeSalle, G. Giribet, and W. Wheeler, eds., Molecular Systematics and Evolution: Theory and Practice. Birkhäuser Verlag, Boston.

LECTURE 18: Development, complex characters and evolution
Wake, D.B., and G. Roth. 1989. The linkage between ontogeny and phylogeny in the evolution of complex systems. Pp. 361-377 in D.B. Wake and G. Roth, "Complex organismal functions: Integration and evolution in vertebrates." John Wiley and Sons, San Francisco.

Atchley, W.R. and B.K. Hall. 1991. A model for development and evolution of complex morphological structures. Biological Reviews 66: 101-157.

Kavanagh, K.D., A.R. Evans and J. Jernvall. 2007. Predicting evolutionary patterns of mammalian teeth from development. Nature 449: 427-433.

PART III Paleontology

LECTURE 19*: *The nature of the fossil record
Kidwell, S. and K. Flessa. 1996. The quality of the fossil record: Populations, species, and communities. Annual Reviews of Earth and Planetary Sciences 24:433–64.

Eldredge, N. and S.J. Gould. 1972. Punctuated Equilibria: An alternative to phyletic gradualism. In Schopf, Thomas J.M. (ed.), Models in Paleobiology, pp. 82-115. Freeman, Cooper and Co., San Francisco.

LECTURE 20: Fossils and phylogeny
Patterson, C. 1981. Significance of fossils in determining evolutionary relationships. Annual Reviews in Ecology and Systematics 12:195-223.

Donoghue, M., J. Doyle, J. Gauthier, A. Kluge, and T. Rowe 1989 The importance of fossils in phylogeny reconstruction. Annual Reviews in Ecology and Systematics 20:431-460.

LECTURE 21: Phylogeny and the stratigraphic record
Smith, A.B. 1994 Systematics and the Fossil Record. Blackwell, Oxford. (Selections)

Pol, D., Norell, M. A. and Siddall, M. E. 2004. Measures of stratigraphic fit to phylogeny and their sensitivity to tree size, tree shape, and scale. *Cladistics* 20, 64-75.

Huelsenbeck, J. and B. Rannala 2000 Using stratigraphic information in phylogenetics. Pp. 165-191 in: J. Wiens, ed., Phylogenetic Analysis of Morphological Data. Washington, DC, Smithsonian Press.

Wagner, P. 2000. The quality of the fossil record and the accuracy of phylogenetic inferences about sampling and diversity. Systematic Biology 49: 65-86.

LECTURE 22: Soft tissues, functional morphology and behavior in fossils
Witmer, L. 1995 The extant taxon bracketing method. Pp. 19-33 in: Functional Morphology in Vertebrate Paleontology, J.J. Thomason, ed. Cambridge Univ. Press, NY.

Rayfield, E.J. 2007. Biomechanics and evolution of living and fossil organisms. Annual Review of Earth and Planetary Sciences 35:541–76.

LECTURE 23*: *Dating molecular divergences times with fossils
Benton, M., P.C.J. Donoghue and R. Asher. 2009. Calibrating and constraining molecular clocks. Pp. 35–86 in *The Timetree of Life*, S. B. Hedges and S. Kumar, Eds. Oxford University Press.

LECTURE 24: Problems with missing data
Kearney, M. and J. Clark. 2003. Problems due to missing data in phylogenetic analyses including fossils: a critical review. Journal of Vertebrate Paleontology 23: 263-274.

Wilkinson, M. 1994 Common cladistic information and its consensus representations: Reduced Adams and reduced cladistic consensus trees and profiles. Systematic Biology 43:343-368.

Wilkinson, M., J.L. Thorley, and P. Upchurch. 2000 A chain is no stronger than its weakest link: Double decay analysis of phylogenetic hypotheses. Systematic Biology 49:754-776.

PART IV Morphometrics

LECTURE 25: Size and allometry
Thompson, D'Arcy 1963 (reprint) On Growth and Form. Cambridge University, Cambridge. (Selections)

Zelditch et al. 2004, Geometric Morphometrics for Biologists, chapter 1.

LAB Geometric morphometrics
Zelditch et al. 2004, Geometric Morphometrics for Biologists, chapter 2.

LECTURE 26
Catalano, S.A., P.A. Goloboff, and N.P. Giannini 2010. Phylogenetic morphometrics (I): the use of landmark data in a phylogenetic framework. Cladistics 26 (2010) 539–549

Zelditch et al. 2004, Geometric Morphometrics for Biologists, chapter 3, skim chapter 4.

LECTURE 27 Geometric morphometrics
Zelditch et al. 2004, Geometric Morphometrics for Biologists, chapter 5.

LAB Geometric morphometrics
Zelditch et al. 2004, Geometric Morphometrics for Biologists, chapter 7.

LECTURE 28 Geometric morphometrics
Zelditch et al. 2004, Geometric Morphometrics for Biologists, chapter 14, skim chapter 13.

FINAL – As scheduled.

LAB TOPICS

1: Editing morphological images

2: Online morphological databases

3: Coding continuous variables

4: Character correlation

5: Bayesian analysis of morphology

6. Paleontological techniques (NMNH)

7. Size and scaling – allometric equations

8. Morphometrics (PCA, DFA)

9. Morphometrics (Geometric morphometrics)

Field trip to Calvert Cliffs