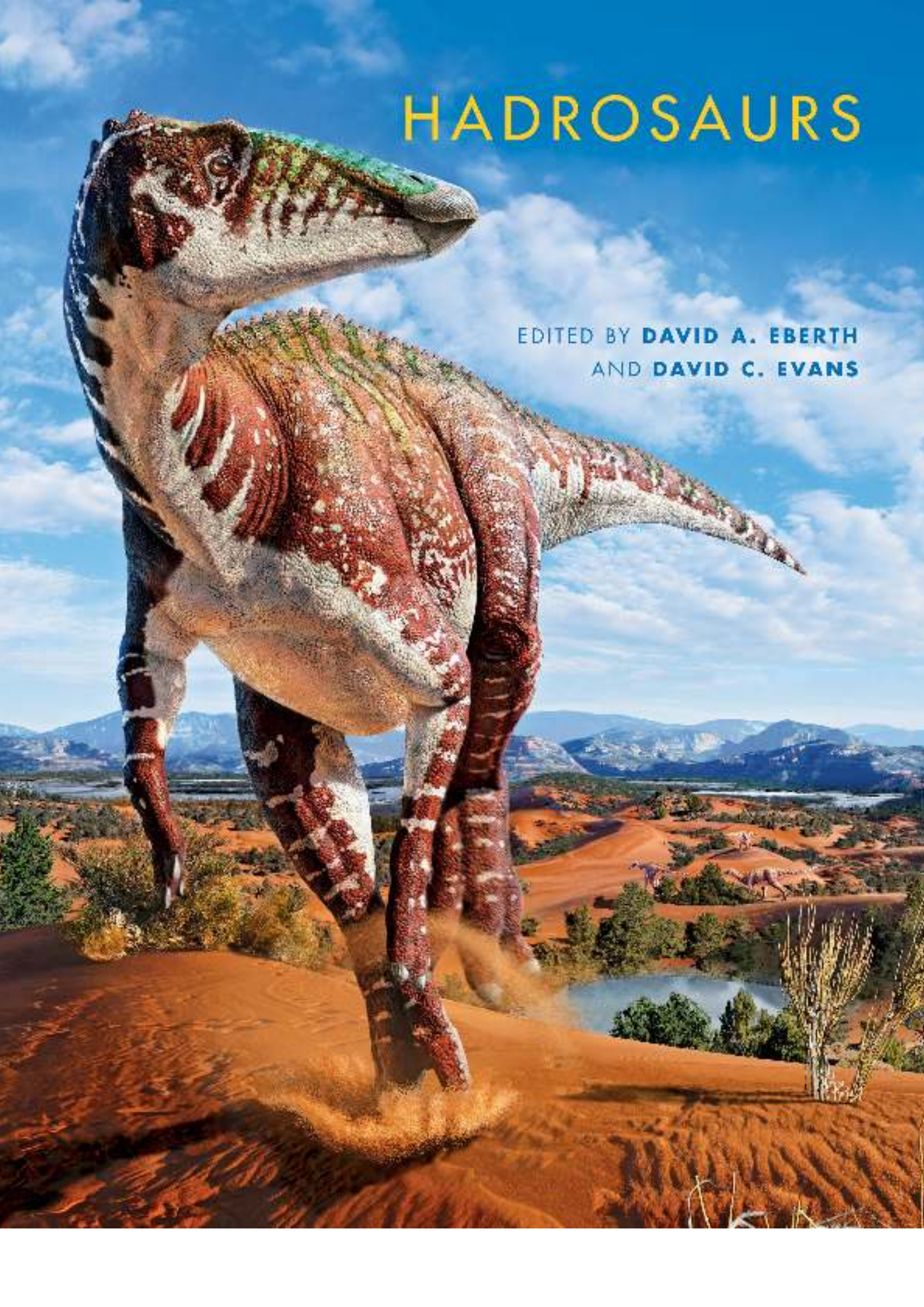


HADROSAURS

EDITED BY **DAVID A. EBERTH**
AND **DAVID C. EVANS**

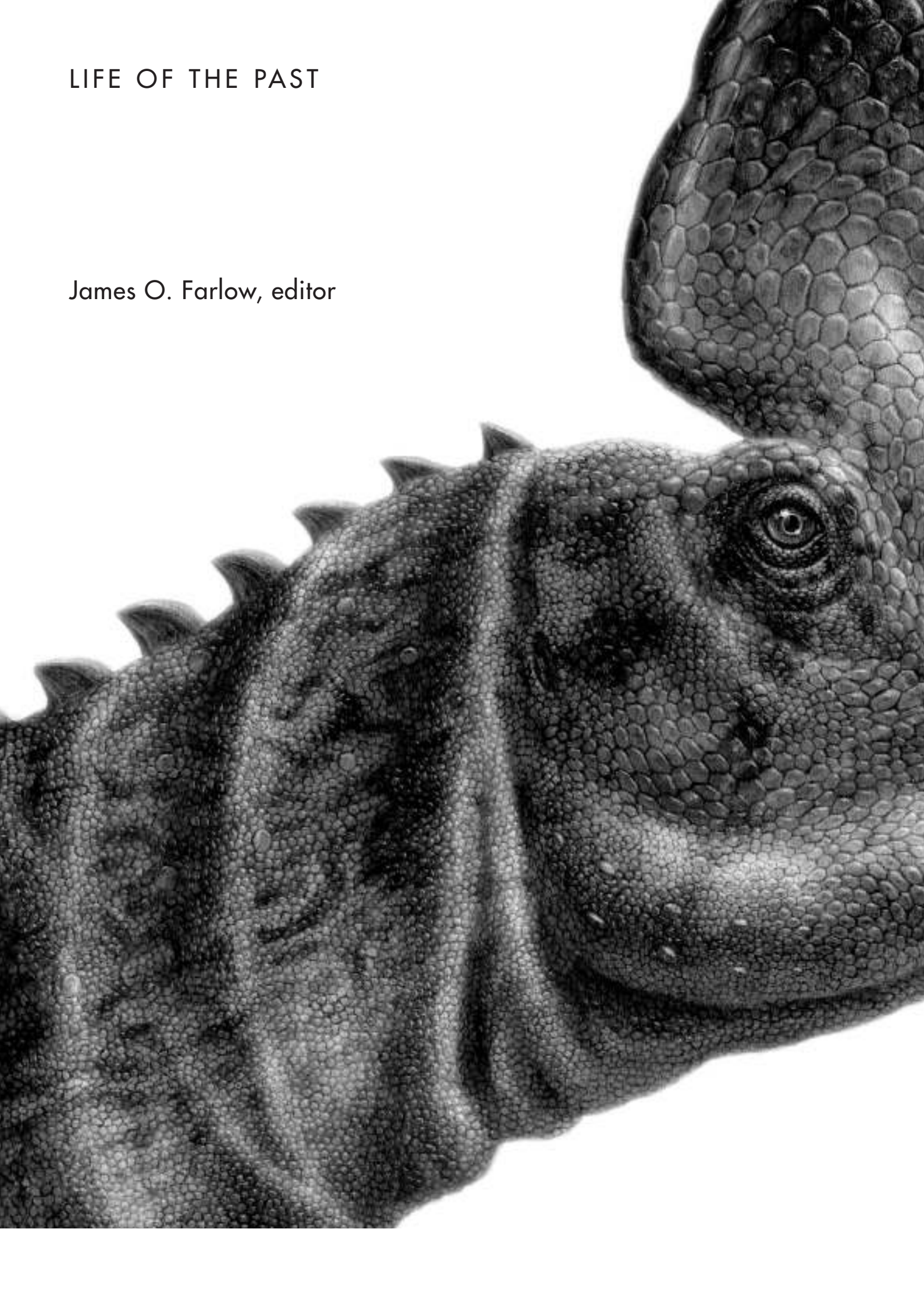


Hadrosaurs



LIFE OF THE PAST

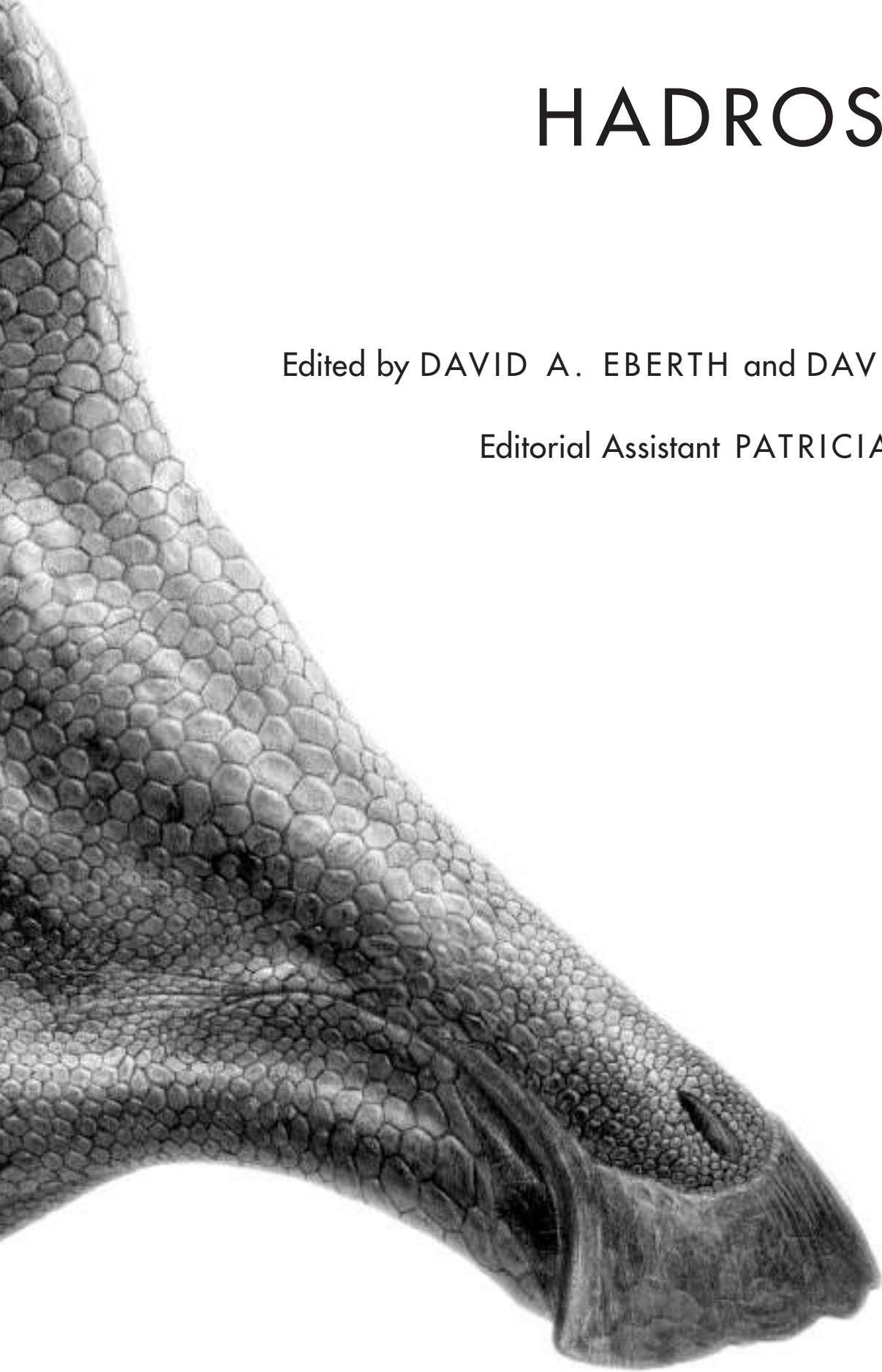
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Edited by DAVID A. EBERTH and DAVID C. EVANS

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To David Weishampel and all those, from J. Leidy onward, who have contributed to our knowledge of hadrosaurs.

In particular, we recognize the efforts of Derek J. Main, a tireless promoter of Earth Science education and research. We value his contribution to this volume and mourn his all-too-soon passing.

Those animals of other days will give joy and pleasure to generations yet unborn.

Charles H. Sternberg

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HADROSAURIDS (ALSO KNOWN AS DUCK-BILLED DINOZOSAURIDS) are one of the best-known groups within Dinosauria due to their relatively recent fossil record, notable diversity, and near global distribution in the Late Cretaceous. Their success was likely driven by a combination of factors that included, most importantly, anatomical, unique and functionally complex innovations and conditions that gressyraptorids were efficiently than those of any “reptile” before or since. Ultimately, the richness of hadrosaurids in the Cretaceous fossil record has allowed us to learn more about dinosauran paleobiology and paleoecology than we have from any other group.

In recent years, a number of dinosaur groups have been the subject of renewed scientific interest. In 2007, sauropod studies experienced a significant resurgence with the seminal monograph *The Sauropods: Evolution and Paleobiology* and Indiana University Press’ *Theodor G. Lönnerdal: The Sauropodomorph Dinosaur*. In 2010, after a decade-long surge of interest, a themed dinosaur “tag” group received annual treatment in Indiana University Press’ *New Perspectives on Hadrosaur Dinosauria*. During the last five years it has been the hadrosaurids’ time in the spotlight. Due to the rapidly growing fossil record as well as gressyraptorid international collaborations, researchers from around the world are now studying new specimens and taxa of hadrosaurids clarify their origins, patterns of evolution, function, paleobiology, paleoecology, and preservation.

It was with this perspective that we (David and I) conceived the “International Hadrosaur Symposium” (September 22–23, 2011). A collaboration between the Royal Tyrrell Museum and the Royal Ontario Museum, the goal of the U.S. was to bring together an international slate of scientists and enthusiasts to share their research on and passion for duck-billed dinosaurs. Hosting the event at the Royal Tyrrell Museum made perfect sense. In one of the few places in the world can boast the abundance and quality of hadrosaur fossils as an iconic “classic Upper Cretaceous non-marine strata of southern Alberta, and the Tyrrell’s collections.

Fifty-plus presentations by international hadrosaur specialists and up-and-coming students rounded out two days of hadrosaur acrophilia in paleontology in Peter Daxson for

skilfully ripping off his terminology. In 1948 was also an opportunity for all of us to honor the contributions of David Weishampel (David 4).

Setting the international tone were our five keynote presenters: Rodolfo Coria (Argentina), Pascal Godefroit (Belgium), Jack Horner (U.S.A.), Khishigjav Tsochbaatar (Mongolia), and our international guest, David Weishampel (U.S.A.). The watershed nature of the meeting was recognized by all attendees and, unfortunately, we managed to overcome logistical obstacles such as an impending strike by Air Canada employees, which resulted in last-minute re-routing of flights and late appearances by some attendees. Be it shown that we truly appreciate the efforts everyone made to attend the symposium.

This volume comprises a part of the content from the symposium, and more. Because we believe this volume and its contents to be a uniquely comprehensive introduction of hadrosaurids, we chose simply to call it *Hadrosaurids*. The scope of the volume encompasses not only the well-known hadrosaurids proper, but also Hadrosauridae, which allows the former group to be evaluated in a broader perspective.

The volume’s 28 chapters are organized into the following six parts, all written by an international by Jack Horner:

Overview includes only one chapter, written by David Weishampel. David has spent a large part of his career studying dinosauran paleobiology and, arguably, has most significant contributions to paleoecology. He has conducted pioneering work on hadrosaurian parental care, feeding (reconstruction), functional morphology of beak structure, and phylogeny. In this chapter he uses data from the second edition of *The Dinosauria* to describe the paleontological research on ornithomimids over the past two centuries, and uses his wisdom to advise where researchers may be focusing in the future.

New Insights Into Hadrosaur Origins includes six chapters that document new and historical materials that shed light on the evolution and diversity of hadrosaurids before the origins of true hadrosaurids. David Norman (David 4) reviews the data and the implications for the origin of Hadrosauridae, and presents some provocative ideas about the evolution of ornithomimid-like group to hadrosaurids. A

standout chapter by Tsogtbataar et al. describes an exciting new taxon from the Djadokhta Formation of Mongolia, important for understanding the origin of hadrosaurids (it is rendered beautifully on the cover of the book by Julius Csotonyi). McDonald et al., You et al., and Barrett et al. provide new information about known specimens, and help sort out some long-standing questions about these specimens. Similarly, Main et al. and Larson et al. remind us of the importance of the North American hadrosauroid record for understanding the origins of Hadrosauridae.

Hadrosaurid Anatomy and Variation includes contributions by Gates, Bell, Farke and Herrero, Evans, Campione, Brink, and colleagues, and focuses on the anatomy of a variety of hadrosaurid taxa from western North America. Gates, Bell, Farke and Herrero, and colleagues describe new specimens from stratigraphic units that are rapidly proving to be important sources of new information about hadrosaur diversity and distributions, whereas the contributions by Evans, Campione, Brink, and colleagues provide in-depth descriptions and interpretations of known taxa and specimens. The morphological details provided here will lead undoubtedly to improved comparative studies.

Biogeography and Biostratigraphy documents the distribution of hadrosaurids in time and space. Here, chapters by Ramírez-Velasco et al. and Dalla Vecchia and colleagues stand out as exceptionally detailed overviews of hadrosaur occurrences in Mexico and Europe, respectively. Similarly, contributions by Bolotsky et al., Coria, and Sullivan and Lucas go a long way to help improve our understanding of hadrosaurian diversity in eastern Asia, South America, and the Southwestern U.S.A. The contribution by Tanke and Evans underscores the importance of properly documenting locality data for specimens.

Function and Growth includes seven contributions that address function, growth, and life habits. Studies of hadrosaur morphology, locomotion, and function by Maidment et al., Persons and Currie, and Henderson employ evolving techniques in computer modeling and engineering that we hope will spark discussion and renewed interest in this topic. Nabavizadeh revisits the all-important question of jaw kinetics via predeantary morphology, and Guenther's com-

parison of postcrania is a step toward identifying different developmental pathways in hadrosaurs. Erickson and Zelenitsky describe ontogenetic changes in tooth morphology/histology in *Hypacrosaurus stebingeri* that reflect dietary changes during development. Lastly, Brinkman's size-distribution data are the basis of conclusions that challenge conventional wisdom related to growth rates in hadrosaurs.

Preservation, Tracks, and Traces is the last part of the volume and includes eight chapters, including contributions by Manning et al., Prieto-Márquez and Wagner, and Bell on skin and skin traces. Of particular note is the chapter on the origins of the classic *Maiasaura* bonebed by Schmitt et al., which many of us have awaited for years (no pressure anymore, Jim!). Contributions by Eberth et al. and Hone et al. present more evidence that some hadrosaurs lived in large, segregated herds, perhaps rivaling in size those of centrosaurian ceratopsians. Back in Alberta, Therrien et al. provide the first evidence of hadrosaur tracks from the Oldman Formation of Alberta, and Tanke and Rothschild provide an exhaustive survey of paleo-osteopathologies in hadrosaurs from Dinosaur Provincial Park.

Nomenclature note—Unlike most forms of science, taxonomy can be quite democratic. Over the last two decades, numerous clade names and definitions have been proposed for the hadrosaurian part of the ornithomimid family tree. Rather than imposing a particular taxonomic scheme on the book's contributors, we chose to allow contributors to employ their preferred taxonomy. Not surprisingly, the book reveals little consensus. In particular, readers may find differential use of the terms Hadrosauridae, Hadrosaurinae, and Saurolophinae across the book's chapters a bit confusing. In order to address this, and other similar confusions, we asked authors to cite their taxonomic sources where necessary.

In summary, we have tried our best to present a group of well-balanced and consistently edited manuscripts, while allowing the authors to express their individual styles. We hope that you all enjoy the volume and find it useful for years to come.

David A. Eberth

David C. Evans

WE THANK ALL OF THE PARTICIPANTS WHO ATTENDED THE International Hadrosaur Symposium in 2011 and helped us realize that this volume would be a successful venture. We thank the authors for helping provide a cohesive and coherent product, and especially for being so patient as the clock kept ticking. Special thanks to the reviewers who did their jobs in a timely manner and were often willing to look at manuscripts more than once, thus ensuring that contributions were of high quality both scientifically and editorially.

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Last, but certainly not least, we recognize P. Ralrick for her colossal contributions to this project. Patty served as our technical editor and editorial assistant, helped review manuscripts, listened to the occasional rant, and also indexed the volume. Without her attention to detail, this project would have taken twice as long and would not have been done half as well. Thanks, Patty, we hope that now you are very satisfied.





A History of the Study of Ornithomorphs: Where Have We Been? Where Are We Now? and Where Are We Going?

David B. Weishampel

ABSTRACT

Where ornithomorph studies have been and where they are going is fascinating. I try to provide answers for the history of the study of ornithomorphs by collecting bibliographic data from the second edition of *The Dinosauria*. The resulting publication trends were examined for initial six factors, nearly all of which increase through the first decade of the twenty-first century. These increases are used to take stock of present-day ornithomorph studies and, finally, to try to predict a future ornithomorph research in this increasingly contingent world.

INTRODUCTION

From a historical perspective, knowledge about a taxonomic group can be judged by its publication rate. A dramatic rise indicates a momentarily stalled interest in the group or a cessation of interest in a lineage (e.g., *Kobayutia* or *Nepesia*, 1901), while a low rate suggests less than vigorous or at least research-entirely focused, on the group (e.g., *Trigys* or when there are few publishing scientists). Finally, a high publication rate may have many reasons, including new discoveries and new taxonomic recognition, and evolutionary convergence, to name a few.

Compilations of taxa are not new to studies of dinosaurs, or even to groups of invertebrates (Sepkoski et al., 1981; Benton, 1987, 1998; Dodson, 1995; Weishampel, 1996; Sepkoski, 2002; Pasteris et al., 2003; Wang and Dodson, 2004). However, this present compilation and survey differs from previous studies in that it focuses on the number of papers published and the research areas these papers address.

For Ornithomorphs, the most abundant and diverse of which are hadrosaurs—the record of publication begins in 1829 with the publication of Mantel's *Iguanodon*, and finishes with the numerous papers, some being issued via conventional journals as well as in line only journals, with no hard copies, of the present day. What this record looks like is presented in Figure 1. How it was obtained and how it is interpreted are the subjects of this chapter.

Central to this volume is the production of a symposium created predominantly to help researchers, which includes a program's program, as well as hadrosaurs, it has been reviewed by the organizers to include iguanodontians as well. By strictly (and slightly more to include iguanodontians, we are practically) down to the base of Ornithomorphs. Hence, this chapter is also Hadrosaurians and more.

MATERIALS AND METHODS

In order to evaluate the rate of publication of papers dealing with ornithomorph dinosaurs, the number of papers was plotted on a graph with x-axis from 1829 to 2004 from an archeography of *The Dinosauria*, second edition (Weishampel et al., 2004). Continuing to publish papers on the main even all dinosaurian taxa, this book is likely to be comprehensive enough for our current purposes. Because the decade of 2005–2009 was incomplete in that volume, the remainder of this decade was filled in proportionally since an approximate representation during the first three and one-half years of the decade. That is, if 2005 produced *n* items are proportions based on tabulations from the first three and one-half years. Total papers and years in each research category (see below) were adjusted by multiplying the number in the first three and one-half years of the 2005–2009 decade by a factor of 2.66 to yield a total proportionally equivalent to other decades. This kind of correction was judged preferable to changing data sources (e.g., Web of Science), which would increase both an inflation of the more obscure literature.

To facilitate the total record, I have then plotted and categorized the papers that went into this total by combining the categories of research (Table 1). I provide general description of these categories, denoted in boldface text below. These categories were usually assessed by title alone, but occasionally it was necessary to consult the paper itself in order to determine which category it belonged to. For example, count of footprints are, eggshell papers, because it was often impossible to assess a unit's of "ornithomorphs" or "beyond Dinosauria" from the title of the paper.

TABLE 1.1. Categories of Ornithomorph Research Identified in This Survey

General taxonomy
Evolutionary paleontology
Phylogeny
Biostratigraphy and taphonomy
Biogeography
Preservation
Soft tissue
Cladistics
Palaeoecology

General taxonomy refers to those publications announcing new species or generic taxa, or new taxonomic revisions that correct errors in the handling of phylogeny (see below). For example, Gilmore's (1913) announcement of *Therapsaloxenus neglectus* is here considered to be in general taxonomy.

Functional morphology is the category for papers involving a biomechanical or functional interpretation of an ornithomorph anatomical system. An example of a functional morphology study is Alexander's (1985) work on stance and gait in ornithomorphs among other dinosaurs.

Phylogeny refers to those studies that attempt to portray the evolutionary history, or phylogeny, of the group. In recent years, these studies have emphasized cladistics in phylogenetic reconstruction (e.g., Prieto-Marquez, 2002), but also include a number of pre-Hennigian analyses (e.g., Colton, 1977).

Biostratigraphy and taphonomy papers involve the geographic distribution of ornithomorphs, either within or among rock units. Rogers (1960) provided an example of how far skeletal taphonomy can provide evidence on long-distance migration in dinosaurs that include hadrosaurs.

Biogeography includes studies that examine the geographic distribution of ornithomorphs either from a dispersal or vicariance perspective, or both. For example, Casanovas et al. (1999) examined the global distribution of archosaurs in the Cretaceous, whereas Luchini et al. (2002) considered the full spectrum of controls on dinosaur diversity, including that of ornithomorphs, as a function of biogeography and biostratigraphy.

Paleoecology papers include those of Corrado et al. (1994) on convergence—or lack thereof—among ornithomorphs and ungulate mammals, and Varricchio and Horner (1997) on the significance of "hotheds" in paleoecological interpretations, and are intended to address the reconstruction of particular taxonomically bound or free ecosystems in the past.

Soft tissue studies have been generally limited to skin impressions. Examples include Ostrom (1975) on the "imprinting" of *Archaeopteryx lithuanica* in the American Museum of Natural History.

Growth includes papers associated with aspects of ontogenetic development. The impact of growth on ornithomorph studies is relatively recent. Here I note Dackon (1974) on the taxonomic significance of growth in *Lambeosaurus* and *Corythosaurus*, as well as various studies by Horner and colleagues (e.g., Horner et al., 1999, 2002) focused on the cellular basis of bone growth.

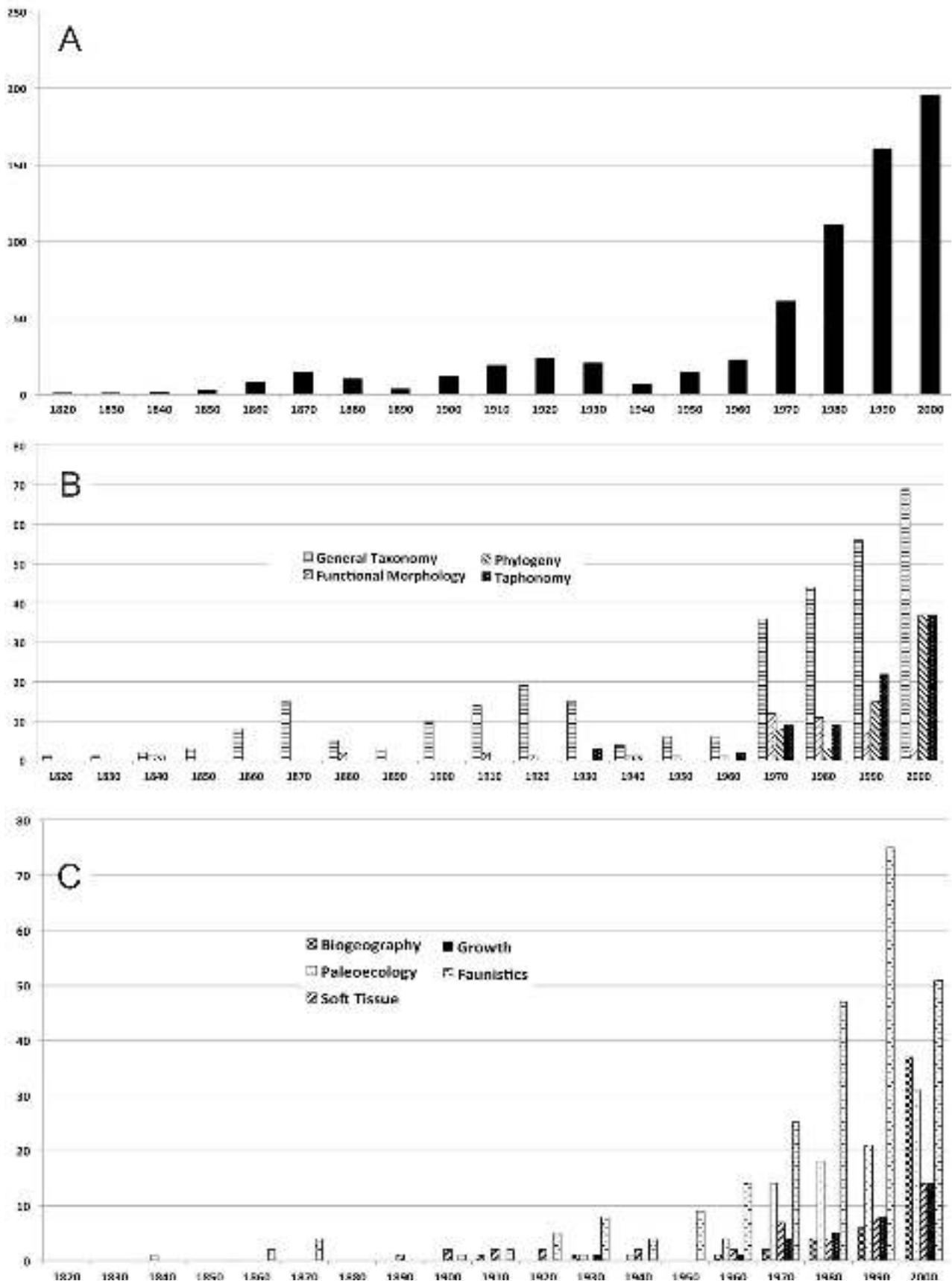
Taxonomies includes papers whose principal purpose is to establish or review a taxonomic classification that include ornithomorphs. For example, Lepparent (1869) reviewed the dinosaurs including many ornithomorphs from the "Cretaceous" of northern Africa.

Usually ornithomorphs were entered into one category. However, a study can contribute here to several categories. For instance, Colton (1977) included dinosaurs in general taxonomy, functional morphology, phylogeny, and other subjects in his major review of North American hadrosaurs, and so it was added to each of these categories.

WHERE HAVE WE BEEN?

Where we have been can be determined by looking at the total curve of ornithomorph publications (Fig. 1.1). Beginning in the 1860s, the number of papers published per decade rises to a high of 5 in the 1870s. It then declines to 1 in the 1890s, and increases again, to 24, in the 1920s. The 1940s see a drop to 7, followed by a persistent, or generally increasing, decade of the 2000s, which is characterized by nearly 200 papers, amounting to almost 2 papers per month.

Before turning to several intrinsic factors, I want to examine three kinds of extrinsic events that may have influenced these numbers and patterns. For possible influences due to world events, the European revolutions of 1848, the American Civil War, World War I, the Russian Revolution, the fall of communism, and the Arab-Israeli and Afghan wars appear to have no substantial influence on rate of publication, whereas the 1929 stock market crash and subsequent worldwide financial depression followed by World War I are likely factors in the cessation of publications in the 1930s and 1940s. Regarding technological influences, there are no great fluctuations in rate of publication for technological events, except for the last two events. It is probably safe to say that the invention of personal computers, particularly laptop (1970s), in combination with the development of the World Wide Web or e-mail (1990s) made a huge impact on the rate of ornithomorph publications. With the initiation of web publishing, this trend is certain to continue. Finally, seasonal fluctuations probably account for smaller perturbations in the total curve. For example, the absence of the 1960s data assemblage from Bernisart probably accounts for the rise in ornithomorph publications during the 1870s and 1880s. The



1.1. Publication trends on ornithomimid dinosaurs. (A) Total publication record of ornithomimid dinosaurs from 1820 to 2000 tabulated by decade; (B) Total publications of general taxonomy, functional morphology, phylogeny, and biostratigraphy and taphonomy, tabulated by decade; (C) Total publications in biogeography, paleoecology, soft tissue, growth, and faunistics, tabulated by decade.

rise in publication rates during the 1910s, 1920s, and 1930s can certainly be attributed to the Great Canadian Dinosaur Rush in Alberta. Finally, as a personal homage, I consider John H. Ostrom's first monographic publication—his 1961 treatment of the hadrosaurids of North America—to signal the beginning of what has turned out to be a plethora of ornithopod publications to the present day.

Intrinsic factors, on the other hand, are some of the subjects that I am interested in, which also have given Ornithopoda pride of place in the world of dinosaur publishing. General taxonomy and faunistics are the largest contributors to the total sample, whereas the rest have relatively low influence.

General taxonomy (Fig. 1.1B) has as long a history, beginning with the first publication on *Iguanodon* by Mantell (1825) and early on encompassing the first publication on *Hadrosaurus* by Leidy (1858). Furthermore, it mirrors fairly well the total publication curve, with a high point of 69 publications during the decade of 2000–2010.

Functional morphology (Fig. 1.1B) has a long, but patchy history, beginning with the publication of Mantell (1848) on the teeth and jaws of *Iguanodon*. It has never been common, but increases significantly in the 1970s and 1980s, with renewed interest in ornithopod jaw mechanics. Functional morphology has been in decline since this time.

Phylogeny (Fig. 1.1B) also has a long and equally patchy history, beginning with Owen's (1842) christening of Dinosauria. Thereafter, there is a long hiatus until the 1970s, when we see an irregular publication record reflecting the large impact of cladistics on phylogeny estimates. The 1990s and 2000s indicate an important increase in cladistic studies, peaking near 40 publications.

Biostratigraphy and taphonomy (Fig. 1.1B) have a relatively short history, confined to the period of the 1930s to the present, and within this span only relatively abundant since the 1970s, with the publications of Dodson (1971), Rogers (1990), and Varricchio and Horner (1993). There is a steady increase in biostratigraphic and taphonomic publications from the 1980s to the 2000s, indicative of increased interest in the sedimentological aspects of ornithopod fossils.

Biogeography (Fig. 1.1C) is in its infancy, with its concentration of publications only evident from the 1960s onward. This is roughly the same time as the scientific ascendancy of plate tectonics and phylogenetic systematics, and thus, may be a direct product of these two revolutions in the natural sciences (Serenó, 1997, 1999a, 1999b; Upchurch et al., 2002). Biogeography reaches its zenith in the decade of 2000; in all likelihood it will continue to increase.

Paleoecology (Fig. 1.1C) has a relatively short history. With a few notable exceptions (Mantell, 1844; Nopcsa, 1934), the history of paleoecology papers really began in the 1960s.

There has been a steady increase in the number of paleoecology publications since then, to a high of more than 30 publications in the decade of 2000–2010.

Soft tissue (Fig. 1.1C), consisting almost entirely of the study of integumentary impressions, has a reasonable steady and long history, increasing steadily since the 1970s. It is presently on a very large upswing, in large part because of the discovery of exceptionally well preserved specimens (particularly in northeastern China) and a more focused evaluation of variation in integumentary patterns (Bell, this volume).

Growth (Fig. 1.1C) has a very modest history. It has been common only since the 1970s, and appears to be on a steep upswing to nearly a dozen papers for the decade of 2000–2010. This increase probably represents the rise in fossil bone histology studies in ornithopods (e.g., Chinsamy, 1995; Horner et al., 2000).

Finally, **faunistics** (Fig. 1.1C) has a long history, approximately paralleling general taxonomy and the total curve, at least since the 1860s. Faunistics seems to drop off during the decade of the 2000s, but this downturn should be treated with skepticism because it is almost certainly an artifact of sampling extrapolation. Examples taken from the 1990s and 2000s include Csiki (1997), Ryan and Russell (2001), López-Martínez et al. (2001), and Zhou et al. (2003).

WHERE ARE WE NOW?

Before we all assembled for the International Hadrosaur Symposium, we all probably thought we knew where our science was. At a minimum, that was what we came to Drumheller to report on. It was hadrosaur taxonomy, North American, Asian, South American, and European hadrosaurs, and ornithopod brains. It was also hadrosaur gigantism and age, hadrosaur jaws and herbivory, locomotor mechanics, taphonomy, integument, tracks, and various aspects of development. This was where we thought our discipline was as we began the symposium.

Eighty-eight percent of the symposium talks ($n = 34$ talks, 16 posters) fall within the categories discussed here (Braman et al., 2011). Most are taxonomic, phylogenetic, or biogeographic in scope. Another half-dozen or more pertain to functional morphology, growth, and taphonomy—a good sampling of the categories examined here (an acclaim delivered independently twice over—the organizers and I both got it right!).

Symposium percentages are all the same order of magnitude compared to those obtained for the decade of 2000–2010, but there are several differences. General taxonomic presentations at the symposium were nearly 25% fewer than from 2000–2010, phylogeny was 19% fewer, taphonomy was 15% fewer, biogeography was 28% fewer, paleoecology was

19% fewer, and faunistics was 13% fewer. Soft tissue remained approximately the same. Interestingly, functional morphology was 14% more and growth was 6% more than from the decade of 2000–2010. While it is tempting to assign significance to individual percentages, they are probably no more than sampling errors when comparing a very small number of symposium talks with the projected breakdown of categories for an entire decade.

WHERE ARE WE GOING?

I am certainly no prognosticator, even about my own research field. Like all historical sciences, our ability to predict the future is fraught with the kinds of unpredictability that derives from historical contingency. There is little inevitability that guides us in the progress of our science—just as there is little that links the hand-cranked ice-cream maker (1840s) to the electron microscope (1930s), a transition that happened in only nine decades. What about going from the invention of the Band-Aid (1930s) to the home computer in five decades? Who would have predicted these changes?

But the contents of this volume give an inkling of where we are headed, at least in the short run. I see continued fieldwork, the wellspring of our science. Its direct consequences—new species and taxonomic revisions—are likely to be accompanied by a healthy continuance of studies focused on comparative anatomy, both bony and inferred soft tissue. To do so requires a healthy dose of phylogenetic systematics, which now should be part of everyone's toolkit.

In functional morphology, finite element analyses and tooth-wear studies have appeared on the horizon and I hope these will be coupled with cladistic analyses to produce even more outstanding work. Finally, growth studies are very likely to continue in the future: the small bit of bone given up for a thin-section is bound to yield disproportionately much more subtle and profound information than if it were left with the rest of the bone.

Still, things do not always work out that way. Contingency makes history messy. Things come out of left field and WHAM! Someone discovers the most amazing specimen or means by which colors can be inferred from skin impressions. All of a sudden, with no way of predicting, we are all scrambling to do research on the melanosomes of what could turn out to be red-, green-, and yellow-striped ornithopods!

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