OEB 213: Macroevolution in Deep Time

Head Instructor: Javier Ortega-Hernández – Associate Professor of Organismic and Evolutionary Biology, and Curator of Invertebrate Paleontology at the Museum of Comparative Zoology

Time: Thursdays, 09:45 to 11:45am.

Location: Northwest Building B-217.

Short description: Understanding the processes responsible for the origin of major animal groups and the composition of the biosphere represent some of the core objectives of evolutionary biology. Despite monumental advances made possible by the onset of molecular techniques that allow to reconstruct phylogenetic relationships between phyla, as well as tracking the intrinsic developmental mechanisms behind their morphology, extant diversity inevitably offers an incomplete view of the evolutionary history of these organisms. This course examines how macroevolutionary processes acting through deep time affect fundamental patterns of animal biodiversity, including topics such as the origin of animals, rapid diversification of major clades, and the impact of extinction in shaping extant biodiversity. The aim is to convey a sense of how evolutionary thinking has changed over the past few decades thanks to a combination of conceptual and technical advances, as well as to instill a sense of the importance of the animal fossil record as a valuable source of data with a uniquely historical component among the biological sciences.

Macroevolution in Deep Time – quick overview

S1: Introductory remarks and key concepts	**S2: The shape of modern animal biodiversity**
S3: Life through deep time: how to read the fossil record	**S4: On the origins of Life, animals and the biosphere**
S5: Replay the tape of Life? Cambrian weird wonders and contingency	**S6: Precambrian ghost lineages and molecular clocks**
S7: The Five Laws of Paleobiology – how extinction shapes biodiversity	**S8: Stem and crown groups: making sense of extinct problematica**
S9: The speed of evolution and the nature of change	**S10: History is written by the victors**
S11: Convergence and the inevitability of complexity	**S12: Experimental evolution**

Assessment: Final grades will be calculated from student presentations and participation in class (40%), and two graded essays (30% each, totaling 60%). Regular attendance and engagement during taught sessions are critical for preparing presentations and essays.

Requirements: No prior courses strictly required, but a basic understanding of evolution is essential.

Required reading: It is expected that students will thoroughly read the material provided in advance of each session (up to three scientific publications) to fully benefit from the discussions and practical activities. The full reading list is available in the course website.

Class activities: Most sessions will involve a practical component aimed at complementing the required reading and topical discussion. Instructions and materials will be provided in advance. Several sessions require access to an individual laptop with internet for practical **online activities**, either individual or working in small groups. Please contact the course instructor if this might cause complications.

Course weekly format: All students will attend a live group discussion/practical session chaired by the course instructor focused on the assigned reading material and relevant activities. During class the course instructor will rely on selected figures from the session's required reading to initiate the discussion and provide context. A typical class will start with a **15-20 minute introduction by the course instructor**, followed by a **30-45 minute literature discussion and Q&A**, then a **30-45 minute practical activity** (e.g. probability games, online resources), and end with a **whole class discussion addressing the topic**.

Academic integrity: Seminar attendees agree to adhere to the Harvard College Honor Code as outlined below (more information at https://honor.fas.harvard.edu/honor-code):

Members of the Harvard College community commit themselves to producing academic work of integrity – that is, work that adheres to the scholarly and intellectual standards of accurate attribution of sources, appropriate collection and use of data, and transparent acknowledgement of the contribution of others to their ideas, discoveries, interpretations, and conclusions. Cheating on exams or problem sets, plagiarizing or misrepresenting the ideas or language of someone else as one's own, falsifying data, or any other instance of academic dishonesty violates the standards of our community, as well as the standards of the wider world of learning and affairs.

Statement of AI use: Use of Artificial Intelligence (AI) based software (e.g. ChatGPT) undermines the objective of this course to encourage critical thinking and the integration of the new information and literature covered. As a result, the use of AI resources for graded course outputs (e.g. essays, presentations) is prohibited. However, students may use AI resources as a complementary tool for studying, revising and when actively encouraged by the course instructor as part of class activities that do not receive a grade or are actively considered towards individual assessment.

September 5, 2024

Session 1: Introductory remarks and key concepts – General course overview, instructor/student expectations, and discussion of core evolutionary concepts.

Class activity: Biodiversity is more complex than you think. **Online activity** with interactive resource Metazooa (https://metazooa.com/). *Please bring your personal laptop or tablet.*

Core question: What is our current view/understanding of animal macroevolution?

September 12, 2024

Session 2: The shape of modern animal biodiversity – Overview of major animal phyla, their phylogenetic relationships, and body plan disparity based on extant biodiversity.

Required reading:

Dunn, C.W., Giribet, G., Edgecombe, G.D. and Hejnol, A., 2014. Animal phylogeny and its evolutionary implications. *Annual review of ecology, evolution, and systematics 45*: 371-395.

Deline et al. 2018. Evolution of metazoan morphological disparity. *Proceedings of the National Academy of Sciences 115*: E8909-E8918.

Class activity: Visualizing the taxonomic richness and morphological disparity of modern animals. **Online activity** with interactive resource OneZoom (https://www.onezoom.org/). *Please bring your personal laptop or tablet.*

Core question: How is diversity (taxonomic and morphological) distributed among extant animal phyla?

September 19, 2024

Session 3: Life through deep time: how to read the fossil record – Introduction to the animal fossil record, including studies that address geologic-scale patterns of marine invertebrate biodiversity.

Required reading:

Sepkoski 1993. Ten years in the library: new data confirm paleontological patterns. *Paleobiology 19*: 43-51.

Alroy et al. 2008. Phanerozoic trends in the global diversity of marine invertebrates. *Science 321*: 97-100.

Class activity: **Diversity and disparity through time I** – modelling the traditional view from shelly fossil record. **Online activity** with the Paleobiology Database (https://paleobiodb.org/navigator/). *Please bring your personal laptop or tablet.*

Core question: How does the fossil record affect our view of diversity/disparity through time?

September 26, 2024 (Remote session)

Session 4: On the origins of Life, animals and the modern biosphere – Discussion on the precise timing for the origin of life on Earth, and the emergence of complex animals.

Required reading:

Marshall 2006. Explaining the Cambrian "explosion" of animals. *Annual Review of Earth and Planetary Sciences 34*: 355-384.

Smith and Harper 2013. Causes of the Cambrian explosion. *Science 341*: 1355-1356.

Class activity: **Graded student group presentations** exploring proposed causes for the Cambrian Explosion, followed by whole class discussion.

Core question: Why is the Cambrian Explosion significant for understanding the modern biosphere?

October 3, 2024

Session 5: Replay the tape of Life? Cambrian weird wonders and contingency – Discussion about the effect of contingency on evolution developed by Stephen J. Gould based on his interpretation of the Burgess Shale and the Cambrian Explosion.

Required reading:

Gould 1989. *Wonderful life: the Burgess Shale and the nature of history*. WW Norton & Company.

Class activity: **Diversity and disparity through time II** – modelling Gould's view of the Burgess Shale and evolutionary implications of "failed evolutionary experiments" during the Cambrian.

Core question: How did the Burgess Shale fossils influence our understanding of evolution?

October 10, 2024

Session 6: Precambrian ghost lineages and molecular clocks – Addresses the fossil evidence for a Precambrian origin of animals and the use of molecular clocks to estimate clade diversification in the presence of an incomplete fossil record.

Required reading:

Erwin et al. 2011. The Cambrian conundrum: early divergence and later ecological success in the early history of animals. *Science 334,* 1091-1097.

Warnock 2015. Molecular clock calibration. *Encyclopedia of scientific dating methods* 576-583.

Cunningham, J.A., Liu, A.G., Bengtson, S. and Donoghue, P.C., 2017. The origin of animals: can molecular clocks and the fossil record be reconciled?. *BioEssays 39*: 1-12.

Class activity: **Online activity** timing for the origin of metazoans (http://www.timetree.org/).

Core question: How did the Burgess Shale fossils influence our understanding of evolution?

October 17, 2024

Session 7: The Five Laws of Paleobiology: how extinction shapes biodiversity – Discusses the main processes that affect biodiversity through time, as well as the influence of extinction.

Required reading:

Marshall 2017. Five palaeobiological laws needed to understand the evolution of the living biota. *Nature Ecology & Evolution 1*: 0165.

Friedman and Sallan 2012. Five hundred million years of extinction and recovery: a Phanerozoic survey of large-scale diversity patterns in fishes. *Palaeontology 55*: 707-742.

Class activity: **Diversity and disparity through time III** – modelling the modern view and the impact of background extinction in shaping the composition of the biosphere.

Core question: How has extinction shaped biodiversity in the past and in the present day?

October 24, 2024

Session 8: Stem and crown groups: making sense of extinct problematica – Introduces the modern approach to the study of problematic fossil taxa as extinct representatives of living phyla.

Required reading:

Budd and Jensen 2000. A critical reappraisal of the fossil record of the bilaterian phyla. *Biological Reviews* 253-295.

Ortega-Hernández 2019. Exceptionally Preserved Cambrian Fossils in the Genomic Era. In *Old Questions and Young Approaches to Animal Evolution* Springer, Cham. pp. 39-54.

Class activity: **Graded student group presentations** on selected case studies that explore evolutionary links between problematic Cambrian organisms to extant biodiversity.

Core question: How do we reconcile extinct Cambrian organisms with modern biodiversity?

October 31, 2024

Session 9: The speed of evolution and the nature of change – Challenges the classical Darwinian notion of evolution as an agonizingly slow process and discusses evidence for accelerated rates of evolution at critical points in the history of life from the perspective of the fossil record.

Required reading:

Lee et al. 2013. Rates of phenotypic and genomic evolution during the Cambrian explosion. *Current Biology 23*: 1889-1895.

Paterson et al. 2019. Trilobite evolutionary rates constrain the duration of the Cambrian explosion. *Proceedings of the National Academy of Sciences 116*: 4394-4399.

Core question: How does the variable rates of evolution affect patterns of diversification through time?

November 7, 2024

Session 10: History is written by the victors – Introduces the idea of the Push of the Past, which posits that lineage longevity is largely reliant on early high rates of evolutionary change, and that extinction fundamentally models our understanding of extant biodiversity.

Required reading:

Budd and Mann 2018. History is written by the victors: the effect of the push of the past on the fossil record. *Evolution 72*: 2276-2291.

Budd and Mann 2020. Survival and selection biases in early animal evolution and a source of systematic overestimation in molecular clocks. *Interface Focus 10*: 20190110.

Hughes et al. 2013. Clades reach highest morphological disparity early in their evolution. *Proceedings of the National Academy of Sciences 110*: 13875-13879.

Class activity: Modeling the modern effects of the Push of the Past and biodiversity with Blackjack.

Core question: How do we explain variable patterns of taxonomic richness among extant biodiversity?

November 14, 2024

Session 11: Convergence and the inevitability of complexity – Discusses the ideas of convergence as a fundamental constrain that may even allow to predict evolutionary change.

Required reading:

Conway-Morris, S.C., 2006. Evolutionary convergence. *Current Biology 16*: R826-R827.

Orgogozo 2015. Replaying the tape of life in the twenty-first century. *Interface focus 5*: 20150057.

Class activity: Inescapable constraints – examples from Cambrian and modern ecosystems.

Core question: How much can we predict of the outcomes of macroevolution through convergence?

November 21, 2024

Session 12: Experimental evolution – Will utilize a recent case study on the evolution of bacterial lineages in response to antibiotics as a demonstration of patterns of early diversification, extinction and convergence.

Required reading:

Conway-Morris 2009. The predictability of evolution: glimpses into a post-Darwinian world. *Naturwissenschaften 96*: 1313-1337.

Baym et al. 2016. Spatiotemporal microbial evolution on antibiotic landscapes. *Science 353*: 1147-1151.

Blount et al. 2018. Contingency and determinism in evolution. *Science 362*: eaam5979.

Core question: What is the true nature of evolution?

Assessment – Student presentations

Instructions: Part of the final assessment will be based on two student presentations (30 to 45 minutes, depending on material) to take place throughout the course. The specifics regarding the number of speakers per topic will depend on the cohort size, and thus further details will be circulated once enrollment has finalized and prior to the corresponding sessions.

Pedagogical goal: The objective of the student presentations is to deepen into the diverse body of work on the topics covered throughout the course in greater detail than that possible within the conventional session format. Presentations should include relevant background information, explain the reasoning behind particular hypotheses discussed, and critically evaluate the body of supporting evidence. Please prepare your presentation in PowerPoint, or alternatively using the online whiteboard if you feel courageous (software details will be provided during the semester).

Assessment – Graded essays

Instructions: A significant component of the final assessment will be based on two graded essays designed around the first and second halves of the course respectively. The main text should comprise between 1,500 to 2,000 words (excluding reference list and/or figure captions). Feel free to include supporting material in the form of figures or schematic diagrams as you consider appropriate to complement the main text. The format should follow that of a manuscript for publication according to the submission guidelines for an "Insights and Perspectives" contribution to the journal *Bioessays* (see Parry et al 2018 in course reading materials as an example). Essays will be assessed based on the clarity, breadth, and depth of the content, as well as overall presentation, similarly to a work submitted for peer-review. The essays should broadly address each of the questions posited below, however, there is ample freedom to choose the best approach and/or specific subject matter for achieving this objective. The essays should be emailed to the course instructor by the due dates specified below. If you foresee any complications in fulfilling these requirements please get in touch as soon as possible.

Pedagogical goal: The objective of the essays is to give the students an opportunity to think critically and broadly about the course material, as well as develop their own informed perspective on the contributions of the animal fossil record for understanding evolution. Since there is no single correct answer to the questions posited below, the essay should demonstrate appropriate mastery over the main ideas and material discussed during the course, and evidence the ability to integrate a diverse body of work into a logical discussion.

Essay due dates:

October 17, 2024 – First essay, encompassing Sessions 1 to 6.

Q: How does the study of animal evolution in deep time inform our current understanding of the origin and composition the modern biosphere?

December 5, 2024 – Second essay, encompassing Sessions 7 to 12.

Q: Consider an idealized scale for the "predictability of evolution" ranging from 0 (evolution is purely the result of random historical contingency) to 10 (evolution is completely deterministic, even

predictable given enough information). What do you think is the current consensus among evolutionary biologists in its broadest sense? What is your own perspective on this topic?

Other formatting requirements:

- Adhere to either American or British spelling consistently
- Font Times New Roman, 12pt for main text, 14pt for headings/subheadings
- 1.5 or double spaced
- Numbered pages
- Include contact details (e.g. full name, email)
- Please limit the graphical content (if any) to a maximum of four accompanying figures.