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### **Jim Hopson and Amniote Paleobiology**

Living amniotes—including all extant mammals, birds, crocodylians, lizards, snakes, and turtles—together comprise an extraordinarily varied array of more than 21,000 species (Pough et al., 1999). These familiar animals are found in every major habitat on earth and are characterized by a dazzling range of morphological, ecological, and behavioral adaptations. The fossil record of the Amniota extends back in time over 300 million years (Carroll, 1988; Benton, 1993; Gauthier, 1994) and encompasses additional thousands of extinct genera (Carroll, 1988). In many respects, this impressive fossil assemblage is even more diverse than are the living amniote taxa. Given that more than ninety-nine percent of all species that have ever existed are extinct (Novacek & Wheeler, 1992), it is not surprising that extant amniote species provide only a glimpse of the total diversity of form and function that have existed historically. As a result, paleobiological analyses of the fossil record are crucial to understanding the origins of modern biological diversity and the processes that shape the patterns we observe today.

Two critical questions are at the core of many paleobiological studies: (1) how are species related to one another and (2) what do species relationships reveal about changes in anatomy and function through time? These two perspectives—phylogenetic and functional—lie at the heart of this volume, which highlights the modern contributions of amniote paleobiology to evolutionary studies. At the same time, this volume serves as tribute to Dr. James A. Hopson, in honor of his retirement after more than thirty-five years of teaching and research at the University of Chicago. Throughout his career, Jim has been a strong advocate for both phylogenetic and functional approaches to studies of vertebrate evolution. Most importantly, Jim's work stands as an example of the successful integration of these two perspectives in amniote paleobiology.

The contributions in this volume focus primarily on phylogenetic and functional themes, but they also reflect the broad range of approaches

used by modern paleobiologists. Therefore, the chapters are divided into four sections; the first two (entitled “New Fossils and Phylogenies” and “Large-Scale Evolutionary Patterns”) are primarily phylogenetic in emphasis, and the second two (entitled “Functional Morphology” and “Ontogeny and Evolution”) focus on other biological issues. However, the reader may be struck by the fact that many of these papers do not fit neatly into the categories that we, the editors, have erected. Indeed, to a certain degree such distinctions are difficult to make in any modern paleobiological compendium, given the importance of bringing varied perspectives to the task of elucidating any group’s evolutionary history. This difficulty in discretely categorizing the various contributions also occurs in part by design, as the contributors were encouraged to integrate phylogenetic and functional perspectives into their work. Thus, it also testifies to the degree of integration increasingly seen in all aspects of modern paleobiology.

### **New Fossils and Phylogenies**

Our knowledge of the amniote fossil record has increased rapidly over the past several decades. For example, Sereno (1997) noted that the diversity of dinosaur taxa alone has doubled in the past twenty years. The discovery, excavation, preparation, and description of new fossils is the most fundamental component of the science of paleontology. Because these actions represent the collection and integration of primary data, they underlie all other aspects of paleontological study. As long as new fossils remain to be discovered, paleontology will maintain this emphasis on descriptive work.

Early descriptions of fossil discoveries in the nineteenth century (and before) are typically used as benchmarks for the slow birth of paleontology as a field of study. Yet even the earliest paleontologists recognized that morphology does not exist in isolation but serves to illuminate the varied and complex connections between organisms. For example, Baron Georges Cuvier’s comments on the first known European dinosaurs included prescient insights into their paleoecological relationships (Taquet, 1994).

With the advent of evolutionary theory and its profound impact on paleontology came an appreciation for the roles fossils could play in understanding the interrelationships of organisms. Description increasingly fed more directly into analyses of phylogenetic relationships for the simple reason that morphology formed the primary basis for such hypotheses until the advent of molecular studies in very recent decades.

New fossils were seen as important markers of transitions between previously known forms and ultimately between distantly related modern groups. Indeed, few new fossils are described even today without accompanying statements or analyses of their phylogenetic placement, and these descriptions typically are written with phylogenetic informativeness in mind. Thus, description and phylogeny have become intertwined.

As is true of many workers in vertebrate paleontology, Jim Hopson's first scientific papers were descriptive (Hopson, 1964a, 1964b), and he continued to offer such studies throughout his later career. It is fitting, therefore, that several of the contributors to this volume describe new fossil taxa or significant new material from previously described taxa. In addition to their particular scientific content, they provide an excellent illustration of the modern state of the oldest of paleontological methods.

Lombard and Bolt (chapter 2) describe the mandibular morphology in *Whatcheeria deltae*, one of the oldest well-preserved tetrapods in North America. The authors then analyze the systematic implications of this morphology for basal tetrapods. As the authors explain, *Whatcheeria* was thought to represent a critical link in our understanding of basal tetrapod relationships, given its proposed phylogenetic position at the base of the anthracosaur radiation (Lombard & Bolt, 1995), which ultimately gave rise to all living amniotes. However, more recent analyses have thrown doubt on its anthracosaur affinities (see references in chapter 2). Nevertheless, Lombard and Bolt's analysis suggests that *Whatcheeria* provides novel insights into mandibular evolution in early tetrapods, and has improved our understanding of this important character complex.

In chapter 3, Munter and Clark describe new remains of small theropod (predatory) dinosaurs from the latest Early Jurassic of Mexico. A formal description is followed by a series of phylogenetic analyses that demonstrate the coelophysoid affinities of these fragmentary remains. The new coelophysoids represent the youngest known fossils of this clade. The group is common throughout Late Triassic and Early Jurassic terrestrial faunas but had disappeared by the Late Jurassic. The poorly known Middle Jurassic terrestrial record has hampered our understanding of their demise, but new fossils such as these ultimately may shed light on this process.

Sidor and Rubidge (chapter 4) discuss the morphology and phylogenetic affinities of a new biarmosuchian, which they named in honor of Jim Hopson. This new taxon is based on a nearly complete skull and broadens our understanding of this relatively poorly known group. The biarmosuchians are particularly important to studies of synapsid evolution,

as they represent the oldest and most basal clade of therapsids. The authors use modern numerical cladistic techniques to elucidate the systematic relationships of the new taxon, ultimately supporting the monophyly of Biarmosuchia.

Sues and Jenkins (chapter 5) present a detailed description of the postcranial skeleton of the tritylodontid therapsid *Kayentatherium*. This taxon contributes greatly to our knowledge of the morphology of these cynodonts (specifically by suggesting that tritylodonts are not nearly as mammal-like as previously had been supposed) and simultaneously offers new clues on their relationships. The authors mine this wealth of new data for important phylogenetic implications, some of which bear directly on the origin of mammals themselves. As they point out, the phylogenetic placement of *Kayentatherium* makes it a particularly appropriate subject for a volume honoring Jim Hopson.

It is noteworthy that all these contributions include data matrices and/or some form of systematic analysis. The ability to place fossils into their appropriate systematic context has long been a central focus of paleontology. However, the role of systematics has changed dramatically since Jim Hopson began his career in the 1960s. At that time, investigations of higher-level vertebrate phylogeny were almost exclusively the domain of paleontologists (Ross, 1974; Patterson, 1981). Groups that lacked a significant fossil record typically were portrayed as having unknown (and by implication unknowable) phylogenetic histories (Patterson, 1981). Patterson (1981; p. 195) described the logical sequence whereby paleontology was granted its pivotal role in the reconstruction of phylogenetic or evolutionary relationships: “evolution is a theory about the history of life; evolutionary relationships are historical relationships; fossils are the only concrete historical evidence of life; therefore fossils must be the arbiters of evolutionary relationships.”

The ensuing years have witnessed a dramatic revolution both in systematic practice and in the role of paleontology in systematics. Beginning in the late 1960s and 1970s, two important objections were raised to traditional systematic practices. The first objection concerned subjectivity in systematics. The practices of traditional systematists came to be viewed as overly dependent on intuition and authority, with groupings often established on the basis of subjective or cryptic selection and weighting of characteristics (e.g., see criticisms by Patterson, 1980; Wiley et al., 1991). Cladistics or phylogenetic systematics rose to prominence in response to such concerns and enjoyed particular success among systematic paleontologists over the past few decades. Indeed, in even a brief scan of

important systematic paleontology journals such as the *Journal of Paleontology* or *Journal of Vertebrate Paleontology*, one would be hard pressed to find more than a handful of papers that used traditional (“evolutionary” *sensu* Mayr [1980]) systematic methodologies over the past decade. In recent years, the incorporation of computer-driven analyses into cladistic methodology has allowed ever more sophisticated investigations of ever larger systematic data sets. This transition in the vertebrate paleontological community from traditional “evolutionary” systematics to cladistic methodology to computer-driven analyses was embraced by Jim Hopson and his students and is mirrored in their systematic publications (e.g., see Hopson & Crompton, 1969; Hopson & Barghusen, 1986; Sidor & Hopson 1998).

The contribution by Gaudin and Wible (chapter 6) is another example of the use of such computer-driven cladistic analysis to analyze large data sets. They examine the phylogenetic relationships among living and extinct armadillos based on a data set of 163 craniodental characters sampled across nineteen taxa. The armadillos are the most diverse of the living members of the placental mammalian order Xenarthra. Along with their extinct kin, armadillos have been placed in the clade Cingulata, a group whose systematic relationships remain poorly investigated (Gaudin, 2003). This contribution overturns many of the traditional ideas about armadillo interrelationships and is notable in that the phylogenetic results for living taxa are changed substantially by adding fossil taxa to the analysis.

The results reported in chapter 6 are particularly pertinent in relation to the second primary objection to traditional systematics that began to surface, particularly in the 1970s and 1980s. This second objection concerned the role of paleontology in systematics. Influential papers published by Patterson (1981), Rosen et al. (1981), and Gardiner (1982) pointed out that, because of gaps in the fossil record, phylogeny could rarely if ever be read from the rocks in any straightforward manner. Cladistic methodology did not depend on stratigraphic information, meaning that living taxa could play a role in cladistic analyses equivalent to that of fossil taxa. Furthermore, because fossils typically do not preserve information on soft tissue structure or molecular composition, they contain only a fraction of the potentially useful systematic information provided by living forms. Patterson (1981, 218) claimed that “instances of fossils overturning theories of relationship based on Recent organisms are very rare, and may be nonexistent.” Patterson (1981), Rosen et al. (1981) and Gardiner (1982) suggested that fossils may play only a minor

role in phylogenetic reconstruction. A number of recent papers addressed their challenge of the relevance of paleontology to systematic analysis (e.g., Gauthier et al., 1988; Smith & Littlewood, 1994; O'Leary, 1999), and readers are referred to these works for more detailed arguments advocating the continued importance of fossils in investigations of phylogenetic relationships. We believe the papers throughout this volume provide further corroboration for the continued relevance of vertebrate fossils in advancing our understanding of amniote phylogeny.

### **Large-Scale Evolutionary Patterns**

One of the benefits of cladistics' emphasis on the importance of living taxa in phylogenetic analysis has been a more widespread realization of the centrality of phylogeny to comparative biology and evolutionary biology. Many authors have discussed the importance of using phylogenetic information to better understand the evolution of myriad aspects of organismal biology, from functional morphology and physiology (e.g., see Lauder et al., 1995, and references therein) to behavior and ecology (Brooks & McLennan, 1991). Morphological, functional, ecological, and behavioral characters can be incorporated into cladograms as a means of elucidating evolutionary patterns and thereby enhancing our understanding of evolutionary processes. The importance of using cladograms to further our understanding of the biology of extinct vertebrates has also been recognized by the vertebrate paleontological community (e.g., see Polly & Sidor, 1999).

Such systematics-driven analyses of evolutionary patterns have long figured importantly in the work of Jim Hopson, who used such analyses to improve our understanding of a variety of topics from the evolution of phalangeal formulas in nonmammalian therapsids (Hopson, 1995) to the evolution of the mammalian ear (Allin & Hopson, 1992).

Modern workers have also developed an array of statistical techniques to address macroevolutionary questions regardless of whether they are based explicitly on a particular phylogeny. Trend analyses (e.g., Stanley, 1973; McShea, 1998; Alroy, 2000) complement cladogram-based analyses by investigating the distributional, variational, and probabilistic aspects of large-scale evolutionary trends. A number of our contributions use both systematic and trend-based techniques as a means of understanding evolutionary patterns of morphological change.

Parrish's work in chapter 7 draws paleoecological inferences from specific morphological observations. On the basis of previously published observations of fossil taxa, Parrish quantifies ranges of motion for cervical

vertebrae in sauropodomorph dinosaurs (often using computer modeling as a guide). These ranges allow him to hypothesize potential feeding regimes for primitive members of this group and subsequently to place them into a larger phylogenetic and faunal context. This type of analysis is especially meaningful for taxa like most dinosaurs that have no obvious functional or behavioral analogues among the modern fauna.

In chapter 8, Carrano takes an even broader look at dinosaur history, quantifying and analyzing patterns of body size evolution in this group. Using several different analytical techniques, he tracks specimen-based size measures through the entire phylogeny of Dinosauria. This allows size changes to be quantified, revealing that most dinosaur lineages seem to follow Cope's Rule, showing marked size increases over time. A few exceptions are also identified, among both theropods and sauropods, that may prove worthy of future paleobiological study.

Finally, Rougier and Wible (chapter 9) examine the evolution of the mammalian ear region and basicranium. This anatomical region is rich in morphological characters, allowing them to investigate important phylogenetic questions surrounding the early evolution of modern mammals. They are also able to draw on a series of previous works to discuss anatomical changes in the mammalian ear region and basicranium in great detail. Of particular note are instances of correlated changes between ear osteology and soft-tissue structures, simplification in vascular patterns, and independent acquisition of several middle ear characters in different mammalian groups.

### **Functional Morphology**

The study of functional morphology is essentially an investigation into the relationship between organismal form and function. Such research is in evidence long before the advent of evolutionary theory (Russell, 1916; Padian, 1995; Ross, 1999). Since its beginnings, functional morphology has had a long and mutually enlightening relationship with the science of engineering, relying substantially on physics to explain the how and why of function (Vogel, 1998). In fact, early concepts of animal and plant "architecture" drew heavily from concepts of human architecture (Vogel, 1998). However, matches between form and function generally were viewed as static reflections of overarching principles of design and frequently were argued to be both purposeful and unalterable (Padian, 1995; Ross, 1999).

The theory of evolution, and specifically the concept of natural selection, altered the relationship between biological study and physics. If the

form of a structure could affect its function, it also could affect the reproductive success of its parent organism (Arnold, 1983; Ross, 1999). Thus, organismal design had the potential to be invested with a selective value. Working alongside studies of developmental biology, sexual selection, and population biology, functional morphology has come to assume a prominent role in the study of evolution, contributing to the broad goal of understanding the origins, evolution, and adaptation of species (Lauder, 1991, 1996).

But why study function in fossil taxa? Links between form and function can be tested effectively in living organisms, and extant taxa are the only source for many kinds of functional data, such as kinematics, muscle activity patterns, and musculoskeletal stress and strain. However, extant species provide only a snapshot of a single cohort of taxa at one evolutionary instant. The study of evolution is the study of biological change through time, and intermediate stages in the transitions toward the character states displayed by living taxa often are documented only in the fossil record. Thus, the interpretation of function in fossil taxa is critical for the examination of such transitions (e.g., Gauthier et al., 1988). Moreover, by studying the functional morphology of extinct species, we can evaluate the full range of possible shapes and behaviors that organisms have exploited through time, gaining insight into constraints on diversity.

The techniques available for investigating functional morphology in organisms are varied, and they reflect both the types of data being collected and the conceptual framework of the questions being addressed.

What was once a largely qualitative, descriptive enterprise (answering the question, “what does it do and how does it do it?”) has become increasingly quantitative and experimental (Ashley-Ross & Gillis, 2002). Studies of function can encompass everything from a complete behavior—which includes a great complexity of activities, from physical to neurological—down to a single motion or action. Experimental studies of biomechanics (i.e., the mechanical roles of biological structures) now play a central role in examinations of function among extant species, providing data on kinematics, transmitted forces, skeletal stresses and strains, muscle contractions, and neurological inputs (Biewener, 1992; Vogel, 2003). Such studies form the ultimate basis for our understanding of functional morphology in extinct species (e.g., Witmer, 1995). As a result, experimental data from extant species are applied as an integral component of many analyses of function in fossil taxa (e.g., Crompton & Hiiemae, 1970; Thomason, 1985; Carrano, 1998; Blob, 2001).

A striking pattern that has emerged in functional studies in recent years has been that the dominant structural materials of the amniote

body—bone, cartilage, muscles, and tendons—tend to have conservative material properties across most taxa (Currey, 1984; Erickson et al., 2002; for exceptions, see Espinoza, 2000; Blob & LaBarbera, 2001). When coupled with the universality of gravity and other physical laws, two powerful conclusions emerge: (1) amniotes face largely similar problems, structurally speaking, and (2) amniotes are restricted to a few, common avenues of response when dealing with these problems. Thus, structural convergences are quite common among amniotes (indeed, as they are among many other organisms), often extending to a remarkable degree. These convergences suggest that similar selective pressures frequently may act in organisms of very different phylogenetic lineages.

Two main approaches have been applied to study the functional morphology of fossil taxa: *historical* (or *phylogenetic*) and *ahistorical* (or *paradigmatic*) (Lauder, 1995; Weishampel, 1995; Ross, 1999). In the former, phylogenetic principles are applied to evaluate the validity of functional inferences in fossil taxa (Bryant & Russell, 1992; Witmer, 1995; Lauder, 1995). Using the Extant Phylogenetic Bracket method (formalized by Witmer, 1995), for example, fossil taxa are analyzed in the context of at least two extant sister lineages. If osteological correlates of the function can be identified, then examination of fossils for those markers provides a test of functional inferences (Witmer, 1995; but see Lauder, 1995). However, historical analyses of function can also draw conclusions strictly from the most parsimonious distribution of features (Lauder, 1995; Witmer, 1995).

In contrast, ahistorical analyses depend critically on morphological data from the fossils in question (DeMar, 1976; Lauder, 1995; Ross, 1999) along with four central methods: qualitative correlation, quantitative correlation, physical modeling, and mathematical modeling. Qualitative correlation is rooted firmly in descriptive anatomy: conclusions about the function of a structure in an extinct species are based on whether its morphology suggests that it appears to have been good at performing that function (e.g., Molnar, 1977). With quantitative correlation, measured morphometric correlations between shape and function in living taxa are used as a guide to draw inferences about function in fossil species (e.g., Coombs, 1978; Van Valkenburgh, 1985; Carrano, 1998). Under physical modeling, replicates of fossil taxa are constructed and their functional responses to various stimuli are measured to evaluate the effects of shape (e.g., Bennett, 1996; Erickson et al., 1996). Finally, mathematical modeling uses physical principles and experimental data from living animals to derive equations that predict functional capabilities and constraints in fossil taxa (e.g., Alexander, 1989; Thomason, 1985; Blob, 2001). Such

“ahistorical” approaches can enlighten evolutionary studies of function when applied within a phylogenetic context.

Two of our contributions focus on questions of functional morphology. They illustrate the breadth of perspectives and techniques available as well as the use of both extinct and extant taxa as focal groups.

Sereno (chapter 10) discusses the morphology of the multituberculate shoulder girdle based on an exceptional specimen from Mongolia that shows well-preserved three-dimensional structures. The specimen provides important data on the evolution of this region in mammals and sheds light on the controversial phylogenetic position of the Multituberculata. This is, perhaps, a best-case scenario for functional inference based on the description of a fossil amniote specimen; here the materials, though lacking soft tissues, nevertheless retain a wealth of morphological information.

In chapter 11, Crompton et al. review mandibular condyle morphology across extant herbivorous mammals, seeking to explain observable variations in functional terms. Their work is grounded in the biomechanics of feeding and a broad examination of living taxa. Using kinematic and morphological data from the bones and teeth, they are able to draw conclusions about the functional implications of mammalian jaw geometry and the changes in morphology in different lineages.

### **Ontogeny and Evolution**

Groundbreaking nineteenth-century studies of vertebrate embryology by workers such as Haeckel and von Baer laid the foundation for a dialogue between researchers in evolution and development (Gould, 1977). Recent decades have witnessed a resurgence of interest in the relationships between development and evolution, and a mutual understanding between workers in these fields has flourished with the widespread use of new analytical and investigative techniques. As finer-scale developmental processes become better understood, so too do their relationships to the evolutionary history of the organisms in which they occur (e.g., Alberch, 1982; Shubin & Marshall, 2000; Donoghue, 2002). The current success of numerous “evo-devo” research programs is but one illustration of the integration of these approaches to understanding organismal diversity.

One of the outgrowths of this renewed relationship between studies in evolution and development has been a widespread appreciation for the importance of ontogenetic and developmental information in studies of paleontology. Ontogeny—with its constituent phenomena such as heterochrony—is now seen as an integral part of organismal evolution and

therefore is of specific interest to paleontologists. Although the determination of specific ontogenetic processes can be difficult at the paleontological scale (e.g., Benton & Kirkpatrick, 1989; Jones & Gould, 1999), such efforts have the potential to yield great insights into the evolutionary process (e.g., Nelson, 1978; Larsson, 1998). As a result, paleontologists have taken new interest in studying the ontogenies of extinct species wherever possible, using information from sources as wide ranging as morphometrics (e.g., Zelditch et al., 2003), growth rates (e.g., Curry, 1999) and curves (e.g., Heinrich et al., 1993; Rinehart & Lucas, 2001), and the developmental biology of modern forms (Brochu, 1996; Maisano, 2002).

Three of our contributions draw on ontogenetic approaches to investigate vertebrate paleobiology and evolution. Together, these chapters provide a broad view of some of the varied ways paleobiological studies are currently emphasizing and utilizing ontogenetic data.

O'Keefe (chapter 12) provides a detailed description of the braincase in several basal sauropterygians and plesiosaurs, representing the onset of an important radiation of Mesozoic marine reptiles. By placing these observations into a phylogenetic context, he is able to determine the plesiomorphic condition for Plesiosauria. This condition is much more similar to that of basal diapsids than to that of basal sauropterygians, providing evidence for character reversal. O'Keefe's study brings an ontogenetic perspective to this pattern by applying a heterochronic interpretation.

In his paper (chapter 13), Blob examines patterns of within-taxon scaling (size-related changes in limb bone morphology and proportions) in cynodont therapsid taxa for which juvenile and subadult fossils have been preserved. Data from extant vertebrates have suggested that such patterns are linked to metabolic rate and could provide insight into the metabolic status of fossil taxa. Blob tests this proposal by analyzing data from a critical fossil lineage, allowing examination of the evolution of locomotor ontogeny and endothermy in the ancestors of modern mammals.

Finally, in chapter 14, Grine et al. tackle the leviathan problems surrounding the taxonomy and ontogeny of the dicynodont therapsid *Lystrosaurus*. This widespread genus has housed an ever-proliferating array of species since its original diagnosis. Grine et al. use several morphometric techniques to analyze the large sample of *Lystrosaurus* skull material in the context of size and stratigraphic position. They conclude that growth changes account for much of the variation seen in this taxon but that valid taxonomy differences are detectable within this context. The bewildering list of *Lystrosaurus* species is reduced to a few well-documented forms.

### **Acknowledgments**

As editors, we offer sincere thanks to the many contributors to this volume. They responded to our request for papers enthusiastically, ultimately providing some of their finest work. We are pleased and proud to offer this volume to Jim on their behalf and hope our work as editors can measure up to theirs as authors.

We initially approached many of Jim Hopson's former students, post-docs, and collaborators with the idea of creating a volume to honor Jim's career and work. We received an overwhelmingly positive response and are pleased that so many people were able to provide papers for this volume. Indeed, even those who for various reasons were unable to contribute nonetheless provided unsolicited praise for Jim and his work.

It has been a pleasure to work with the University of Chicago Press on this project. From the beginning, the editors were unanimous in their feeling that the Press would be the most appropriate home for a book honoring the career of Jim Hopson, and we were pleased to find our opinion shared by people at the Press. Nonetheless, this work would have been much more difficult, and its success less assured, without the sincere efforts, enthusiasm, and support offered to us by Christie Henry. The importance of her guidance to these four novice editors should not be underestimated.

Claire Vanderslice has worked as a scientific illustrator with Jim Hopson for more than twenty years, and her skills are evident in many of Jim's publications. Here again, we thought she was the single most appropriate person to work with in designing the cover of this volume. We thank her for producing the wonderful image of *Thrinaxodon* that graces this book's cover. We also thank Claire, Jim Hopson, and Edgar Allin for providing the previously published illustrations that are placed at the head of each section of the book as a tribute to their long and productive collaborations.

Finally, this book could not have proceeded without the generous efforts of numerous outside reviewers, who agreed to treat these manuscripts as they would submissions to any scientific journal. Their expertise and assistance elevated both the content and the organization of this work. We thank numerous anonymous reviewers as well as Gerardo de Iuliis, Zofia Kielan-Jaworowska, Timothy O. Koneval, Michael W. Maisch, Sean Modesto, Michael J. Novacek, Olivier C. Rieppel, and Sergio Vizcaíno.

It has been our honor and privilege to serve as coeditors of this volume honoring the occasion of Jim Hopson's retirement from the University of Chicago. Three of us (M.T.C., T.J.G., R.W.B.) are former graduate students of Jim's, and the other (J.R.W.) is a former post-doc. Jim has

shared with each of us his tremendous enthusiasm for paleontology and his interest in our work and our development as scientists. Jim's knowledge of paleobiology across the entire taxonomic spectrum of vertebrates is extraordinary; he has used this knowledge to encourage each of us to pursue our own taxonomic and methodological interests in a rigorous fashion. We have enjoyed his wide-ranging intellectual pursuits and his willingness to share these interests with those around him. We have benefited from his and his family's hospitality on many occasions as well as from their kindness and friendship. It is therefore with love and gratitude that we offer this volume in tribute and profess our hope that he finds it a scientific enterprise worthy of his own high standards of professional excellence.

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