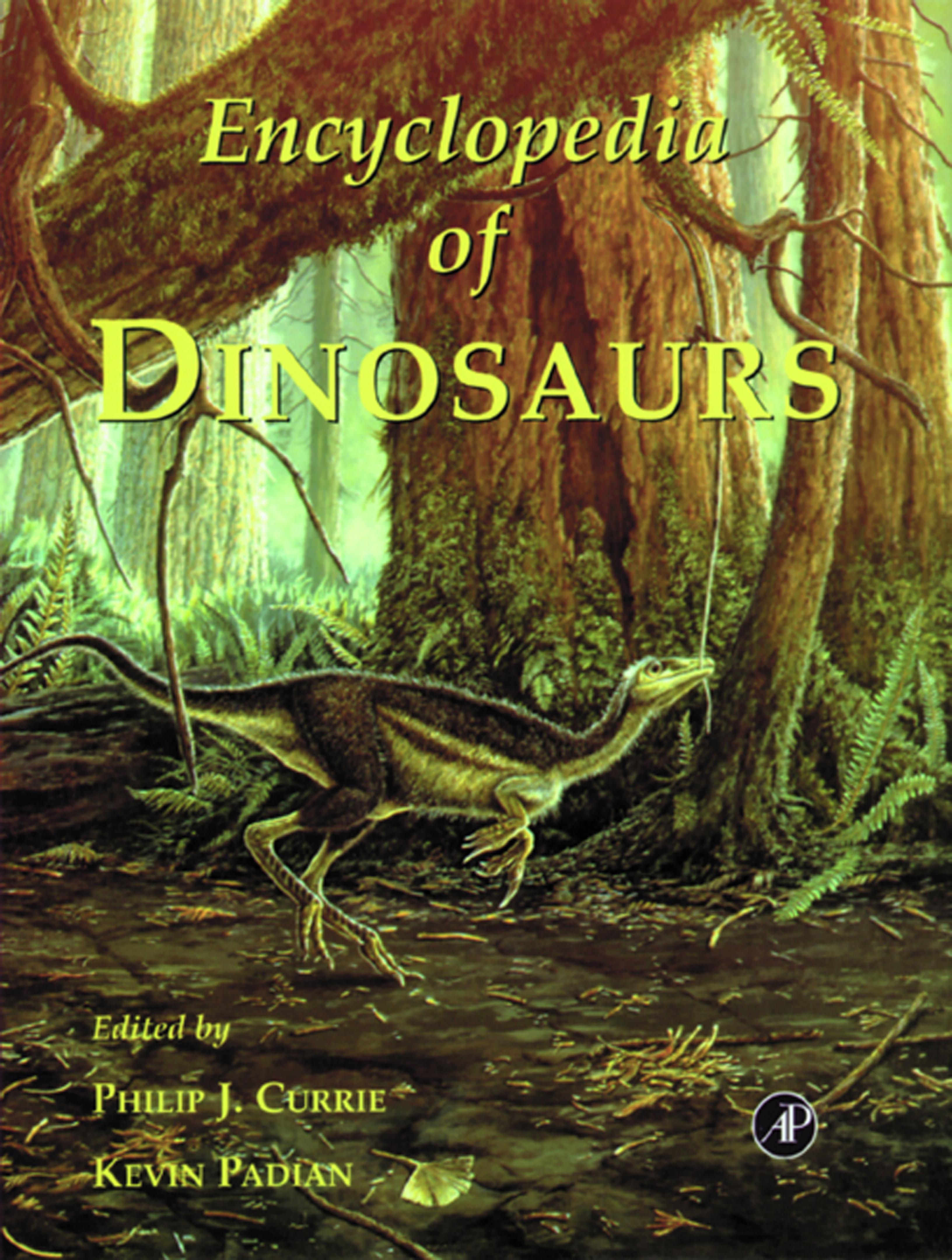


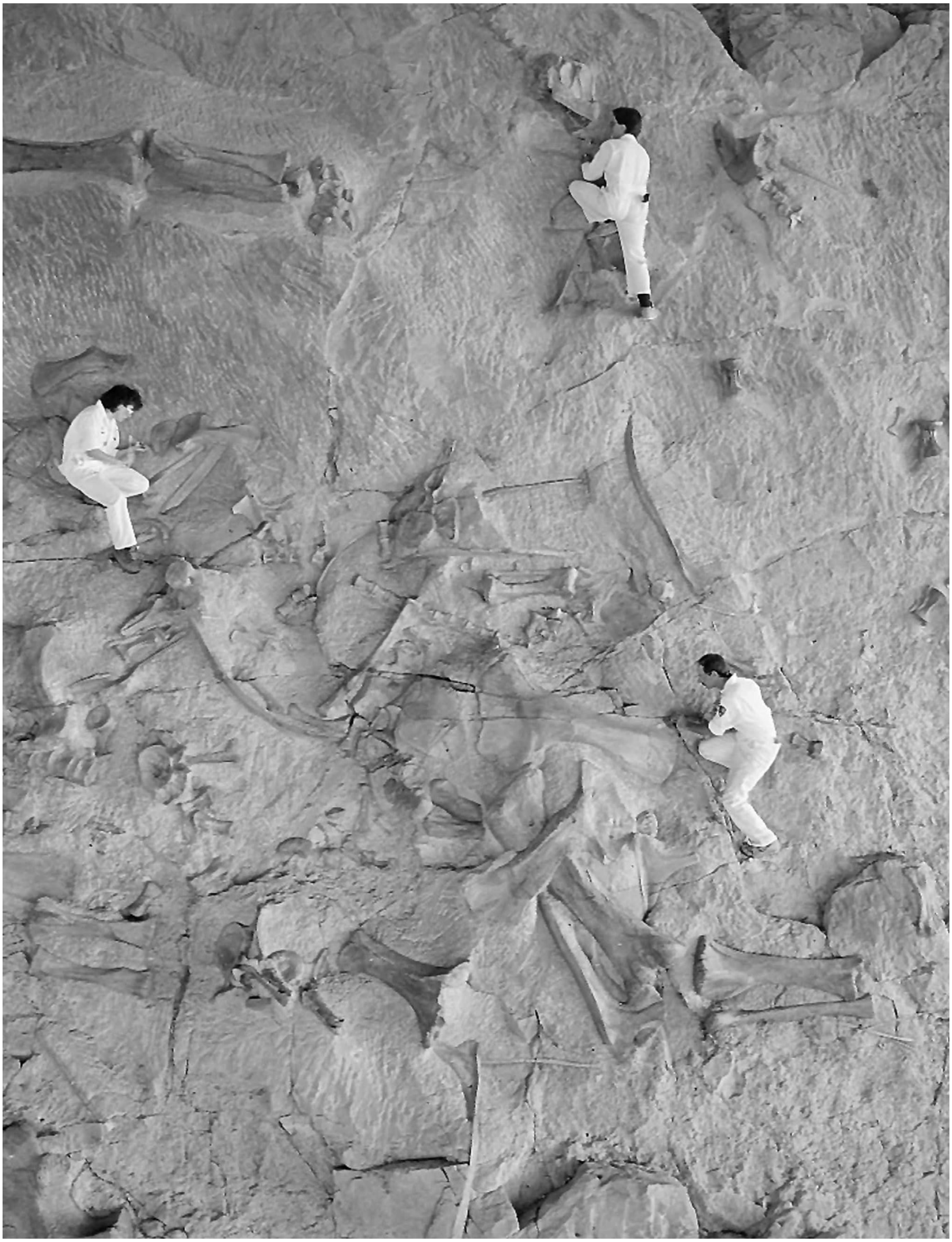
Encyclopedia of Dinosaurs

Edited by

Philip J. Currie
Kevin Padian

Encyclopedia of

DINOSAURS



Encyclopedia of

DINOSAURS

EDITED BY

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A Guide to Using the Encyclopedia

The *Encyclopedia of Dinosaurs* is a complete source of information on the subject of dinosaurs, contained within the covers of a single volume. Each article in the Encyclopedia provides an overview of the selected topic to inform a broad spectrum of readers, from researchers to the interested general public.

In order that you, the reader, will derive the maximum benefit from the *Encyclopedia of Dinosaurs*, we have provided this Guide. It explains how the book is organized and how the information within it can be located.

Subject Areas

The *Encyclopedia of Dinosaurs* presents 275 separate articles on the whole range of dinosaur study. It includes information not only on the organisms themselves, of course, but also on all other aspects of this field.

The articles in the *Encyclopedia of Dinosaurs* fall within nine general subject areas, as follows:

- Kinds of Dinosaurs Around the World
- Groups of Dinosaurs and Related Taxa
- The Biology of Dinosaurs
- Environments of the Past
- Important Dinosaur Localities
- Geology and Dinosaurs
- Institutions of Dinosaur Study
- Dinosaur Expeditions
- Dinosaur Research and Techniques

A Thematic Table of Contents appears in the introductory section of the Encyclopedia on page xv. It has a complete list of all the articles in the book, placed according to subject area and in relation to other topics.

Organization

The *Encyclopedia of Dinosaurs* is organized to provide the maximum ease of use for its readers. All of the articles are arranged in a single alphabetical sequence by title, from ''A'' (Abelisauridae, African Dinosaurs, etc.) to ''Z'' (Zigong Museum). An alphabetical Table of Contents for the articles can be found on p. v of this introductory section.

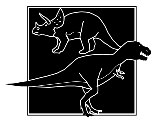
As a reader of the Encyclopedia, you can use this alphabetical Table of Contents by itself to locate a topic. Or you can first identify the topic in the Thematic Table of Contents and then go to the alphabetical Table to find the page location.

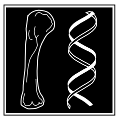
So that they can be more easily identified, article titles begin with the key word or phrase indicating the topic, with any descriptive terms following this. For example, ''Pelvis, Comparative Anatomy'' is the title assigned to this article rather than ''Comparative Anatomy of the Pelvis,'' because the specific term *Pelvis* is the key word.

Article Format

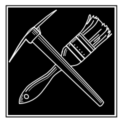
Articles in the *Encyclopedia of Dinosaurs* are divided into three general categories. The first category includes concise entries that deal with highly focused topics, such as ''Albany Museum,'' ''Cañon City,'' ''Dinoturbation,'' ''Gastralia,'' and ''Tooth Marks.'' These entries vary in length from one to several paragraphs. The second category, the bulk of the text, includes entries of the standard length of 1 to 4 pages, such as "African Dinosaurs," "Djadokhta Formation," "Dry Mesa Quarry," "Egg Mountain," "Musculature," "Paleoclimatology," and "Trace Fossils."

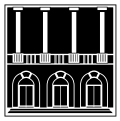
Major articles constitute the third category. They deal with broad areas of dinosaur study, such as "Behavior," "Bird Origins," "Evolution," and "Systematics." These articles are of extended length, typically 5 to 15 pages, and are identified as to general theme by the following system of symbols:


Kinds of Dinosaurs


Dinosaur Biology


Geology & Sites


Research Methods


Dinosaur Institutions

Articles in all three categories have been written by individual contributors, as indicated in the article heading. The only exception is that some shorter entries are unsigned. These have been prepared collectively by the general editors, Drs. Currie and Padian.

Cross-References

The *Encyclopedia of Dinosaurs* has an extensive system of cross-referencing. Cross-references to other articles appear in three forms: as marginal headings within the A-to-Z article sequence; as designations within the running text of an article; and as indications of related topics at the end of an article.

As an example of the first type of reference cited above, the following marginal entry appears in the A-to-Z article list between the entries "Archosauria" and "Arctometatarsalia:"

Arctic Dinosaurs *see* POLAR DINOSAURS

This reference indicates that the topic of dinosaurs of the Arctic region is discussed elsewhere, under the article title "Polar Dinosaurs."

An example of the second type, a cross-reference within the running text of an article, is this excerpt from the entry "Central Asiatic Expeditions":

> Discovery of non-avian dinosaurs in Central Asia was pioneered by the AMERICAN MUSEUM OF NATURAL HISTORY (AMNH) during a series of swashbuckling Central Asiatic Expeditions in the 1920s.

This indicates that the item "American Museum of Natural History," which is set off in the text by small capital letters, appears as a separate article within the Encyclopedia. (This reference appears here because the Museum was the sponsor of these expeditions.)

An example of the third type, a cross-reference at the end of the article, can be found in the entry "Distribution and Diversity." This article concludes with the statement:

> See also the following related entries:
> BIOGEOGRAPHY • MIGRATION • PLATE TECTONICS

This reference indicates that these three articles all provide some additional information about the distribution and diversity of dinosaurs.

Bibliography

The bibliography section appears as the last element in an article, under the heading "References." This section lists recent secondary sources that will aid the reader in locating more detailed or technical information. Review articles and research papers that are important to a more detailed understanding of the topic are also listed here.

The bibliographic entries in this Encyclopedia are for the benefit of the reader, to provide references for further reading or research on the given topic. Thus they typically consist of a limited number of entries. They are not intended to represent a complete listing of all materials consulted by the author or authors in preparing the article.

Index

The Subject Index for the *Encyclopedia of Dinosaurs* contains more than 5,840 entries. Within the entry for a given topic, references to general coverage of the topic appear first, such as a complete article on the subject. References to more specific aspects of the topic then appear below this in an indented list.

Encyclopedia Website

The *Encyclopedia of Dinosaurs* maintains an editorial Web Page on the Internet at:

http://www.apnet.com/dinosaur/

The *Encyclopedia of Dinosaurs* site provides information about this project and links to many related sites that feature dinosaurs. The site will continue to evolve as more information becomes available.

FOREWORD

We human beings are fascinated by dinosaurs. The first reports of the giant bones of extinct creatures caused a worldwide sensation, and in the century and a half since then, our interest has never diminished. In every country of the world, children and adults are entranced by dinosaurs.

It is often imagined that the current dinosaur mania is a recent phenomenon; in fact it is not. When I first started writing a novel about dinosaurs, back in 1981, I put the project aside because at that time, Americans seemed to be in the grip of an unprecedented dinosaur mania. There were dinosaur cups and saucers, dinosaur toys, dinosaur bedspreads; museums were having dinosaur shows; it seemed there were dinosaurs everywhere you looked. I did not want to write a book that exploited a fashion of the moment. So I waited. But year after year, the fashion never went away. Finally I realized that our fascination with dinosaurs is a permanent phenomenon. It is always there.

Children, of course, have always been captivated by dinosaurs. To go to a museum and see young children, barely able to walk and talk, shrieking "Stegosaurus" and "Tyrannosaurus" as they view the creatures is a very striking thing. Why does it happen? What is going on in their minds as they shout out those complex Latin names? How do we explain the fact that dinosaurs excite the imagination of adults and children throughout the world?

Over the years, I have entertained many theories. For a while, I thought the phenomenon might be characteristic of those countries, like the United States, where many fossils have been found—a kind of nationalistic interest, if you will. But dinosaurs are just as popular in countries such as Japan and Italy, where few remains have been found.

For a while, I thought it was primarily a childish interest. But in museums, you'll notice that adults are equally fascinated. To be honest, it often seems that children are only an excuse for adults to visit the dinosaurs.

Later on, I suspected the interest in dinosaurs might be something that children passed on to each other, a trait of a children's subculture. But my own daughter showed a marked interest in dinosaurs long before she went to preschool—indeed, before she was even very verbal.

Still later, I thought this enthusiasm was provoked by the great size of these creatures. But smaller dinosaurs excite just as much interest among children. Baby dinosaurs are very appealing. And in any case, the dinosaur toys are all small. . . .

For a time, I wondered whether the interest had something to do with the fact that the dinosaurs had become extinct. But children are not clear about this. When my daughter was two years old, she asked to see dinosaurs at the zoo. She had been to the zoo several times, and apparently believed the dinosaurs were housed in some section we hadn't visited yet. When she was told that she could not see dinosaurs, she gave a resigned shrug—parents never do what you want them to do!

Perhaps, I thought, that was a clue. Children spend much of their lives powerless and frustrated. I began to entertain a Freudian notion that being able to pronounce the complex names of huge creatures afforded children a sense of control. In a child's world, after all, everything is big—parents, cars, everything. And naming things is a classic human procedure to reduce anxiety. (Patients are always relieved to hear that they have "idiopathic hypertension," even though the term is literally meaningless.) But once again, careful observation cast doubt on this idea. When my daughter was four, I took her and two friends to Stan Winston's workshop to see the dinosaurs being constructed for Jurassic Park. I thought they'd enjoy it, but they didn't. Although the dinosaurs were then only sculpted in clay, the girls were distressed by what they saw. The animals were simply too big, and too real-looking. It is one thing to play with little dinosaur toys. It is quite another to walk beneath the enormous scaly legs of a towering tyrannosaur, or to touch the big claw of a Velociraptor. The kids were very uneasy. They wanted to leave.

So in the end, I decided I just don't understand why children are fascinated by dinosaurs. And I don't believe anybody understands. In the end, it is a mystery.

And it may be that the mystery is part of the fascination. Certainly for adults, dinosaurs present an intriguing puzzle, in which fantasies are inevitably provoked. Although we know far more about dinosaurs than we did a few decades ago, the truth is that we still know very little. We don't really know what these creatures looked like, or how they behaved. We have some bones, impressions of skin, some trackways, and many fascinating speculations about their biology and social organization. But what hard evidence remains of their long-vanished world is tantalizing and incomplete.

And so they still provoke our dreams. And, probably, they always will.

Michael Crichton

PREFACE

Is it possible that the scientific understanding of dinosaurs has now come so far that a volume such as this, as big as the Manhattan telephone directory, is necessary to compile even a synopsis of what we know about them?

Could Dr. Gideon Mantell and Dean William Buckland, when they described the first remains of what would become known as dinosaurs, have ever imagined the scientific attention that would be paid to them more than 170 years later?

Could Richard Owen, who gave Dinosauria its name in 1842, have intended that his "fearfully great lizards" would be used as metaphors for both evolutionary success and obsolescence?

As we sit today on three decades of the most awesome explosion of knowledge about dinosaurs in history, can we imagine how much more will be learned before most of us now active in the field reach retirement age?

The answers to these questions are probably yes, no, yes, and no, perhaps in no particular order. This is not the first phonebook-sized compendium of dinosaur information, and we wish at the outset to acknowledge both our debt to and admiration for the already classic work, *The Dinosauria* (D. B. Weishampel, P. Dodson, and H. Osmólska, eds.; University of California Press, 1990), which organizes so much of what is known in such an accessible way. This volume should be seen in many respects as a companion to that one, which was dedicated to exploring the individual dinosaurian groups in considerable depth.

Our focus in this *Encyclopedia* is to provide background and a point of reference to the recent literature on dinosaurian subjects in general. The two books can be read in similar and completely different ways; in the organization of the *Encyclopedia* we have tried to foresee the uses that it may serve for its audience. It is unlikely, of course, that Mantell and Buckland could have foreseen much of what has transpired around their *Iguanodon* and *Megalosaurus*, and hundreds of their reptilian kin, so far into the future; indeed, in the 1820s these men had themselves only the scarcest idea of the nature and importance of the fossil bones they were describing. As for Richard Owen, there was little that escaped his eye, and he was always looking to posterity. In his own time he regarded his creations as approaching the great mammals in physiological sophistication; yet, like all reptilian forms of the Secondary Era (Mesozoic), they were doomed to extinction and replacement. But even he, like us toiling in the fields today, can have no idea of what will come next. The possibilities seem almost limitless.

A few words about what this book is and is not. (This part seems to be read only infrequently by reviewers, but we hope it will help the general reader.)

An encyclopedia is designed to be a concise summary of knowledge, ideas, historical background, and current thinking on a general topic. The information for a given entry is not exhaustive; rather, through cross-references and citations to other literature, readers are invited to learn more and explore wider resources. Consequently, the name of every dinosaur, geological formation, quarry, museum, and idea about how dinosaurs lived and died will not be found under its own entry. Many of these names may be found in the indexes at the end of the book, subsumed under other entries, and still others will be gleaned by surfing the cross-references as one would on the Internet. We have assembled a most knowledgeable contingent of experts from all over the globe on various subjects, and we hope that they, and you, enjoy and learn as much from perusing this book as we did in editing it.

For more exhaustive listings of dinosaurian names and histories, a good start can be made in *The Dinosauria* or in Don Glut's *Dinosaurs, the Encyclopedia* (McFarland & Company, Inc., 1997). For an entry into the primary literature about dinosaurs and all extinct backboned things, there is no finer source than the many volumes of the *Bibliography of Fossil Vertebrates*, produced over the years by A. S. Romer, Charles L. Camp, Joseph T. Gregory, Judy Bacskai, George Shkurkin, and a host of colleagues, under the most recent auspices of the American Geological Institute and the Society of Vertebrate Paleontology.

Recent textbook-style works about dinosaurs include D. B. Norman's *The Illustrated Encyclopedia of Dinosaurs* (Salamander, 1985), Spencer G. Lucas's *Dinosaurs: The Textbook* (William C. Brown, 1996), and D. E. Fastovsky and D. B. Weishampel's *The Evolution and Extinction of the Dinosaurs* (Cambridge University Press, 1996). Finally, for younger dinosaur enthusiasts, The Dinosaur Society (East Islip, New York) works with both professional paleontologists and educators to provide the best of what is new and what is known to the many children and adults who want to learn more.

The taxonomic conventions of this book do not follow the venerable Linnean System, in place since 1763 (well before evolution was a mainstream scientific concept), but the newer Phylogenetic System, based on phylogenetic systematics or cladistics. The principles of this system are explained in this work and in others referenced herein, and need not be detailed at this point. Cladistic conventions hold that all taxa (named groups of organisms) must include a common ancestor and all its descendants in theory (i.e., monophyletic groups). All taxa must have both a definition of their ancestry and membership and a diagnosis of the uniquely shared evolutionary features by which they may be recognized. For the sake of stability, we have restricted definitions to node-based and stem-based kinds, as explained in the entry ''Phylogenetic System.'' We have tried to provide definitions for every taxon (stem- and node-based) and diagnoses for every node-based taxon in this book, though many will change with future research. A data matrix of the characteristics and taxa used in phylogenetic analyses is a *sine qua non* of formal systematic research, and it was our initial hope to include matrices in this work; however, the constant revision and expansion of these matrices would soon outdate any printed effort, and we are now more hopeful that these may be made available and updated on CD-ROM or in World Wide Web format in the future.

Controversies are the business of science, which thrives by expanding, testing, or overturning what we think we already know. And dinosaurs are no strangers to debate; many questions from phylogeny to physiology have strong cases for divergent conclusions. In this book we present these controversies as they are seen today. Many are new, some are old; some may well be resolved with further work, and some may never be. The viewpoints of the authors of individual entries may not always coincide; the authors were not recruited because they agreed with each other's conclusions, but because they had something intelligent to say. Of course, not all apparent controversies are real; some have been settled, at least to the satisfaction of the paleontological community's consensus, and excessive attention is not paid to these here. Many apparent controversies regarding dinosaurs live more in the minds of the representatives of the press than in those of the scientists.

Finally, we express our appreciation to our editorial crew at Academic Press, including Gail Rice, Chris Morris, and especially Chuck Crumly, who remained the driving force behind this volume's realization; to Eva Koppelhus, John Hutchinson, and Leakena Au, for pragmatic assistance beyond the call of duty; to the staff of the Tyrrell Museum of Palaeontology, particularly Pat Bobra, and the support of the University of California Museum of Paleontology; to the various individuals, journal editors, publishers, and copyright holders who allowed us to reprint many of the wonderful illustrations in this book; and especially to all our authors, who met deadlines, extraordinary requests, and last-minute pleas with patience and cooperation. To everyone, our best thanks.

Philip Currie and Kevin Padian
Drumheller, Alberta, and Berkeley, California

DEDICATION

To

John H. Ostrom

In a career spanning some forty years in vertebrate paleontology, John Ostrom has worked on so many groups of dinosaurs, and on so many problems relating to the paleobiology of dinosaurs, that he has become *the* central figure in dinosaur research since the mid-1960s. Originally headed for a career in medicine, John became sidetracked under the spell of George Gaylord Simpson and Ned Colbert, from whom he learned vertebrate paleontology at the American Museum of Natural History while a student at Columbia University in the 1950s. He produced several studies of living and extinct amphibians and reptiles, and finally settled on a Ph.D. thesis project studying the skulls of North American hadrosaurs, mainly using the spectacular collections of the AMNH. It was not long before he challenged prevailing ideas about the paleoecology of hadrosaurs, too, suggesting that they were not aquatic but terrestrial. This approach of using anatomy and functional morphology to ask broader questions about paleobiology and behavior would become a hallmark of John Ostrom's work.

After a brief stint teaching at Beloit College, John joined the faculty at Yale, where he has spent the rest of his career. Undoubtedly his most important contributions to the collections of the Yale Peabody Museum were those from the Cloverly Formation of Wyoming, which included various remains of ornithopods, ankylosaurs, and particularly an ''unusual'' theropod dinosaur that John christened *Deinonychus,* or ''terrible claw,'' in 1969. This beast was to change our concept of dinosaurs in more ways than one. John brought to life an animal that stalked its prey with jaws full of large teeth, long arms with prehensile hands and sharp talons, and a foot that bore a huge curved claw on its second toe, which could not have been used in walking. *Deinonychus* captured the imagination of dinosaur fans everywhere, notably in Michael Crichton's *Jurassic Park.* But that was only a small part of the maelstrom of interest in dinosaurs that grew from John's work.

In 1970 John attended the First North American Paleontological Convention and presented an innocent-sounding paper called ''Terrestrial Vertebrates as Indicators of Mesozoic Climates.'' In it, he maintained that the zoogeography and behavior of living reptiles were inappropriately stereotyped, and that Mesozoic dinosaurs were at least as widespread and ecologically varied. His ideas on the subject were amplified and studied further by his student Robert Bakker, who was largely responsible for popularizing the ''renaissance'' of ideas about dinosaurian warm-bloodedness. These debates thrived for a decade, and still survive today in modified form.

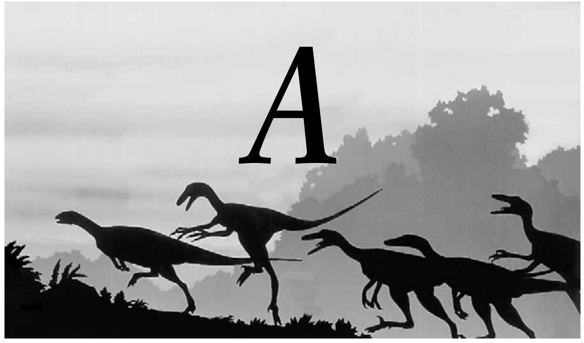
Perhaps John's greatest contribution to dinosaurs was to recognize that a whole group of them was largely unrecognized: namely, birds. In 1973 John first advanced a synopsis of the evidence that birds had descended from small coelurosaurian dinosaurs. He had gotten this idea (which can be traced back to T. H. Huxley, but was long abandoned) while in Germany studying pterosaurs in the company of his old friend Peter Wellnhofer. John had traveled to Haarlem, in The Netherlands, to look at their relatively small collection of Solnhofen pterosaurs, when he found that one specimen, known only from a hindlimb, had a very dinosaur-like foot. When he looked more closely, he also saw impressions of feathers. This was obviously not a pterosaur, but an *Archaeopteryx*.

As John tells the story, he was faced with a dilemma. Should he ask to borrow the specimen, bring it home, and then ''suddenly'' discover its true identity? Or should he come clean from the start, risking the loss of ever seeing it again once its value became apparent? He took the latter course. The old, white-haired curator was nonplussed; he gasped and wiped his brow. ''You have made our museum famous,'' he managed to say gratefully, and walked away with the newly precious relic. John forlornly began to gather his things, and was about to leave when the curator reappeared—with the world's newest *Archaeopteryx* specimen wrapped in a shoebox, tied with string. He handed John the box, and history took its course.

The *Archaeopteryx* specimen at Teyler, like the others, had reminded John not only of dinosaurs, but of theropod dinosaurs—particularly of the ones he had been recently studying at Yale, such as *Deinonychus* and *Ornitholestes,* and *Compsognathus* in Munich. Detailed comparisons of these animals, as well as living birds and more distantly related archosaurs, resulted in a series of papers in which John established that birds evolved from small coelurosaurs, probably sometime in the Middle or Late Jurassic. Controversy has flared around this issue intermittently for nearly 25 years, yet it is one of the more firmly established hypotheses in vertebrate history. But John was not content with the origin of birds; he wanted to explore the origin of their flight. To him, the terrestrial, predatory habits of the theropod relatives of birds suggested their origin from the ground up, running and flapping, perhaps initially after small insects. John's heuristic model of *Archaeopteryx,* using its wings as flyswatters, attracted support, intrigue, and brickbats, but stimulated a look into this question from many disciplines and a great deal of further research on the origin of major evolutionary adaptations.

Perhaps one of the reasons for John's pervasive influence, both in the professional field and among interested laymen, is the clarity and simplicity of his writing style. Had he chosen to obfuscate his ideas in a mountain of impenetrable scientific prose, they would not have gotten much of the attention they have. But he has always written directly, modestly, and accessibly, avoiding hyperbole and dogma. (How many paleontologists could have confined themselves to the understatement of calling *Deinonychus* ''an unusual theropod''?) He has been a model for his students and colleagues alike, and many entries in this book testify to the endurance and importance of his work and his thought. On behalf of all the authors, it is our great pleasure to dedicate the *Encyclopedia of Dinosaurs* to John Ostrom.

The Editors



Abelisauridae

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Abelisauridae constitutes a clade of CRETACEOUS theropods widely documented in the Gondwanan continents (South America, Madagascar, and India). As far as Argentina is concerned, abelisaurids are the best represented group of predatory dinosaurs from the Cretaceous deposits in both number of specimens and species diversity. Abelisaurids underwent a significant evolutionary radiation during the Cretaceous in South America, becoming active predators of large size (see SOUTH AMERICAN DINOSAURS).

Abelisauridae was originally established by Bonaparte and Novas (1985) to include the Late Cretaceous Patagonian dinosaur *Abelisaurus comahuensis* as a mean of emphasizing the distinctness of this taxon with respect to the remaining theropods. The list of abelisaurids, however, rapidly increased: *Carnotaurus sastrei* (Bonaparte *et al*., 1990), *Xenotarsosaurus bonapartei* (Martínez *et al*., 1986), *Indosaurus matleyi* and *Indosuchus raptorius* (both taxa from the Lameta Group, Late Cretaceous of India; von Huene and Matley, 1933; Chatterjee, 1978; Bonaparte and Novas, 1985; Bonaparte, 1991), yet undescribed *Carnotaurus*-like creatures (Coria and Salgado, 1993), and *Majungasaurus crenatissimus* (Maevarano Formation, Campanian; Madagascar; Lavocat, 1955; Bonaparte; 1991; Sampson *et al*., 1996) were added to the family.

Abelisauridae is defined to include the previously listed taxa and all the descendants of their common ancestor. Diagnostic characters of Abelisauridae include craniocaudally short and deep premaxilla; dorsoventrally deep snout at the level of the narial openings; frontals dorsoventrally thickened resulting in a dorsal bulking (*Abelisaurus*), paired horn-like structures (*Carnotaurus*) or a dome-like prominence (*Majungasaurus*; Sampson *et al*., 1996); posterior surface of basioccipital wide and smooth below occipital condyle; dentary short, with convex ventral margin; and loose contacts among dentary, splenial, and postdentary bones.

Abelisauridae seems to be related to the small theropod *Noasaurus leali* (Bonaparte and Powell, 1980) because both taxa share maxillae with subvertical ascending rami and cervical vertebrae with hypertrophied epipophyses and reduced neural spines (Bonaparte, 1991; Bonaparte *et al*., 1990; Novas, 1991, 1992). Novas (1991) coined the name Abelisauria to encompass Abelisauridae, *Noasaurus*, and their most recent common ancestor. *Ligabueino andesi* resembles abelisaurs in the morphology of the cervical vertebrae (Bonaparte, 1996).

Interestingly, abelisaurids show close resemblances with the Cenomanian carcharodontosaurids *Giganotosaurus carolinii* and *Carcharodontosaurus saharicus* (Coria and Salgado, 1995; Sereno *et al*., 1996). These taxa exhibit many derived traits in common (e.g., antorbital fossae reduced, similar patterns of rugosities on external surfaces of nasals and maxillae, preorbital openings anteroposteriorly expanded, wide contacts between lacrimals and postorbitals forming thick ''brows'' above orbits, and eyes enclosed by sinuous orbital margins of lacrimals and postorbitals), suggesting that they are more closely related than previously thought (Coria and Salgado, 1995; Rauhut, 1994; Sereno *et al*., 1996). The resemblances noted among the different South American, Malagasian, and Indian taxa suggest Gondwanan origins for abelisaurs plus carcharodontosaurids, contrary to some recent proposals (e.g., Sereno *et al*., 1996).

The phylogenetic relationships of Abelisauridae need to be studied in depth. *Abelisaurus* and *Carnotaurus*, at least, exhibit several apomorphic resemblances in the morphology of the dorsal and sacral vertebrae with the JURASSIC *Ceratosaurus nasicornis*, and the taxon Neoceratosauria has been erected for this clade (Novas, 1991, 1992).

References

Bonaparte, J. F. (1991). The Gondwanan theropod families Abelisauridae and Noasauridae. *Historical Biol.* **5,** 1–25.

Bonaparte, J. F. (1996). Cretaceous tetrapods of Argentina. *Münchner Geowissenchaftliche Abhandlungen (A)* **30,** 73–130.

Bonaparte, J. F., and Novas, F. E. (1985). *Abelisaurus comahuensis*, n.g. et n.sp., Carnosauria del Cretácico Tardío de Patagonia. *Ameghiniana* **21**(2–4), 259–265.

Bonaparte, J. F., and Powell, J. E. (1980). A continental assemblage of tetrapods from the Upper Cretaceous beds of El Brete, northwestern Argentina. *Mem. Soc. Geol. France N. Ser.* **139,** 19–28.

Bonaparte, J. F., Novas, F. E., and Coria, R. A. (1990). *Carnotaurus sastrei* Bonaparte, the horned, lightly built carnosaur from the middle Cretaceous of Patagonia. *Contrib. Sci. Nat. History Museum Los Angeles County* **416,** 1–42.

Chatterjee, S. (1978). *Indosuchus* and *Indosaurus*, Cretaceous carnosaurs from India. *Journal of Paleontology* **52,** 570–580.

Coria, R. A., and Salgado, L. (1993). Un probable nuevo neoceratosauria Novas, 1989 (Theropoda) del Miembro Huincul, Formación Río Limay (Cretácico presenoniano) de Neuquen. *Ameghiniana* **30**(3), 327.

Coria, R. A., and Salgado, L. (1995). A new giant carnivorous dinosaur from the Cretaceous of Patagonia. *Nature* **377,** 224–226.

Lavocat, R. (1955). Sur une portion de mandibule de théropode provenant du Crétace supérieur de Madagascar. *Bull. Musee Natl. d'Histoire Nat. Ser. 2* **27,** 256–259.

Martínez, R., Ginmenez, O., Rodriguez, J., and Bochatey, G. (1986). *Xenotarsosaurus bonapartei* gen. et. sp. nov. (Carnosauria, Abelisauridae), un nuevo Theropoda de la Formación Bajo Barreal, Chubut, Argentina. *IV Congr. Argentino Paleontol. Bioestratigr. Actas* **2,** 23–31.

Novas, F. E. (1991). Relaciones filogenéticas de los dinosaurios terópodos ceratosaurios. *Ameghiniana* **28**(3/4), 410.

Novas, F. E. (1992). La evolución de los dinosaurios carnívoros. In *Los dinosaurios y su entorno biótico. Actas II Curso de Paleontología en Cuenca* (J. L. Sanz and A. Buscalioni, Eds.), pp. 125–163. Instituto "Juan de Valdés," Ayuntamiento de Cuenca, España.

Rauhut, O. (1994). Zur systematischen Stellung der afrikanischen Theropoden *Carcharodontosaurus* Stromer 1931 und *Bahariasaurus* Stromer 1934. *Berliner Geowissenchaften Abhandlungen* **16,** 357–375.

Sampson, S., Krause, D., Forster, C., and Dodson, P. (1996). Non-avian theropod dinosaurs from the Late Cretaceous of Madagascar and their paleobiogeographic implications. *J. Vertebr. Paleontol.* **16**(3). [Abstract]

Sereno, P., Dutheil, D., Iarochene, M., Larsson, H., Lyon, G., Magwene, P., Sidor, C., Varrichio, D., and Wilson, J. (1996). Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. *Science* **272,** 986–991.

von Huene, F., and Matley, C. (1933). The Cretaceous Saurischia and Ornithischia of the central provinces of India. *Mem. Geol. Survey India* **21,** 1–74.

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Specimens collected by Joseph Leidy are a part of this collection, but specimens that were the basis of many of E. D. Cope's publications are now at the American Museum of Natural History.

see MUSEUMS AND DISPLAYS

African Dinosaurs

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The fossil record of dinosaurs in Africa extends from the Late TRIASSIC, over 200 million years ago, until the Late CRETACEOUS, presumably 65 million years ago, although the extinction event that ended the reign of dinosaurs has yet to be documented in Africa. Throughout this length of time, Africa remained relatively stable geologically, changing position only slightly by drifting and rotating northward. By contrast, Africa's neighboring continents moved greatly, resulting in ocean barriers between what were once contiguous land masses. The changing geography of Africa and its neighbors throughout the MESOZOIC is fundamental to understanding the dinosaurs found there.

During the Late Triassic through the Early JURASSIC, major continental land masses were united into the supercontinent of Pangaea. Because the land was not divided into separate continents, dinosaurs and other animals were more or less free to expand across the entire area, not constrained by ocean barriers but rather by environmental and ecological differentiation of this large land area. Thus, the dinosaur fauna of the Late Triassic and Early Jurassic is generally similar across the globe because the globe had only one continent rather than several continents acting as separate theaters of evolution.

Late Triassic dinosaur sites are found extensively in southern Africa (particularly South Africa, Lesotho, and Zimbabwe) and to a lesser extent in northern Africa (Morocco). Herbivorous prosauropods (*Azendohsaurus*, *Blikanasaurus*, *Euskelosaurus*, and *Melanorosaurus*) are the best known of African Triassic dinosaurs. Footprints and incomplete remains indicate the presence of small THEROPODS and ORNITHISCHIANS. The Triassic–Jurassic boundary is marked by extinctions globally, but the boundary has not been studied in detail in Africa.

Early Jurassic localities, like those of the Late Triassic, are concentrated in southern (Lesotho, Namibia, South Africa, and Zimbabwe) and northern Africa (Algeria and Morocco). The northern record is predominantly footprints, although tracks are also found in the south. PROSAUROPODS, represented by *Massospondylus*, appear to be relatively abundant. *Massospondylus* and the ceratosaur *Syntarsus* are also known from North America. SAUROPODS are represented by *Vulcanodon*, a primitive genus known from Zimbabwe. ORNITHOPODS are small and primitive but apparently diverse, being represented by *Abrictosaurus*, *Heterodontosaurus*, *Lanasaurus*, *Lesothosaurus*, and *Lycorhinus*.

The Middle Jurassic is poorly represented and poorly studied in Africa. Large sauropods, usually referred to *Cetiosaurus*, are known from Morocco and Algeria. There are few Late Jurassic localities. Theropod, sauropod, and ornithopod footprints are reported from Morocco and Niger. However, the most impressive concentration of Late Jurassic dinosaurs in Africa is TENDAGURU, Tanzania. This collection of sites was worked first by Germans, until they were disrupted by World War I, then by British. Although theropods, including the ornithomimosaur *Elaphrosaurus*, are present, by far the bulk of the material pertains to large sauropods (*Barosaurus*, *Brachiosaurus*, *Dicraeosaurus*, and *Janenschia*). ORNITHISCHIANS are represented by the ornithopod *Dryosaurus* and the stegosaur *Kentrosaurus*. Perhaps most surprising about the Tendaguru fauna is the similarity it shows to that of the Morrison Formation of North America.

Madagascar has a history separate from that of Africa for the latter half of the Mesozoic Era. *Bothriospondylus* and *Lapparentosaurus*, both sauropods, are reported from the Jurassic. Those records are particularly important because Madagascar separated from Africa approximately 160–150 million years ago, at approximately the same time or slightly postdating the Jurassic fossils. They are perhaps among the last dinosaurs that could have inhabited a Madagascar connected to the African mainland. Although separated from Africa, in the Jurassic and Early Cretaceous Madagascar remained conjoined with India, and through India, to the land masses now known as Antarctica and Australia, and through Antarctica to South America. In the Early Cretaceous, Madagascar plus India separated from Australia and Antarctica. Then, in the Late Cretaceous, they separated from each other to drift to the configuration they have now achieved. This sequence of geographic events is important because it means that the biogeographic affinities of Late Cretaceous Madagascan dinosaurs may lie elsewhere than Africa.

Recent work in the Late Cretaceous of Madagascar is greatly improving our knowledge of that island. Theropods are best represented by the probable abelisaurid *Majungasaurus*. Sauropods are best represented by a derived titanosaurid that was referred to as *Titanosaurus* in earlier literature, a genus first named from India. In addition to the biogeographic implications, titanosaurid remains in Madagascar include the first documented bony dermal armor from a sauropod. Of particular interest among recent finds are birds found in the quarries with the dinosaurs. Earlier studies indicated the presence of a pachycephalosaur, *Majungatholus*, but this animal is an ABELISAURID.

Localities are more widespread across the continent during the Cretaceous Period, but with the Cretaceous lasting from 144 to 65 million years, with few radiometric dates in Africa, and with the density of localities sparse relative to the area and the time involved, it is not surprising that chronological resolution is poor. During the Early Cretaceous Africa remained connected to South America. By the end of the Early Cretaceous or in the early portion of the Late Cretaceous, Africa and South America split apart with the completion of the South Atlantic. This was an important event because, with the completion of the Atlantic, new ocean current patterns were established, distributing heat across the globe and affecting climates. Besides the ecological changes this would bring about, the growing Atlantic formed a widening barrier, allowing the prediction that the similarity of South American and African dinosaur faunas decreases after the Early Cretaceous. Recent work suggests this may be the case.

Most Early Cretaceous localities have yielded fragmentary theropod and sauropod material lacking detailed contextual data. Notable exceptions are the tetanuran *Afrovenator* from Niger, the primitive titanosaurid sauropod *Malawisaurus* from Malawi, the high-spined ornithopod *Ouranosaurus* from Niger, and the stegosaur *Paranthodon* from South Africa. The Late Cretaceous is equally in need of more field work and discovery, although numerous localities are scattered through northern Africa in particular. Notable taxa from the Late Cretaceous of Africa include the coelurosaur *Deltadromeus*, the tetanuran *Spinosaurus*, and the allosauroid *Carcharodontosaurus*, all from northern Africa, and *Kangnasaurus*, an ornithopod from southern Africa. In terms of collected and adequately described taxa, this is clearly unbalanced for both the Early and Late Cretaceous, indicating the fertile ground that Africa is for discovery.

In the current geography of the earth, the Middle East is distinct from Africa. In the Mesozoic it was not. Therefore, indeterminate sauropod remains from Late Jurassic coastal deposits in Yemen and Late Cretaceous theropod footprints from Israel must be considered African. In addition, Croatian localities from a Mesozoic carbonate platform yield fragmentary bones and dinosaur footprints that may have been made on land that was originally a broad, intermittently submerged promontory of Africa or possibly a microplate that drifted northward to join Europe. Either way, the Croatian sites have great implications for the biogeography of African dinosaurs in the Cretaceous.

See also the following related entries:

BIOGEOGRAPHY • EXTINCTION, TRIASSIC • FOOTPRINTS AND TRACKWAYS • INDIAN DINOSAURS • PLATE TECTONICS • SOUTH AMERICAN DINOSAURS

References

Attridge, J., Crompton, A. W., and Jenkins, F. A. (1985). The southern African Liassic prosauropod *Massospondylus* discovered in North America. *J. Vertebr. Paleontol.* **5**(2), 128–132.

Dalla Vecchia, F. M. (1994). Jurassic and Cretaceous sauropod evidence in the Mesozoic carbonate platforms of the southern Alps and Dinarids. *Gaia* **10,** 65–73.

Jacobs, L. L., Winkler, D. A., and Gomani, E. M. (1997). Cretaceous dinosaurs of Africa: Examples from Cameroon and Malawi. In *Gondwana Dinosaurs* (R. Molnar and F. Novas, Eds.), in press. Memoirs of the Queensland Museum, Brisbane.

Krause, D. W., Hartman, J. W., and Wells, N. A. (1997). Late Cretaceous vertebrates from Madagascar: Implications for biotic change in deep time. In *Natural and Human-Induced Change in Madagascar* (B. Patterson and S. Goodman, Eds.), in press. Smithsonian Institution Press, Washington, DC.

Padian, K. (Ed.) (1986). *The Beginning of the Age of Dinosaurs: Faunal Change across the Triassic–Jurassic Boundary,* pp. 378. Cambridge Univ. Press, Cambridge, UK.

Weishampel, D. B., Dodson, P., and Osmólska, H. (1990). *The Dinosauria,* pp. 733. Univ. of California Press, Berkeley.

Age Determination of Dinosaurs

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Early attempts to estimate the longevity of dinosaurs used allometric scaling principles. Ages were determined by dividing individual mass estimates by rates of growth for extant taxa. For very large species, growth rates were extrapolated to dinosaur proportions using regression analysis. The results of these investigations have been extremely variable because they depend on mass estimates and growth rates that are highly disparate. For example, longevity estimates for the sauropod *Hypselosaurus priscus* range from a few decades to several hundred years (Case, 1978). Recently it has been shown that most dinosaur bones have growth lines that are visible in thin sectioned material viewed under polarized light (e.g., Reid, 1990; Fig. 1). Two types of growth lines exist: annuli and lines of arrested growth (Francillon-Vieillot *et al.*, 1990). Histological examinations have re-

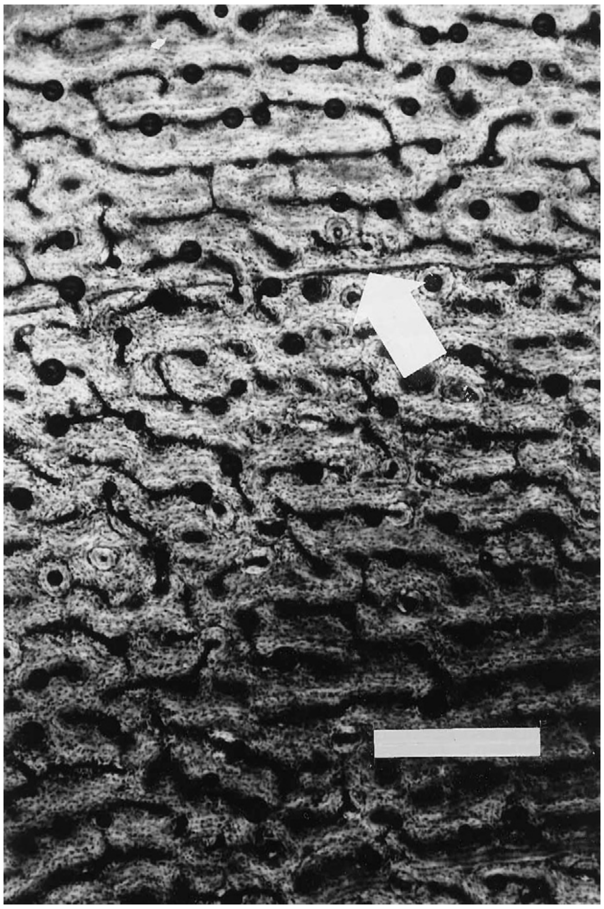

FIGURE 1 Thin-sectioned tibia of the tyrannosaur *Albertosaurus lancensis* (LACM 23845) exhibiting a line of arrested growth (arrow) between zones of highly vascularized fibrolamellar bone. Scale = 1 mm.

vealed that annuli are composed of thin layers of avascular bone with parallel-aligned bone fibers. The growth line annuli are sandwiched between broad vascularized regions of bone with more randomly oriented fibrillar patterns known as zones (Fig. 1). Lines of arrested growth, like annuli, are found between zones and are avascular. They are, however, thinner and have relatively fewer bone fibers by volume (Fig. 1). Studies on extant vertebrates indicate that the vascularized zones form during moderate to rapid skeletogenesis, and that abrupt metabolic disruptions of bone formation trigger growth line deposition. Interruptions that significantly reduce bone growth cause the genesis of annuli, whereas lines of arrested growth form in response to near or complete cessations in bone formation (Francillon-Viellot *et al.*, 1990).

Both types of growth lines may be deposited in synchrony with endogenous biorhythms. For example, captive crocodilians exposed to constant temperature, diet, and photoperiod still exhibit the periodic and cyclical skeletal growth banding of their wild counterparts. In many extant vertebrates, including most actinopterygian fish, amphibians, lepidosaurian reptiles, and crocodilians, the growth lines have an annual periodicity of deposition (Castanet *et al.*, 1993). Consequently, it is assumed by many paleontologists that the growth lines of dinosaurs reflect annual rhythms and that they can be used to determine individual ages. However, in the long bones of many taxa, resorption of internal and external bone proceeds even as new external cortical bone continues to be deposited, so growth lines deposited early in development may need to be inferred. The results of pioneering efforts to age dinosaurs using growth ring counts suggest that the longevity of the basal ceratopsian *Psittacosaurus mongoliensis* was 10 or 11 years (G. Erickson and T. Tumanova, unpublished data), the prosauropod *Massospondylus carinatus* 15 years (Chinsamy, 1994), the sauropod *Bothriospondylus madagascariensis* 43 years (Ricqlès, 1983), the ceratosaur *Syntarsus rhodesiensis* 7 years (Chinsamy, 1994), and the maniraptor *Troodon formosus* 3–5 years (Varricchio, 1993). These data are being used in conjunction with mass estimates to infer the metabolic status and growth rates of dinosaurs and to reconstruct the trophic dynamics of Mesozoic ecosystems.

See also the following related entry:

Growth Lines

References

Case, T. J. (1978). Speculations on the growth rate and reproduction of some dinosaurs. *Paleobiology* **4,** 320–328.

Castanet, J., Francillon-Viellot, H., Meunier, F. J., and Ricqlès, A. de (1993). Bone and individual aging. In *Bone* (B. K. Hall, Ed.), pp. 245–283. CRC Press, Boca Raton, FL.

Chinsamy, A. (1994). Dinosaur bone histology: Implications and inferences. In *Dino Fest* (G. D. Rosenberg and D. L. Wolberg, Eds.), pp. 213–227. The Paleontological Society, Department of Geological Sciences, Univ. of Tennessee, Knoxville.

Francillon-Viellot, H., de Buffrénil, V., Castanet, J., Géraudie, J., Meunier, F. J., Sire, J. Y., Zylberberg, L., and Ricqlés, A. de (1990). Microstructure and mineralization of vertebrate skeletal tissues. In *Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends* (J. G. Carter, Ed.). Vol. 1, pp. 471–530. Van Nostrand–Reinhold, New York.

Reid, R. E. H. (1990). Zonal "growth rings" in dinosaurs. *Mod. Geol.* **15,** 19–48.

Ricqlès, A. de (1983). Cyclical growth in the long limb bones of a sauropod dinosaur. *Acta Palaeontol. Polonica* **28,** 225–232.

Varricchio, D. V. (1993). Bone microstructure of the Upper Cretaceous theropod dinosaur *Troodon formosus*. *J. Vertebr. Paleontol.* **13,** 99–104.

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The Albany Museum, established in 1855, has postcranial material of *Euskelosaurus* and *Massospondylus*. It also houses probable *Paranthodon africanus* fossils, including several bone fragments. In a recent expedition to the Kirkwood beds of the Algoa Basin, soon-to-be described HYPSILOPHODONTID skeletal elements recovered included a partial jaw. Titanosaurid-like, brachiosaurid-like, and theropod teeth from the Kirkwood formation are represented in the collections. The paleontology section of the Albany Museum is currently being renovated. Dinosaurs from the Eastern Cape will be represented by recently collected brachiosaurid material and by full-scale models of *Paranthodon africanus* (the first dinosaur discovered in South Africa) and *Syntarsus rhodesiensis*.

See also the following related entries:

AFRICAN DINOSAURS • BERNARD PRICE INSTITUTE FOR PALAEONTOLOGICAL RESEARCH • NATIONAL MUSEUM, BLOEMFONTEIN • SOUTH AFRICAN MUSEUM

Algerian Dinosaurs

Fragmentary remains of dinosaurs have been recovered from the Late Cretaceous of Algeria.

see AFRICAN DINOSAURS

Allosauroidea

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Allosauroidea (Fig. 1) subsumes by content the concepts Allosauria, Allosauridae, and *Allosaurus.* As recently constituted, Allosauroidea includes the Allosauridae and Sinraptoridae (Currie and Zhao, 1993; Sereno *et al.*, 1994; Holtz, 1994, 1996). Because CARNOSAURIA is defined as all TETANURAE closer to *Allosaurus* than to birds, Allosauroidea are by definition carnosaurs, and any potential members of Carnosauria must be evaluated against *Allosaurus*.

Resolution of allosauroid phylogeny beyond this statement is a difficult matter, partly because many taxa that are clearly allied to the group are incompletely known or have had their systematic characters interpreted differently by different workers. Consequently, the membership of Allosauridae and Sinraptoridae is currently not agreed upon apart from their eponymous genera. Sereno *et al.* (1994), for example, place *Sinraptor* and *Yangchuanosaurus* in Sinraptoridae and *Acrocanthosaurus, Allosaurus, Cryolophosaurus,* and *Monolophosaurus* in Allosauridae. Holtz (1994) placed only *Allosaurus* and *Acrocanthosaurus* in Allosauridae. Holtz (1995) regarded *Monolophosaurus* as a tetanurine outside AVETHEROPODA, but in 1996 found it to be the sister taxon to Allosauroidea,

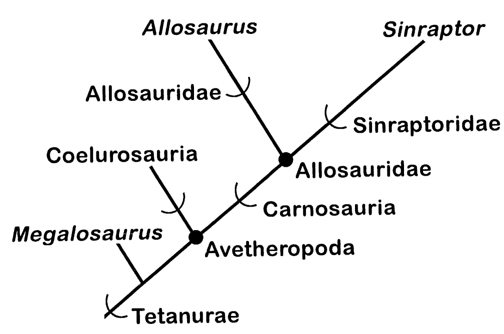

FIGURE 1 Phylogeny of Allosauroidea. For synapomorphies see text. Taxa of debated placement, not listed here, include *Acrocanthosaurus, Monolophosaurus, Cryolophosaurus, Chilantaisaurus, Piatnitzkysaurus, Carcharodontosaurus,* and *Giganotosaurus*. These are all recognized as Carnosauria and a possible phylogeny is given under that entry.

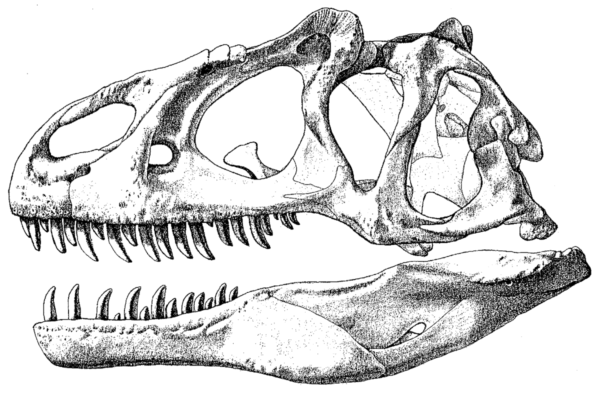

FIGURE 2 Skull of *Allosaurus* (after Madsen, 1976).

with *Cryolophosaurus* as a more basal carnosaur. Holtz (1996) also found *Giganotosaurus* and the Carcharodontosauridae to be allosauroids closer to Allosauridae than to Sinraptoridae. Meanwhile, Sereno *et al.* (1996) also found Carcharodontosauridae to be in Allosauroidea but suggested that *Acrocanthosaurus* and *Giganotosaurus* might belong in Carcharodontosauridae instead of in Allosauridae. *Acrocanthosaurus* was known until recently only from incomplete specimens, but more material has been discovered in the past few years and awaits formal description. Other poorly known taxa, such as *Pianitzkysaurus* and *Chilantaisaurus,* may be allosauroids as well, but their exact relationships have not yet been conclusively established.

Sereno *et al.* (1994) provided four synapomorphies of Allosauroidea, including the participation of the nasal in the antorbital fossa, a flange-shaped lacrimal process on the palatine, the basioccipital excluded from the basal tubera, and the articular with a pendant medial process (Fig. 2). The synapomorphies of Allosauridae include a short quadrate with the head level with the middle of the orbit, a deep anterior ramus of the surangular, and the small diameter of the external mandibular fenestra. Sinraptoridae (Currie and Zhao, 1993) is characterized by two accessory pneumatic excavations on the maxilla, an external nares with a marked inset of the posterior margin, a bulbous, anteriorly projecting rugosity on the postorbital, and a flange on the squamosal that covers the quadrate head in lateral view (Sereno *et al.*, 1994). Holtz (1994) diagnosed Allosauridae by the possession of a pubic "foot" that is longer anteriorly than posteriorly and triangular in ventral view. Because the synapomorphies diagnosing other nodes in his 1995 and 1996 works have not yet been published, differences in phylogenetic conclusions cannot currently be evaluated.

Given the current instability in diagnosing the content and hence the synapomorphies of the allosauroid groups, Allosauridae and Sinraptoridae can be defined only with reference to their eponymous genera. Hence, Allosauridae comprises *Allosaurus* and all Allosauroidea closer to it than to *Sinraptor;* Sinraptoridae comprises *Sinraptor* (Fig. 3) and all Allosauroidea closer to it than to *Allosaurus.* Allosauroidea is a node-based taxon, diagnosed by the synapomorphies previously discussed, that includes *Allosaurus* and *Sinraptor* and all descendants of their most recent common ancestor. It will be noted that Allosauridae and Sinraptoridae are herein defined as stem-based taxa; neither Sereno *et al.* (1994) nor Holtz (1994) indicated node- or stem-based definitions but rather used characters and included taxa (see PHYLOGENETIC SYS-

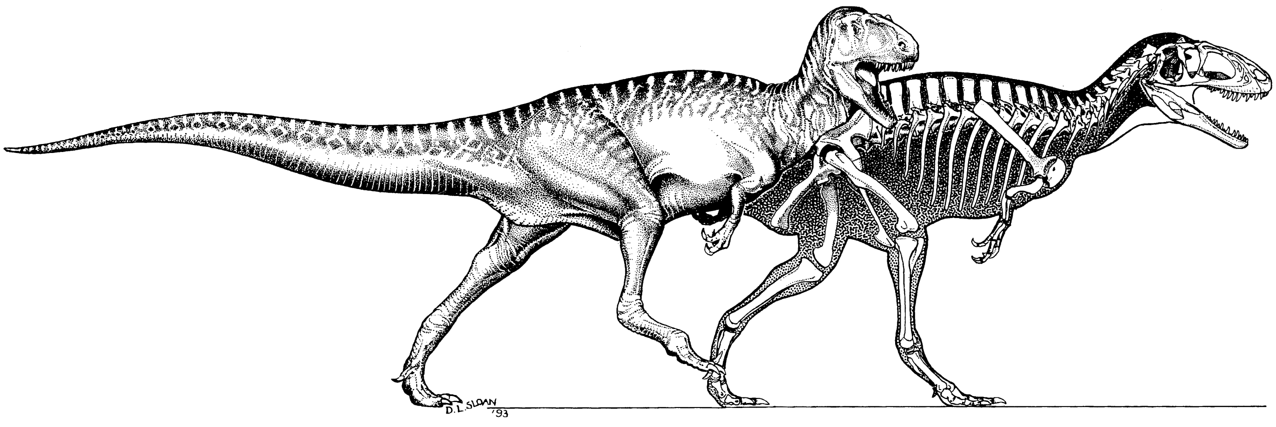

FIGURE 3 *Sinraptor* (after Currie and Zhao, 1993).

TEM). Stem-based definitions are included here because currently the taxa are minimally monotypic: No consensus exists on the membership of more than one genus per taxon.

The genus *Allosaurus* has had a slightly confusing history. Leidy (1870) assigned a partial caudal vertebra, collected from Colorado by the Ferdinand Hayden expedition, to *Poicilopleuron* [sic] *valens*, noting its putative similarity to the European genus *Poikilopleuron* (which has had its own tortured history and has usually been synonymized with, or allied to, *MEGALOSAURUS*). However, Leidy also provided the generic name *Antrodemus,* should his specimen eventually prove different from *Poikilopleuron.* Marsh (1877) described a tooth, two dorsal vertebrae, and a phalanx, collected by Benjamin Mudge from the Late Jurassic MORRISON FORMATION of Fremont County, Colorado (''Garden Park Quarry''), as *Allosaurus fragilis*, and Marsh eventually described some of the further remains from the same quarry, excavated by M. P. Felch, which included an almost complete skeleton, several partial skeletons, and other bones. Hence, *Allosaurus* came to be well known. Gilmore (1920), however, in describing the full material from Garden Park, decided that Leidy's caudal half-centrum of *Antrodemus valens* had diagnostic characters also seen in the *Allosaurus* material, so he regarded all the material as belonging properly to *Antrodemus.* Gilmore's judgment, however logical at the time, has not been sustained by character analysis, and the name *Allosaurus* is accepted today (Madsen, 1976).

The greatest collection of *Allosaurus* material has been made at the CLEVELAND–LLOYD QUARRY, discovered in 1927 and worked intermittently by crews from the University of Utah, Princeton University, and the Earth Science Museum, Brigham Young University, where most of the material is now jointly stored (see Miller *et al*., 1996). Several thousand bones now provide a very full picture of this animal, including its osteology and ontogeny, which preserve bones of individuals (unfortunately, none articulated) ranging from approximately 3 to 12 m in length. A detailed study and map of the Cleveland–Lloyd Quarry (Miller *et al*., 1996) and recent Ph.D. work by David K. Smith at Brigham Young University on the morphometrics of the *Allosaurus* material testify to the continuing importance of this bonanza of skeletal material.

Allosaurus was the largest well-known carnivore in the Morrison Formation, presumably feeding on SAUROPODS, HYPSILOPHODONTIDS, STEGOSAURS, ANKYLOSAURS, and probably other animals; *Ceratosaurus,* another large carnivore, is present but rarer, and an even larger, possibly allosauroid theropod, *Saurophaganax* (which apparently reached the size of some adult *Tyrannosaurus* specimens) has not yet been well described. *Torvosaurus* is a basal tetanurine theropod also from the Morrison Formation (see DRY MESA QUARRY) and it reached comparable size, plus a few other taxa have been reported from fragmentary material that may or may not be diagnostic; therefore, at least four large theropods are known from the Morrison Formation, and there may well have been a considerable diversity of large carnivores feeding on the other components of the Morrison fauna and perhaps on each other. Fragmentary specimens referable to *Allosaurus*, or at least to Allosauridae, are reported from the TENDAGURU Beds of Tanzania and the Strzelecki Group of Victoria, Australia, extending the survival of the allosaurid lineage into the Early CRETACEOUS Period (Molnar *et al.*, 1981, 1985).

The upper jaw of *Allosaurus* bears 20 or more trenchant, laterally compressed teeth; the dentary bears up to 13, but the lower tooth row does not extend as far posteriorly as the upper row, as in most theropods. An extensive system of pneumatic spaces characterizes the orbital ''brow ridge'' and the skull roof bones behind the orbit (see CRANIOFACIAL AIR SINUS SYSTEMS). The brow ridge in *Allosaurus, Sinraptor,* and apparently *Yangchuanosaurus* is centrally excavated in a particular way, but the function is unknown.

One of the most important recent discoveries concerning *Allosaurus* is that it has a furcula (Chure and Madsen, 1996). This was first discovered during the excavation of a still undescribed, *Allosaurus*-like theropod from DINOSAUR NATIONAL MONUMENT. Comparison of this specimen's furcula with *Allosaurus* material from the Cleveland–Lloyd Quarry revealed that such elements were common at Cleveland–Lloyd Quarry but had been taken for median bones of the ventral cuirass, or gastralia (Madsen, 1976). Gilmore (1920) had figured them as proceeding down the length of the abdomen, when in fact there was only one per individual, situated properly between the pectoral girdles. Their anatomy is easily distinguished from that of the true median gastral elements (Chure and Madsen, 1996). As Holtz (1996) noted, the possession of this distinctive, boomerang-shaped furcular morphology is a synapomorphy of AVETHEROPODA (see also PECTORAL GIRDLE).

References

Chure, D. J., and Madsen, J. H. (1996). On the presence of furculae in some non-maniraptoran theropods. *J. Vertebr. Paleontol.* **16,** 573–577.

Currie, P. J., and Zhao, X. J. (1993). A new carnosaur (Dinosauria: Theropoda) from the Jurassic of Xinjiang, People's Republic of China. *Can. J. Earth Sci.* **30,** 2037–2081.

Gilmore, C. W. (1920). Osteology of the carnivorous Dinosauria in the United States National Museum, with special reference to the genera *Antrodemus (Allosaurus)* and *Ceratosaurus.* Smithsonian Institution, United States National Museum Bulletin No. 110, pp. 1–159.

Holtz, T. R., Jr. (1994). The phylogenetic position of the Tyrannosauridae: Implications for theropod systematics. *J. Paleontol.* **68,** 1100–1117.

Holtz, T. R., Jr. (1995). A new phylogeny of the Theropoda. *J. Vertebr. Paleontol.* **15**(Suppl. to No. 3), 35A.

Holtz, T. R., Jr. (1996). Phylogenetic analysis of the nonavian tetanurine dinosaurs (Saurischia: Theropoda). *J. Vertebr. Paleontol.* **16**(Suppl. to No. 3), 42A.

Leidy, J. (1870). [Remarks on *Poicilopleuron valens*, etc.] *Proc. Acad. Nat. Sci. Philadelphia* **1870,** 3–5.

Madsen, J. H. (1976). *Allosaurus fragilis*: A revised osteology. *Bull. Utah Geol. Miner. Survey* **109,** 1–163.

Marsh, O. C. (1877). Notice of new dinosaurian reptiles from the Jurassic formation. *Am. J. Sci.* **3**(14), 513–514.

Miller, W. E., Horrocks, R. D., and McIntosh, J. H. (1996). The Cleveland–Lloyd Quarry, Emery County, Utah: A U.S. national landmark (including history and quarry map). *Brigham Young Univ. Geol. Stud.* **41,** 3–24, 4 maps.

Molnar, R. E., Flannery, T. F., and Rich, T. H. V. (1981). An allosaurid theropod dinosaur from the Early Cretaceous of Victoria, Australia. *Alcheringa* **5,** 141–146.

Molnar, R. E., Flannery, T. F., and Rich, T. H. V. (1985). Aussie *Allosaurus* after all. *J. Paleontol.* **59,** 1511–1513.

Sereno, P. C., Wilson, J. A., Larsson, H. C. E., Dutheil, D. B., and Sues, H.-D. (1994). Early Cretaceous dinosaurs from the Sahara. *Science* **265,** 267–271.

A diorama of *Albertosaurus* over a prey item, *Centrosaurus*, perhaps a common scene from the Cretaceous of Alberta, Canada. (Photo by François Gohier.)

American Dinosaurs

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The United States has a great diversity of dinosaurs spanning a wide stratigraphic range. Although the concept of dinosaur was born in England, it found fertile ground in the United States. The United States has more different kinds of dinosaurs than any other country by a wide margin. A recent tabulation based on data as of 1988 shows that the United States has 64 known genera of dinosaurs compared with 40 for Mongolia and 36 for China. Such figures rapidly become dated as new kinds from around the world are described. In 1993, for instance, four new dinosaurs were described from the United States: *Shuvosaurus* from Texas, *Utahraptor* from Utah, and *Naashoibitosaurus* and *Anasazisaurus* from New Mexico. In 1994, *Mymoorapelta* from Utah was added, and in 1995 the ceratopsids *Einiosaurus* and *Achelousaurus* from Montana were formally described (see Variation). Forthcoming are a theropod from the Early Cretaceous of Utah, an ankylosaurian and an ornithopod from Texas, and a basal ornithischian from New Mexico. Thus, growth of knowledge of new kinds of dinosaurs continues at least as rapidly in the United States as in China and at a greater rate than in Argentina or in Mongolia.

There are four fundamental reasons why the United States has so many different kinds of dinosaurs: stratigraphy, climate and geography, human resources, and history. Like Argentina and China, and unlike Canada and Mongolia, the United States has dinosaur-bearing continental strata that span most of the stratigraphic interval in which dinosaurs may be expected from the Carnian stage of the Late Triassic to the Maastrichtian stage of the Late Cretaceous. The United States has large areas of outcrop in semiarid climates, principally in the west, where erosion is relatively unencumbered by vegetation, unlike Canada, England, or the eastern United States, for example. There is also a large corps of professional, commercial, and amateur dinosaur collectors in this country, all of whom contribute to ongoing discoveries.

The explicit history of dinosaur paleontology in the United States extends back to 1856, when Joseph Leidy applied names to a collection of teeth from the Judith River beds along the Missouri River in Montana that was sent to Philadelphia by Ferdinand Hayden. The four names are *Deinodon, Trachodon, Paleoscincus,* and *Troodon*. Unfortunately, the first three names are *nomina dubia*, as these teeth are diagnostic only at the family level (this being the rule for dinosaur teeth, making it generally unwise to name dinosaurs on that basis). Before this time, an interesting bone had turned up in Cretaceous deposits from Woodbury, New Jersey. Such material had been discussed as early as 1787 at the American Philosophical Society in Philadelphia, but dinosaurs had not yet been recognized scientifically, and the report was forgotten. (Donald Baird has proposed that a hadrosaur metatarsal in the collection of the Academy of Natural Sciences of Philadelphia is this specimen.)

The discovery and description of *Hadrosaurus foulkii* from Haddonfield, New Jersey, by Leidy in 1858 marks the first time that a major portion of a dinosaur skeleton, including fore- and hind-limbs, had been found. This allowed Leidy to reconstruct *Hadrosaurus* as a biped, showing that the Owen–Hawkins reconstruction of *Iguanodon*, exhibited at the Crystal Palace since 1854, was incorrect. The reconstruction and exhibition of *Hadrosaurus* at the Academy of Natural Sciences in 1868 marked the first time that a dinosaur skeleton had ever been exhibited anywhere in the world. Casts of this specimen were exhibited at Princeton University Geology Museum, the Smithsonian, and the Field Columbian Museum in Chicago, but it was not until the first decade of the 20th century that other dinosaur skeletons were exhibited at the American Museum of Natural History, Yale Peabody Museum, and the Smithsonian. E. D. Cope described a partial skeleton of the enigmatic theropod *Laelaps* (preoccupied; renamed *Dryptosaurus* Marsh 1877) from New Jersey in 1868. Cope named the ceratopsids *Agathaumas* in 1872 and *Polyonax* in 1874 from Wyoming and Colorado, respectively, but these are *nomina dubia* based on fragmentary material. In 1876, he collected and named *Monoclonius* from the Judith River Formation of Montana, the first valid ceratopsid. Up to this point, dinosaur finds had been geographically widespread and generally of poor quality. Montana had produced the most dinosaurs up to this time, but most finds were not memorable.

In 1877, dinosaurs were discovered in abundance for the first time anywhere in the world at three separate localities: CAÑON CITY and Morrison, both in Colorado, and COMO BLUFF, Wyoming. The beds proved to be of Late Jurassic age and have produced a remarkable fauna dominated by large sauropods, with stegosaurs also important; theropods and ornithopods were less abundant; recently an ankylosaur was reported. Intensive examination of the Morrison fauna waned after 1885. Renewed interest in the Morrison at the turn of the century, after Marsh and Cope had died, produced further sauropods (*Brachiosaurus* and *Haplocanthosaurus*) and the small theropod *Ornitholestes*. Beds of Triassic age were documented with the description of *Coelophysis bauri* by Cope in 1889. The study of beds of latest Cretaceous age began with the description of *Triceratops* Marsh 1889, followed by *Torosaurus* Marsh 1891, and then *Tyrannosaurus* (1905) and *Ankylosaurus* (1908) early in this century. Lancian hadrosaurine species were described by Marsh in 1890 and 1892, but the proper generic assignments (to *Anatotitan* and *Edmontosaurus*) were not recognized until much more recently. The United States lacks a major dinosaur fauna correlative with the Horseshoe Canyon Formation (early Maastrichtian) of Alberta, Canada, although the TWO MEDICINE FORMATION of Montana, first studied by C. W. Gilmore beginning in 1914, contains an antecedent fauna, as do the FRUITLAND/KIRTLAND FORMATIONS of New Mexico and the Aguja Formation of Texas. A major fauna of Early Cretaceous age, very broadly correlative with the British WEALDEN fauna, was unknown in the United States until John Ostrom described the fauna of the CLOVERLY FORMATION of Wyoming and Montana in 1970. Lateral equivalents of the Cloverly (CEDAR MOUNTAIN FORMATION of Utah is partially equivalent; Trinity Group, TX) are now producing important specimens (*Utahraptor*; Proctor Lake ornithopod). Late Cretaceous dinosaurs from New Mexico began to be described in 1910. The Late Triassic is sparsely productive of dinosaurs, the rich deposits of *Coelophysis* being a conspicuous exception. There are Early Jurassic dinosaurs in Connecticut and the southwest; the Middle Jurassic is essentially unknown.

Primitive theropods are well represented, the most prominent being *Coelophysis* (known from scores of skeletons from the mass death assemblage at GHOST RANCH, NM), *Dilophosaurus*, and *Ceratosaurus*. Large theropods are represented by two principal taxa, the Allosauridae (*Allosaurus*) and the TYRANNOSAURIDAE. *Tyrannosaurus* now appears to be one of the most common large theropods. Good specimens of *Albertosaurus* are common in Canada but are very rare in the United States. The fossil record of maniraptorans in the United States is rather sparse, apart from the imperfect material of *Ornitholestes* and *Coelurus*. *Deinonychus* is the most important American maniraptoran, and recently the larger *Utahraptor* has been described. Ornithomimids are poorly represented but were surely present. Many MANIRAPTORAN taxa are documented principally by teeth (e.g., *Aublysodon, Paronychodon,* and *Ricardoestesia*) and thus are in perilous condition taxonomically. No segnosaurs have been confirmed.

"Prosauropods" (basal SAUROPODOMORPHS) are somewhat sparse in the American fossil record. *Anchisaurus* and *Ammosaurus* are the principal taxa, although *Massospondylus* has been reported from the Early Jurassic of Arizona. No sauropods of Early and Middle Jurassic age are known, but the Late Jurassic Morrison Formation contains a sauropod assemblage that is rivaled in quality, quantity, and diversity only by the correlative assemblages from China. For nearly a century, these sauropods presented the basis for understanding sauropods everywhere in the world. The important taxa Camarasauridae (*Camarasaurus*), Brachiosauridae (*Brachiosaurus*), and Diplodocidae (*Diplodocus, Apatosaurus,* and *Barosaurus*) were established on Morrison sauropods. The taxa Cetiosauridae (*Haplocanthosaurus*) and Titanosauridae (*Alamosaurus*) are known but are much less important here.

Basal ornithischians are poorly represented at present, but *Technosaurus* from Texas seems representative of such basal taxa. In addition, teeth of basal ornithischians have been documented in Late Triassic sediments from Pennsylvania to Arizona. *Scutellosaurus* and *Scelidosaurus* are good basal thyreophorans. The Stegosauridae are magnificently characterized by *Stegosaurus*, but there is otherwise very low diversity of this family, in contrast to China. There are few basal ankylosaurians, but there are good representatives of the Nodosauridae (*Sauropelta*) and of the Ankylosauridae (*Ankylosaurus*), both taxa being established on American taxa. A very important recent discovery is that of the ankylosaur *Mymoorapelta* from the MORRISON FORMATION of Colorado. The nodosaur *Edmontonia* is now reported from Alaska. For both families, there are more skulls than skeletons, with no complete skeletons in either taxa having yet been collected. ORNITHOPODS are well represented in the United States. Hypsilophodontids are somewhat fragmentary (*Othnielia* and *Orodromeus*), although there are several good specimens of the enigmatic *Thescelosaurus*. Basal iguanodontians are also well represented by *Dryosaurus* and *Tenontosaurus*, the latter of which is particularly abundant and widespread with specimens being reported from Montana, Wyoming, Utah, Oklahoma, and Texas (possibly Maryland as well). *Camptosaurus* is an abundant American iguanodontian, and a fine skull of *Iguanodon* itself, named *I. lakotensis*, has been described. HADROSAURS are abundant in the United States, including both lambeosaurines and hadrosaurines. The former are represented only by *Parasaurolophus* from New Mexico and Utah and *Hypacrosaurus* from northern Montana. Hadrosaurines come from New Jersey (*Hadrosaurus),* Alabama (*Lophorothon*), New Mexico (*Kritosaurus*), and extensively from Wyoming, Montana, North Dakota, and South Dakota (*Anatotitan* and especially *Edmontosaurus*, which is one of the most abundant dinosaurs both in the United States and in the world). *Edmontosaurus* is also reported from the North Slope of Alaska. Pachycephalosaurs are principally represented by crania, particularly of *Pachycephalosaurus* itself. Protoceratopsids are documented by a few incomplete specimens of *Leptoceratops* and by a specimen of *Montanoceratops*. Ceratopsids include both centrosaurines (*Monoclonius*) from Montana and chasmosaurines, especially *Triceratops,* from Wyoming, Montana, North Dakota, South Dakota, and Colorado; *Chasmosaurus* from Texas; *Torosaurus* from Montana and South Dakota; and *Pentaceratops* from New Mexico. Ceratopsids are endemic to North America. *Triceratops* is among the most abundant of all dinosaurs. There is a fragmentary occurrence of *Pachyrhinosaurus* from the North Slope of Alaska.

Because dinosaurs are so diverse in the United States, it is tempting to think of this country as a center of evolution for worldwide faunas. This may not be so. In the Late Triassic, plateosaurids, common in Europe, Asia, and South America, are rare in the United States. Rare Early Jurassic sauropodomorphs have been found in Arizona and Connecticut. There are significant resemblances between Late Triassic *Coelophysis* of New Mexico and Early Jurassic *Syntarsus* of Zimbabwe and South Africa, but the resemblances between these relatively primitive theropods include few derived characters. There are essentially no Middle Jurassic beds in the United States to document the antecedents of the marvelous Late Jurassic sauropods, ornithopods, and stegosaurs of the Morrison Formation. *Haplocanthosaurus* may be presumed to be representative of the basal cetiosaurid radiation better documented in England, Europe, and South America. *Brachiosaurus* from Colorado has affinities with congeneric fossils from Tanzania. Other faunal elements having congeners in East Africa are *Dryosaurus*, probably *Barosaurus*, and less certainly *Ceratosaurus* and *Allosaurus*. It is significant that stegosaurs are much less diverse in the United States than they are in China, although *Stegosaurus* itself may be the most highly derived stegosaur. *Camptosaurus* is an important basal iguanodontian in the United States, with a sister species in the Middle Jurassic of England. In the Early Cretaceous, *Tenontosaurus* is an endemic ornithopod more basal than *Camptosaurus*. Although *Iguanodon* appears to have reached North America, it seems to have been uncommon there. Important new evidence suggests that *Polacanthus* from the WEALDEN of England also lived in Utah. In the Late Cretaceous, there is scant evidence for the titanosaurid sauropod fauna that dominated much of the world. It is postulated that *Alamosaurus* was a late migrant from South America, reintroducing sauropods which had been absent since the Early Cretaceous. There is evidence of faunal interchange with Asia based on similarities at the level of family and genus. A close relationship, possibly at the species level, of *Tyrannosaurus* with the Asiatic *Tarbosaurus* is recognized. Other evidence for exchange is better documented by Canadian dinosaurs, notably the hadrosaurine *Saurolophus*. Due to the relatively impoverished faunas of the Judith River Formation and dearth of early Maastrichtian dinosaurs in the United States, coupled with the relatively restricted area of late Maastrichtian strata in Alberta and Saskatchewan, faunal overlap between the United States and Canada is not as great as expected, and the greater diversity and completeness of specimens favors Canada. Although ceratopsids range from Alaska to Mexico, the only identifiable specimens of this family in Asia are teeth and horn core fragments from Uzbekistan. Mid-Cretaceous dinosaurs are found in Maryland, and Late Cretaceous dinosaurs are known from the eastern seaboard of the United States, from New Jersey to North Carolina, and also along the Gulf Coast and Mississippi embayment from Alabama to western Tennessee and Missouri. Few skeletons have been described (*Hadrosaurus* and *Dryptosaurus* from New Jersey), and the faunal relationship to dinosaurs in the West, across the Inland Sea, is not evident. *Hadrosaurus* appears to be a sister group of *Kritosaurus* from New Mexico and / or *Gryposaurus* from Alberta. *Dryptosaurus* is a nonarctometatarsalian of unclear relationship to any other theropod. It is claimed that there is a specimen of *Albertosaurus* from Alabama, but it is undescribed. This would present the same biogeographic challenge that *Hadrosaurus* presents. The mechanism of faunal exchange across a 1000- to 1500-km inland sea has yet to be elucidated.

See also the following related entries:

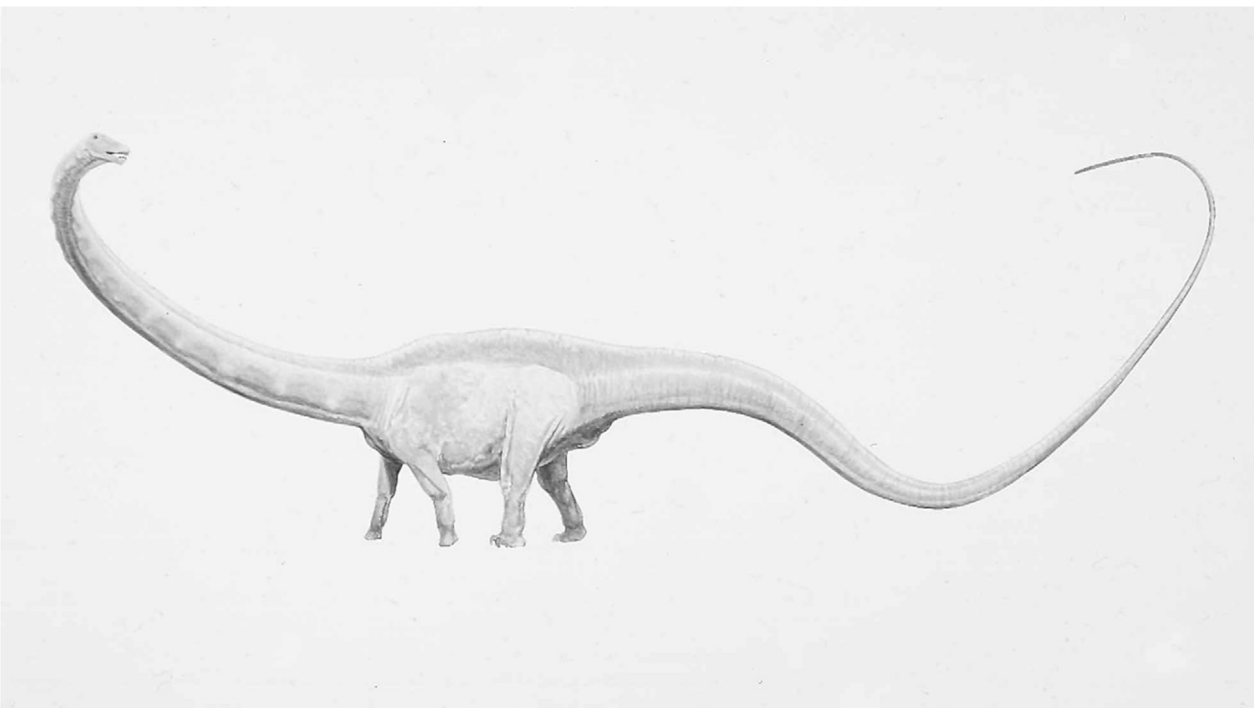
CANADIAN DINOSAURS • HADROSAURIDAE • MEXICAN DINOSAURS • POLAR DINOSAURS • SOUTH AMERICAN DINOSAURS

References

Dodson, P. (1990). Counting dinosaurs: How many kinds were there? *Proc. Natl. Acad. Sci. USA* **87,** 7608–7612.

Russell, D. A. (1993). The role of Central Asia in dinosaurian biogeography. *Can. J. Earth Sci.* **30,** 2002–2012.

Weishampel, D. B., Dodson, P., and Osmolska, H. (Eds.) (1990). *The Dinosauria,* pp. 733. Univ. of California Press, Los Angeles.



Perhaps the largest dinosaur of all time, *Seismosaurus* dwarfs most other large sauropods. (Illustration by Donna Braginetz.)

American Museum of Natural History

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The American Museum of Natural History (AMNH) in New York City is the largest private museum in the world, and it has made a similarly large contribution to vertebrate paleontology. The museum attracts millions of visitors each year to its famous dinosaur displays. Some of the most notable dinosaur discoveries have been made by field expeditions sponsored by the AMNH, including the excavations by Barnum Brown and others at Como Bluff and Hell Creek in the 1890s, the Roy Chapman Andrews expeditions in the Gobi Desert in the 1920s, and the recent trips back to Gobi by AMNH curators Michael Novacek and Mark Norell.

The AMNH was incorporated in 1869 in New York City. In 1877 the first permanent building opened at the current site, in midtown Manhattan west of Central Park. Albert S. Bickmore, a zoologist who studied under Louis Agassiz at Harvard, is regarded as the founder of the museum. He envisioned a natural science museum in the center of the metropolis of New York, comparable to the Museum of Comparative Zoology founded in Cambridge by Agassiz in 1859. Bickmore brought together a group of prominent New Yorkers who raised the money for the museum, including the financier J. P. Morgan.

In its earliest years the AMNH had virtually no vertebrate fossils, a fact that museum president Morris K. Jesup set out to rectify in 1891 by his hiring of Henry Fairfield Osborn, a noted paleontologist and a faculty member at Princeton University. Osborn founded the museum's Department of Vertebrate Paleontology and staffed it with an outstanding group of paleontologists, including Barnum Brown, William Diller Matthew, Jacob Wortman, Walter Granger, and Albert ''Bill'' Thomson. They were supplemented by preparators such as Peter Kaisen, Otto Falkenbach, and Adam Hermann.

Field Expeditions of the Museum

During the Jesup–Osborn era, the museum initiated a series of highly productive field expeditions. Beginning in 1897, Wortman, Brown, Granger, and others explored the Jurassic fossil beds in the Como Bluff area of Wyoming. Although this area had already been extensively worked by the expeditions of Othniel Charles Marsh, the AMNH group made many additional important finds, including the sauropods *Apatosaurus, Diplodocus, Allosaurus,* and *Ornitholestes.* In 1898, museum paleontologists in this area located the distinctive Bone Cabin site.

In 1902 Barnum Brown led an AMNH expedition to the Cretaceous beds of the Hell Creek region of Montana. This resulted in the first known specimen of *Tyrannosaurus rex,* in 1902, and a second, more highly preserved specimen in approximately 1908. This second specimen is generally regarded as the most famous dinosaur fossil in the world and has long been a centerpiece of the AMNH. Brown went on to lead museum-sponsored expeditions in 1910–1915 to the Red Deer River region of Alberta, Canada. These also yielded rich discoveries, especially of hadrosaurs such as *Saurolophus* and *Corythosaurus.* In the 1930s another AMNH expedition led by Brown excavated a large collection of Jurassic fossils from the Howe Ranch site in Wyoming.

What has been termed the golden age of the museum's field expeditions extended from 1890 to 1930. In addition to Brown's highly publicized efforts, various other paleontologists from the AMNH staff also made important finds in this period, including Matthew, Granger, Thomson, and Henry Fairfield Osborn himself. Osborn also obtained many specimens from independent collectors, such as Charles H. Sternberg.

Expeditions of Roy Chapman Andrews

The expeditions described previously all were situated in western North America, but the most renowned expeditions sponsored by the AMNH were carried out in central Asia. These took place in Mongolia in the period 1920–1930 under the leadership of the legendary Roy Chapman Andrews.

Andrews originally went to Mongolia's remote Gobi Desert region at the invitation of Henry Fairfield Osborn, who had succeeded Morris K. Jesup as president of the museum. Osborn believed that an investigation of the region could substantiate his theory that Asia, not Africa, was the original site of human habitation.

Andrews found no human fossil evidence to support Osborn's theory but did find many other significant vertebrate fossils, including the first dinosaur bone discovered in eastern Asia. The Flaming Cliffs region in particular produced important remains of dinosaurs such as *Protoceratops, Oviraptor, Saurornithoides, Pinacosaurus,* and *Velociraptor,* as well as Cretaceous mammals. The most noted single discovery was that of the predatory dinosaur *Oviraptor* lying on a clutch of supposed *Protoceratops* eggs.

Later Expeditions

Both Barnum Brown and Roy Chapman Andrews achieved celebrity status as dinosaur hunters, and Andrews is now often cited as the model for the Hollywood character Indiana Jones. However, after 1930 a combination of reduced museum funds and the historic circumstances of the Depression and World War II meant that high-profile expeditions such as theirs were no longer feasible.

The AMNH nevertheless continued to sponsor important expeditions such as Roland T. Bird's examination of the GLEN ROSE, TEXAS, dinosaur trackway site in the 1930s and Edwin Colbert's discovery of *Coelophysis* skeletons at GHOST RANCH, New Mexico, in the late 1940s.

The AMNH has maintained this tradition of field explorations to the present day. The most notable recent example was a program to revisit the sites explored by Roy Chapman Andrews. Since 1990, field crews from the museum have participated in annual expeditions to the Gobi Desert in conjunction with colleagues from the Mongolian Academy of Sciences. These efforts have resulted in the discovery of a new Late Cretaceous flightless bird, *Mononykus*, and the first known embryo of a theropod dinosaur.

Exhibits

In the new Halls of Ornithischian and Saurischian Dinosaurs, the AMNH exhibits the largest collection of real dinosaur fossils anywhere in the world. More than 100 specimens are on display, and approximately 85% of them include real fossil material. Many new specimens have been added, and several of the older mounts have been modified, including those of *Tyrannosaurus* and *Apatosaurus*.

In contrast to most exhibitions, the primary organizing framework is based on systematics rather than geologic time. Labels have intentionally been developed at different levels of technical difficulty to address the needs of a diverse audience. A main path down the center of each hall represents the trunk of an evolutionary tree. By walking down this path, one can see the most spectacular specimens and encounter labels addressing the major themes. Collection alcoves along the sides of the halls represent branches that contain fossil representatives of the principal dinosaurian clades. One system of computer interactives located in each alcove is utilized to present curatorial views about the evolutionary relationships of the dinosaurs on that branch. A second system of computer interactives is used to present the ''walk-through time'' approach utilized in most exhibitions.

The main point of the presentation is to illustrate for the visitor what we really know about these extinct animals. Many controversial issues are addressed by simply presenting the evidence for different ideas and letting the visitor make up his or her own mind about what to think. This is intentionally done in order to provide visitors with some insight into how the scientific process works.

The two dinosaur halls are part of a loop of six halls on the fourth floor of the museum that are designed to tell the story of vertebrate evolution. In all, these halls contain 57,000 square feet of exhibition space.

In emphasizing evolutionary relationships based on cladistic methods, the dinosaur exhibits also help make visitors aware of the kind of scientific research conducted in the museum's Department of Vertebrate Paleontology. In terms of dinosaurs, the curatorial staff and associates actively pursue research and