

INTRODUCTION

Monoliths of the Mesozoic

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GEORGE GAYLORD Simpson (1987:71) expressed his impressions of the well-known North American sauropod *Diplodocus* in the form of a poem to his mother, written while he was studying Mesozoic mammals at Oxford University:

*Oh! Thou imbecile reptile Diplodocus!
Whoever created so odd a cuss?
With a tail like a neck,
And a neck like a tail—
I wonder, by heck,
If you ever do fail
To remember your ends,
And when danger impends
Do stand still, which is bad,
or still more, run tail first,
Or indeed run both ways, which is rather worst!*

Simpson adorned his poem with a caricature of *Diplodocus longus* (fig. 1.1), which—it must be said—looks very sauropod-like. That the anatomy of a sauropod can be adequately conveyed in a humorous sketch attests to the relatively simple and recognizable body plan that characterizes the group. Sauropods have deep, barrel-shaped chests supported by four pillarlike legs. They have a relatively small skull that is perched at the end of an

elongate neck, which in turn is balanced by a long tail that tapers tipward. Numerous synapomorphies reflecting this general body plan diagnose the basalmost sauropod nodes, and small and large differences in all regions of the skeleton allow recognition of 121 sauropod species (Upchurch et al. 2004) that were globally distributed during most of the Mesozoic Era.

Sauropods are paradoxical animals because they are built on an obvious and memorable body plan but are nonetheless one of the most taxonomically diverse dinosaur groups. This volume is dedicated to exploring sauropod systematics and paleobiology by presenting an up-to-date summary of our knowledge and remaining questions in these areas. While acknowledging and embracing the paradoxical nature of sauropods, we hope to explain how their body plan was constructed, explore its variations, and dispel the myth that it led to evolutionary stagnation and eventual replacement by more “advanced” herbivorous dinosaurs.

SAUROPODS AS MONOLITHS

Sauropods are the largest animals known to have walked the earth, as recorded in numerous

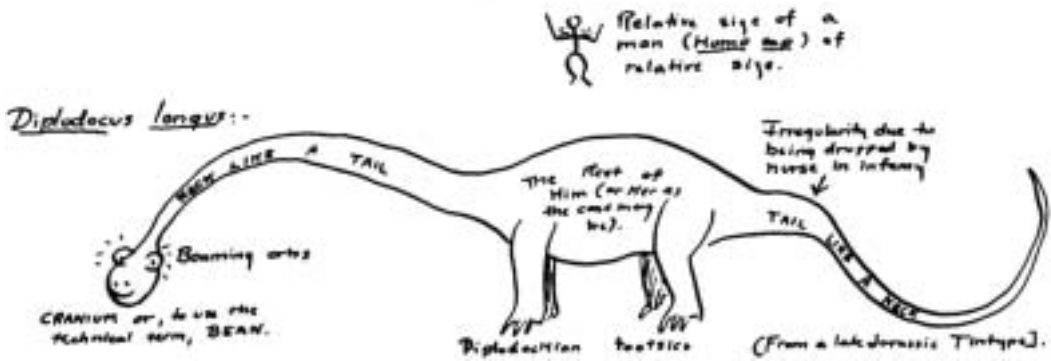


FIGURE I.1. Caricature of *Diplodocus longus* by George Gaylord Simpson (from Simpson 1987).

footprints found around the globe (e.g., Bird 1941, 1944; Hunt et al. 1994). “Monolithic” seems an apt descriptor of both their size and their tight adherence to the body plan described above, of which there are few reversals observed during the nearly 150 million years of sauropod evolution.

The recently published second edition of *The Dinosauria* (Weishampel et al. 2004) contains 22 chapters focused on “dinosaur systematics.” The partitioning of chapters and number of pages devoted to each offer insight into specialists’ perception of different dinosaur groups as well as the attention each has been given historically (table I.1). Not surprisingly, theropods have garnered the most attention, with their diversity (282 species) partitioned among nine chapters and 185 pages. Thyreophorans (68 species, 58 pages), ornithopods (107 species, 71 pages), and marginocephalians (56 species, 53 pages) are partitioned into three chapters each. Prosauropods (23 species, 27 pages) and sauropods (121 species, 64 pages) are the only major dinosaur groups represented by single chapters in *The Dinosauria* 2. This allotment may be justified for Prosauropoda, which is the smallest of the groups mentioned yet the only to receive more pages than its species count. In contrast, Sauropoda is the second most diverse dinosaur group, representing 18%, or nearly one-fifth, of the 661 recognized dinosaur species. Together, sauropods and theropods encompass >60% of dinosaur species diversity. That sauropods are lumped into a single

chapter and given approximately half a page per species suggests that they are at least perceived as monolithic by dinosaur specialists. Is there any justification or explanation for this characterization?

SAUROPOD FOSSIL RECORD

The sauropod fossil record itself may be responsible for the monolithic perception of sauropods. Sauropods first appear in the fossil record during the Late Triassic, during which there are currently several candidate earliest-appearing sauropods. Together, these body fossils and ichnofossils suggest a late Carnian or Norian origin for the group (summarized in Wilson 2005). Possible Carnian sauropods include *Blikanasaurus* (Yates 2003, 2004; Yates and Kitching 2003; Upchurch et al. 2004) and the Portezuelo Formation trackmaker (Marsicano and Barredo 2004); probable Norian sauropods include *Antenonitrus* (Yates and Kitching 2003) and the *Tetrasauropus* trackmaker (Lockley et al. 2001).

The notion of Triassic sauropods is new to this century but was expected based on the first appearance of other saurischians (e.g., Upchurch, 1995; Wilson and Sereno 1998). Prior to this, a lengthy ghost lineage implied by these relationships preceded the exclusively post-Triassic sauropod record (fig. I.2), which began with the fragmentary remains of the Lower Jurassic sauropods *Vulcanodon* (Raath 1972) and *Barapasaurus* (Jain et al. 1975) and the complete remains of the Middle Jurassic *Shunosaurus* (Zhang 1988; Chatterjee and Zheng 2003).

TABLE I.1
Species Counts and Pages Devoted to Systematics in The Dinosauria, 2nd Edition

CHAPTER		PAGES	SPECIES	PAGES/SPECIES
1	Basal Saurischia	22	11	2.00
	Theropoda			
2	Ceratosauria	24	33	0.73
3	Basal Tetanurae	40	74	0.54
4	Tyrannosauroidae	26	19	1.37
5	Ornithomimosauria	14	12	1.17
6	Therizinosauroidae	14	12	1.17
7	Oviraptorosauria	19	18	1.06
8	Troodontidae	12	9	1.33
9	Dromaeosauridae	14	20	0.70
10	Basal Avialae	22	74	0.30
11	Prosauropoda	27	23	1.17
12	Sauropoda	64	121	0.53
13	Basal Ornithischia	10	4	2.50
	Thyreopoda			
14	Basal Thyreophora	8	5	1.60
15	Stegosauria	20	17	1.18
16	Ankylosauria	30	46	0.65
	Ornithopoda			
17	Basal Ornithopoda	20	24	0.83
18	Basal Iguanodontia	25	38	0.66
19	Hadrosauridae	26	45	0.58
	Marginocephalia			
20	Pachycephalosauria	14	17	0.82
21	Basal Ceratopsia	16	21	0.76
22	Ceratopsidae	23	18	1.28
	Total Dinosauria	490	661	—
	Sauropoda contribution	13.06%	18.31%	—

NOTE: Introductory chapters that contained no species descriptions (i.e., "Saurischia," "Ornithischia") are not included in the page tally.

Together, these taxa indicate that the sauropod body plan was constructed early in their evolutionary history and that the earliest sauropods resemble later sauropods more than they do sauropod outgroups (such as prosauropods). That is, until recently, few fossils have been available to document the transition between sauropods and their hypothesized sister-taxa. This fact of the fossil record was borne out in lower-level phylogenetic analyses of sauropod

dinosaurs. Upchurch (1998) recorded 60 synapomorphies diagnosing nodes basal to Eusauropoda, and Wilson (2002) identified 74 synapomorphies arising at Sauropoda and Eusauropoda. These two analyses independently recognize that synapomorphies appearing at basal sauropod nodes represent 26% of *all* synapomorphies identified. Few, if any, dinosaur groups have such a base-heavy distribution of synapomorphies. Thus the sauropod fossil

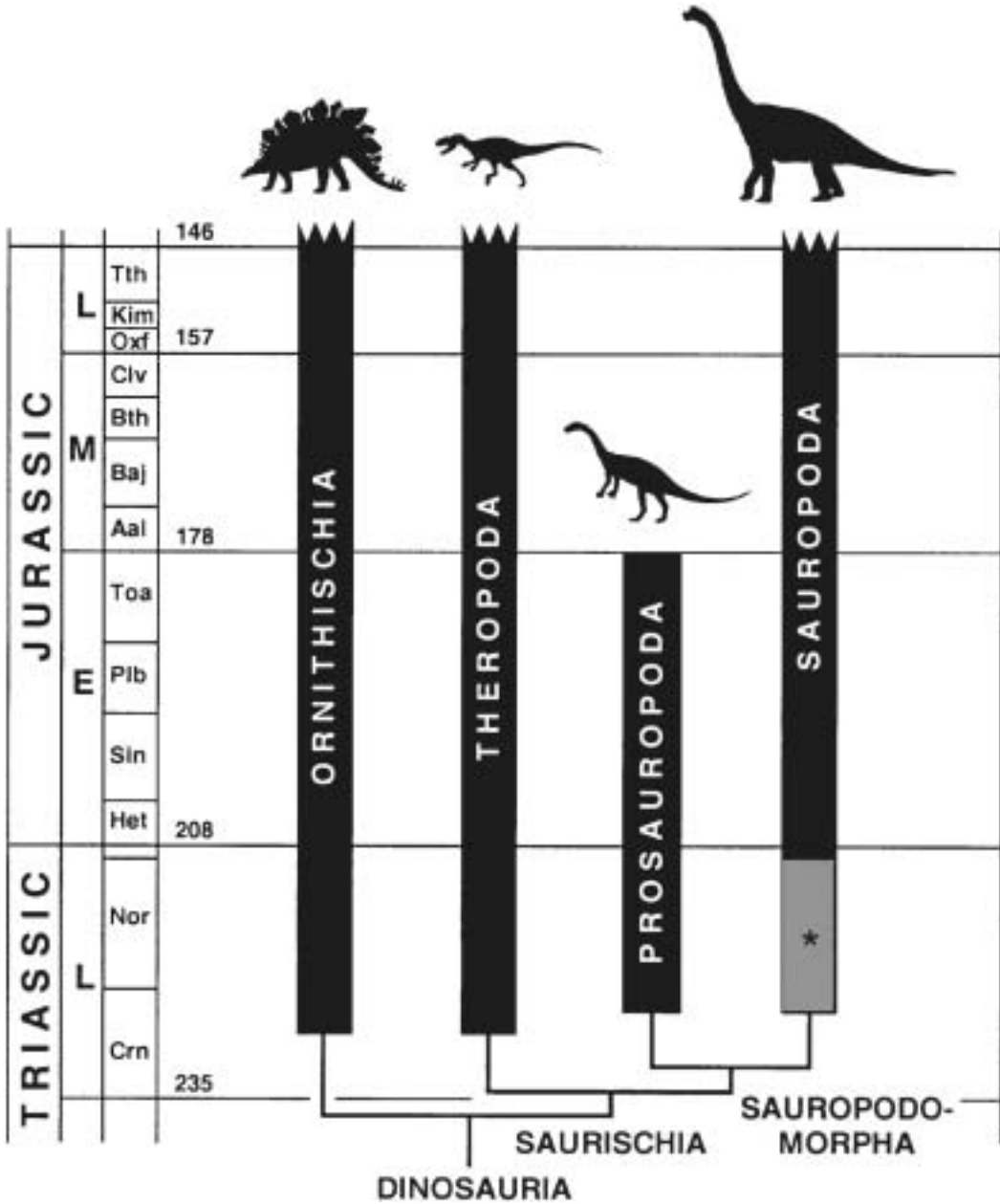


FIGURE 1.2. Temporal distribution and relationships of major lineages of dinosaurs during the Triassic and Jurassic. The vertical bar representing sauropod lineage duration is divided into a black section (pre-2000) and a gray section with asterisk (post-2000). Icons from Wilson and Sereno (1998) and Sereno (1999); timescale based on Harland et al. (1990). (Modified from Wilson 2002:fig. 2.)

record has in part led the monolithic depiction of sauropods.

As new Triassic sauropods are discovered, many of the synapomorphies identified by Upchurch (1998) and Wilson (2002) will likely diffuse stemward and articulate the transition from bipedal, short-necked, nonspecialized her-

bivores to quadrupedal, long-necked, herbivorous monoliths.

SAUROPOD SYSTEMATIC RECORD

Romer (1968:137–138) bookended his discussion of sauropods in his *Notes and Comments on Vertebrate Paleontology* with the following

laments: “A proper classification of the great amphibious sauropods has been the despair of every one working on the group,” and “It will be a long time, if ever, before we obtain a valid, comprehensive picture of sauropod classification and phylogeny.” The perception that sauropod interrelationships were intractable has contributed to their monolithic status, perhaps even more than do the circumstances of their fossil record. How can it be otherwise if subgroups are not identifiable?

Although a “valid” and “comprehensive” sauropod phylogeny was not available during Romer’s time, steps had already been initiated to resolve the relationships of constituent taxa. Sauropod interrelationships were resolved in stages, beginning with early classifications by Marsh (1895, 1898), Janensch (1929), and Huene (1932), followed much later by Bonaparte’s (1986a, 1986b) recognition of “eo” and “neo” sauropods, McIntosh’s (1989, 1990a, 1990b) delineation of numerous sauropod families, and the relatively recent use of cladistic techniques (Russell and Zheng 1993; Calvo and Salgado 1995; Upchurch 1995, 1998; Wilson and Sereno 1998; Wilson 2002; Upchurch et al. 2004). Together, these and other studies have gained substantial consensus on the interrelationships of sauropods, although several contentious areas remain (see chapters by Wilson and Curry Rogers).

THE PACE OF DISCOVERY

Romer (1968:137–138) suggested that the fragmentary nature of many sauropod taxa contributed to their unresolved interrelationships: “The reasons for our difficulties are apparent. Few complete skeletons exist; feet and skulls are rare; many of the numerous described forms are based on fragmentary material.” This was certainly the case, and the improvement in our understanding of sauropod phylogeny is the result of an improved sauropod fossil record. Recent key discoveries, in stratigraphic order, include the discovery of primitive sauropods in Africa (e.g., Charig et al. 1965; Raath 1972; Yates

and Kitching 2003; Allain et al. 2004) and India (e.g., Jain et al. 1975; Yadagiri 2001); Middle Jurassic sauropods from China (Zhang 1988; He et al. 1988, 1998; Tang et al. 2001; Ouyang and Ye 2002) and Argentina (Bonaparte 1986b); and well preserved sauropod skeletons from the Cretaceous of Asia (Borsuk-Bialynicka 1977; Suteethorn et al. 1995), South America (Salgado and Bonaparte 1991; Calvo and Salgado 1995; González Riga 2003; Martínez et al. 2004), India (Jain and Bandyopadhyay 1997), Africa (Jacobs et al. 1993; Sereno et al. 1999), and Madagascar (Curry Rogers and Forster 2001).

The history of discovery of the 121 sauropod species recognized as valid by Upchurch et al. (2004) is summarized in figure I.3. Prior to the “Dinosaur Renaissance,” inaugurated with Ostrom’s (1969) description of *Deinonychus*, sauropod discoveries rarely topped more than a handful every five years. A notable outlier, however, is the burst of sauropod discoveries and descriptions in the late 1870s that coincides with peak Cope–Marsh activity. Following 1969, however, sauropod discoveries always exceed five per five years, steadily increasing through the late 1990s, when 25 sauropods were named. The subsequent drop in sauropod discoveries in figure 3 is an artifact of only counting up to the year 2002. Projecting to 2005 based on these numbers suggests an excess of 10 sauropods for this interval. This relatively sudden surge in sauropod discoveries is more striking when we consider that 50 sauropod species were named since the first edition of *The Dinosauria*, and that one-third of all sauropod species have been named *since* the first cladistic analyses of Sauropoda (Calvo and Salgado 1995; Upchurch 1995).

Both the steady improvement of the sauropod fossil record and the intensified interest in and resolution of sauropod phylogeny are beginning to differentiate the group into more manageable pieces, such as basal sauropods, macronarians, and diplodocoids. Both of these advances are relatively recent—cladistic analyses and escalation in sauropod

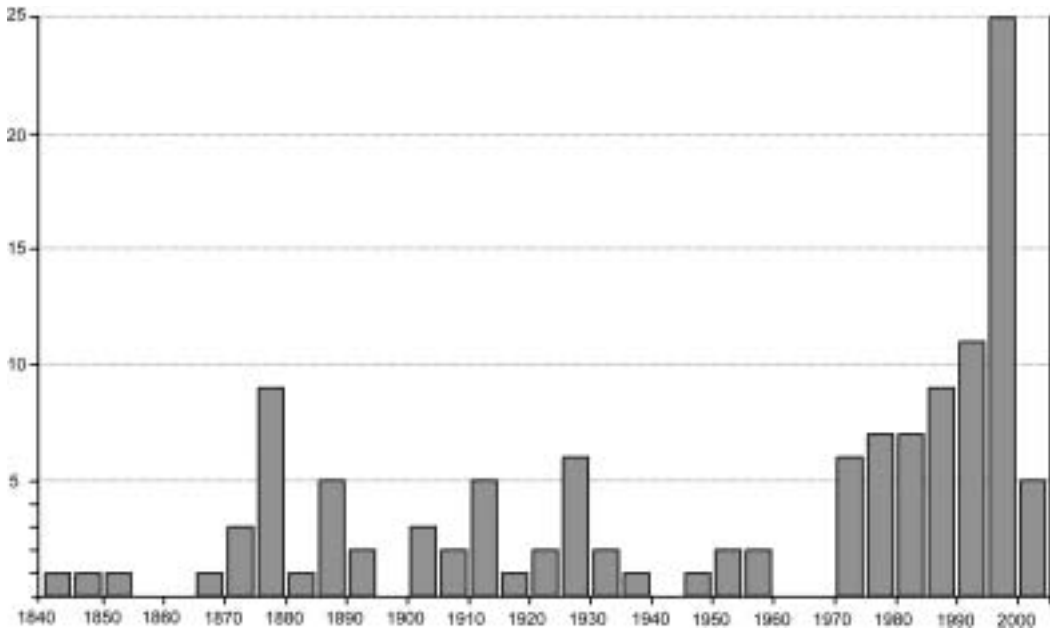


FIGURE 1.3. Sauropod species named since the description of *Cetiosaurus* (Owen, 1841) and recognized as valid by Upchurch et al. (2004).

discoveries postdate the first edition of *The Dinosauria* (1990) but predate *The Dinosauria 2* (2004).

SAUROPODS LIVING LARGE

Body size is the most recognizable characteristic of sauropods, and can be expected to have influenced all aspects of their biology (Peters 1983; LaBarbera 1989). The largest sauropods are estimated to have reached adult body masses of 40 to 70 metric tons or more (Peczkis 1994:appendix), an upper bound reached independently within multiple sauropod lineages (Diplodocoidea, “*Seismosaurus*”; Macronaria, *Brachiosaurus*; Titanosauria, *Argentinosaurus*). The smallest sauropods (e.g., *Magyarosaurus*, *Saltasaurus*) may have weighed between 1.5 and 3 metric tons (Erickson et al. 2001) and represent one of the few phylogenetic decreases in body size among dinosaurs.

Sauropods appear to have attained large adult body size by rapid post-hatching growth (e.g., Rimblot-Baly et al. 1995; Curry 1999; Sander 2000; Erickson et al. 2001; Sander and Tückmantel 2003) rather than by the slow, pro-

longed growth strategy common in other reptiles (e.g., Enlow and Brown 1956, 1957; Case 1978a; Francillon-Vieillot et al. 1990). Interestingly, although other vertebrates attained comparable body sizes, sauropods may be the only giants whose young hatch from eggs. Even the largest of adult sauropods began as hatchlings measuring only one meter long and weighing less than 10 kg (Chiappe et al. 1998, 2001), a range of ontogenetic size exceeding that for any other dinosaur lineage. In contrast, other large-bodied vertebrates bore live young, including chondrichthyans (sharks [Dulvy and Reynolds 1997]), mammals (whales [Clapham et al. 1999]), and marine reptiles such as plesiosaurs (Cheng et al. 2004), ichthyosaurs (Böttcher 1990; Maxwell and Caldwell 2003), and mosasaurs (Caldwell and Lee 2001).

The enormity of sauropod dinosaurs has cast a shadow over studies of their paleobiology. Struggling to find adequate descriptors for sauropod size—“ponderous,” “behemoth,” “enormous,” “stupendous,” and “massive” being a few—many early paleontologists assumed that sauropods could not support their body weight on

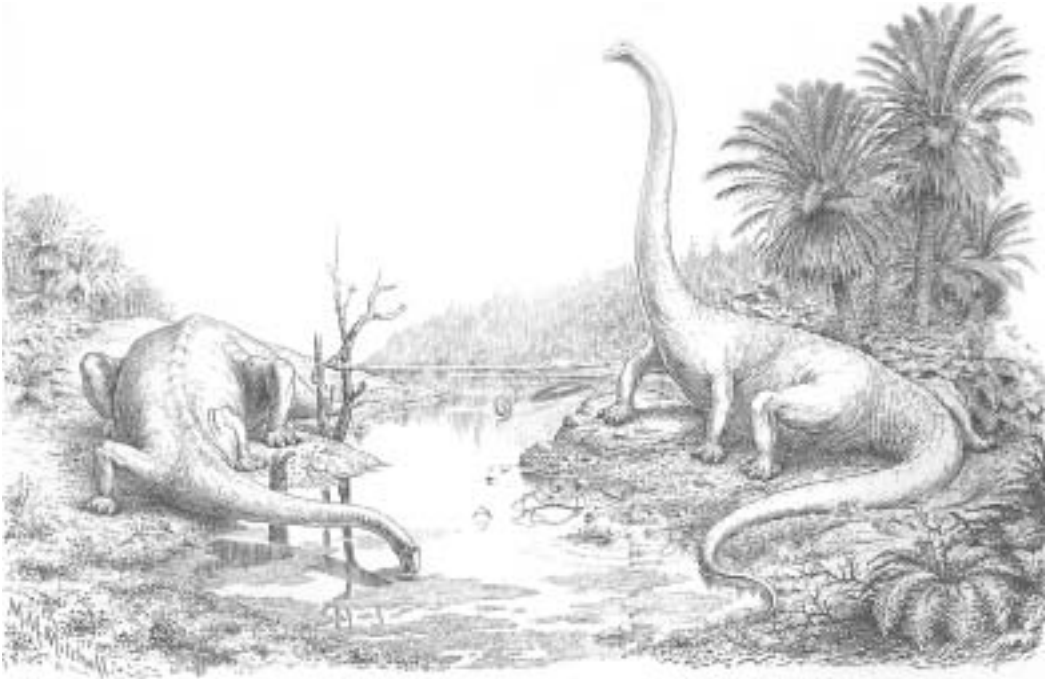


FIGURE 1.4. Oliver P. Hay's 1910 reconstruction of "The Form and Attitudes of *Diplodocus*." Hay's interpretation of sauropod paleobiology—lazing on beaches of ancient rivers, lizardlike in their stance and habit—was common until quite recently.

land (e.g., Owen 1875; Osborn 1899; Hatcher 1901). Although their anatomy was trumpeted as a "marvel of construction . . . a mechanical triumph for great size, lightness, and strength" (Osborn 1899:213), early life reconstructions depicted sauropods as large, lumbering, and near or up to their necks in ancient swamps (fig. 1.4). Even the first-described sauropod footprints were initially interpreted as having been made in an aquatic environment (Bird 1941, 1944). This perception of sauropods as unwieldy, archaic herbivores relegated to evolutionary backwaters was prominent as recently as the early 1990s:

Their large sizes, small heads, simple teeth, and tiny brains served them well for millions of years. But in the Cretaceous, more progressive, large-headed, larger-brained dinosaurs appeared (the ornithomorphs and marginocephalians) and vegetation changed. . . . The old giants retreated to southern continents, where the newcomers did not flourish.

(Dodson 1991:34).

Consequently, Cretaceous Gondwanan sauropods were viewed as Jurassic relics rather than thriving

lineages (Gilmore 1946; Lucas and Hunt 1989; Dodson 1991).

Ironically, some of these interpretations themselves can be looked on as holdovers from a previous era. Studies by Walter Coombs (1975, 1978) and Robert Bakker (1968, 1971a, 1971b, 1986) reinvented sauropods as dynamic, terrestrial vertebrates that might have been agile enough to feed tripodally, use their tails as weapons, and generate their own body heat via high food consumption capabilities (fig. 1.5). These interpretations challenged the prevailing perception of sauropods as archaic dinosaurs destined for extinction and helped underscore how little we know about sauropod paleobiology. The recent surge in sauropod discoveries around the world, combined with the taxonomic revision of fragmentary genera and the first testable hypotheses of relationship, provide the requisite framework for delving deeper into these questions of sauropod paleobiology. In this volume, we attempt to gain new understanding of "nature's grandest extravagances" (Dodson 1991:34).

FIGURE 1.5. John Gurche's dramatically posed *Barosaurus* protecting its young from an attacking *Allosaurus*. This depiction casts sauropods as active animals capable of rearing up on their hind legs.



SAUROPOD EVOLUTION AND PALEOBIOLOGY

The Sauropods: Evolution and Paleobiology opens with three chapters aimed at delimiting the evolutionary history and diversity of Sauropoda. These chapters provide a phylogenetic context for the subsequent chapters on sauropod paleobiology. Chapter 1 highlights our current view of sauropod phylogeny and concludes that sauropods were successful in terms of their geographic and temporal distributions, biomass, morphological complexity, and diversity at both higher and lower levels. Our understanding of sauropod phylogeny is particularly lucid with regard to the Diplodocoidea and Macronaria and the cranial specializations in each of these major

groups. Wilson highlights the difficulties in tracing two major parts of the sauropod phylogeny—even the earliest known sauropods have the features of the axial and appendicular skeletons that characterize all sauropods, implying a 10 million- to 15 million-year ghost lineage. Similarly, the preponderance of partial material and relative conservatism of the postcranial skeleton has obfuscated the other end of sauropod evolution, that of Rebbachisauridae and Titanosauria. Wilson highlights the importance of these taxa for biogeography during the Late Mesozoic as the continents attained their current positions. Similarly, rebacchisaurids and titanosaurs bear dental specializations and were coeval with the burgeoning ornithischian populations in both the northern and the southern hemisphere. The

connections between Late Cretaceous survivorship and narrow-crowned dentition provide an interesting opportunity for future work.

In chapter 2, Curry Rogers expands on the work of Wilson and examines the interrelationships among Titanosauria, a significant yet poorly understood sauropod clade. She outlines the current consensus with regard to titanosaur phylogeny and highlights the skeleton of *Rapetosaurus krausei*, the first titanosaur with associated cranial and postcranial remains, as a keystone taxon in current phylogenetic analyses. Her chapter concludes with one of the first detailed analyses of lower-level titanosaur relationships, which helps set the stage for a more detailed analysis of the paleobiology of this unique, derived group of macronarians.

Building on recent phylogenetic analyses, Upchurch and Barrett investigate sauropod “success rate” in chapter 3 by taking a closer look at taxic and phylogenetic estimates of sauropod diversity. Both estimates compare favorably with other estimates of sauropod diversity, indicating that important radiations occurred in the Middle and Late Jurassic, as well as at the end of the Cretaceous. Such results contradict the longstanding view that sauropod diversity reached its zenith in the Jurassic and its nadir in the Cretaceous, and highlights the high diversity of particular sauropod clades late in the history of sauropod evolution. Barrett and Upchurch expand on this analysis of sauropod diversity in chapter 4 by exploring the effects of macroevolutionary mechanisms potentially responsible for these patterns. The authors determine that proposed causes and their effects do not always fit the observed sauropod diversity pattern (i.e., competition between rebbacchisaurids and titanosaurs; competition between sauropods and ornithomorphs). In addition, the authors highlight the potential for coevolution among titanosaurs and angiosperms.

The theme of complex dentitions and herbivory during the last radiation of sauropods is apparent in the description of the unique dental battery present in *Nigersaurus* presented in chapter 5. Sereno and Wilson compare the dental bat-

teries of *Nigersaurus* to those of euornithomorphs and neoceratopsians, and conclude that divergent functions and uncorrelated progression signal independent causes for the evolution of dental batteries. This contrasts with the view that a single environmental cue (i.e., the evolution of angiosperms) prompted the evolution of complex dental batteries, and that sauropods and ornithomorphs were in direct competition for resources during the last stages of the Mesozoic.

In chapter 6, Stevens and Parrish present and implement their method for three-dimensional reconstructions of sauropod skeletons, focusing on the pose of the neck and its implications for sauropod herbivory. Their reconstructed feeding envelopes challenge the view that all sauropods were high browsers. In contrast to the giraffelike reconstructions of *Brachiosaurus*, or the tripod stance that is so often depicted in the popular media, Stevens and Parrish identify most sauropods as medium to low browsers. In their view, sauropod feeding is constrained not only by the dentition, but also by the axial flexibility and forage availability and abundance.

Although sauropod vertebrae have long been touted as being specialized for reducing weight while providing strength, the relationship has not been systematically analyzed and the implications of potential weight-reducing methods qualified. In chapter 7, Wedel investigates the axial skeleton from the perspective of pneumaticity and “efficiency of design.” Concluding that most eusauropod vertebrae were pneumatic, Wedel estimates that these vertebrae are in most cases between 50% and 60% air. The effects of pneumaticity might reduce sauropod mass estimates by as much as 10%, and provide some interesting new possibilities for interpreting sauropod physiology.

Chapters 8 and 9 focus on sauropod limbs and their significance for interpreting locomotor capabilities in sauropods. In chapter 8, Carrano utilizes a phylogenetic framework to address the morphological and functional diversity observed in the secondarily quadrupedal sauropods. Without question, the appendicular morphology of sauropods is constrained by

being big in a terrestrial environment. Carrano concludes that sauropods exhibit considerable morphological diversity associated with varying locomotor patterns. For example, titanosaurs can be characterized in part by their wide-gauge gaits and the coeval development of reduced body size in some clades, potential tripodality, and so forth. As outlined by Wright in chapter 9, sauropod trackways have provided widely divergent views of sauropod habits during the history of discovery, with early tracks thought to demonstrate that sauropods spent more time wading than walking in more terrestrial settings (Bird 1939, 1941, 1944). Wright outlines the history of discovery of sauropod tracks, summarizes our understanding of trackmakers, and critiques the ichnological evidence that sauropods traveled in organized herds.

Sauropod size and reproduction are discussed in chapter 10. Chiappe et al. document the first discoveries of identifiable sauropod embryos and nests—the fantastic accumulation of fossils from Auca Mahuevo, Argentina. This site provides definitive evidence that sauropods were egg-laying reptiles. Chiappe et al. analyze the taphonomy and morphology of this amazing assemblage of sauropod eggs, providing us with a clearer understanding of how sauropods reproduced and what hatchlings looked like, an example of nesting structure, and the first unspeculative interpretations of sauropod nesting behavior.

In chapter 11, Curry Rogers and Erickson survey sauropod growth rates from the perspectives of bone histology, long bone growth, and developmental mass. Instead of the century-long ontogenies predicted by early workers extrapolating from reptilian growth rates for the large-bodied sauropods (e.g., Case 1978a, 1978b), Curry Rogers and Erickson present a dramatically different view of the ontogeny for *Apatosaurus*. Growth rates on par with those of some of the largest living vertebrates were normal for sauropods, and development of a characteristic trend for dinosaur growth allows predictions of growth rates for the largest sauropods ever known. They suggest that sauropods reached their enormous adult sizes quickly—likely within 15 years. To compare—at

age 5, an African elephant is only ~1 metric ton; at the same age, *Apatosaurus* might have been closer to 20 metric tons.

FUTURE DIRECTIONS

New sauropods will continue to be discovered in Mesozoic strata from around the world, despite the improbability of the preservation of their enormous bodies and fragile skulls and axial bones. These future discoveries will surely remedy some of the temporal and geographic gaps in our current record of Sauropoda and reveal anatomical surprises that will revise our estimates of their genealogy. *The Sauropods: Evolution and Paleobiology* not only documents what is currently known about sauropod evolutionary history, but also highlights deficiencies in our understanding. In that sense, we hope this volume sparks interest, provokes questions, and provides fresh ground for continued research on sauropod dinosaurs.

Several gaps in our understanding of sauropod paleobiology are not addressed in this volume. Many of these are directly related to the sauropod fossil record, which documents as few as 20 genera known from better than 90% of the skeleton (Upchurch et al. 2004). One of the most conspicuous deficiencies is the absence of transitional Triassic forms bridging the morphological gap between sauropods and their closest relatives, prosauropods, which obfuscates the origin of the sauropod body plan. Other poorly sampled horizons include the Middle Jurassic, during which nearly all the main neosauropod lineages are hypothesized to have evolved, and the Early Cretaceous, when rebbachisaurid and titanosaur sauropods underwent interesting changes in herbivory and locomotion that were manifest in later Cretaceous forms. Geographical biases in the sauropod fossil record also persist. Australia and Antarctica stand out as southern continental landmasses that have produced only a few, fragmentary sauropod taxa. Similarly, with the exception of a few well-preserved taxa from North Africa, the continent has only provided a

glimpse of later-stage sauropod evolution. North America, despite its rich Late Jurassic sauropod record, hints of an as-yet-undiscovered Cretaceous sauropod fauna. These large-scale evolutionary questions are not the only ones impeded by an imperfect fossil record; straightforward anatomical questions also persist. Examples include the arrangement and diversity of body armor (osteoderms), the configuration and embryological identity of carpal bones, and the nature and arrangement of gastralia and clavicles.

Other questions are not necessarily dependent on discoveries of new and better fossils, but on our ability to interpret those already collected. Although we have made inroads, summarized in several chapters in this volume, sauropod life history stands out as a complex issue knotting physiology, development, ecology, and behavior. Basic questions remain, including the trajectory of body size change within the phylogenetic, temporal, and geographic distribution of sauropods; the sequence of fusion of skeletal elements (particularly in the vertebral column) throughout ontogeny; the masticatory forces producing wear facets on teeth; the composition of sauropod diets; and the relative roles of oral and gastric maceration of plant material. More challenging still are questions of sauropod thermal biology and energetics, reproductive behavior, and social interactions. These and other questions will propel future sauropod research.

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