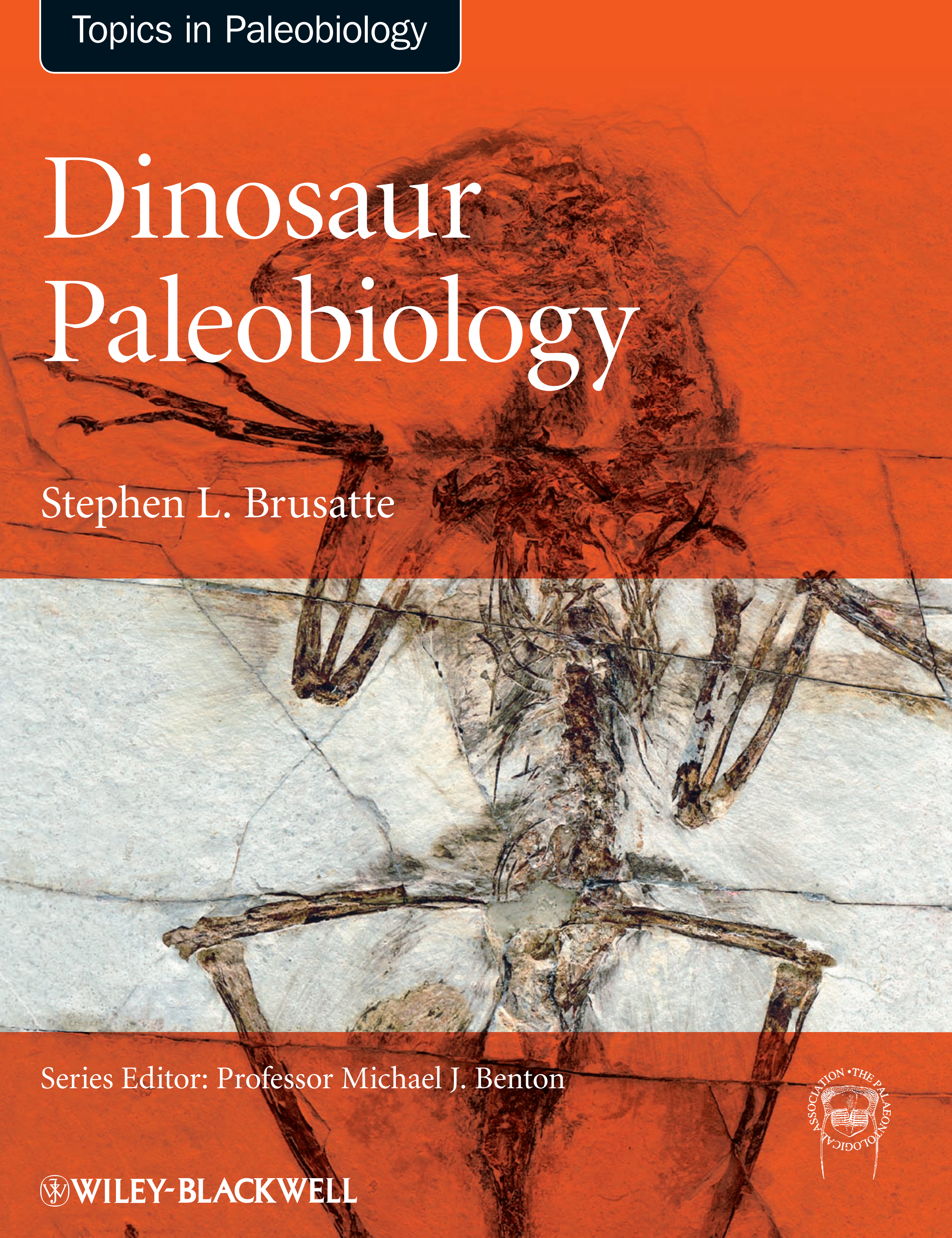

Topics in Paleobiology

Dinosaur Paleobiology

Stephen L. Brusatte

Series Editor: Professor Michael J. Benton

THE PALAEONTOLOGICAL ASSOCIATION

WILEY-BLACKWELL

Dinosaur Paleobiology

Books in the **Topics in Paleobiology** series will feature key fossil groups, key events, and analytical methods, with emphasis on paleobiology, large-scale macroevolutionary studies, and the latest phylogenetic debates.

The books will provide a summary of the current state of knowledge and a trusted route into the primary literature, and will act as pointers for future directions for research. As well as volumes on individual groups, the Series will also deal with topics that have a cross-cutting relevance, such as the evolution of significant ecosystems, particular key times and events in the history of life, climate change, and the application of new techniques such as molecular paleontology.

The books are written by leading international experts and will be pitched at a level suitable for advanced undergraduates, postgraduates, and researchers in both the paleontological and biological sciences.

The Series Editor is *Mike Benton*, Professor of Vertebrate Palaeontology in the School of Earth Sciences, University of Bristol.

The Series is a joint venture with the *Palaeontological Association*.

COMPANION WEBSITE

This book has a companion website:

www.wiley.com/go/brusatte/dinosaurpaleobiology

with Figures and Tables from the book for downloading

Dinosaur Paleobiology

Stephen L. Brusatte

WILEY-BLACKWELL
A John Wiley & Sons, Ltd., Publication

Wiley-Blackwell is an imprint of John Wiley & Sons, formed by the merger of Wiley's global Scientific, Technical and Medical business with Blackwell Publishing.

Registered office: John Wiley & Sons, Ltd, The Atrium, Southern Gate, Chichester, West Sussex,
PO19 8SQ, UK

Editorial offices: 9600 Garsington Road, Oxford, OX4 2DQ, UK
The Atrium, Southern Gate, Chichester, West Sussex, PO19 8SQ, UK
111 River Street, Hoboken, NJ 07030-5774, USA

For details of our global editorial offices, for customer services and for information about how to apply for permission to reuse the copyright material in this book please see our website at www.wiley.com/wiley-blackwell.

Library of Congress Cataloging-in-Publication Data

Brusatte, Stephen.
Dinosaur paleobiology / Stephen L. Brusatte.
p. cm. – (Topics in paeobiology)
Includes bibliographical references and index.
ISBN 978-0-470-65657-0 (hardcover : alk. paper) 1. Dinosaurs. 2. Paleobiology. I. Title.
QE861.4.B786 2012
567.9–dc23 2011050466

A catalogue record for this book is available from the British Library.

Wiley also publishes its books in a variety of electronic formats. Some content that appears in print may not be available in electronic books.

Set in 9/11.5pt Trump Mediaeval-Roman by Thomson Digital, Noida, India

1 2012

Dedication

To my wife, Anne

Contents

Foreword

Paleobiology is a vibrant discipline that addresses current concerns about biodiversity and about global change. Further, paleobiology opens unimagined universes of past life, allowing us to explore times when the world was entirely different and when some organisms could do things that are not achieved by anything now living.

Much current work on **biodiversity** addresses questions of origins, distributions, and future conservation. Phylogenetic trees based on extant organisms can give hints about the origins of clades and help answer questions about why one clade might be more species-rich ("successful") than another. The addition of fossils to such phylogenies can enrich them immeasurably, thereby giving a fuller impression of early clade histories, and so expanding our understanding of the deep origins of biodiversity.

In the field of **global change**, paleobiologists have access to the fossil record and this gives accurate information on the coming and going of major groups of organisms through time. Such detailed paleobiological histories can be matched to evidence of changes in the physical environment, such as varying temperatures, sea levels, episodes of mid-ocean ridge activity, mountain building, volcanism, continental positions, and impacts of extraterrestrial bodies. Studies of the influence of such events and processes on the evolution of life address core questions about the nature of evolutionary processes on the large scale.

As examples of **unimagined universes**, one need only think of the life of the Burgess Shale or the times of the dinosaurs. The extraordinary arthropods and other animals of the Cambrian sites of exceptional preservation sometimes seem more bizarre than the wildest imaginings of a science fiction author. During the Mesozoic, the sauropod dinosaurs solved basic physiological problems that allowed them to reach body masses ten times those of the largest elephants today. Further, the giant pterosaur *Quetzalcoatlus* was larger than any flying bird, and so challenges fundamental assumptions in biomechanics.

Books in the **Topics in Paleobiology** series will feature key fossil groups, key events, and analytical methods, with emphasis on paleobiology, large-scale macroevolutionary studies, and the latest phylogenetic debates.

The books will provide a summary of the current state of knowledge, a trusted route into the primary literature, and will act as pointers for future directions for research. As well as volumes on individual groups, the Series will also deal with topics that have a cross-cutting relevance, such as the evolution of significant ecosystems, particular key times and events in the history of life, climate change, and the application of new techniques such as molecular paleontology.

The books are written by leading international experts and will be pitched at a level suitable for advanced undergraduates, postgraduates, and researchers in both the paleontological and biological sciences.

Michael Benton,
Bristol,
November 2011

Preface

Dinosaurs are everywhere these days. They are the most popular exhibits in many museums, the stars of movies and the focus of television documentaries, the pitchmen in advertising campaigns and the subject of gushing articles in magazines and newspapers. Looking at how dinosaurs are portrayed in the popular press, it is easy to lump them together with leprechauns, unicorns, and dragons – creatures of myth and iconic lore that only exist in the imaginations of children and the whimsy of pop culture. But dinosaurs are not creatures of fantasy – they were real animals, of many fantastic shapes and sizes, that dominated terrestrial ecosystems for an astounding span of over 160 million years. They were living, breathing, feeding, moving, reproducing, evolving organisms that originated in the aftermath of the worst mass extinction in earth history, rose to dominance as a supercontinent was splitting and climates were fluctuating, evolved into some of the largest and most fearsome animals the planet has ever seen, and then suddenly went extinct right at the same time that a giant comet or asteroid slammed into the earth and supervolcanoes were belching rivers of lava. And perhaps most astonishing of all, these ancient creatures, so often symbols of lethargy and failure, were the ancestors of one of the most successful groups of living animals: the birds.

The scientific study of dinosaurs has been experiencing a remarkable renaissance over the past couple of decades. Scientific understanding of dinosaur anatomy, biology, and evolution has advanced to such a degree that paleontologists often know more about 100 million-year-old dinosaurs than many species of living organisms. Research is proceeding at a frenetic pace, as illustrated by a simple statistic: during 2010, the year I proposed and began writing this book, some 63 new species of dinosaurs were discovered. That's a stupendous rate of over one new species per week, which has largely been fueled by a great increase in fieldwork exploration (especially in China and South America) and an ever-expanding roster of graduate students and other young researchers choosing to study dinosaurs. And not only is our stockpile of dinosaur fossils growing at an exponential pace, but so is the development of new research techniques. It used to be that paleontologists could pontificate on the biology, evolution, and extinction of dinosaurs based only on the flimsiest scraps of evidence, interpreted with a healthy dose of imagination and a snickering dismissal of the explicit, quantitative, repeatable methodologies that have long been the norm in most other sciences. Those days are long gone. Today, dinosaur paleontology is a dynamic science that demands evidence-based rigor and is firmly integrated with many other scientific disciplines. Indeed, researchers often draw from a diverse repertoire of anatomy, geology, chemistry, physics, mathematics, and statistics when studying dinosaurs. It is not uncommon to see advanced calculus used to estimate dinosaur body masses, computerized engineering analyses marshaled to test whether certain dinosaurs were capable of feeding or moving a certain way, or statistics utilized to explicitly assess whether some dinosaurs were evolving faster or slower than others.

The breadth of current dinosaur research is vast. Some scientists spend their careers discovering and describing new species, others may focus solely on anatomy or genealogy, and others concentrate on studying dinosaur locomotion or feeding. In general, though, all contemporary work on dinosaurs provides evidence for addressing two main questions. First, how did dinosaurs function as living animals? Second, what is the grand narrative of dinosaur evolution across the Mesozoic? The only way to attack these questions in a defensible competent manner is to interpret the primary evidence – the actual dinosaur fossils that provide a bedrock for the entire enterprise of dinosaur research – using explicit quantitative methodologies. The emerging answers to these questions, and the evidence and methods that are revealing them, are the focus of this book. Like any science, dinosaur paleontology is constantly changing as new fossils are found and new research techniques are developed and refined. Our knowledge of dinosaur biology and evolution is shifting fast, and this book is an attempt to capture what is currently known about this remarkable group of ancient creatures that dominated our planet for so long.

From a more personal standpoint, this book is also a young, perhaps brazen, researcher's examination of his field of study. I am in the somewhat unusual position of writing this book as a PhD student – a scientist without an advanced degree, with less than a decade of research experience, who has not had the time and wisdom to (at least yet) make a substantial mark on the field. But although I may not be the most traditional author of a technical dinosaur book, and although perhaps I should be focusing more on my thesis than on writing books, I feel that I am able to present a perspective that has yet to be tapped by the oversaturated dinosaur book market. I have been brought up and trained within the dynamism of contemporary dinosaur research, and have been experiencing the explosive growth of this field as a dizzying cocktail of new discoveries and techniques have enabled modern scientists to understand dinosaurs in unprecedented detail. In many ways this book is a personal journey. I do not pretend that this book is an exhaustive encyclopedia of everything that is currently known about dinosaurs, or a technical critique of the minutiae of every method and each piece of evidence. Instead, what I present is my understanding of dinosaur biology and evolution – the understanding of a student actively learning about dinosaurs and in the midst of planning his own research program and career. I present what I find interesting and empowering, what I think is most important and exciting about contemporary research, and where I think the field is heading.

So, then, what do scientists actually know about dinosaurs? As it turns out, the truth about dinosaur biology and evolution is surely more fascinating than even the most sensational dinosaur documentary or movie, and more than fascinating enough to fuel the passion of this member of the MTV generation. Indeed, without even a hint of hyperbole, the story of dinosaur evolution is one of the greatest stories ever told.

Steve Brusatte
New York, USA
September 1, 2011

Acknowledgments

Writing a book is a lot of fun, but also a lot of work. Although my name may appear on the cover, this book could never have been written without the help of so many friends and colleagues across the globe. One of my favorite aspects of paleontological research is the friendships and collaborations that are fostered, and I'm pleased to be able (even if in a small way) to showcase the work of many of my colleagues and include their contributions in the form of photos and illustrations. This book relects my personal journey studying paleontology, and building a career in research, over the past decade. I have tried, wherever possible, to include photographs and figures that I have compiled during my research work, fieldwork, and museum visits, or those provided by trusted colleagues and friends. These colleagues are too numerous to thank here, but individuals who helped with images are credited in the figure captions. To all of them, let me apologize one final time for all my nagging questions.

I have been very fortunate in my young career to have been mentored by three very excellent advisors: my undergraduate advisor Paul Sereno at the University of Chicago, my Master's advisor Mike Benton at the University of Bristol, and my PhD advisor Mark Norell at Columbia University and the American Museum of Natural History. I recognize how lucky I have been to study under three of the most prominent luminaries in the field, and thank them for all of heir guidance, advice, and support over the years. Specific to this book, I would like to offer my sincere thanks to Mike Benton, the editor of the Topics in Paleobiology series, who invited me to write a book on dinosaurs for Wiley-Blackwell. I am humbled that he would place such trust in me at such a young stage in my career, and I hope that I have seized this remarkable opportunity and written a book that justifies his confidence in me. And to Mark Norell, my current advisor, please know that I will always appreciate the freedom that you have provided me as a student to pursue whatever interests me. Not every PhD advisor would allow his student to put a doctoral thesis on the backburner to write a book.

Although many colleagues helped with images and advice, a few people deserve special mention here. I am very pleased to feature the skeletal reconstructions of Scott Hartman, the photographs of Mick Ellison, and the artistic life reconstructions of Jason Brougham. Scott, Mick, and Jason are three of the best artists in the business, and are consistently producing beautiful and scientifically accurate work that, at least in my opinion, sets a benchmark for the field. Without their contributions this book would be little more than a jumble of 130,000 words; if this book does succeed in bringing dinosaurs to life, it is largely due to their reconstructions, photos, and illustrations. A lot of the work they have provided here has not been reproduced before, and all three worked tirelessly to help make this book something more than just a run-of-the-mill dinosaur tome. Several trusted colleagues also read large portions of this book, including Roger Benson, Mike Benton, Richard Butler, Matt Carrano, Greg Erickson, Paul Gignac, John Hutchinson, and Pat O'Connor, as well as the formal reviewers (Paul Barrett and Larry Witmer). Their advice was instrumental, and I thank them for their encouragement, suggestions, and frank criticism that helped tighten my writing and improve the text. All mistakes, however, are of course mine.

My continuing development as a scientist has been facilitated by the friendship, collaboration, advice, and assistance of many trusted colleagues. I would like to especially acknowledge my two closest colleagues, Roger Benson and Richard Butler, whom I consider something of scientific blood brothers. I've been fortunate to work on many projects with Richard and Roger, and have shared many long car journeys, evenings over beers, and hours in museum collections learning from them. They are two of the most dynamic, thoughtful young researchers in the field, and I have no doubt that they will emerge as among the most respected voices in dinosaur research as their careers unfold. I've also enjoyed fruitful collaborations and friendships with many other close colleagues, including Thomas Carr, Zoltán Csiki, Phil Currie, Graeme Lloyd, Octavio Mateus, Josh Mathews, Grzegorz Niedźwiedzki, Marcello Ruta, Steve Wang, Scott Williams, and Tom Williamson. My fellow graduate students and advisors have provided constant inspiration, including Carol Abraczinskas, Marco Andrade, Amy Balanoff, Robin Beck, Mark Bell, Gabe Bever, Jianye Chen, Jonah Choiniere, John Flynn, Andres Giallombardo, Christian Kammerer, Mike LaBarbera, Shaena Montanari, Sterling Nesbitt, Paul Olsen, Rui Pei, Albert Prieto-Márquez, Manabu Sakamoto, Michelle Spaulding, Mark Webster, Hongyu Yi, and Mark Young. Three colleagues that I have only worked with briefly, but have long admired for their adherence to quantitative rigor and ability to ask and answer interesting questions, are Matt Carrano, Greg Erickson, and John Hutchinson. Many other colleagues also have helped me along, including Robert Bronowicz, Dan Chure, Julia Desojo, Phil Donoghue, Gareth Dyke, Jerzy Dzik, Martin Ezcurra, Dave Gower, Mike Henderson, Dave Hone, Steve Hutt, Randy Irmis, Max Langer, Pete Makovicky, Darren Naish, Chris Organ, Emily Rayfield, Nate Smith, Tomasz Sulej, Corwin Sullivan, Alan Turner, Mátyas Vremir, Anne Weil, Jessica Whiteside, Zhao Xijin, and Xu Xing.

And finally, but most importantly, I must thank my family and close personal friends. My parents (Jim and Roxanne Brusatte) have long fostered my passion for paleontology and writing, even going as far as letting me plan whole days of family vacations dedicated to museum hopping (which my brothers, Mike and Chris, must have really enjoyed). My parents and in-laws (Peter and Mary Curthoys) have generously provided space in their homes for me to write this book. A handful of good personal friends have helped fuel my passion for writing and have molded me (gradually, and surely with much pain) into a competent author: Fred Bervoets, Lonny Cain, Lynne Clos, Allen Debus, Mike Fredericks, Richard Green, Joe Jakupcak, Mike Murphy, and Dave Wischnowsky. I sincerely thank all of the help that my editor, Ian Francis, has provided with this book. And last, but certainly not least, I dedicate this book to my patient and beautiful wife Anne, who someday (I hope) will understand that it isn't too strange for a grown man to spend his days thinking about 65 million-year-old, 6-tonne, killer-toothed megapredators.

1

An Introduction to Dinosaurs

It is necessary to begin with a straightforward, if not pedantic, question: what is a dinosaur? In popular parlance a dinosaur is often anything that is old, big, or frightening. Any kindergartner could identity *Tyrannosaurus* or *Triceratops* as dinosaurs, and they would be correct, but newspapers will often sloppily use the term ''dinosaur'' to refer to flying reptiles (pterosaurs), marine reptiles (plesiosaurs, ichthyosaurs, etc.), or even large mammals (such as the woolly mammoth). ''Dinosaur'' has become a cultural and political idiom as well: out-of-touch politicians or washed-up celebrities are often mockingly ridiculed as ''dinosaurs,'' a synonym for lethargy, obsolescence, and inevitable extinction.

Although the term ''dinosaur'' is firmly established in the popular lexicon, it is also a scientific term that refers to a specific group of organisms that shared particular anatomical features and lived during a certain period of time. While the popular definition of ''dinosaur'' is amorphous, the scientific definition is precise. We will get to that definition in a moment, but first it is necessary to review exactly where dinosaurs fit in the tree of life – when they evolved, what they evolved from, and who their closest relatives are – so it is easier to comprehend the explicit distinction between dinosaur and non-dinosaur. Some of the following discussion may seem elementary to more advanced readers, and I intentionally use a more conversational tone in this introduction to appeal to non-specialists and younger students. It is important, however, to set the stage for this book by first painting in broad strokes, before progressing to a more nuanced discussion of dinosaur anatomy, ecology, behavior, and function.

Dinosaur Paleobiology, First Edition. Stephen L. Brusatte.

Dinosaurs: A Brief Background

Dinosaurs are one of the best-known, most intensively studied, and most successful groups of tetrapods: animals with a backbone that have limbs with digits (fingers and toes) (Fig. 1.1). Within the tetrapod group, dinosaurs are members of a speciose subgroup of reptiles called the Archosauria, which literally means "ruling reptiles" in Greek (Cope, 1869; Romer, 1956; Carroll, 1988; Benton, 2005) (Figs 1.1–1.6). This is a fitting moniker, as archosaurs have been a major component of terrestrial ecosystems since the early Mesozoic, and for large swaths of time have been ecologically dominant and incredibly diverse (Benton, 1983; Fraser, 2006). Living archosaur subgroups include two major clades, birds and crocodylomorphs, which are among the most familiar and successful groups of extant vertebrates (note that a "clade" refers to a group of animals that includes an ancestor and all of its descendants; Fig. 1.5) (Gauthier, 1986; Sereno, 1991a; Nesbitt, 2011). However, the great majority of archosaur diversity is extinct, and the two main living groups merely represent two highly aberrant body types (fliers and semiaquatic sprawlers) that were able to endure several mass extinction events that pruned most other lineages on the archosaur family tree. Dinosaurs, without a doubt, are the most familiar of these extinct archosaurs.

The archosaur clade is an ancient group that originated approximately 250 million years ago (Nesbitt, 2003, 2011; Brusatte et al., 2010a, 2011a; Nesbitt et al., 2011). Some of the closest archosaur relatives are known from the Late Permian (e.g. Dilkes, 1998; Nesbitt et al., 2009a), and archosaurs themselves arose within the first few million years after the devastating Permo-Triassic mass extinction, the largest instance of mass death in earth history, estimated to have eradicated 75–95% of all species (Raup, 1979; Stanley and Yang, 1994; Benton, 2003; Erwin, 2006; Clapham et al., 2009). The Permo-Triassic extinction interval was a time of death and destruction on a massive scale, but its aftermath was a time of equally large-scale rebirth: ecosystems were reshuffled, organisms that were once overshadowed had the freedom to flower, and entirely new groups originated and

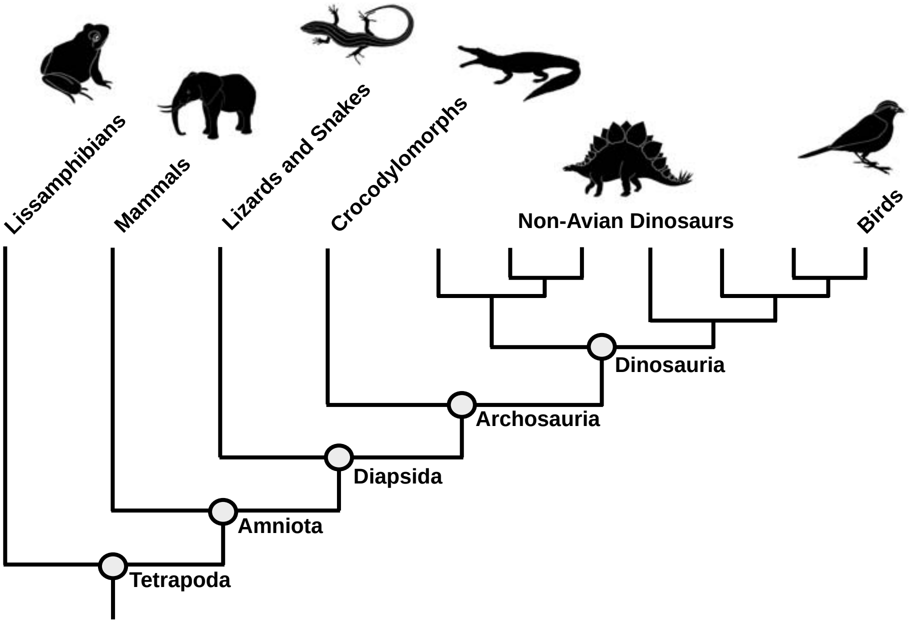

Figure 1.1 A simplified genealogical tree (cladogram) of tetrapods (limbed vertebrates) showing the position of dinosaurs and their closest relatives. Artwork by Simon Powell, University of Bristol.

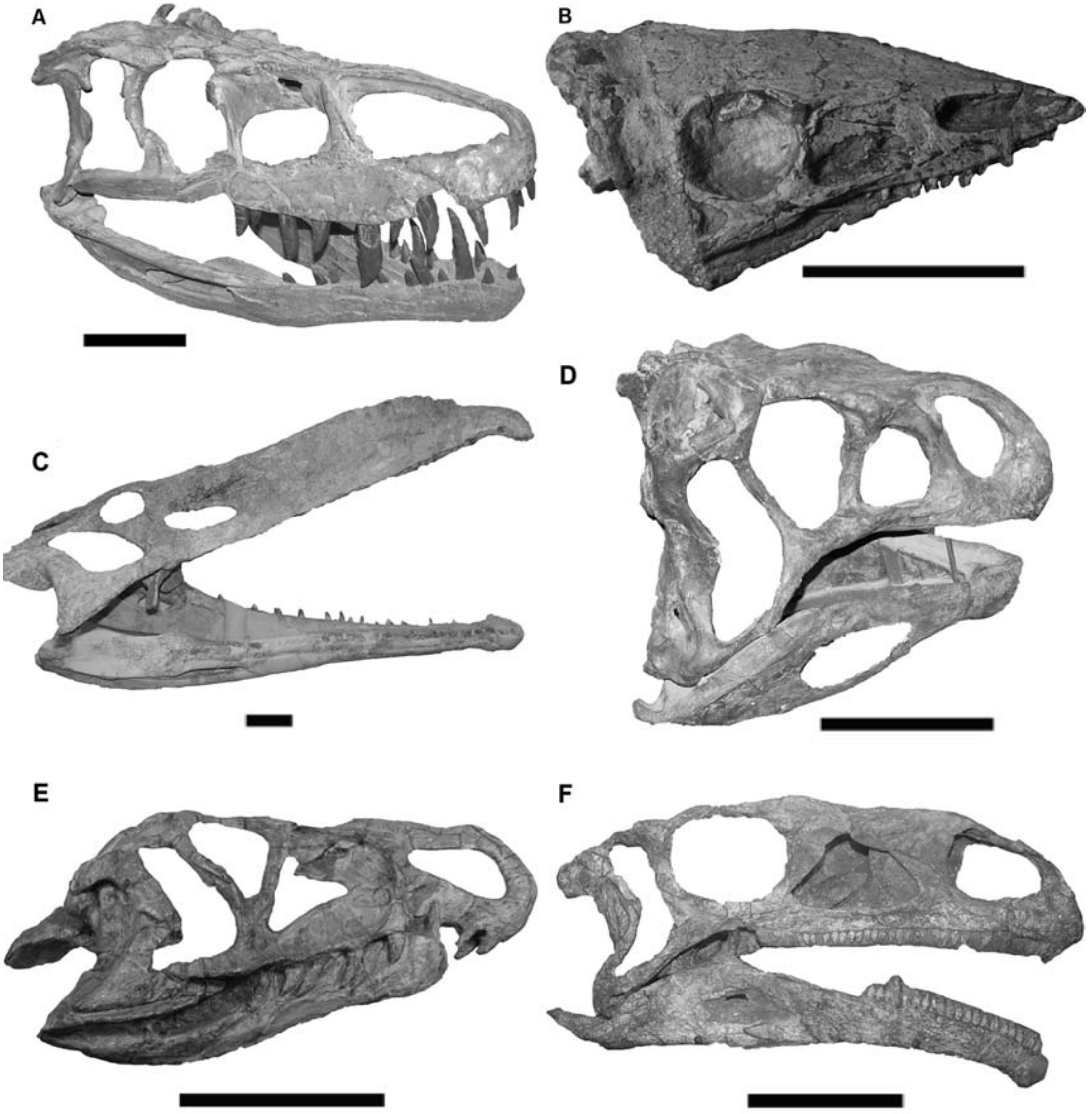

Figure 1.2 A montage of the skulls of various archosaurs, including the rauisuchian crurotarsan *Batrachotomus* (A), the aetosaurian crurotarsan *Aetosaurus* (B), the phytosaurian crurotarsan *Nicrosaurus* (C), the poposauroid crurotarsan *Lotosaurus* (D), the ornithosuchid crurotarsan *Riojasuchus* (E), and the sauropodomorph dinosaur *Plateosaurus* (F).

diversified in the barren, post-extinction landscape (Benton et al., 2004; Sahney and Benton, 2008). Among these entirely new groups were "modern" lineages such as turtles, mammals, lepidosaurs (lizards and their relatives), lissamphibians (frogs and salamanders), and archosaurs. It is no wonder that the Triassic Period is often called the "birth of modern ecosystems," as so many of today's most distinctive and successful clades originated during this time.

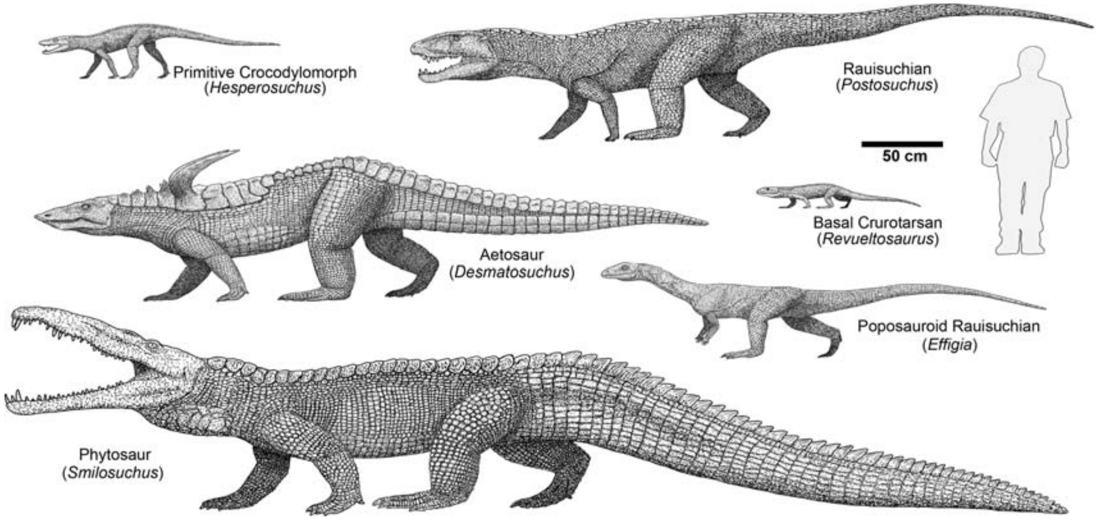

Figure 1.3 A montage of life reconstructions of various crurotarsan (crocodile-line) archosaurs. Illustrations courtesy of Dr Jeff Martz, National Park Service.

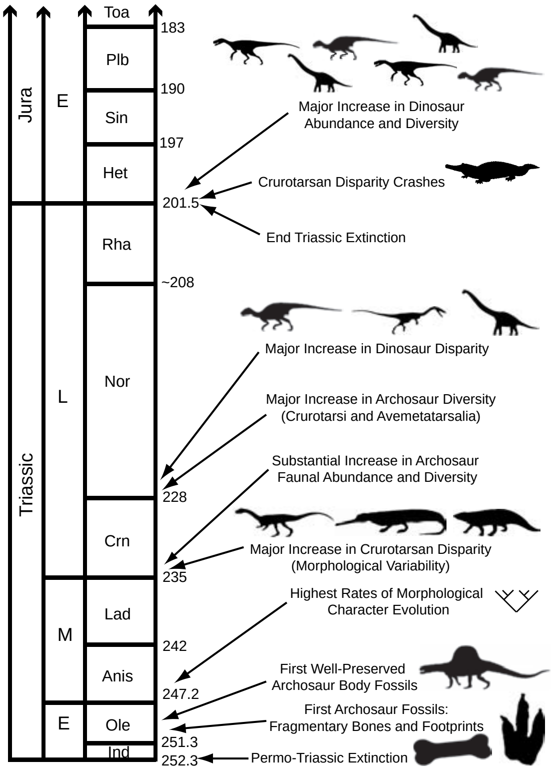

Figure 1.4 A general timeline of important events during the first 70 million years of archosaur evolution during the Triassic and early Jurassic. Image based on illustration in Brusatte et al. (2011a).

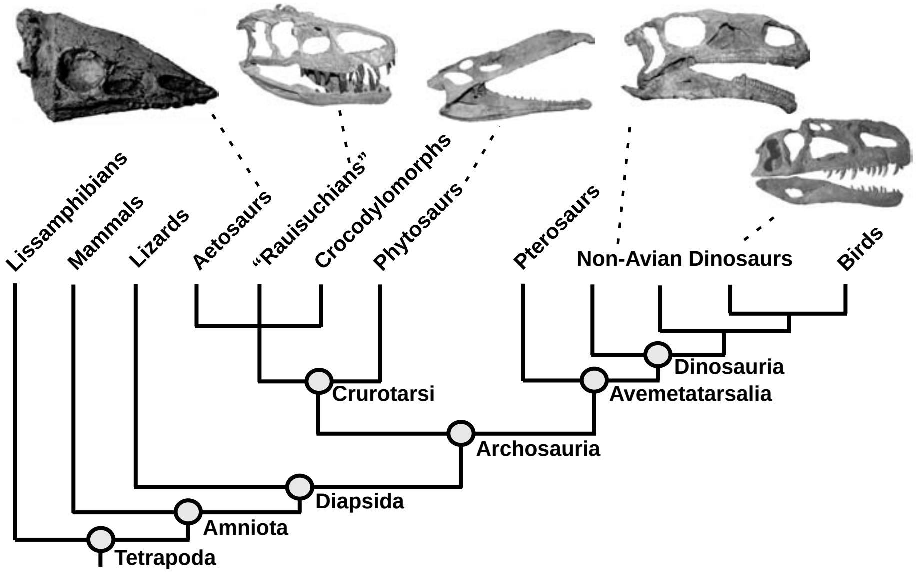

Figure 1.5 A simplified genealogical tree (cladogram) of archosaurs, showing the position of dinosaurs and their closest relatives. Artwork by Simon Powell, University of Bristol.

The archosaur clade diversified rapidly after its origination, as most of the major archosaur subclades and body plans were established by the end of the Early Triassic, a mere 5 million years after the mass extinction (Brusatte et al., 2011b) (Fig. 1.4). The oldest unequivocal archosaur body fossil with a well-constrained age and phylogenetic position is *Xilousuchus*, from the late Olenekian/early Anisian (c.247–248 million years ago) of China (Nesbitt et al., 2011). This species is a derived member of the "crocodile line" of archosaur phylogeny, which is properly referred to as Crurotarsi (also sometimes called Pseudosuchia). Crurotarsi includes crocodylomorphs and their closest extinct relatives, whereas the other half of the archosaur clade, the "bird-line" group Avemetatarsalia (sometimes also called Ornithodira), includes birds, dinosaurs, and pterosaurs (the familiar flying

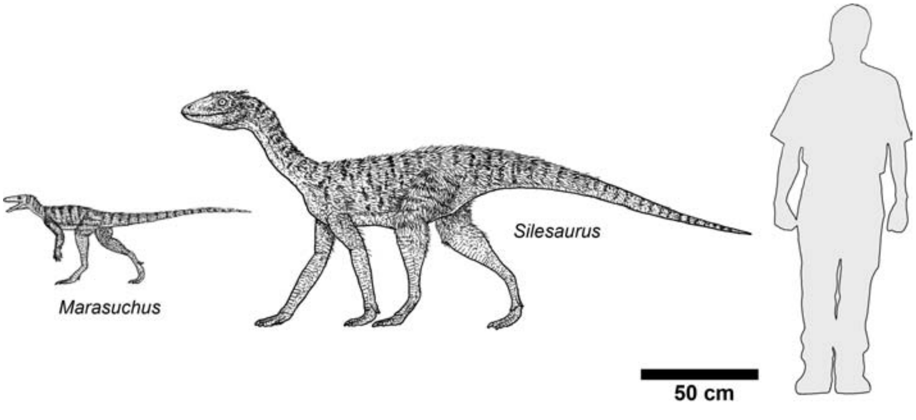

Figure 1.6 Life reconstructions of the basal non-dinosaurian dinosauromorphs *Marasuchus* and *Silesaurus*, two of the closest relatives to dinosaurs. Illustrations courtesy of Dr Jeff Martz, National Park Service.

reptiles) (Gauthier, 1986; Sereno, 1991a; Benton, 1999, 2004; Irmis et al., 2007a; Brusatte et al., 2010a, 2011b; Nesbitt, 2011) (Fig. 1.5). Because *Xilousuchus* is a member of the crocodile lineage, then the bird line (but not true birds themselves) must have also been present by approximately 248 million years ago, because these two lineages are each other's closest relative, and the presence of one implies the contemporary existence of the other (see Norell, 1992, 1993 for details of such "ghost lineages," which will be discussed later in the text).

Although the bird lineage, of which dinosaurs are a part, must have been present by the Early Triassic, the first body fossils of truly dinosaur-like animals are not known until the late Anisian (c.243–244 million years ago) (Nesbitt et al., 2010). These fossils do not belong to true dinosaurs, as will become clear below, but are among the handful of closest relatives to dinosaurs, and likely resembled and behaved like their more famous cousins (Fig. 1.6). More properly, they are members of the "dinosaur stem clade," technically known as Dinosauromorpha (Sereno, 1991a; Benton, 1999, 2004; Ezcurra, 2006; Brusatte et al., 2010a; Nesbitt, 2011). Among the best known species are *Lagerpeton* (Sereno and Arcucci, 1993), *Marasuchus* (Sereno and Arcucci, 1994), *Dromomeron* (Irmis et al., 2007a), *Silesaurus* (Dzik, 2003), and *Asilisaurus* (Nesbitt et al., 2010). Middle to Late Triassic dinosauromorphs were small animals, no bigger than a small dog, and were incredibly rare in their ecosystems. The tiny fragile footprints of some of these close dinosaur cousins are known from several fossils sites in the western United States (Peabody, 1948) and Europe (Haubold, 1999; Ptaszynski, 2000; Klein and Haubold, 2007; Brusatte et al., 2011a), and these are remarkably scarce compared with the footprints of other characteristic Triassic animals, especially crocodile-line archosaurs (Fig. 1.7). It seems therefore that these dinosaur stem taxa were small, rare, only represented by a few species, and overshadowed by other contemporary reptiles. From such a humble beginning came the dinosaurs.

True dinosaurs likely originated some time in the Middle Triassic, although it is difficult to pinpoint the exact time. The first dinosaur body fossils

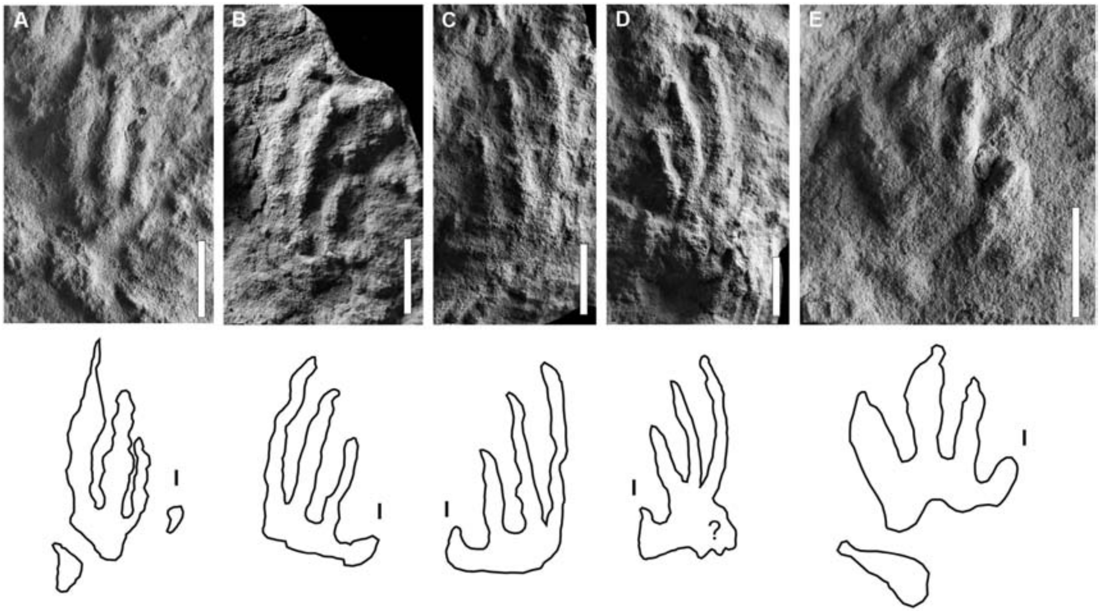

Figure 1.7 A montage of photographs and illustrations of the footprints (A–D) and handprint (E) of a small-bodied quadrupedal dinosauromorph from the Early Triassic of Poland. These fossils are currently the oldest known fossil evidence of the dinosauromorph lineage. Scale bars equal 1 cm. Images by Grzegorz Niedźwiedzki and modified from Brusatte et al. (2011a).

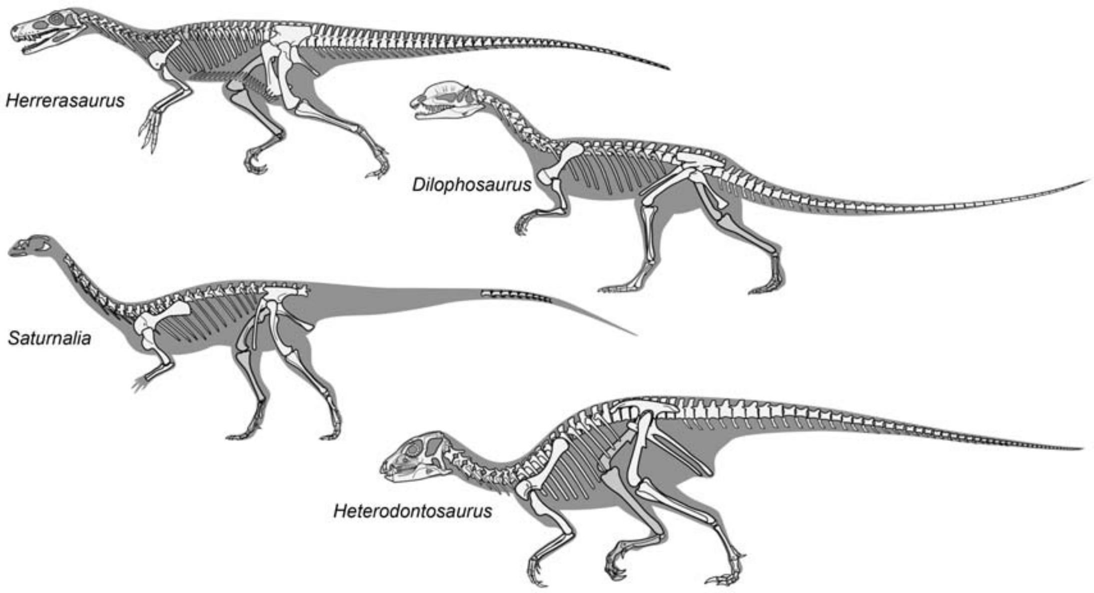

Figure 1.8 Skeletal reconstructions of four early dinosaurs from the Late Triassic to Early Jurassic: the theropod *Herrerasaurus*, the theropod *Dilophosaurus*, the sauropodomorph *Saturnalia*, and the ornithischian *Heterodontosaurus*. Illustrations by Frank Ippolito (American Museum of Natural History) and modified from Brusatte et al. (2010b).

are known from rocks that were deposited in Argentina at approximately the Carnian–Norian boundary (c.228 million years ago) (Rogers et al., 1993; Shipman, 2004; Brusatte et al., 2010b; Ezcurra, 2010a; Langer et al., 2010; Martinez et al., 2011) (Figs 1.8 and 1.9). However, it is almost certain that dinosaurs arose several million years earlier. First, the closest relatives of dinosaurs were clearly present by at least 243 million years ago, as outlined above, and it is reasonable to hypothesize that dinosaurs originated around this time (Nesbitt et al., 2010). Second, there are a number of provocative footprints, which closely match the feet of primitive dinosaurs, that have recently been described from the Ladinian (c.242–235 million years ago) of Europe and South America (Gand and Demathieu, 2005; Melchor and de Valais, 2006). Regardless of the exact timing of dinosaur origins, which will surely become clearer as new fossils are found, it is undeniable that dinosaurs began to diversify quickly once they originated. By the time the first dinosaur body fossils appear in the fossil record, representatives of the three major subgroups of dinosaurs – the carnivorous theropods, long-necked sauropodomorphs, and herbivorous and often armored or crested ornithischians – are already present (Sereno and Novas, 1992; Sereno et al., 1993; Langer et al., 1999, 2010; Butler et al., 2007; Martinez and Alcober, 2009; Brusatte et al., 2010b; Ezcurra and Brusatte, 2011; Martinez et al., 2011).

Therefore, by the Late Triassic, the Age of Dinosaurs was in full swing, and over the course of the next 50 million years dinosaurs would continue to diversify into new species and body types, before ultimately becoming the dominant mid-to-large size vertebrates in terrestrial ecosystems globally in the Early Jurassic, about 176 million years ago (Benton, 1983; Brusatte et al., 2008a, 2008b, 2010b) (Fig. 1.4). From this point on, throughout the remainder of the Jurassic and the Cretaceous, from approximately 175 to 65 million years ago, dinosaurs truly were "ruling reptiles" in every sense of the phrase. They lived in all corners of the globe, including the Arctic highlands, and reached some of the most stupendous sizes ever seen in land-living animals. Some species developed absurdly long necks, others extravagant horns and armor that would make a medieval

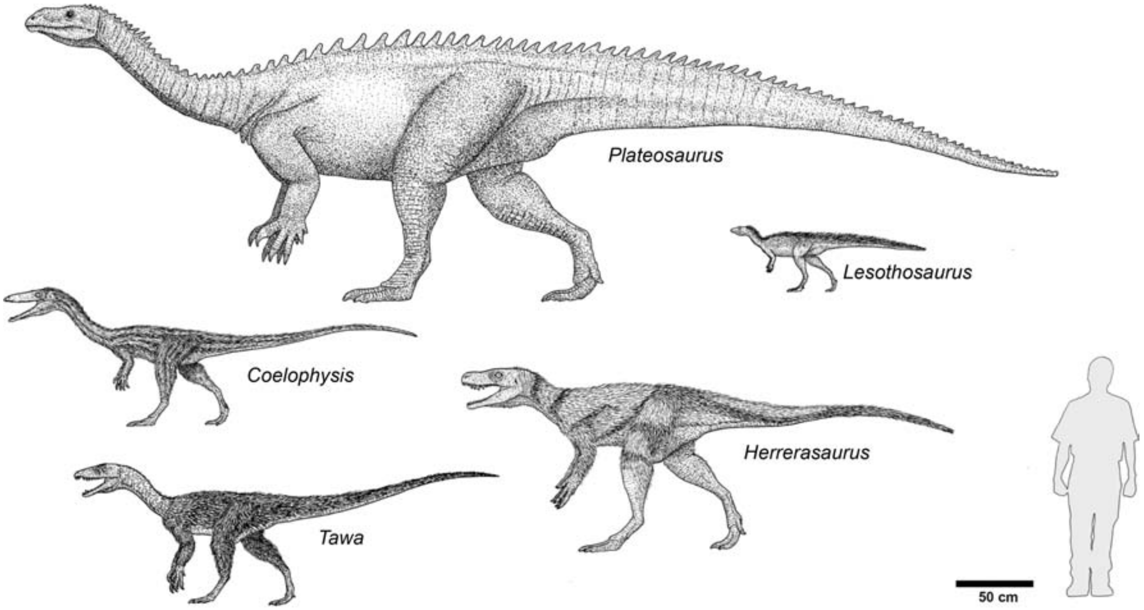

Figure 1.9 Life reconstructions of early dinosaurs from the Late Triassic. Illustrations courtesy of Dr Jeff Martz, National Park Service.

knight blush, and yet others grotesque skulls, longer than an average man is tall and packed with dagger-like teeth, perfect for delivering bone-crunching bites. This fantastic array of dinosaurs – predators and herbivores, dwarves and 50-m long behemoths and all sizes in between – continued to evolve in concert with the slow drift of the continents and the roller-coaster wiggles of climate change, until an unexpected visitor from outer space smashed into the planet 65 million years ago, snuffing out the Age of Dinosaurs and permitting the survival of only one marginal, aberrant dinosaur subgroup: the birds.

The Scientific Definition of Dinosaurs

The above review liberally used terms like "true dinosaur" and "close dinosaur cousin." Vague terminology like this can often be maddening, and can sadly obstruct communication between scientists. Thankfully, however, there is an explicit definition of what constitutes a dinosaur (the "true dinosaurs"). Dinosaurs are defined by scientists as "members of the least inclusive clade containing *Triceratops horridus* and *Passer domesticus* (the living house sparrow)" (Padian and May, 1993; Sereno, 1998; Sereno et al., 2005). At first this definition may seem confusing, and perhaps even counterintuitive, but in fact it is quite straightforward.

Most modern biologists define groups of organisms, such as dinosaurs or mammals or birds, based on ancestry, not on the possession of certain characteristics (e.g. de Queiroz and Gauthier, 1990, 1992; Sereno, 2005). An animal is a dinosaur if it falls in a certain place on the family tree of life, in this case that group of organisms that includes *Triceratops*, the living sparrow (*Passer*), and all descendants of their common ancestor. This hypothetical common ancestor can be visually traced on a family tree (properly called a cladogram, or a phylogeny) of reptiles: simply find *Triceratops*, then *Passer*, and then trace the branches leading to both species down to their common meeting point (Fig. 1.10). Any species that can also be traced down to this common ancestor – in other words, any species that descended from this ancestor – is by definition a dinosaur.

Phylogenetic definitions may seem confusing, but they can be understood with analogies to our own family histories. Some of my ancestors, for instance, immigrated to the United States from northern Italy. As the story goes, my great grandfather, upon hearing distressing rumors of anti-Italian sentiment in his soon-to-be new homeland, decided to change his surname from the obviously Italian "Brusatti" to the somewhat more ambiguous "Brusatte" when registering as a new citizen. This name change can be thought of as the origin of a new group of organisms, in this case the Brusatte family, and anybody who has descended from my great grandfather is by definition a Brusatte. It doesn't matter what we look like – whether we are tall, short, fat, thin, or bald – or when or where we live. We are simply Brusattes by definition.

The definition of Dinosauria given above is called a phylogenetic definition, and it is a general definition that can be applied to any cladogram. Clearly, however, this definition needs a phylogeny for context, and it is unintelligible without a cladogram to refer to. The first scientists to study dinosaurs did not define them this way, which is unsurprising given that these pioneering paleontologists were working in a pre-Darwinian world in which evolution (and hence common ancestry) was regarded as heresy. The man who named Dinosauria, Richard Owen (1842), followed the custom of the time and defined dinosaurs as those animals possessing a certain set of anatomical features, which included various traits relating to body size, posture, and locomotion (see below). Owen saw these features as essential characteristics – an unchangeable blueprint that set dinosaurs apart from other reptiles – but today we simply recognize them as products of common ancestry, as traits that all dinosaurs inherited from that distant ancestor that unites *Triceratops* and *Passer*. These are so-called synapomorphies: shared derived characters – evolutionary novelties – that unite a group on the tree of life.

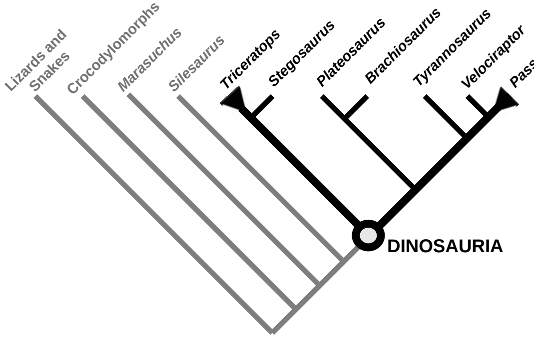

Figure 1.10 A schematic illustration showing how a group (such as Dinosauria) is defined in a phylogenetic sense. Dinosauria is formally defined as "members of the least inclusive clade containing *Triceratops horridus* and *Passer domesticus*." This definition requires a genealogical tree, or phylogeny, to make sense. In this case, locate *Triceratops* and *Passer* on the tree and then trace both branches back to their common ancestral meeting point (denoted by a circle). All species that also descended from this common ancestor are dinosaurs by definition (those species shown in black), whereas other species that fall outside this group are not dinosaurs by definition (those species shown in gray).

This clarifies an important point: animals such as dinosaurs are not strictly defined by their anatomical features, but every group on the tree of life possesses a characteristic set of traits inherited from their common ancestor and thus absent in other organisms. These features are said to diagnose dinosaurs, rather than define them. An analogy can be seen in medicine: cancer is defined as a disease in which cells grow uncontrollably (a process), but is diagnosed by symptoms such as headaches, swelling, or abnormal breathing. Doctors never rigidly define a disease based on symptoms, but a certain disease usually has a characteristic set of symptoms, and by noticing and studying these symptoms a doctor can pinpoint the disease that is causing them. Dinosaurs, therefore, are defined based on ancestry, but share a common set of features, and by identifying and studying these features scientists can be sure that a certain specimen or organism is truly a dinosaur.

Characteristic Features of Dinosaurs

With the above semantics out of the way, we can now focus on those features that distinguish dinosaurs. After all, these anatomical features, and their biological and ecological significance, are much more interesting than the subtleties of cladograms, and the mundane quibbles about whether a certain species did or did not descend from a certain common ancestor. This criticism is not to trivialize phylogenetic definitions – their strength is in their explicitness and stability – but unfortunately tedious debates have raged over whether a certain species is a proper dinosaur or falls just outside of the group defined by *Triceratops* and *Passer*. These academic quarrels can be maddening, because the focus is on a technicality of nomenclature rather than much more illuminating discussions of biology, function, and evolution. And in one sense these debates miss the point, because even if an animal is not quite a dinosaur by definition, it may still have many features common to other dinosaurs, and may have resembled and behaved like true dinosaurs.

A prime example concerns a recently described group of peculiar Middle to Late Triassic archosaurs called the silesaurids. There is no question that these animals were very similar to dinosaurs, as they share several derived features with species that are unequivocally part of the *Triceratops–Passer* group. But there is debate over whether they are true dinosaurs: whether they descended from the common ancestor of *Passer* and *Triceratops*, or whether they are the closest relatives of true dinosaurs (i.e., are immediately outside the *Triceratops–Passer* group) (Dzik, 2003; Ferigolo and Langer, 2007; Irmis et al., 2007a; Brusatte et al., 2010a; Nesbitt et al., 2010; Nesbitt, 2011). This debate is indeed important for that narrow group of specialists which focuses on reptile phylogeny, and does have important ramifications for understanding patterns of character evolution, but is of little concern even for most dinosaur paleontologists. Therefore, in this section, I take a more catholic view of dinosaurs and focus not only on those features that precisely diagnose Dinosauria, but also features that are seen in a handful of the closest dinosaur relatives, which are not dinosaurs by definition but likely were very similar to dinosaurs in a biological sense. Throughout the remainder of this book the focus will be on true dinosaurs, but close dinosaur cousins ("stem dinosaurs") will sometimes be discussed for context or to flesh out exploration of biology, function, or large-scale evolutionary patterns.

When outlining features common to all dinosaurs, it is wise to begin with some historical background. Dinosauria was first established as a distinctive group by Owen (1842), who recognized that three extinct genera of large reptiles – *Megalosaurus*, *Iguanodon*, and *Hylaeosaurus* – shared several unusual features that were unknown in other reptiles, both living and extinct. These included features of the hips, limbs, and body posture, which generally indicated that dinosaurs had a more upright stance than other reptiles (see review in Cadbury, 2002). Discoveries of new fossils continued at a frenzied pace during the remainder of the 19th century, and by the dawn of the 20th century paleontologists had recognized that not only did all known dinosaurs share many features – including several additional hallmarks revealed by the new finds – but that they could be divided into two major subgroups: the "lizard-hipped" saurischians, which include theropods and sauropodomorphs, and the "bird-hipped" ornithischians (Seeley, 1887). These groups are recognized to this day as the two major subdivisions of dinosaurs. Over the next several decades, however, scientists gradually changed their conception of dinosaurs. For much of the 20th century, paleontologists considered saurischians and ornithischians to be separate lineages, which independently diverged long ago from separate "thecodont" (primitive archosaur) ancestors. Therefore, all the features common to saurischians and ornithischians were not seen as the product of common ancestry – characteristics that united all dinosaurs relative to other animals – but rather as insignificant nuances of the anatomy that evolved in parallel in both groups. The very idea of a single, distinctive dinosaur group had fallen out of favor.

This view began to change in the mid 1970s and within a few years was widely dismissed as outdated and incorrect. A new generation of paleontologists, motivated by new discoveries and conceptual advances, resurrected Owen's (1842) original notion of a single, unique group of Mesozoic reptiles – Dinosauria – that could be distinguished from all other organisms based on their possession of shared derived characters. This revolution in thinking was driven by two major factors. First, if saurischians and ornithischians were descended from separate ancestors, then the most primitive members of both groups should look very different from each other.

However, as new fossil finds of early saurischians and ornithischians were discovered in Triassic rocks across the world, this prediction was utterly rejected (Welles, 1954; Crompton and Charig, 1962; Reig, 1963; Colbert, 1970). Instead, primitive theropods, sauropodomorphs, and ornithischians were remarkably similar to each other, exactly as would be predicted if they diverged from a single common ancestor. Second, the advent of an explicit, numerical methodology for inferring genealogical relationships – cladistics – swept through the field of biology in the 1970s and 1980s (Hennig, 1965, 1966). Cladistic principles hold that a lengthy roster of shared anatomical features between two groups is much more likely to indicate close relationship than parallel evolution, and it would take quite a bit of special pleading to retain saurischians and ornithischians as separate entities that evolved so many eerily similar features independent of each other.

It was more plausible, therefore, that the myriad similarities between saurischians and ornithischians meant that these two groups descended from a common ancestor, and could be united as a single, larger group: Dinosauria. This view was persuasively articulated in a seminal 1974 paper by Robert Bakker and Peter Galton. In doing so, Bakker and Galton (1974: 168–169) highlighted a surprisingly long list of characteristic dinosaur features, many of which had been revealed by new discoveries during that long dark period when saurischians and ornithischians were assumed to be nothing but distant, convergent relatives. These features included an upright and fully erect posture, an enlarged deltopectoral crest on the humerus (which anchors large shoulder and chest muscles), a perforated hip socket for articulation with the head of the femur, a well-developed fourth trochanter and lesser trochanter on the femur (which anchor hindlimb muscles), and an ankle joint in which the proximal tarsals (astragalus and calcaneum) were ''fixed immovably on the ends of the tibia and fibula [resulting in a] simple unidirectional hinge between the astragalus–calcaneum and distal tarsals.'' As is evident, many of these features have to do with the posture, strength, and range of motion of the forelimbs and hindlimbs: compared with their closest relatives, dinosaurs had a more upright stance and stronger, more muscular legs, which moved in a more restricted fore–aft direction, ideal for fast running and keen balance. Importantly, Bakker and Galton (1974) acutely recognized that many of these hallmark dinosaur features are also present in living birds, and thus support a close relationship between dinosaurs and birds. This was not a new idea, but one that was rapidly gaining traction in the field at the time. It had been proposed as early as the 1860s (Huxley, 1868, 1870a, 1870b), but had largely been ignored until the pioneering studies of John Ostrom in the 1960s and 1970s (Ostrom, 1969, 1973).

It is a great testament to the work of Bakker and Galton (1974) that many of the features they described as dinosaur trademarks are still considered valid today. This is no small feat, as the exact characteristics that diagnose a clade on the tree of life, such as Dinosauria, are constantly changing as new fossils are discovered and ideas are reinterpreted. At one point in time a certain character, such as a large deltopectoral crest, may only be known in one group, such as dinosaurs. It is easy to envision, however, how a single new fossil discovery, such as a new close dinosaur cousin with a large crest, could reveal that this feature is more widely distributed. This has, in fact, happened to several of Bakker and Galton's diagnostic characters but, importantly, most of the features they described are still only known in dinosaurs and a handful of their closest cousins, and their general argument that dinosaurs are distinguished from other reptiles by their posture and hindlimb anatomy still stands. But perhaps most important of all, Bakker and Galton's (1974) paper was a catalyst for future studies, and authors continue to actively debate exactly what characters unite dinosaurs.

Over the past four decades, beginning with Bakker and Galton's (1974) paper, approximately 50 characters have been identified as potential dinosaur synapomorphies. Many of these have emerged from detailed, higher-level cladistic analyses of archosaur phylogeny (Benton, 1984, 1999, 2004; Gauthier, 1986; Benton and Clark, 1988; Novas, 1989, 1992, 1996; Sereno, 1991a, 1999; Sereno and Novas, 1994; Fraser et al., 2002; Ezcurra, 2006, 2010a; Langer and Benton, 2006; Irmis et al., 2007a; Nesbitt et al., 2009b, 2010; Brusatte et al., 2010a; Martinez et al., 2011; Nesbitt, 2011). Of course, different phylogenies may imply different patterns of character evolution, and the exact

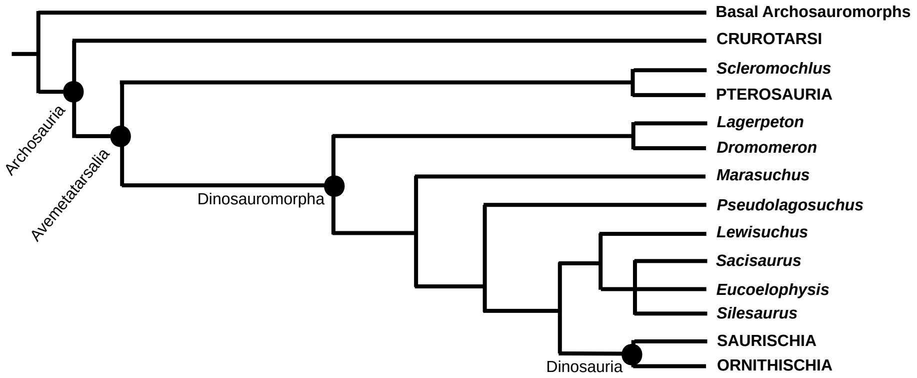

Figure 1.11 The genealogical relationships of "bird-line" archosaurs (Avemetatarsalia) based on the phylogenetic analysis of Brusatte et al. (2010a).

characters that diagnose Dinosauria often differ depending on the phylogeny being considered. To avoid the risk of getting mired in a tedious catalogue of different phylogenies, the discussion here uses the recent phylogeny of Brusatte et al. (2010a) and the review of dinosaur origins by Brusatte et al. (2010b) as guides. This phylogenetic context is graphically shown in Fig. 1.11.

Taking at first a reductionist view, seven features are currently recognized as unequivocal synapomorphies of Dinosauria. In other words, these characters are only known in true dinosaurs, and are absent even in the closest dinosaur cousins. These bona fide dinosaur hallmarks are known from across the skeleton, and include the following.

1 Temporal musculature that extends anteriorly onto the skull roof. The mandibular adductors (temporal muscles) are among the fundamental muscles of mastication in vertebrates: when they contract they elevate the lower jaw, allowing the mouth to close. Dinosaurs have an unusually large and extensive set of mandibular adductor muscles, which expand anteriorly onto the top of the skull (see Holliday, 2009 for review). Although muscle tissue is rarely preserved in dinosaur fossils, the location and size of the mandibular adductors can be deduced based on the position and size of a smooth fossa on the skull roof, to which these muscles attached. In most reptiles, including most archosaurs and even close dinosaur kin such as *Silesaurus*, the fossa is restricted to the parietal bone, and is only expressed as a narrow depression in front of the supratemporal fenestra (one of the main diapsid skull openings, which will be described in more detail below) (Dzik, 2003). In dinosaurs, however, the fossa extends further anteriorly onto the frontal bone, and is a much deeper and more discrete depression (Fig. 1.12A,B). This indicates that the mandibular adductor muscles were larger and more powerful in dinosaurs than in close relatives, and probably implies that dinosaurs had a stronger bite than most other archosaurs.

2 Posterior process of the jugal bifurcates to articulate with the quadratojugal. The jugal bone forms the lateral "cheek" region of the skull underneath the eye and articulates posteriorly with the quadratojugal bone. Together these two bones define the ventral margin of the lateral temporal fenestra, the second of the two main diapsid skull openings. In all archosaurs other than dinosaurs, including *Silesaurus*, the posterior process of the jugal tapers and meets the quadratojugal at a simple overlapping joint (Dzik and Sulej, 2007). In dinosaurs, by contrast, the posterior process bifurcates into two prongs, which clasp the anterior process of the quadratojugal (Fig. 1.12C,D). The biological significance of these two conditions is uncertain, but it is likely that dinosaurs had a stronger jugal–quadratojugal articulation, and this may be functionally associated with their larger mandibular adductor musculature and inferred stronger bite force.

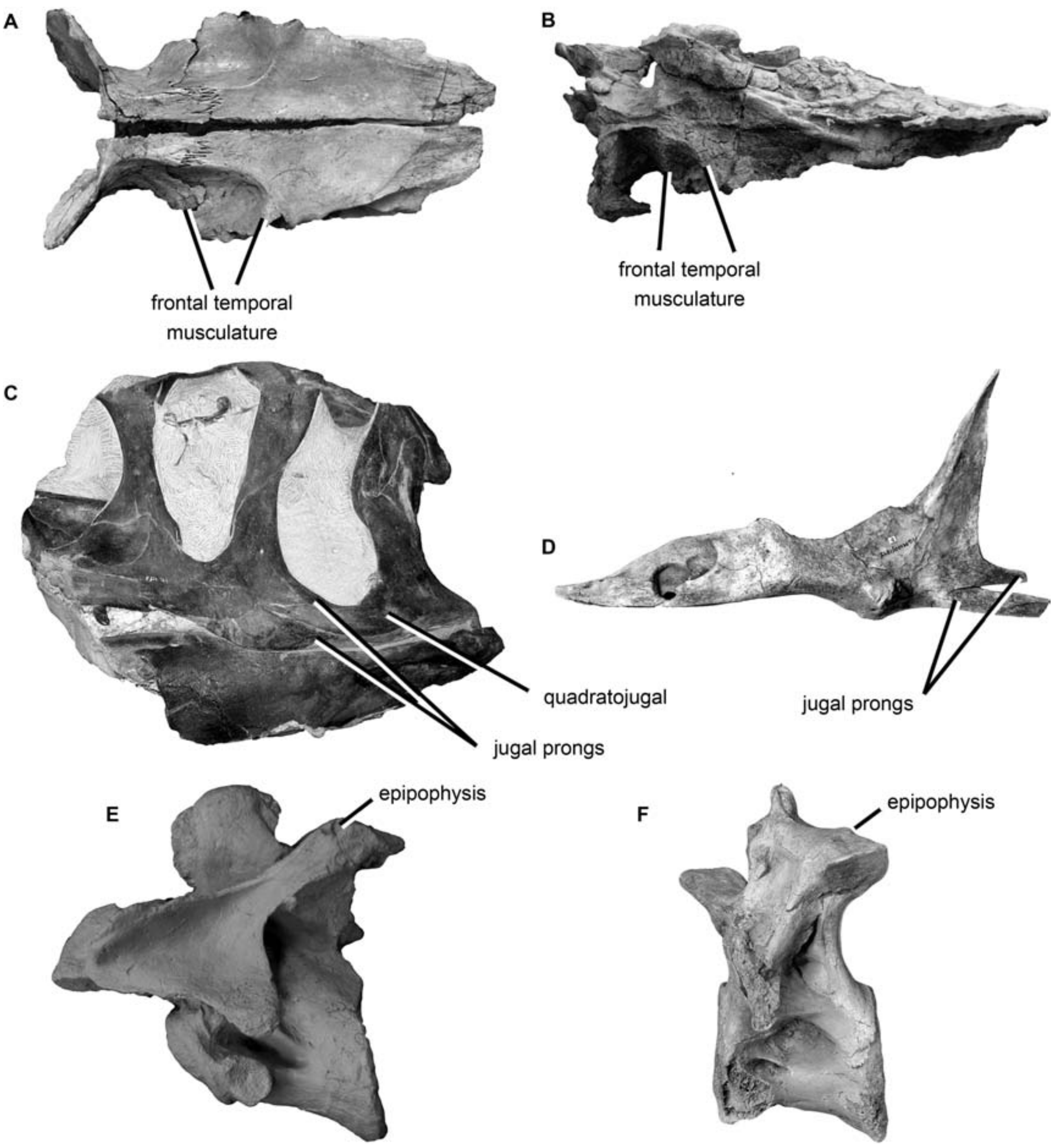

Figure 1.12 Distinctive features of dinosaurs. (A, B) Portions of the skulls of two theropod dinosaurs in dorsal view (*Dubreuillosaurus* and *Guanlong*) showing the anterior extension of the fossa for the temporal jaw muscles onto the frontal. (C, D) The bifurcated posterior process of the jugal, for articulation with the quadratojugal (jugal and quadratojugal of the theropod *Allosaurus* shown in articulation in C, only the jugal of the tyrannosaurid theropod *Alioramus* shown in D). (E, F) The epipophysis, a bump-like projection of bone on the dorsal surface of the postzygapophysis of the cervical vertebrae of the large theropod *Aerosteon* (E) and the tyrannosaurid *Alioramus* (F). Photographs (D) and (F) by Mick Ellison; image (E) courtesy of Dr Roger Benson.

3. Epipophyses on the cervical vertebrae. Epipophyses are projections of bone, which range from small mounds to more elaborate flanges, that protrude from the dorsal surfaces of the postzygapophyses of the cervical vertebrae (those parts of the vertebra that articulate with the following vertebra) (Fig. 1.12E,F). These are present in all dinosaurs, but not close relatives such as *Marasuchus* (Sereno and Arcucci, 1994) or *Silesaurus* (Dzik, 2003; Piechowski and Dzik, 2010). Various muscles of the neck would have attached to these structures, as well as some muscles that may have extended onto the back and thorax (Tsuihiji, 2005; Snively and Russell, 2007a, 2007b). The primary function of these muscles is to extend, rotate, and reinforce the neck and back. Although these muscles would have been present in other archosaurs, the epipophyses in dinosaurs would have increased their available attachment area, perhaps indicating that these muscles were stronger or capable of a greater range of motion (see Snively and Russell 2007a, 2007b for functional considerations).
4. Elongate deltopectoral crest. The deltopectoral crest is a ridge of bone on the humerus, the upper bone of the arm, that anchors the deltoid muscle of the shoulder and the pectoralis muscle of the chest (Coombs, 1978a; Nicholls and Russell, 1985; Dilkes, 2000; Jasinoski et al., 2006). Its primary purpose is to support the latter muscle, whose contraction brings the arm closer to the body. A discrete deltopectoral crest is present in many animals, but it is especially prominent and elongate in dinosaurs, in which it is expressed as an offset flange that extends for 30–40% of the length of the entire humerus (Fig. 1.13). In most other archosaurs, including close dinosaurian relatives such as *Marasuchus* (Sereno and Arcucci, 1994) and *Silesaurus* (Dzik, 2003), the deltopectoral crest is shorter, less offset, and restricted to the proximal portion of the humerus. The large deltopectoral crest of dinosaurs indicates that forelimb motion, particularly adduction towards the body, was especially powerful.
5. Open acetabulum in the pelvis. The acetabulum is the joint surface on the pelvis that articulates with the femur (thigh bone). In humans this is a ball-and-socket joint: the globular head of the femur fits into a deep depression on the pelvis. A similar condition, although with a much shallower socket and a less spherical head of the femur, is present in most reptiles, including most archosaurs. In these animals, the acetabulum is always a discrete socket, which is backed by a medial wall of bone. Dinosaurs, by contrast, have a very different morphology (Fig. 1.14). In all primitive dinosaurs, and most species of more derived dinosaurs, the acetabulum is "open" like a window, because there is no medial wall. This condition is readily apparent in even fragmentary fossils, as a concave ventral margin of the ilium (the most dorsal of the three pelvis bones) is a surefire hallmark of an open acetabulum. The closest relatives of dinosaurs, including *Marasuchus* and *Silesaurus*, have a ventral ilium that is essentially straight, but punctuated by a small concave divot (Sereno and Arcucci, 1994; Dzik, 2003). This is often referred to as an "incipiently open" acetabulum, and is hypothesized to be a transitional morphology that was later elaborated into the fully open condition of dinosaurs.

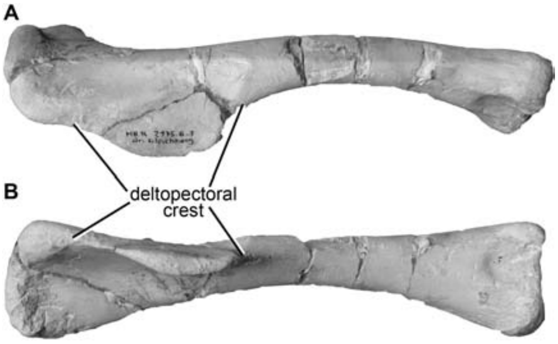

Figure 1.13 Distinctive features of dinosaurs. The humerus of the Late Triassic theropod *Liliensternus* in lateral (A) and anterior (B) views showing the expanded deltopectoral crest.

The opened and closed acetabular morphologies have clear functional significance (Fig. 1.15). Many reptiles, including primitive archosaurs, have a sprawling posture. In these sprawling forms, of which crocodiles are a prime example, the femur is angled outwards to a near horizontal inclination, and during locomotion the full weight of the body is transmitted medially, directly between the femur and the medial wall of the acetabulum. Therefore, it is no surprise that