MEASUREMENT, SCALE, AND PREDICTION: CAVEAT EMPTOR

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Confuting Darwinism’s Enemies—and False Friends Too


Referring to the aura of mystery surrounding the ancient Etruscans and their supposedly indecipherable language, D. H. Lawrence once wrote, “I don’t think there is any other field of human knowledge in which there is such a daft cleavage between what has been scientifically ascertained and the unshakeable beliefs of the public” (quoted in Robert Hughes, Things I Didn’t Know: A Memoir [New York: Knopf, 2006], p. 246). Lawrence must not have known about evolutionary biology—or was unaware of the gap between his own daft view of it and what had been scientifically ascertained even in his day.

I mention this because it gives a feel for the situation to which Michael Ruse addresses himself in Darwinism and Its Discontents. In part because he has been more willing than most biologists and philosophers of biology to engage in the rough-and-tumble of public debate, Ruse has been an effective advocate for Darwinism. The present book follows on the heels of Ruse’s The Evolution–Creation Struggle (Cambridge, MA: Harvard University Press, 2005). It thus reflects his keen awareness that, although they have lost every court case since they began their most recent crusade to get Darwinism out of the schools, creationists and their kissing cousins in the intelligent design (ID) movement (who take Darwinism’s opposite number to be Paley’s design, who take Darwinism’s opposite number to be Paley’s design) have nonetheless managed to throw so much sand in the eyes of the general public that many people actually think that evolution—specifically, the common descent of all organisms from a common ancestor—is still in dispute. Worse, the public has been led to believe that the factuality of evolution is hostage to Darwin’s theory of natural selection as its cause, and therefore that the mere existence of controversies among Darwinians throws doubt on the phenomenon of evolution itself. Commendably, Ruse’s aim in this book is to wise up the public.

Ruse’s strategy is to update Darwin’s own argument. With respect to evolution itself, Darwin cited converging facts from a variety of different sciences—embryology, biogeography, classification, and so forth—and inferred that evolution is their best explanation. (This is a proof procedure that William Whewell, whom Ruse somewhat controversially takes to be Darwin’s primary methodological mentor, called “consilience.”) Ruse points out that evolution (a “theory” only in the nontechnical sense in which any factual conclusion drawn from reasoning rather than direct observation alone is a theory) remains the best explanation of the fact that “missing links” have been popping up regularly since Darwin’s day, with no countervailing finds; that phylogenies first established by traditional systematic methods have been corroborated, except for details, by phylogenetic systematics; and that recently these phylogenies have been shown to be beautifully consilient with molecular sequencing data coming from a flood of genome sequencing projects.

Ruse’s account of natural selection follows suit. Selection is the best explanation of evolution. Selection has been confirmed in the lab and, with increasing success and sophistication, in the wild. In the second connection, Ruse cites the well-known work of Peter and Rosemary Grant on Darwin’s finches. Is there empirical evidence for speciation, too? Ruse cites apple maggot flies, which parasitize both apple trees and hawthorns. Although capable of interbreeding, the sexual unattractiveness of these subpopulations to each other suggests a speciation event in the making.

Ruse’s portrait of Darwinism as a continuous, cumulative, progressive research tradition set on the correct path by its ingenious founder is a good part of the persuasive strategy of the book. After all, we do like our science to be cumulative. The very idea that it might not be is what bothers people about Thomas Kuhn’s paradigms. But this strategy also commits Ruse to (or perhaps springs from) a substantive claim according to which the main line of Darwinism always has been, and presumably always will be, one in which the targets and beneficiaries of adaptive natural selection are individual organisms considered as members of discrete interbreeding populations. The discovery of genes, Ruse assures us, did not affect this continuity. “The genes (genotype),” he declares, “and the physical features (phenotype)...are not rivals” (p. 108). Accordingly, Ruse thinks that group-level selection either is rare or turns out to be individual selection after all. So much for groups, above the level of the individual. What about genes below? Ruse’s assurance of preestablished harmony between genes and adapted traits implies that “selfish gene theory” is just another way of formulating organism-centered Darwinism, perhaps more useful on some problems than others. This is controversial, and I would have welcomed some discussion.

Ruse’s claim about the continuity of the organism-centered Darwinian main line may well be historically and theoretically defensible. It is far from self-evident, however, if only because Ruse burdens it with a more contentious line of argument. He claims that self-proclaimed Darwinians who depart from the main line are not Darwinian at all, but constitute a fifth column of false friends whose ill-disguised “visceral hatred” of Darwinism gives aid and comfort to the creationist enemy and might even spring from psychological disorders. The context indicates that Ruse has at least partially in mind the late Stephen Jay Gould and the distinguished population geneticist Richard Lewontin. Their famous criticism of “the adaptationist program” sprang, Ruse implies, from a prior commitment to Marxism that trumped their
supposed Darwinism. For Ruse, the cure for bad adaptationist arguments is good ones, not confessions of failure invoking phylogenetic constraints, hopeful monsters, or species selection.

If I were a creationist or ID enthusiast, I would take comfort from the heresy-hunting and ad hominem quality of this dismissal. To me, these arguments sound more like politics than science or philosophy. But I must confess that I am a bit sensitive about the issue. At one point in Ruse’s book, I myself am excommunicated. In *Darwinism Evolving: Systems Dynamics and the Genealogy of Natural Selection* (Cambridge, MA: MIT Press, 1994), Bruce Weber and I never claimed that Darwinism needs to be “augmented” by nonlinear dynamics, as Ruse reports. We suggested only that the mathematical models used by Darwinian research programs associated with the modern evolutionary synthesis do. Our remark can be interpreted Ruse’s way only if any departure from the main line is called “non-Darwinian,” the point at issue. Darwinism’s history itself suggests that sometimes departures from the main line are actually causes of its ultimate continuity. Ruse himself reports that by using Sewell Wright’s “not very Darwinian” theory of genetic drift, Mayr’s hypothesis of allopatric speciation unified selection and isolation—and did so by discounting Darwin’s own commitment to sympatric speciation. Other, similar stories suggest that if the hypotheses and conjectures of evolutionists hug the shore as closely as Ruse seems to recommend, Darwinism even of his preferred sort might be badly served—especially now that a revolution in developmental genetics is putting pressure on existing models of gene–environment interaction, a topic Ruse does not discuss.

A difficult issue looms here. Is it better to admit the contentiousness of the Darwinian tradition, thereby giving scandal to people who want their science smoothly cumulative, or to exploit the public’s assumptions by portraying Darwinism as always piously conforming to conventional notions of what science must be like? The choice is especially vexed because—as Ruse acknowledges in his critique of Karl Popper’s doubts about whether Darwinism is science at all—evolutionary science is more focused on particular cases than, say, physics. Physics-envying evolutionists like R. A. Fisher have tried to portray the mathematicization of selection as a step toward the discovery of universal laws. It is more likely, however, that mathematical modeling serves evolutionary biologists as an increasingly powerful toolkit for finding the best explanation of particular cases—and is “good quality science” for all that. Nonetheless, physics-oriented scientists and philosophers will always worry about this difference, and creationists will always exploit their worries by exaggerating to nontechnical audiences the significance of controversies among evolutionists, making too much of rare cases of fraud, and proclaiming in consequence that it is metaphysical materialism rather than science that holds Darwinism together.

This unedifying argumentative dynamic is especially important now that
Darwinian naturalism is steadily encroaching on the territory of the human sciences, including psychology. In the last third of his book, Ruse draws attention to the possibility—for him a strong probability—that our reasoning powers (or rather their endemic defects) and our ethical norms “have the pragmatic origin of having proven themselves in the struggle for existence.” I resonate with Ruse’s argument that these encroachments are sufficiently powerful to undermine the indifference to the consequences of Darwinism (as well as the misunderstanding that for him divine design remains a plausible alternative. Ruse’s rejection of Plantinga’s hyperbolic standard of reasoning is of practical, as well as theoretical, importance. ID adherents have used the same tactic as opponents of global warming, stem cell research, and other bêtes noires of the right: Exploit the public’s high regard for the validity of science by setting the bar for what will count as good science so high that even the best actual science must fail to meet it. Whether knowingly or not, Plantinga gives these folks undeserved cover.

Ruse acknowledges that Darwinism and religious belief are not logically inconsistent and that, this being so, Darwinism has no a priori commitment to philosophical materialism. To be sure, by any reasonable standard of proof, Darwin did “undermine the argument from design” and with it “all of natural theology.”

Ruse’s reply to Plantinga is all the more effective because Ruse acknowledges that Darwinism and religious belief are not logically inconsistent and that, this being so, Darwinism has no a priori commitment to philosophical materialism. To be sure, by any reasonable standard of proof, Darwin did “undermine the argument from design” and with it “all of natural theology.” So distancing religious belief from natural theology is especially important in light of Richard (“Selfish Gene”) Dawkins’s claim in a highly publicized trade book (The God Delusion [New York: Houghton, 2006]) that the invalidity of the argument from design turns Darwinism into a defense of atheism. In the final chapter, Ruse opposes this argument: Religious belief and practice have very little to do with the argument from design, and Darwinism has little to say about the many religious beliefs and practices that are not predicated on strict Biblical literalism.

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TO WHOM AM I SPEAKING?

Animal Communication Networks.

Sometimes, when we want to be careful about our communication or we are not sure who is listening, we adopt a formal tone and say something like, “To whom am I speaking?” This can be a humorous inquiry when we know very well who is listening and we do not have to be careful. Or it can be a serious question when, as observers, we are not sure who is being addressed. An animal communication network approach, as outlined by Peter McGregor in his previous writings and now in his excellent book Animal Communication Networks, asks us to reconsider to whom animals are speaking when they signal. Are they being careful in ways we have not previously considered? Are they addressing a number of different recipients in ways we have not understood? What are the implications of these, and other, considerations for the study of signaling strategies?

For years, researchers in the field of animal communication have focused primarily on the dyad of sender and receiver. Although they were aware that communication events were actually more complex, it was often necessary to first demonstrate more straightforward aspects of these events to provide a strong basis for further study. The dyad was also often the easiest and quickest aspect that could be analyzed—especially before the development of such things as handheld electronic event recorders, compact digital audio and video equipment, and computers with statistical packages.

In this book, Peter McGregor shows us that it is difficult to build a strong basis for understanding communication if one looks only at dyads, and that the time has come to build on the dyad information base. He offers a network approach as a logical next step in a maturing field. It seems we live in an age of networks—brain networks, genetic networks, and,
now, communication networks. McGregor is a pioneer in this area. This book is a wonderful introduction to the ideas in the field of animal communication networks and to the steadily growing set of data that seem to support them, building on the foundational studies of animal communication.

McGregor is currently a reader in applied zoology at Cornwall College, United Kingdom, and has also been a Marie Curie Fellow at Cornwall College; a professor of behavioral biology in, and head of, the Department of Animal Behaviour at the University of Copenhagen, Denmark; and a special professor at the Institute of Applied Psychology in Lisbon, Portugal. He is the editor of Bioacoustics. His own research focuses on social behavior and communication in birds, fish, and fiddler crabs, and on the implications of communication studies for conservation issues. His previous work about communication networks is perhaps best known from publications with two collaborators, Tom M. Peake (McGregor and Peake 2000) and Torben Dabelsteen (McGregor and Dabelsteen 1996). This book is an important next step in bringing the concepts from this earlier work to a larger audience.

The volume provides an excellent outline of the concepts the editor and his close collaborators would like researchers to consider. (McGregor wrote the preface and general introduction; Peake and Dabelsteen wrote the first two chapters.) There are carefully crafted definitions, clear statements of what is being considered and what is not, and a wonderful collection of examples and thoughtful comments by all three of these scientists. But McGregor is not simply attempting to push his own idea with this volume. He is more interested in having colleagues clearly see the concepts and decide if and how they might be of value to them in their studies. As he states in his excellent introduction to the first section of the book, “A network perspective will become more commonly adopted only if it is clearly better able to explain communication behaviours than a dyadic approach” (p. 9).

This editorial approach makes the collection unusual, in that it approaches the reader with an open mind. Although the focus of the book is on explaining and refining the communication network approach, McGregor included researchers who do not profess to be using this approach, and he asked them to consider whether it would add to their understanding in a meaningful way. This makes for especially interesting reading; it is not often that contributors to a collection are allowed, and even encouraged, to question the very focus they were asked to discuss. This openness, and the inclusion of researchers from a broad spectrum of approaches and considerations (in lab and field, studying invertebrates through vertebrates, using a variety of techniques in both terrestrial and aquatic habitats), makes it easy for researchers who have not thought about the network approach to see whether or not it would be helpful for them to do so. In short, there is something here for everyone, information that almost any researcher can relate to. The last section of the book even includes unusual perspectives, such as the implications of networks for using modeling approaches (chapter 26, by Andrew M. R. Terry and Robert Lachlan).

McGregor defines a communication network most simply as “groupings of several individuals that constitute the social context in which communication takes place.” He points out that “communication is inherently social, but the wider social context in which communication takes place is rarely considered explicitly,” and that “if a signal travels further than the average spacing between individuals, then there is potential for a communication network to exist, so it could be considered the commonest context in which communication occurs.” I would have liked to have seen more credit given to W. J. Smith (1977) for stressing the importance of context as a major player in any communication event; however, it is good to see someone seriously address the issue once again.

McGregor includes the concepts of eavesdropping and audience effects as important aspects of network communication; however, the various chapter authors provide many other ideas and considerations of what should and should not be included in this perspective. They point out alternative explanations, problems, and assumptions and often outline further testing that might help resolve issues.

I found this book exciting, thought-provoking, and an important contribution. Every chapter was strong. This was helped in large part by several technical requirements imposed by the editor:

- The 26 chapters were divided into four sections so that chapters within each section clearly related to one another.
- McGregor wrote clear, concise introductions to each of those sections; these alone provide an excellent introduction to the concepts, questions, and problems discussed in each section and could be read separately for a quick but excellent overview of the important aspects of the book.
- There was an excellent organizational structure imposed on each chapter: an introduction that sets the stage and explains how the chapter authors feel it relates to the focus of the book, followed by details of each author’s own and related research, a summary, and suggestions for future research. This organization allows each set of authors to place the concepts in their own context, define and redefine terms to fit their own research, raise questions, elucidate new problems, and outline future directions. The chapter introductions, in particular, are often extremely insightful about the issues raised when considering a network approach for a particular research area.
- The editor also asked authors to comment on each other’s chapters and incorporate comments and cross-references into their own chapters, making for a much more cohesive book than most edited volumes.
There are a number of other strengths as well. Animal Communication Networks is a great resource for those seeking a good basic review of information about a specific taxon, technique, or communication situation (e.g., dawn chorusing in birds). Many chapters also provide excellent reviews of important concepts in a particular research area. For example, Karen E. McComb and David Reby (chapter 17) give a concise review of sound generation in terrestrial animals; Vincent M. Janik (chapter 18) provides a similar review of aquatic communication, including a compelling explanation for why dyadic signaling was studied first; and Irene M. Pepperberg (chapter 24) offers a clear restatement of the “cognitive question” in communication. The volume also includes several chapters on human communication, bringing our own species back into the fold of communication studies (rather than leaving it to linguistics or studies of consciousness), and it is exciting to see how a network approach might provide insights into our own behavior. But perhaps most important, each set of authors pulls together diverse literature from their field and considers it in new and interesting ways. The insights gained are at least thought-provoking, and when the new perspective seems to enhance our understanding, as in nestling begging (chapter 9, by Andrew G. Horn and Marty L. Leonard), they are inspiring.

I urge all communication researchers to read this book. It is clear and accessible, allowing readers to see how this perspective might or might not apply to behaviors both seemingly already understood and currently mysterious. As I read it, I found myself rethinking and reevaluating my own studies. To whom are prairie dogs, monkeys, and domestic cats “speaking” when they use tail signals in social groups, where the signal is visible to many individuals and where individuals are often simultaneously signaling and receiving? A communication network approach may offer the best perspective on these questions, and I am already thinking of new observations and experiments that could be attempted.

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BIOLOGICAL COLLECTIONS: THE BASIS OF EVOLUTIONARY THEORY


Robert Kohler says he wrote All Creatures: Naturalists, Collectors, and Biodiversity, 1850–1950 to answer the question, “Hundreds of expeditions launched to every corner of the world: millions of specimens assembled and lovingly preserved—what made that happen?” In typical historian fashion, Kohler documents his answer to that question with 776 endnotes—a gold mine of information for anyone wanting to explore further. He writes an excessively long (90-page) introduction before he ever gets to the major collecting expeditions, discussing patterns of land use and recreation across the United States (which is important for documenting his idea that hunting, fishing, and camping were the ancestral requirements for large-scale collecting). Kohler also provides an excellent discussion of how Americans’ view of nature evolved over 100 years, noting that amateur collections of birds’ eggs and other biological specimens turned out to be valuable additions to the collections of major museums. Kohler’s skillful writing helped sustain my interest through the parts of his discussion that I thought were quite outside the main themes of the book.

The title All Creatures is an exaggeration—the book refers only to creatures with fur or feathers, and only to collections within the United States. Insects get very short shrift, and slugs, snails, worms, and other invertebrates none at all. Kohler has a few comments on botanical collections, and I hope he writes another book on exploring the world for plants. He generally stays within the subtitle’s 1850–1950 boundaries, but he does mention DNA at the end of the volume, and understandably so: Data and methods developed from 1950 to date have totally revised our concepts of how to classify collections, especially insect collections.

Chapter 3, “Patrons,” describes how important the millionaires were in supporting grand expeditions in the late 19th and early 20th centuries, with their small armies of men ready to kill every bird and animal in their gun sights. Although Kohler says the records are complete, he avoids telling us how many thousands of animals were killed in the cause of obtaining specimens for museums. The mass slaughter would be prohibited today by law and, perhaps more important, condemned by public sentiment for conservation. Kohler does not indicate whether there is any evidence that the scientists who were complicit in the slaughter contributed to the extinction of any species. Patrons were essential for obtaining the big game animals and an entire family group of elephants for the American Museum. We are fortunate that these collections were made then, and they are still enchanting millions of visitors. It would be virtually impossible to construct such multimillion-dollar dioramas today.
The next big challenge I see for museums is to make dioramas of insects that truly show their incredibly detailed morphology. The simplistic ones at the American Museum and the Field Museum show only caricatures of insects, lacking all their wondrous detail. I am waiting for an exhibit based on scanning electron microscopes that will show insects as they really are. The current crop of nature videos appears to be attempting to make all Americans hate and fear insects. Kohler claims that “tiny insects and invertebrates lack the human appeal” that led to dioramas and collecting expeditions, but that is the fault of our education, not the fault of the insects, which are much more spectacular than most birds. People cannot relate to creatures they can hardly see. Correct scientific depictions of insects could help recruit the army of new taxonomists needed to tackle the millions of incredible insects in the rainforests.

The illustrations in All Creatures are mostly photographs of people who did the collecting. I was disappointed that there were no illustrations of the field data sheets used to record information, and no photographs of the equipment used during the expeditions. There are few good photographs of people actually working, although there is a wonderful shot of Francis Sumner with his half-car, half-truck, taken in 1920 in the Panamint Mountains of California. In spite of “accurate” records, in one photograph the burro “Pardo” is identified but the collector is only “possibly” J. H. Barry, collecting for the American Museum in Mexico. Another unknown collector is shown with more than 60 skins drying in the Mexican sun in 1904. It is clear that the all-important specimens are well labeled, but the photographs of people are not. Of the four men examining the Rothschild bird collection being unpacked in February 1935 at the American Museum, only Ernst Mayr is identified.

Few women are shown, not even Annie Alexander, one of the founders and a patron of the Museum of Vertebrate Zoology at Berkeley. There is a wonderful shot of Edith Clements repairing the field vehicle while the men are off collecting, however. Women played a small but important role in many of the early expeditions, in striking contrast to circumstances today, when women make up about half of field researchers and collectors.

I am much impressed with Kohler’s knowledge and appreciation of taxonomists and how they work. As he points out, taxonomy has been a second-class biological occupation, usually dismissed as unimportant and second-rate by experimental biologists. I am an ecologist–behaviorist who has been forced to do taxonomy on flies and mites because I could find no one to study my collections. My brief exposure to taxonomy convinced me that it is amazingly difficult. Even big animals such as giraffes are still causing taxonomic dispute. I applauded Kohler for his sympathy for the taxonomists, who do not often get much credit.

Although All Creatures supposedly ends at 1950, it mentions E. O. Wilson’s 1980 plea for a complete inventory of world species. Kohler questions why we “spend billions exploring extraplanetary space but balk at the cost of exploring our own earthly environment.” I think this is another manifestation of how the military-industrial complex rules our world. The world for the taxonomist is not likely to change until insects become weapons of mass destruction.

Taxonomists who feel depressed about their lack of recognition should read this book. Experimental biologists who believe in the superiority of their own approach should also read it to learn that the whole field of evolutionary biology is supported at the roots by the taxonomists.

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The 18 chapters of this book are arranged into three sections. The first section reviews concepts and defines terms. Chapters 1 and 2, by Wu and Li, are well-constructed overviews with clear expositions of issues concerning extrapolation across scale. Those unfamiliar with this subject will appreciate these chapters and the perspective they provide. The third chapter, also by Li and Wu, reviews the history and methods employed in the analysis of uncertainties of model predictions. There has been a recent resurgence of interest in uncertainty analysis, making this review timely and useful. Because complex systems often have many variables with high uncertainties, this chapter leaves the reader with the pessimistic view that reliable predictions may be beyond current capabilities. In fact, a central point of earlier work revolved around the fact that only a few variables are usually responsible for most of the uncertainties associated with predictions. The importance of this result is that it focuses future studies on measuring specific processes that will most increase our confidence in predictions. This feedback between prediction and measurement should be an organic component of all ecological studies.

The remaining chapters of this section provide a diverse set of approaches to scale-dependent analysis and prediction. The discussion of multilevel statistical models by Richard A. Berk and Jan de Leeuw provides access to these methods for the ecological community; the contrasting requirements of nonspatial, spatially implicit, and spatially explicit methods, reviewed by Debra P. C. Peters and colleagues, are fundamental to the problems of spatial prediction; and the discussion of landscape prediction by Carol A. Wessman and C. Ann Bateson succinctly summarizes all spatial extrapolations by stating that “heterogeneity and non-linearity are the two factors determining the magnitude of scaling errors and bias.”

The second section of the book presents a series of case studies. As in most edited volumes, there is much of interest here, but it is difficult to extract governing principles or unifying themes that will resolve the problems of measurement, scale, and prediction. There are four chapters on nutrient dynamics, each with different scale-dependent perspectives; two chapters on avian habitat issues; two chapters on landscape analysis; and a single chapter on policy issues associated with water quality. Undoubtedly the reader will find these examples interesting, but will be forced to parse and select among the different approaches. Because the stated goal of this volume was to “provide a synthesis useful for management, planning and decision making,” it would have been helpful to provide at the start of each chapter a bulleted list of topics considered, methods employed, and principles explained. A nice overall chapter outline is provided late in the text (table 18.1, p. 332), but this summary is limited to an indexed list of keywords that does not exhaustively cover the concepts and applications essential for planning and management.

The final section comprises a single synthesis chapter written by the four editors. This chapter emphasizes the importance of scale and uncertainty for prediction. Although most of the discussion consists of caveats and warnings, a systematic and pluralistic philosophy is outlined. The final conclusions provide a useful summary, echoing observations found early in the text:

In general, only when the scales of observation and analysis are properly chosen, may the characteristic scale of the phenomenon of interest be detected correctly; only when the scales of experiments and models are appropriate, may the results of experiments and models be relevant; only when the scale of implementation of policies is commensurate with the intrinsic scale of the problem under consideration, may the policies be effective. (p. 7)

Scaling and Uncertainty Analysis in Ecology is an expensive book to add to a personal library—the cloth edition costs more than $100, and the paperback about $50. Nevertheless, it may be a wise purchase for those seeking a coherent introduction to the issues of scale, measurement, and prediction. I am pleased to have a copy on my shelf, and I plan on referring to it often for its exposition of concepts and for the diversity of examples presented.

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ONE STEP AT A TIME


Amniote Paleobiology: Perspectives on the Evolution of Mammals, Birds, and Reptiles is a Festschrift honoring Jim Hopson, recently retired from his long-time post as a vertebrate paleontologist at Chicago University. From both the introductory remarks by the editors and the final chapter eulogizing Jim, it is clear that he has inspired great affection and intellectual respect among his students and collaborators, 24 of whom have contributed to the volume. In these days of
intense pressure to acquire research grants, and competition to publish in the most prestigious journals, it is refreshing to have such a reminder of the overarching value of teaching. Much university research is frankly more of an enjoyable personal indulgence than a direct means of significantly addressing the needs of society. But using one’s active research as an integral part of the process of teaching students how to explore problems, handle information, think about complex issues, and develop habits of intellectual rigor seems to me the most important, if underrated, aspect of the work of a university academic. How many more of Jim Hopson’s former students no longer work on fossil vertebrates, but are nevertheless all the better equipped by his example for pursuing whatever other career they chose?

Sandwiched between the first and last chapters lies a collection of 13 specialist papers. It has to be said that the publisher’s blurb verges on the disingenuous by seeming to imply that the book is a far more comprehensive study of fossil amniotes than it is. In fact, like Festschriften in general, it is akin to an issue of an academic journal in the subject, and it will be of direct value only to those who might subscribe to such an organ. To be precise, lest a purchaser be disappointed by the highly selective nature of the contents, there are four papers on mammal-like reptiles, four on mammals, three on dinosaurs, one on plesiosaurs, and one on the early Carboniferous *Watcheria*, a basal tetrapod (which was indulgently allowed into an amniote volume).

Of these papers, let me turn at once to the area over which the recipient of the Festschrift and I most overlap, the “non-mammaliaform synapsids,” as we are supposed to call the mammal-like reptiles of old. This is the extraordinary range of animal fossils that combine ever fewer primitive, reptilian characters with ever more mammalian ones, offering what is by far the best paleontological window onto how a new higher taxon arises. In chapter 5, Hans-Dieter Sues and Farish A. Jenkins Jr. provide a welcome description of the postcranial skeleton of the tritylodontid *Kayentatherium*, an event we have been awaiting for two or three decades. The tritylodontids are the most contentious of all the synapsid groups, illustrating as effectively as any taxon the problem of inferring phylogenetic relationships from fossil material. On the one hand, they have a number of mammalian characters, such as loss of the postorbital bar. On the other, they have characters of the highly specialized, herbivorous diademodontoid cynodonts, such as enlarged, multicusp postcanine teeth, suggesting that this group is not closely related to the lineage that led to the mammals.

Current cladistic practice necessarily requires that morphological characters be treated as independent of one another, and as having equal probabilities of evolving. This avoidance of a priori weighting of characters creates an illusion of objectivity. Yet both assumptions are counterintuitive of the real world, and worse still, the principle of objectivity is immediately violated by the selection of what an author takes to be the unit characters. Is the postcanine tooth structure of a tritylodontid a single character—an enlarged, multicusp tooth—or several characters, one for each dimension, each cusp, each crest? Both views of tritylodontid relationships are current, and depend respectively on such decisions as this. The call is always for yet more characters to help resolve the dispute, and Sues and Jenkins provide a number of these. Several of the previously acknowledged mammal-like characters of the tritylodontid postcranial skeleton are noted but, on the basis of this material, are promptly dismissed as “only superficial in nature,” and the authors conclude that “scoring them as representing the same character-state in phylogenetic analyses obscures the real structural differences in these features between tritylodontids and basal mammals.” Well, maybe so or maybe not—the argument will continue.

Richard Blob’s contribution attacks another category of paleobiological problem, that of inferring the function and physiology of organisms represented by no more than their bare bones. Specifically, he addresses the question of whether the cynodonts had actually achieved a significant degree of endothermic temperature physiology, as most commentators believe. One way to test this is to find correlations between skeletal features and temperature physiology strategies in living organisms and apply them to the fossils. In this case, Blob notes an allometric relationship in mammals, in which the rate of increase in limb diameter is less than the rate of increase in body mass. In ectothermic reptiles, these two dimensions scale isometrically. He finds that the relationship within a growth series of cynodonts matches the reptilian pattern, implying that cynodonts were ectothermic. This is a rather disconcerting result in light of the evidence for enhanced feeding, ventilation, and locomotory functions that most of us take to be clear signs of an elevated metabolic rate. Blob is commendably cautious in evaluating the result, but nevertheless we should not lose sight of the fact that many a new insight began life as an anomalous result.

Fred Grine and three colleagues offer an admirably detailed biometric, species-level analysis of the South African specimens of *Lystrosaurus*. This genus was the most abundant, widespread mammal-like reptile of all time and has the distinction of being one of the very few amniote genera to have survived the great end-Permian mass extinction.

The third paper on mammal-like reptiles concerns evolution at the lowest taxonomic level, a level not often amenable to study in fossil amniotes, but of fundamental importance if community evolution and the rates and controls of extinction and speciation are ever to be understood. Fred Grine and three colleagues offer an admirably detailed biometric, species-level analysis of the South African specimens of *Lystrosaurus*. This genus was the most abundant, widespread mammal-like reptile of all time and has the distinction of being one of the
very few amniote genera to have survived the great end-Permian mass extinction. Grine and colleagues reduce the existing plethora of ill-defined species to five, and define their respective stratigraphic occurrences. Only one species, Lystrosaurus curvatus, occurred during the latest Permian, while the others are all first found in the subsequent lowermost Triassic, which generates interesting thoughts about patterns of survival during and radiation after the end-Permian crisis. For example, was it the evident burrowing ability that allowed Lystrosaurus both to avoid extinction and to undergo speciation before any other terrestrial taxon, once the crisis was over?

The final contribution on mammal-like reptiles is a reminder of what lies at the very heart of paleobiology—new fossil discoveries. Christian Sidor and Bruce Rubidge describe Herpetoskylax hopsoni, a new member of the most basal therapsid taxon, Biarmosuchia. Studying this species gives us new anatomical details about the skull and jaws of one of amniote phylogeny’s most interesting groups. The ancestral therapsids were the first animals to show serious evidence—including changes in their jaws, teeth, limbs, girdles, ears, and undoubtedly many more features—of setting off down the evolutionary lineage that eventually ended up as mammals. The more we know of this grade of amniote evolution, the closer we may come to understanding just how and why mammals evolved, complete with their amazing potential to radiate into all the great variety found today.

Other contributions to the volume address a similar range of issues, but in other taxa. Dinosaur buffs will appreciate Matthew Carrano’s demonstration that most—though not quite all—dinosaur lineages really did evolve increasing body size, and Michael Parrish’s analysis of the relationship between neck length and body size in sauropods. For me, the pick of the mammal papers is Paul Sereno’s investigation of the long-standing problem of how and when the parasagittal forelimb gait evolved.

Attending a contemporary vertebrate paleontology conference, one is immediately struck by a revolutionary change that is currently affecting the subject, in the form of new techniques for studying old problems. We can now create detailed three-dimensional reconstructions of extinct organisms, using CT (computerized tomography) and laser scanning to reveal the detailed internal structure of fossils and associated computer algorithms to correct for distortion and damage. Sequences of hypothetical evolutionary stages can be drawn by the computer rather than merely imagined. The engineer’s methods of finite element analysis of stress patterns in skulls and limb bones lead to new biomechanical hypotheses about how and why inferred morphological changes occurred. Molecular-based phylogenetic trees may not be directly applicable to fossil material, but examples of taxa that have living members, such as placental mammals, are nevertheless warning us about how unreliable traditional morphological-based methods can be, and are therefore stimulating a search for independent guides to relationships such as paleobiogeography and functional analysis. Stable isotopes can reveal the diets and habitats of animals that lived tens or hundreds of millions of years ago.

Amniote Paleobiology stands at the threshold of this exciting new future for its subject. It contains little that is based on these new methods of investigation, but offers instead a snapshot of the range of paleobiological problems for which provisional solutions have been developed over the last half-century—solutions whose further refinement awaits new insights based on such new techniques. A historian of science 50 years hence will undoubtedly find this attractive, well-produced volume a timely portrait of the subject as it stood at the start of the 21st century.

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