How well can we reconstruct the appearance, movements, and behavior of extinct vertebrates from studies of their bones and other, more rarely preserved parts? Where is the boundary between the scientific evidence for reconstruction and the need to resort to imagination? In this book, sixteen paleontologists and biologists discuss these questions, review the current status of functional studies of extinct vertebrates in the context of similar work on living animals, and present a broad philosophical view of the subject’s development within the framework of phylogenetic analysis. The authors describe and debate methods for making robust inferences of function in fossil vertebrates and present examples where we may be confident that our reconstructions are both detailed and accurate. The area of greatest success is in reconstructing masticatory mechanics in mammals and their cynodont ancestors; several chapters address aspects of this work. Further chapters consider the cranial and postcranial skeletons of a range of vertebrates.

The detailed studies are placed in the context of their contribution to the understanding of evolutionary processes and will be valuable reading for vertebrate paleontologists, comparative anatomists, and evolutionary biologists.
Functional morphology in vertebrate paleontology
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Edited by

Jeff Thomason

University of Guelph
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Contributors

Harold N. Bryant
Vertebrate Morphology Research Group
Department of Biological Sciences
The University of Calgary
Calgary, Alberta T2N 1N4
Canada
Current address:
Provincial Museum of Alberta
Mammalogy Program
12845–102 Avenue
Edmonton, Alberta T5N 0M6

Arthur B. Busbey
Department of Geology, Box 30798
Texas Christian University
Fort Worth, TX 76129

Alfred W. Crompton
Department of Organismic and Evolutionary Biology
Harvard University
Cambridge, MA 02138

Stephen M. Gatesy
Museum of Comparative Zoology
Harvard University
Cambridge, MA 02138

Emily B. Giffin
Department of Biological Sciences
Wellesley College
Wellesley, MA 02181

Walter S. Greaves
Department of Oral Biology, Anatomy, and Cell Biology and Department of Biology
University of Illinois at Chicago
801 S. Paulina St.
Chicago, IL 60612

Christine M. Janis
Program in Ecology and Evolutionary Biology
Division of Biology and Medicine

Brown University
Providence, RI 02912

Rolf E. Johnson
Milwaukee Public Museum
800 W. Wells St.
Milwaukee, WI 53233

George V. Lauder
School of Biological Sciences
University of California
Irvine, CA 92717

Virginia L. Naples
Department of Biological Science
Northern Illinois University
DeKalb, IL 60115

John H. Ostrom
Peabody Museum
Yale University
170 Whitney Avenue
New Haven, CT 06511

Kevin Padian
Department of Integrative Biology
University of California
Berkeley, CA 94720

John M. Rensberger
Department of Geological Sciences and Burke Museum
University of Washington, DB-10
Seattle, WA 98195

Anthony P. Russell
Vertebrate Morphology Research Group
Department of Biological Sciences
The University of Calgary
Calgary, Alberta T2N 1N4
Canada
Contributors

Jeffrey J. Thomason
Department of Biological Sciences and College of
Osteopathic Medicine
Ohio University
Athens, OH 45701
Current address:
Department of Biomedical Sciences
Ontario Veterinary College
University of Guelph
Guelph, Ontario N1G 2W1
Canada

Keith S. Thomson
Academy of Natural Sciences
1900 Benjamin Franklin Parkway
Philadelphia, PA 19103-1195

David B. Weishampel
Department of Cell Biology and Anatomy
The Johns Hopkins University School of Medicine
Baltimore, MD 21205

Lawrence M. Witmer
Department of Cell Biology and Anatomy
The Johns Hopkins University School of Medicine
Baltimore, MD 21205
Current address:
Department of Anatomy
New York College of Osteopathic Medicine
New York Institute of Technology
Old Westbury, NY 11568
Preface

The primary intent of this book is to provide a snapshot of the current status of functional studies of fossil vertebrates in North America. Half of the contributions are based on presentations at a symposium of the same title as this book that was held in conjunction with the Annual Meeting of the Society of Vertebrate Paleontology in Toronto, October 1992. The other contributions were solicited. To give coherence to both the symposium and this volume I sent some questions for each author to consider while writing:

1. On what philosophical premises are functional interpretations of fossil vertebrates based, and what contributions do they make to our understanding of evolutionary processes? For example, what do functional studies draw from phylogenetic reconstruction, and what do they add back to phylogenetic methods?

2. What are the conceptual and methodological links between functional studies of fossil vertebrates and corresponding neontological work? Is it a two-way interchange, or unidirectional from extant to extinct?

3. How does functional morphology relate to the other subdisciplines of paleontology? The interaction with phylogenetic methods has been mentioned; what interactions may exist with paleoecology, stratigraphy, taphonomy, etc.?

4. What methodologies are appropriate for assessing function in an extinct beast? Describe any relevant assumptions and caveats in addition to areas where functional inference may be robust.

As a result, the book does more than illustrate the kinds of functional work currently under way in vertebrate paleontology. It is a forum of discussion on how to study functional morphology of fossils, the levels of resolution we might expect in reconstructing function from structure, and the position of functional studies in the broader context of paleontology and evolutionary biology. The strongest theme to emerge is that of methodology, with several authors proposing or discussing general protocols for robustly inferring function from structure in fossils.

Traditionally, the functional reconstruction of fossils has been open to the criticism of excessive subjectivity. Even though individual workers have usually had good backgrounds in the osteology of extinct vertebrates and the comparative anatomy of living ones, reconstructions often still came down to individual interpretation and opinion. The same was true of systematic methods, but the past 20 years have seen a revolution in systematics, resulting in the quantifiable and repeatable methods of phylogenetic analysis. Procedures have been developed for linking the inference of function in fossils to phylogenetic analyses, providing paleontologists with some confidence in the robustness of their reconstructions. Witmer and Weishampel describe one such procedure; Bryant and Russell and Gatesy present variants. (Lauder and Padian dissent, for entirely different reasons.)

In marked contrast to the emerging confidence among “functional paleontologists” is the situation among neontologists (here represented by George Lauder, though Gatesy, Janis, and Crompton work from a strong base of experiments on living animals when inferring function in fossils). Current technology has allowed neontologists to study some of the functions of living organisms in precise detail, so function and form (morphology) can be assessed independently and compared (rather than the circular procedure of some studies in which function was inferred from morphology, then compared with it). The more animals that are investigated, the looser the coupling between form and function appears to be. Lauder documents examples from his own work that demonstrate that details of function are controlled to a greater extent by motor innervation than
by morphology. The nervous system is never preserved, and is only marginally represented in the preserved parts of vertebrates (see Giffin).

Lauder concludes that paleontologists are largely confined to determining function in only the most general terms for fossils. This pessimistic statement opens the book. The subsequent chapters are by paleontologists presenting, discussing, and defending their methods for assessing function in specific cases. There is, therefore, a tension in the book that I have made no attempt to resolve.

Witmer and Weishampel follow Lauder, presenting a method for inferring function that is linked to phylogenetic assessment: a fossil is bracketed between living animals on a cladogram and their function is used to infer that in the extinct form (cf. Bryant & Russell 1992 and herein). One of the areas remaining problematical to this procedure is when a fossil appears to have functioned differently from the bracketing living forms. An example cited by Weishampel is the evolution of the mammalian jaw joint, which is described in detail in the chapter by Crompton. His chapter provides a transition to a series of chapters on functional studies of the jaws, skull, and dentition. Functional analysis of mammalian dentitions, in particular, is one area in which the interpretation of extant material has been accomplished successfully and at quite a detailed level of resolution.

Janis reviews the past few decades of work on inferring dental function from increasingly finer details of structure: jaw mechanics, occlusal morphology of the teeth, general wear patterns, microwear patterns, and crystalline orientation in enamel. She also shows how studies of fossils can enhance the interpretation of population structure and ecology of living forms. Specific examples of the methods she reviews follow in the chapters by Greaves on jaw mechanics, Bryant and Russell on carnassial wear in sabertoothed cats, Naples on producing dental wear artificially, and Rensberger on comparing stress patterns and crystal alignment in enamel. Greaves’s piece is a prime example of an alternate methodology to those based on phylogeny: the paradigm method described by Rudwick (1964). Greaves infers the constraints of “natural design” of (primarily) mammalian jaws from geometrical models illustrating the principles of their mechanical behavior. Bushby also uses mechanical modeling to interpret the evolutionary changes in the crocodilian skull, whereas Thomson devises an entirely novel method for analyzing sutural orientation in the dermal skull of lower tetrapods, interpreting his results in terms of cranial function.

We then move back from the skull to a lesser number of papers on the postcranial skeleton. I believe the relative weighting of cranial to postcranial chapters reflects the preponderance of cranial research, as does the general emphasis on mammals. Among nonmammalian taxa, dinosaurs are certainly underrepresented here compared with the amount of scientific and public interest in them, but they are well covered elsewhere. Johnson and Ostrom and Gatesy provide the only two pieces focused on dinosaurs and their avian descendants. Johnson and Ostrom remind us that the structural data set for fossil vertebrates is largely limited to the skeleton, and we had better make the most of the functional inferences that can be made directly from osteology. Gatesy returns us to the themes of the earlier chapters, describing his own methods for combining anatomical, phylogenetic, and experimental methods for inferring the change in function of the tail from theropods to birds. Giffin then tackles the problem of the nervous system. Although nerves are not preserved, the cranial cavity and neural canal do contain evidence of the gross anatomy of the central nervous system. Giffin shows how estimates of the change in cross-sectional area of the spinal cord along its length can be used to generate or support inferences of general locomotor patterns in fossil mammals and reptiles. My own chapter argues that, given that bones are our primary data base, we could be missing a whole category of functionally relevant structural information: that encoded in the internal structure of bones.

Kevin Padian rounds out the book with a historical essay that traces the influence of contemporaneous philosophy on functional interpretations of form, from Aristotle to the present day. He ends by presenting a prospectus for the future of functional studies in paleontology that is more optimistic than the opening statements of George Lauder and includes a role for functional work in systematics.

Several authors build their discussions around the phrase “form and function.” For functional studies to be viable, the two have to be related in ways that are amenable to interpretation. Older studies were largely based on the assumption that the relationship was tight, regular, and easy to reconstruct for both fossils and living animals. The situation has changed. There is no longer any excuse for paleontologists to reconstruct fossils based on informed opinion. Rigorous tests of the robusticity of functional inferences are now available. At the same time, “functional paleontologists” need to keep a wary eye over their shoulder to see what the neontologists are reporting. Their work defines the extent to which function can be inferred from structure, and that question seems to be undergoing considerable flux at the moment. If this book achieves its intended purpose of assessing the status quo of functional morphology in vertebrate paleontology in North America, I hope it will also provide a guide and
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stimulus to workers in the field. The field is changing and will continue to change; if this volume stimulates ideas and work that contribute to the change it will have achieved a measure of success.

The idea for this work came from a similar venture: the Symposium Biomechanics in Evolution organized by Jeremy Rayner for a joint meeting of the Society of Experimental Biology and the Palaeontological Association in Manchester, England, 1987 (now published under the same title with R.J. Wootton as coeditor).

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Jeff Thomason

Guelph, Ontario

REFERENCES


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