Systematic fundamentals, paleontological questions.

GEO 391/371C 27740/27970

Rm 3.218, 2-3:30 Mondays and Wednesdays

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Office hours: Wed 3:30-5pm and by appointment.

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Course Description: This reading-intensive course will focus on 1) the philosophical/ historical underpinnings of, and 2) practical approaches to, the study of morphological evolution using discrete cladistic characters. Active participation in class discussion is expected.

Topics covered: Theories of the anatomical character and of character systems. Debates: character independence and functional linkages, characters as the unit of morphological evolution- natural kinds and characters as observations. Practical approaches to character construction and state discrimination in phylogenetic analysis. Morphoclines and multistate vs. single state characters, other debates concerning ordering. The role of post-analysis character exploration. Primary/ secondary homology. Terminal taxa: composite supraspecific vs species or specimen exemplar approaches. Sampling and scoring issues and debates. Dataset exploration: "Support metrics" and indices. Congruence, consistency, branch lengths and their relationship with the inferred strength of phylogenetic hypotheses. Homoplasy and missing data in 'parametric' and 'non-parametric' approaches. Simulation, the comparative method and debates over their roles in considering unique events in the history of life. Investigating hypotheses of adaptation, ecological shifts, rate shifts, disjunctive morphological evolution in the context of parsimony-based, likelihood and Bayesian contexts.

Grading: Assignments 1- 4 (see due dates below) and the abstract of your proposed research (due March 19) are each worth 10% of your grade for a total of 50%. Participation is 20%. Final written assignment: 30% of your grade.

Final Assignment: See description at the end of this syllabus. You will be expected to have an abstract of your proposed research just after spring break (March 19) so a topic should be chosen early in the semester. Ideally this research will be a short paper modifiable for submittal to a journal and a viable part of one of the chapters of your thesis.

Date and time of Final Exam: There is no final exam.

Materials: Papers and assignments are distributed via Blackboard. You must regularly check for new posting and download all readings to have them available in each class. In each class, students will choose one of the assigned papers and be responsible for co-presenting its main points. We can cover more of the relevant literature in this way.

*Course plan: NOTE reading assignments and topics will shift as the course progress necessitates – it is your responsibility to follow changes announced to the course plan. These changes will be announced in class or via email so please make sure I have your preferred email contact. Note based on the interest and experience of the class primary and suggested readings may be swapped.

Week 1. Introduction: Phylogenetic dataset properties

Jan. 18. **Course overview and discussion.** Questions: what are properties of a dataset? How do datasets differ? What is a character? What are properties of a character?

Week 2. The character, Part I.

Jan. 23. **No Class. Prepare for Assignment 1.** Spend appropriate course prep and course time: 1. **Finding and installing a data editor** (Mesquite, MacClade, WinClada) on your computer or locate one you will use throughout the class or establishing an account: Morphobank), and **2) locating, uploading into this data editor, formatting your target dataset** and **3) prepare (copy with citation) the corresponding character list into an editable word document.**

Jan. 25. **Due: Discussion of your character sets: Be prepared in just 3 well organized powerpoint slides** (**in-class component of Assignment 1**) to 1) introduce your dataset, 2) state your target question(s) and 3) briefly introduce your target taxonomic group.

Written Assignment 1 Due. Bring (on one printed page): a 1) one line statement of a proposed target question, 2) relevant formatted citation(s) and 3) attach a print out of your working character list.

Week 3. Philosophy of "the character": Question to be discussed in class: How would your perspective on the nature of the character directly impact establishing decisions about your dataset and analytical approach?

Jan. 30. **Readings:**
Wagner G. 2001. "Characters, units and natural kinds: an introduction" In: GP Wagner, Editor, The Character Concept in Evolutionary Biology, Academic Press, San Diego, pp. 1–10.

Fristrup K. 2001 "A history of character concepts in evolutionary biology" In: GP Wagner, Editor, The Character Concept in Evolutionary Biology, Academic Press, San Diego, pp. 13–35.

Feb. 1. **Reading:**

Schwenk K. 2001. Functional Units and their evolution. In: GP Wagner, Editor, The Character Concept in Evolutionary Biology, Academic Press, San Diego, pp. 165–198.

Other suggested readings:

Rieppel. O. 2001. "Preformationist and Epigenetic Biases in the history of the Morphological Character Concept." In: GP Wagner, Editor, The Character Concept in Evolutionary Biology, Academic Press, San Diego, pp. 13–35.

Week 4: Relationship between philosophies of the character and systematic practice.

Feb. 6: Lecture/discussion: Character construction: Morphoclines, Multistate/single state, Ordering. Post analysis character exploration. Primary/ Secondary Homology

Readings: 67
Pimentel R.A. and Riggins. R 1987. The Nature of Cladistic data. Cladistics 3:2001-2009.

Slowinski, J. 1993. ''Unordered'' versus ''Ordered''characters. Systematic Biology 42: 155–165.

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

Pleijel F. 1995. On character coding for phylogeny reconstruction. Cladistics 11:309-315.

Feb. 8. **Readings**

Hawkins, J, C. E. Hughes and R. W. Scotland. 1997. Primary Homology Assessment, Characters and Character States. Cladistics. 9pp.

Strong and Lipscomb 1999, Character coding and Inapplicable data. Cladistics. 15:363-371.

Other suggested readings on ordering and multistate characters: N.B. available hardcopy only (no UT online access).

DL HAUSER, W PRESCH 1991. The effect of ordered character on phylogenetic reconstruction. Cladistics 7:33, 243-265, Academic Press, 1991.

DL LIPSCOMB 1992. Parsimony, homology and the analysis of multistate characters. Cladistics 8:11, 45-65.

WILKINSON, M. 1992. Ordered versus unordered characters. Cladistics 8: 375-385.

DL HAUSER. 1992. Similarity, falsification and character state order: a reply to Wilkinson. Cladistics 8:44, 339-344, Academic Press.

Week 5. Character writing workshop

Feb. 13. **Students Present. <u>Assignment 2 Due.</u>**

Character writing workshop I. Character wording, construction, issues, state discrimination. Problems of the composite state and non-equivalence of the "0" state. **Due:**

bring examples of characters for discussions and workshop- suitable for the overhead projector, as handouts or as powerpoint slides.

Instructions for assignment:

1. Bring 3 characters for discussion: at least one ordered multistate, unordered multistate, and one binary. If there are no multistates in your analysis bring 2 examples of sets of additive binary characters that could arguably be made into multistates. Be ready to explain the features addressed –bring along visuals or draw on the board…

2. Be prepared to discuss: What kinds of features are multistates are in your dataset? Where are they in the skeleton/organism? Is there any pattern? Why did you (or the authors) choose an ordered multistate in one example, and why did you choose an unordered in another case? Is redundancy introduced? Composite 0 states? Where "O" compasses a variety of disparate conditions?

Feb. 15. **Workshop continued and discussion** concerning the relationships between philosophies of the character and systematic practice.

Reading:
P. Wagner 2000. EXHAUSTION OF MORPHOLOGIC CHARACTER STATES AMONG FOSSIL TAXA Evolution, 54(2), 2000, pp. 365-386.

Week 6. Taxon sampling, terminal taxa and exemplar choice. **What are appropriate terminal taxa?: composite supraspecific vs species or specimen exemplar approaches. Sampling. Scoring issues. Polymorphic Terminals. Potential sources of error. Infraspecific variation? Polymorphism.**

Feb.20. **Readings**

Simmons, N.B. 2001. Misleading results from the use of ambiguity coding to score polymorphisms in higher-level taxa. Systematic Biology 50(4): 613–620.

Simmons N.B. and Giesler J. 2002. Sensitivity analysis of different methods of coding taxonomic polymorphism: an example from higher-level bat phylogeny. Cladistics. 18: 571-584.

Prendini, L. 2001. Species or supraspecific taxa as terminals in cladistic analysis? Ground plans versus exemplars revisited. Systematic Biology 50: 290–300.

Weins. J.J. 1998. The Accuracy of Methods for Coding and Sampling Higher-Level Taxa for Phylogenetic Analysis: A Simulation Study Syst. Biol. 47(3): 397 - 413.

Feb 22**. Readings**

Hillis D. 1998. Taxonomic Sampling, Phylogenetic Accuracy, and Investigator Bias. Systematic Biology 47: 3-8.

Poe S and Swofford D. 1999. Taxonomic Sampling revisited. Nature 398:299-300.

Zwickl D and Hillis D. 2002. Increased Taxon sampling greatly reduces phylogenetic error. 51: 588-598.

Week 7. Missing data

Feb 27. Readings:

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

Kearney, M. 2002. Fragmentary taxa, missing data, and ambiguity: mistaken assumptions and conclusions. Systematic Biology 51: 369-381.

Feb. 29. Readings:

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

Weins, J.J. 2003. Missing data, Incomplete taxa, phylogenetic accuracy. Syst. Bio. 52:528-538.

Wiens, J.J. 2009. Paleontology, phylogenomics, and combined-data phylogenetics: can molecular data improve phylogeny estimation for fossil taxa? Systematic Biology 58: 87-99.

Week 8. Character analysis, missing data & taxon sampling – discussion and workshop

Mar. 5. <u>Assignment 3 Due:</u> Choose 2 of the below: 1 well written page single spaced. One figure.

1. Ordering: Chose a minimum of 2 multistate characters (preferably some we discussed), run an appropriate analysis or use a tree from the literature and bring Macclade or Mesquite output screen shots (or similar) to show character optimizations (use the "show states changing option") when the characters are ordered and unordered. Be prepared to present and discuss these results (ordered vs. unordered, implications for character evolution in trait).

2. Terminal taxa: Go from species or other exemplar scoring to composite (e.g.) supraspecific for one set of taxa or specimens (minimum 2!) *or* Go from supraspecific/composite to a species based exemplar approach (from higher taxa to species or species to specimen).

3. Missing data: Explore your dataset for example iteratively deleting the most incomplete taxa by percent missing data. What is the effect on the recovered topology? If there are apparent wild card taxa in your dataset is lack of resolution driven by operational taxonomic equivalents or by homoplasy? How would you investigate this?

Mar. 7. Continued.

<u>Mar. 12-18 Spring Break</u>

Week 9. Morphological evolution, models and methods for considering rate heterogeneity

Mar. 19. <u>Abstract Due.</u> Readings:

Clarke, J. A. and K. Middleton. 2008. Mosaicism, modules, and the evolution of birds: results from a Bayesian approach to the study of morphological evolution using discrete character data. Systematic Biology, 57: 185-201.

Dececchi and Larsson, H. 2009. Patristic evolutionary rates suggest a punctuated pattern in forelimb evolution before and after the origin of birds. Paleobiology 35:1-12

Wagner. P.J. 2011. Modeling rate distributions using character compatibility: implications for morphological evolution among fossil invertebrates. Biology Letters. http://dx.doi.org/10.1098/rsbl.2011.0523.

Mar. 21. Readings:

Blomberg.S.P. Garland, T. and Ives, A. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. Evolution 57: 717-745.

Smith, N. D. 2011. Body mass and foraging ecology predict evolutionary patterns of skeletal pneumaticity in the diverse "waterbird" clade. Evolution. Doi:10.1111/j.1558-5646.2011.01494.x

Other suggested readings:

Gonzalez-Jose et al. 2008. Cladistic analysis of continuous modularized traits provides phylogenetic signals in Homo evolution. Nature, 435: doi:10.1038/nature06891.

Week 10. Dataset exploration, homoplasy, "Support metrics" and indices.

Mar. 26. Readings:

Sanderson, 1991 In search of homoplastic tendencies: statistical Inference of topological patterns in homoplasy Evolution, 45(2), 1991: 351-358.

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

Hauser D. and G. Boyajian 1997. Proportional change and patterns of homoplasy: Sanderson and Donoghue revisited Cladistics [0748-3007] Hauser yr:1997 vol:13:97-100.

Källersjö M, VA Albert, JS Farris. 1999. Homoplasy Increases Phylogenetic Structure. Cladistics. 15 Issue 1, Pages 91 – 93.

Mar.28: Readings:

Trueman JW. 1998. Reverse successive weighting. Systematic Biology. 47:733-737.

Brochu. C.A. 1999. Taxon Sampling and Reverse Successive Weighting. Syst. Biol. 48:808-813.

Williams. B.A. 2007. Comparing levels of homoplasy in the primate skeleton Journal of Human Evolution 52: 480-489.

Brandley et al. 2009. Homoplasy and Clade Support. Systematic Biology 58:184-198.

Week 11. Discussion/workshop of methods for dataset exploration

Apr. 2. Assignment 4 Due – hard copy in class:
Exercise – Sensitivity analyses and post-analysis data exploration: Choose 2 of the below: 1 well written page single spaced. One figure.

1. **Implement a minimum of 2 rounds of reverse successive weighting on CI** (or CI *and* RI **if you want**).
   Present results:
   a. What characters were removed in the first round? What is their distribution over the skeleton? What are their properties: Ordered? Unordered? Multistate?
   b. Summarize resultant tree topologies minimally as strict consensus cladogram after each round. Present these. What other signal is/maybe present in your dataset? Are other topologies recovered inconsistent with the primary topology based on all of the data?

2. **Partition your dataset into at least 2 anatomical subregions or hypothesized "data types" based on evolutionary hypotheses of your group.** Run separate analyses iteratively including characters from one subregion and then the other. Compare resulting trees to each other and to the primary analysis of all data: topological differences? L? CI and other metrics? Present these trees and metrics.
3. **Take another approach to exploration of your dataset.** For example, the effect of iterative taxonomic deletion or inforcement of a backbone constraint tree on the distribution of characters of interest? You may choose any methods. Please include the relevant cite either from this syllabus or other.

Apr. 4. Continued.

Week 12. Incongruence, Combined analyses, the place of morphology in phylogenetic analyses

Apr. 9. **Readings:**

Lee, M. 2001. Uninformative Characters and Apparent Conflict Between Molecules and Morphology. Molecular Biology and Phylogenetics. 18: 676-680.

Weins. JH. 2004 The role of morphological data in phylogeny reconstruction. Systematic

Biology, 53: 653-661.

Smith, N and Turner, A. 2005. Morphology's Role in Phylogeny Reconstruction: Perspectives from Paleontology. 54:166-173.

Apr. 11. **Readings:**

Wortley A. and R. Scotland. 2006. The Effect of Combining Molecular and Morphological Data in Published Phylogenetic Analyses. Systematic Biology 55: 677-685.

Giribet, G. 2010 A new dimension in combining data? The use of morphology and phylogenomic data in metazoan systematics. Acta Zoologica, 91:11-19.

Other suggested readings:

Jenner, R. 2011. The use of morphology in criticizing molecular trees. Journal of Crustacean Biology, 31(2):373-377.

Assis, A. and O. Rieppel. 2010. Are monophyly and synapomorphy the same or different? Revisiting the role of morphology in phylogenetics. Cladistics 27:94-102.

Lopardo L. G. Giribet and G. Hormiga. 2011. Morphology to the rescue: molecular data and the signal of morphological characters in combined phylogenetic analyses—a case study from mysmenid spiders (Araneae, Mysmenidae), with comments on the evolution of web architecture. Cladistics 27: 278-330.

Week 13. Introduction to debates over the comparative method & and the nature of hypothesis testing in the historical sciences.

Apr. 16 Hypotheses and the Historical Sciences

Readings:

Rieppel. O. 2003. Popper and Systematics. Systematic Biology 52: 259-271.

Apr. 18. The comparative method: fundamentals and critiques

Readings:

Doughty P. 1996. Statistical Analysis of Natural Experiments in Evolutionary Biology: Comments on Recent Criticisms of the Use of Comparative Methods to Study Adaptation. American Naturalist 148: 943-956.

Frumhoff P.C. and K. Reeve. 1994. USING PHYLOGENIES TO TEST HYPOTHESES OF ADAPTATION: A CRITIQUE OF SOME CURRENT PROPOSALS. Evolution, 48: 172-180

Other suggested reading:

Losos, J.B., and D.B. Miles. 1994. Adaptation, constraint, and the comparative method: phylogenetic issues and methods. Pp. 60-98 in P.C. Wainwright and S. Reilly, Eds., Ecological Morphology: Integrative Organismal Biology. University of Chicago Press: Chicago.

Week 14. Diversification

Apr. 23. Rates of character evolution: molecules and morphology.

Readings:

K. E Omland 1997. Correlated rates of molecular and morphological evolution. Evolution 51: 1381-1393

Bromham L., Woolfit M., M. S. Y. Lee, A. Rambaut. 2002. Testing the Relationship between Morphological and Molecular Rates of Change along Phylogenies. Evolution, 56: 1921-1930.

Apr. 25. Diversification: rate or age?

Readings:

McPeek M.A. and J. M. Brown. 2007. Clade Age and Not Diversification Rate Explains Species Richness among Animal Taxa. Am Nat 2007. 169: E97–E106.

Heath T, D. Zwickl, J. Kim, D. Hillis. 2008. Taxon Sampling Affects Inferences of Macroevolutionary Processes from Phylogenetic Trees. Systematic Biology 57: 160-166.

Tarver, J. and P. Donoghue. 2011. The Trouble with Topology: Phylogenies without Fossils Provide a Revisionist Perspective of Evolutionary History in Topological Analyses of Diversity. Systematic Biology, 60:700-712.

Week 15. Comparative method- Biogeography

Apr. 30. **Readings:**

Morrone J. J. and J. V. Crisci. 1995. Historical Biogeography: Introduction to Methods. Annual Review of Ecology and Systematics, Vol. 26: 373-401.

May 2. **In class workshop: examples of biogeographical inference from paleontological data.**

Readings:

Donoghue 2008. A phylogenetic perspective on the distribution of plant diversity. PNAS 105: 11549–11555.

Other suggested readings:

Donoghue M. and B. Moore. 2003. Toward an Integrative Historical Biogeography. INTEGR. COMP. BIOL., 43:261–270.

Weins J.J. and M. Donoghue. 2004. Historical biogeography, ecology and species richness. Trends in Ecology & Evolution, 19: 639-644.

San Martin et al. 2007. West Wind Drift revisited: testing for directional dispersal in the Southern Hemisphere using event-based tree fitting. Journal of Biogeography 34:398–416

May. 9 Final paper due. (see next page).

Final paper:

1. Chose a topic covered in one of our 4 modules – e.g. the character, taxon sampling, homoplasy, patterns of morphological evolution, comparative methods and hypothesis testing. N.B. since independent research is expected- there will be no way to complete all relevant work at the very end of the semester.
2. Critically evaluate the prior literature on your topic and/or method. (e.g., an aspect of character philosophy). Please remember that you are expected to explore the literature on one of these subjects not to primarily cite papers from class. No more than 30% of the references can be from class.
3. Empirically investigate an aspect of this topic with your dataset or through simulation (see "character philosophy" example below). You are also expected to present something new- not something from a prior assignment - although you may include results from a prior assignment as a limited part of the data discussed in the paper or presentation.
4. All papers will take the general form of manuscripts for submittal to a journal (e.g., Systematic Biology, Evolution, Paleobiology, Biology Letters) (Maybe you will submit them?!).
   a.   All have a well crafted abstract, introduction, methods, results, discussion, conclusions and formal reference section. They also have figures.
   b.   Length is not the primary concern but papers are anticipated to be 15+ double spaced pages not including references. The emphasis is up to you: you may focus primarily on a novel critical evaluation of the literature and only have a brief empirical portion or vice versa.

I have included an example sketch for the outline of a final project (below). Please discuss your project concept with me well prior to the end of the semester.

-Critically review the prior literature regarding aspects of a debate, for example, concerning character identity/ontology, transformational vs. taxic homology etc., issues with choice of terminals implications for your understanding of the relationships in your group and the evolutionary history of that group.

Through your concise and thoughtful discussion of the relevant literature, your unique perspective (e.g., on the character, taxon sampling/taxon choice, hypothesis testing and comparative method, homoplasy) as the author of the paper will be come clear. This discussion would generally comprise the introduction (may be lengthy) and contextualize your empirical exercise.

-Methods and Results would present how you investigated, for example, the impact of enforcing your philosophy/ methodological approach (e.g., on character concept, taxon choice etc.) in the revision of the characters in your data matrix (or if you are building a data matrix - in your interpretation and 'translation' of the prior literature to make your dataset).

-Results: explore the implications of, for example, your revised characters etc. on the outcomes of your analysis. How may have your "dataset properties" have changed?

-Discussion and Conclusions: synthesize your results and present your recommendations for other workers based on your critical evaluation of the literature and your analytical results.

-References: Formatting matters.

Grading of final project: Approximate breakdown: 20% Originality of question, articulation of topic/hypothesis, 15% fit of methods/approach to chosen question, 20% relevant literature cited, 20% thorough discussion of implications, 25% quality of the written document, figures and citations.

Policies and other information:

University of Texas Honor Code
The core values of The University of Texas at Austin are learning, discovery, freedom, leadership, individual opportunity, and responsibility. Each member of the university is expected to uphold these values through integrity, honesty, trust, fairness, and respect toward peers and community. We maintain a zero-tolerance policy on cheating. Scholastic dishonesty includes, but is not limited to, cheating, plagiarism, collusion, using, buying, stealing, and/or divulging the contents of an examination, removing a test from the examination room, substituting for another person, having someone take a test for you, misplacing or damaging property of the University or destroying information so another student may not have materials, falsifying research data, misrepresenting facts including providing false grades or resumes, presenting someone else's work as one's own academic work, and falsifying academic records. A full and comprehensive statement about what constitutes academic dishonesty can be found in Appendix C, section 11-802 in the General Information bulletin. The Student Judicial Services office in the Office of the Dean of Students has the responsibility for following up and making the final determination.

Documented Disability Statement
The University of Texas at Austin provides upon request appropriate academic accommodations for qualified students with disabilities. For more information, contact Services for Students with Disabilities at 471-6259 (voice) or 232-2937 (video phone) or **http://www.utexas.edu/diversity/ddce/ssd**

Use of E-Mail for Official Correspondence to Students
E-mail is recognized as an official mode of university correspondence; therefore, you are responsible for reading your e-mail for university and course-related information and announcements. You are responsible to keep the university informed about changes to your e-mail address. You should check your e-mail regularly and frequently—I recommend daily, but at minimum twice a week—to stay current with university-related communications, some of which may be time-critical. You can find UT Austin's policies and instructions for updating your e-mail address at **http://www.utexas.edu/its/policies/emailnotify.php**

Religious Holy Days
By UT Austin policy, you must notify me of your pending absence at least fourteen days prior to the date of observance of a religious holy day. If you must miss a class, an examination, a work assignment, or a project in order to observe a religious holy day, I will give you an opportunity to complete the missed work within a reasonable time after the absence.

Behavior Concerns Advice Line (BCAL)
If you are worried about someone who is acting differently, you may use the Behavior Concerns Advice Line to discuss by phone your concerns about another individual's behavior. This service is provided through a partnership among the Office of the Dean of Students, the Counseling and Mental Health Center (CMHC), the Employee Assistance Program (EAP), and The University of Texas Police Department (UTPD). Call 512-232-5050 or visit **http://www.utexas.edu/safety/bcal**