

My fundamental research interest is the movement of vertebrate lineages in morphospace. Evolution is change over time, and an important index of change is change in shape; the shape of an animal's skeleton can give deep insights into locomotion, feeding, and other aspects of function, thereby documenting how a lineage responds to physical and biotic constraints. Access to time is the other critical component in the study of large-scale evolution, and shape has the added advantage of being recoverable on geologic time scales via the fossil record. That record is profoundly limited, however, and nowhere more so than for vertebrates. But if one is careful one can choose groups and time periods where preservation is high above the norm, and the complexity of the vertebrate skeleton yields fossils of high information content and correspondingly robust phylogeny estimates. Therefore there are instances where the large-scale evolution of vertebrate lineages over geologic time can be studied quantitatively.

My research to date has concentrated on secondarily marine tetrapods. The fossil record of these animals is superior to that of comparable terrestrial groups in both specimen number and completeness. I utilized the excellent record of nothosaurs from the Triassic deposits of Monte San Giorgio, Switzerland in an analysis of multivariate allometry, heterochrony, and speciation mode. This analysis of evolving ontogenetic trajectories demonstrated that growth is loosely integrated in this clade. My later thesis work and the publications stemming from it concerned a related group of marine tetrapods, the Plesiosauria. The fine record of this group allowed me to track the convergent evolution of ecomorphs using complimentary studies of comparative anatomy and morphometrics. Additional theoretical work also allowed the demonstration of correlation in cladistic characters related to this convergence. Extreme, stereotyped morphologies evolve repeatedly in plesiosaurs, and while these morphologies appear tightly constrained, the paths that lineages take to reach them are not. Lastly, recent work on the evolution of plesiosaur locomotion has demonstrated the powerful influence of body size constraints on locomotor morphology across the clade. The tetrapod fossil record is a powerful tool for the study of clade-level evolution over geologic time, if one selects the right group and asks the right questions.

This analysis of clade dynamics is the goal of my research, but I believe that no scientist should focus on higher-level questions to the exclusion of the pursuit of more simple questions. Basic research such as the discovery and description of new taxa is critical in developing that 'feel for the organism' that must accompany theoretical exposition. I conceptualize the study of evolution in vertebrate paleontology as a pyramid of three tiers: synthetic studies aimed at evolutionary generalization (e.g. extrinsic constraints, clade dynamics) form the apex, while intra- and intertaxon comparative studies of various kinds comprise the intermediate level (comparative anatomy and ontogeny, systematics, and morphometrics). The lowest and broadest level is single-taxon field work and description, where new morphological information is discovered and described. My present research program contains research and funding goals at each level of this pyramid.

Current Field/Descriptive Projects

I am currently engaged in several field work projects yielding fossils for primary description. My field program in the Jurassic of Wyoming, funded by the National Geographic Society, aims to find new material of an enigmatic group of plesiosaurs. Thought by some to be filter feeders, these animals are presently known only from tantalizing fragments. A preliminary museum survey in the spring of 2002, and a pilot collecting trip in 2003, demonstrated that the potential of the Jurassic Sundance Formation is high; two recent publications have summarized this early work. I mounted a full expedition to Wyoming in the summer of 2004 and found excellent

material, including a complete pelvis and associated vertebral column, associated adult and juvenile vertebrae and paddle bones, and a fragmentary braincase of enigmatic relationships. When combined with further preparation of museum specimens funded by the grant, I expect to produce major papers on two of the three known plesiosaur taxa from the Sundance Formation, as well as several smaller papers on the juvenile elements and the stratigraphic context of the finds. A follow-up expedition in the summer of 2005 was very successful, resulting in the location of articulated plesiosaur fossils and the gathering of much geological data.

A second target of primary description is the fossils gathered by the NYCOM 2003 expedition to the Permian of Niger. My area of responsibility is the description of the derived captorhinid *Moradisaurus*, a poorly known primitive reptile. We gathered significant new material of this animal, including several skulls and articulated postcrania. Preparation and description of this material is ongoing. Work on this primitive reptile also informs my work on previous Permian diapsids such as *Youngina*. Perspectives gained from sauropterygians have allowed me to interpret the morphology of these animals in a new light. Findings will have systematic implications for the evolution of later diapsids, possibly including turtles.

La Brea Database Project

My work at the second, comparative level of paleontological inference is probably the most exciting to me personally, because it will determine the direction of my research over the next five years, and is a true departure. The vast collection of Pleistocene fossils found in the Rancho La Brea tar pit deposits in California attracts me for two reasons. The first is that the sample of carnivores includes many thousands of specimens, and therefore comprises an excellent record of animals such as saber-tooth cats and dire wolves. The second is that these large population samples span a time range of 44000 to 4000 bp, and that this time period brackets the transition from the Pleistocene glacial to Holocene interglacial climate regimes. The potential for studying the impact of climate change on carnivore population phenotype has been obvious for years; however, issues concerned with taphonomy and accurate carbon dating have prevented much progress. Fortunately, recent work by Blaire Van Valkenburgh and colleagues has gone a long way to solving these problems-- accurate dating *is* possible for these samples, and taphonomic effects are manageable.

I am currently working with Van Valkenburgh on an NSF grant proposing the La Brea Database Project. The Database will contain craniometric measurements of adult dire wolves and saber-tooth cats, along with biological age, chronological age, and various taphonomic factors. The core question will be an attempt to document population-level morphometric change (or the lack thereof) across the climatic transition. Calibration of this study will be provided by a companion study of latitudinal variation in extant wolves. Findings may have implications for wildlife management responses to anthropogenic climate change. The La Brea sample is enormous, and that is the real attraction for me. The Database will be a powerful tool applicable to a range of evolutionary questions at the population level, and should result in a productive synthesis among population biology, evolution, species interaction, and climate change.

Clade Dynamics

The third level of paleontological inference-- synthetic studies-- is the most exciting and challenging type of research, but must be founded on solid morphological and comparative knowledge. My theoretical phylogenetic work resulting in a new method for detecting correlated sets of cladistic characters appeared in *Systematic Biology* in 2001. This method has proved to

be a powerful tool for the generation of functional and other models one can use to understand patterns in homoplasy. I believe that homoplasy (the convergent evolution of character states) is fascinating; repeated appearance of the same adaptations in a group of animals tells us something fundamental about the constraints governing the evolutionary process. This method may be combined with established techniques in cladistics, morphometrics, and functional inference to yield a set of questions I call 'clade dynamics'. Discerning the phylogenetic relationships of a group of animals is the first step. Determining patterned homoplasy, heterogeneous rates of character change, patterns of diversification, and other phenomena then allows insights into the intrinsic and extrinsic constraints governing that evolution. My work on plesiosaurs has hopefully illustrated this conception at the clade level; my move to the La Brea mammals will enable me to quantify the influence of extrinsic constraints on evolution at the population level. Synthetic questions such as these tie together the lower levels of paleontological study, adding meaning to descriptive and comparative research and illuminating the connections between animal and environment.