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THE INTERFACE OF PALEONTOLOGY AND MAMMALOGY: PAST, PRESENT, AND FUTURE

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For nearly a century the fields of mammalogy and paleomammalogy have complemented each other, although the relative influence of one on the other has waxed and waned. The development of new techniques, databases, and information-handling capabilities in the past decades have enhanced the potential for working at the interface between these 2 fields in ways never before possible. This portends an elevated role for mammalogy in the development of ecological and evolutionary theory and serves as a model for merging paleontological and neontological data in other disciplines.

Key words: conservation, ecology, evolution, mammalogy, paleomammalogy

After several decades of going their separate ways, the fields of mammalogy and paleontology are reuniting, with exciting results. The purpose of this special feature is to explore the reintegration of these 2 fields and highlight the promise of the merger for significant advancements in the future of modern biology.

The field of paleontology has been at the heart of mammalogy since its inception. Paleontologists such as J. Leidy, W. D. Matthew, J. C. Merriam, and H. F. Osborn were important in the early days of the American Society of Mammalogists (ASM); W. D. Matthew was one of the early presidents of the society (Layne and Hoffman 1994). The major contributions of paleomammalogists have been in the arena of form, function, and phylogeny (Zakrzewski and Lillegraven 1994). Paleontology always has been influential in defining Mammalia and its origin (e.g., Lillegraven et al. 1979; Rowe 1988; Szalay et al. 1993), in biogeographic fundamentals of distribution and abundance (e.g., Matthew 1939; Simpson 1934, 1952), in comparative anatomy (e.g., Crompton 1971; Rowe 1996; Szalay 1994; Van Valkenburgh 1985), in classification, and later, in phylogenetics (e.g., McKenna and Bell 1997; Novacek 1992; Simpson 1945), and in the study of extinction and diversification (e.g., Martin and Klein 1984; Martin and Wright 1967). Paleomammalogist G. G. Simpson, along with evolutionary biologists T. Dobzhansky, R. A. Fisher, and E. Mayr, as draftsmen of the Modern Synthesis, combined Darwinian evolutionary theory, genetics, and paleontology. Mammals provided key examples important for this neo-Darwinian revolution (Simpson 1944).

Paleontology has declined considerably in its influence and inclusion in the field of mammalogy in the past 50 years, judging by the numbers of papers presented at ASM meetings and articles emphasizing paleontological perspectives in the *Journal of Mammalogy* (Gill and Wozencraft 1994). Although its role in mammalogy has diminished, paleontology as a discipline has matured considerably in the past several decades (e.g., Hall 2002). Paleontologists are globally active in geographic areas only cursorily investigated before (e.g., Antarctica, Mongolia, Patagonia, Uzbekistan, Pakistan, Myanmar, China), and the reward has been a collection of riches such as extraordinarily preserved early mammals (e.g., Ar-

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chibald et al. 2001; Dashzeveg et al. 1995; Flynn et al. 2002), elucidation of paleocommunity diversity patterns (e.g., Barnosky, in press; Barry et al. 2002; Flynn et al. 1995), and ''missing-link'' fossils of mammals such as early whales (Gatesy and O'Leary 2001; Gingerich et al. 2001; Thewissen et al. 2001) and early primates (Gebo et al. 2000, Tavaré et al. 2002). Techniques for fossil excavation and preparation have revolutionized numbers and size ranges of specimens, and computerized tomography scans have enabled investigations of morphology heretofore unimagined (Rowe 1996; Rowe et al. 1997). Cladistic methods, which have introduced scientific rigor to systematics, have resulted in many provocative hypotheses about mammalian relationships that are being tested with molecular and fossil data (Novacek 2001). These methods have been used recently to address the timing of the origins of Mammalia and clades within eutherian mammals through a dialog between neontologists and paleontologists (e.g., Murphy et al. 2001; Springer and de Jong 2001). Community ecology has been influenced profoundly by the work of mammalian paleontologists intent on discerning coherence of species assemblages and their interactions through time (e.g., Graham 1997; Graham and Grimm 1990; Guilday and Hamilton 1978; Hadly and Maurer 2001; Owen et al. 2000).

Indeed, such studies have helped to define and bring focus to questions that are of intense interest in modern biology. For example, is the concept of a niche valid? Do communities evolve? How stable are communities? How do immigration, speciation, and extinction influence ecosystem function? Are abiotic or biotic factors more important drivers of evolution? Why are there apparent differences in relative rates of evolution between molecules and morphology? Does evolution proceed gradually or in fits and starts? Which evolutionary mechanisms underlie diversification events?

The 7 articles presented in this special feature address some of these questions and highlight a few of the new and exciting avenues of research that mammalian paleontologists are following. Disciplines covered by the contributions include evolution (genetic, population, species, and higher taxonomic levels), ecology (predator–prey interactions, behavior, community ecology, macroecology), and technical breakthroughs (ancient DNA, calibration of molecular clocks, quantification of geographic ranges, taxonomy). All the articles demonstrate the advancement to biology made by the integration of neontology and paleontology. The importance of this linkage was emphasized in the early history of paleontology and mammalogy (e.g., Matthew 1925; Romer 1969).

In the 1st article, Barnosky et al. (2003) address the questions: how out-of-the-ordinary is the current global warming episode, and how does rate and severity of climate change actually influence evolution? These questions have gained importance because of the current global-warming crisis. By querying the fossil record specifically about organismal response to warming, they ask whether abiotic or biotic drivers influence evolutionary processes more strongly. The investigation of the evidence of mammalian response to warming across incrementally larger temporal scales emphasizes the importance of scale on evolutionary and ecological response of mammals. Barnosky et al. (2003) used an intuitively obvious, but little recognized, analysis of the influence of temporal scale on degree of warming to make several points. They demonstrated that the predicted amount of temperature change in the near future (whether using conservative temperature change scenarios or not) is in fact far above the background rate of temperature change that characterized the last 60 million years. Even so, based on response to past warming, mammalian response to warming in the future, such as changes in community diversity and population and phenotypic change, is predictable in some ways; however, because the degree of future warming is so far outside previous warming intervals, there may be unexpected organismal responses. Unanswered questions stimulated by this article about the timing of climatic change and the spatial scale of the mammalian response are exciting avenues for future research.

The 2nd feature article by Polly (2003) applies phylogeographic techniques to morphological analyses of spatially and temporally discrete fossil and modern populations to ask: how is differentiation within species partitioned in time and across space? He uses an innovative approach to match morphological analyses to those produced by molecular data by computing morphological divergence through time, which allows a novel comparison with molecular divergence of cytochrome *b* (Steppan et al. 1999). Conclusions from this study suggest that morphological evolution through several glacial–interglacial cycles is greater for some species than for others. An assessment of present geographic portioning of variation suggests that species evolving at a faster tempo are more phylogeographically concordant than those evolving over a longer time. These results have valuable implications for understanding the mode of speciation and suggest that some species may have initiated and experienced their evolutionary histories in different geographic locations than they occupy today. This conclusion has obvious implications for the study of phylogeography (Avise 2000).

In the 3rd feature article, Lyons (2003) uses the FAUNMAP database of mammalian Quaternary fossil localities (Graham et al. 1996) to study volatility of mammalian geographic ranges through time. Her quantitative analysis is the 1st of its kind to address the sum of mammalian geographic range adjustments in North America. Her conclusions focus on fundamental issues at the heart of ecology: individualistic species response to climatic change and no-analog assemblages (Graham 1997). This issue underlies ecological discussion about Gleasonian versus Hutchinsonian niche space and effects on community assembly. Lyons (2003) effectively demonstrates that mammals in fact maintain community associations over long periods of time. Mammalian geographic ranges showed variation in the past, but many time periods witness few range adjustments, and many species respond in similar directions and distances. This results in little assembly change throughout the Quaternary, a conclusion also drawn by Alroy (1999), with a very different analysis.

Use of ancient DNA for assessing population and species dynamics over time is an exciting new technique that allows investigation of actual genetic evolution through time. This technique, although presenting many methodological challenges, holds promise for situations where species are morphologically cryptic and as a direct comparison between rates and magnitudes of morphological and genetic evolution. In the 4th article, Hadly et al. (2003) use this technique to examine whether environmental perturbation influences genetic variation of a geographically restricted endemic rodent (*Ctenomys sociabilis*). Contrary to the expectation that human and climatic disturbances in northern Patagonia have affected this species, there is no evidence that the reduction in population size occurred during the last 1,000 years. Instead, the species has persisted with low levels of genetic variation throughout that time. These results suggest that ancient DNA can be used in novel ways to address issues at the heart of conservation biology and population genetics by examining effective population size over time.

The 5th article in this special feature is by Steele (2003) and presents methods for interpretation of predator behavior from the fossil record. She compares human-collected red deer (*Cervus elaphus*) fossils throughout the Pleistocene of Europe with a wolf (*Canis lupus*)–kill collection of elk (*C. elaphus*) bones from Yellowstone National Park. The article tests the prediction that early European humans, with more limited hunting toolkits, acted more like other carnivorans than do modern *Homo sapiens*. Steele (2003) rejects this hypothesis by a thorough analysis of mortality profiles of red deer in the fossil assemblages. Her analyses provide guidelines for future work of this type and hold promise for use of modern and fossil comparisons to interpret behavior in the fossil record.

Information that can be extracted from large databases is exemplified in the 6th article by Alroy (2003). He uses a large mammalian paleontological database that he compiled to assess the per-year, per-taxonomist rate of species name validity. This technique allows for the quantification of ‘‘lumping’’ versus ‘‘splitting’’ as a function of mammalian body size. Alroy’s (2003) assessment of taxonomic error provides a stimulus to the study of the evolution of mammalian body size and is provocative particularly with regard to diversification rates of different mammalian clades. Indeed, the article by Alroy (2003) is a call for similar analyses on extant mammals and is a valid rationalization for prioritizing the studies of taxonomy and systematics.

The last article by Conroy and van Tuinen (2003) presents a standardized approach to the calibration of molecular clocks with fossil data. The article emphasizes the interplay of molecular and fossil data and provides a paradigm for this approach to mammalogists. It is perhaps with mammals that our best opportunities lie because of the comparatively excellent quality of the mammalian fossil record, the amount of molecular phylogenetic resolution that has been accomplished already, and the recency of the mammalian radiations.

These contributions to the integration of neontology and paleontology are but a hint of the future. Additional examples of how the 2 disciplines are uniting include evolutionary development (‘‘evo-devo’’), population biology, macroecology, and contributions to understanding the global impact of humans. Further synthesis in the field of evolutionary development has the potential to advance our understanding of the evolutionary innovations of mammals and other organisms (Carroll 2000). New developmental techniques (e.g., Hall 2002; Jernvall et al. 2000; Sanchez-Villagra et al. 2002) are yielding evolutionary hypotheses that can only be tested with data from the fossil record. For example, Boyce and Knoll (2002) used a phylogenetic perspective to test the development and independent origin of venation patterns in several clades of plants by using both developmental biology and paleontology. The melding of these disciplines holds great potential to refine our understanding of the tempo and modes of organismal evolution, and mammals provide an ideal model system.

From the perspective of population biology, the interplay of morphologic plasticity, population genetics, and environmental perturbation is an area of research that is underdeveloped but holds great promise in discovering how the processes of speciation and extinction actually work. Examples of work that is underway in this regard include studies of population variation that are being used to address evolutionary constraints and plasticity in morphologic variation over long periods of time (e.g., Dayan et al. 2002; Hadly 1997; Smith et al. 1995). Data sets characterized by large samples with broad temporal and geographic coverage have only recently made such work possible. With new advances in the field of ancient DNA, a temporal genetic component can now be added that should make it possible to better understand the phenotype–genotype response of species to the environment over thousands of years (Hadly et al. 1998; Leonard et al. 2000; Pääbo 2000). The Quaternary, with its excellent fossil record of extant mammals and known climatic changes, perhaps holds the most promise for population studies of this type.

In ecology and environmental studies, a sense of urgency has been imparted to the study of fossils by conservationists anxious to understand the demise of present global ecosystems (e.g., Vitousek et al. 1997), define ‘‘native’’ species (e.g., Jackson 2001), ascertain the influence of climate on evolution (e.g. McLaughlin et al. 2002), help describe the bounds to resilience of communities in the face of environmental change (Roy et al. 2002), and impart knowledge about the impact of humans on extinction of species (e.g., Steadman 1995). Already, evidence is mounting that organisms are responding to global warming (Post and Forchhammer 2002; Root et al. 2003). A look at the past is essential to ascertain whether these responses are anomalous.

These issues suggest that students of mammalogy today live in exciting times with challenging issues on the horizon. The examples in this special feature and considerations noted above highlight that key responses to these challenges will come from working at the interface between mammalogy and paleomammalogy. It has long been recognized that fundamental breakthroughs in evolutionary and ecological issues can best be explored with a firm grasp of all that history can offer. New technologies and information-processing abilities that recently have become available make it possible to merge the historical and neontological in ways that early founders of mammalogy could have only imagined. Active pursuit of the merger will be decisive for deciphering critical questions about dynamics of populations, species, and communities. Working at the paleontological–neontological interface has come of age in mammalogy and, more than ever before, has a major role to play in the future of modern biology.

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