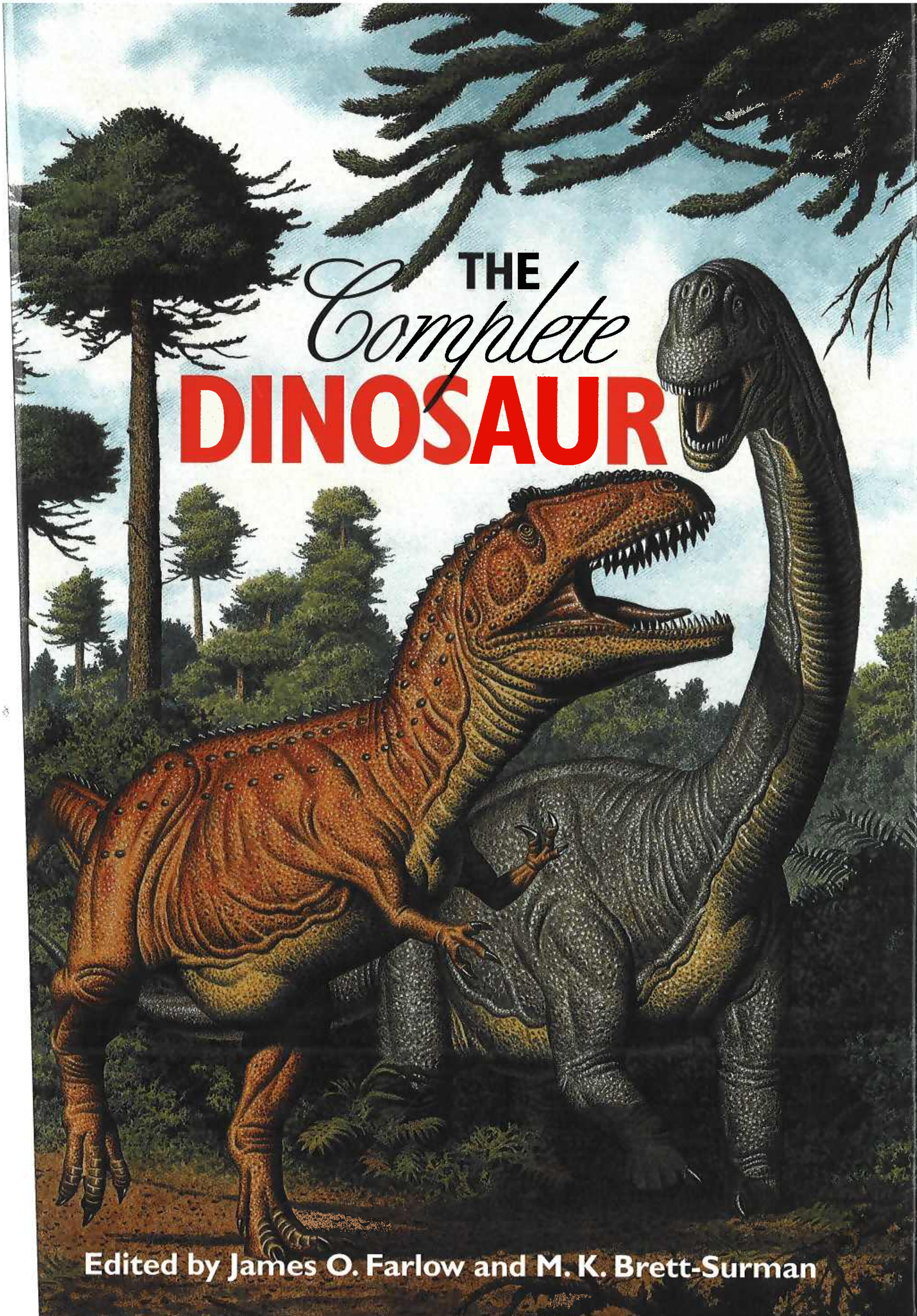
THE
Complete
DINOSAUR
Edited by James O. Farlow and M. K. Brett-Surman

Part Four

Biology of the Dinosaurs

> There were, as I say, five of them, two being adults and three young ones. In size they were enormous. Even the babies were as big as elephants, while the two large ones were far beyond all creatures I have ever seen. They had slate-coloured skin, which was scaled like a lizard's and shimmered where the sun shone upon it. All five were sitting up, balancing themselves upon their broad, powerful tails and their huge three-toed hind-feet, while with their small five-fingered front-feet they pulled down the branches upon which they browsed. I do not know that I can bring their appearance home to you better than by saying that they looked like monstrous kangaroos, twenty feet in length, and with skins like black crocodiles.
>
> —Sir Arthur Conan Doyle, *The Lost World*

Many people think that a new classification is the end product of paleontological research. In fact, it is just the beginning. We can think of three levels of intellectual inquiry that result from the discovery of a new dinosaur fossil.

"First level" questions are based on the actual fossils themselves. The primary pieces of evidence come from bones, teeth, tooth wear patterns, skin impressions, muscle attachment sites, joint articulation configurations, bone pathologies, gut contents, coprolites, trackways, and nests, to name the more obvious of these. Such fossils can be used to address questions about the overall size of the dinosaur, changes in its skeletal proportions during growth, the processes by which the animal grew, the kinds of movements of which it was capable, the injuries or illnesses that afflicted it, and something about the likely acuity of its senses, and perhaps even its intelligence.

"Second level" questions try to go beyond these bits and pieces of dinosaur natural history; these questions build upon the answers to "first level" questions, and represent hypotheses about dinosaurs that are not readily testable. What was the dinosaur's likely ecological role? How long did it take to reach sexual maturity, and at what point in the animal's life history did any sexual characters appear? What was its reproductive rate? What was the mortality rate for different age classes of its species?

The final level of inquiry relates to evolutionary theory. How do dinosaurs (and other organisms) fit into the big picture? Can we discern any evolutionary "laws" from major trends in dinosaurian adaptations over time? Are there any patterns in the evolution of dinosaurian clades above the species or genus level? Do dinosaurs fit into any long-term trends in the evolution of terrestrial ecosystems?

Dinosaur fossils do not exist in a vacuum. They are part of an overall fossil assemblage, and a fossil fauna is in turn a component of the sedimentary rocks that accumulated in a particular depositional setting. Consequently we can attempt to fit dinosaurs and other organisms not just into the big picture of biological evolution; we can also consider how the evolution of life has been affected by, and has affected, the development of the earth's physical systems.

In the previous section of this book, each of the chapters describing a dinosaur group presented ideas about what the dinosaurs of that chapter were like as living animals. Part Four returns to that theme, but in a more general manner, by taking a topical approach to various aspects of dinosaur biology. The emphasis in this section, then, is mainly on the second level of inquiry described above, with a few peeks here and there at the big picture as well.

One of the four basic activities of any animal (along with fighting, fleeing, and reproducing) is finding food. The bloodthirsty denizens of Hollywood's version of prehistory notwithstanding, the vast majority of dinosaurs were plant-eaters. To understand dinosaur ecology, therefore, it is necessary to know something about the plant communities in which they lived. This section of the book therefore begins by surveying present knowledge of Mesozoic floras. What kinds of plants were available to herbivorous dinosaurs, what was their quality as fodder, how did plant communities change over the course of the Mesozoic Era, and how did this affect dinosaur communities?

Having considered what plant-eating dinosaurs might have eaten, we then turn to consider the evidence for what herbivorous and carnivorous dinosaurs actually *did* eat. Information from trackways, death assemblages, bite marks, stomach contents, and coprolites is summarized.

If a species is to survive over the long term, reproductive rates must at least balance mortality losses. Reproduction is therefore another essential aspect of animal biology, and so two chapters consider how dinosaurs went about ensuring that there would be a new generation. The first step in making babies is finding a mate, and so we begin by examining how male dinosaurs might have courted their ladies, and at the same time kept rival males out of the picture. This is one area where the analogous behavior of living animals plays a big part in interpretations of dinosaur behavior.

More from lack of fossilizable information than from any excessive prudery on our part, we skip the obvious sequel to success in finding a mate and move right on to how the new generation began life. Most (if not all) dinosaurs were probably egg-layers, and in recent years there has been an explosion of interest in dinosaur nesting sites and eggs. Chapter 28 discusses what we know about dinosaur eggs, and the problems of assigning eggs to the dinosaurs that laid them.

Once it had hatched from its egg, a baby dinosaur was ready to take its place in the Mesozoic world. It, too, would ultimately try to find a mate, but first it would have to grow to adulthood. Chapter 29 considers the processes by which dinosaurs grew, as inferred from the tissues of their bones.

Dinosaurs were not all giants, but a significant trend in dinosaurian evolution was toward gigantism. Dinosaurs included the largest land-living animals in the history of our planet. How did nature engineer such behemoths? Could sauropods rear up on their hind legs to stick their long necks high into treetops? Could big dinosaurs run quickly, or were they restricted to slow, lumbering movements? How did dinosaurs fight? Chapter 30 addresses such questions.

As well-constructed as dinosaurs seem to have been, they were no doubt subject to the same misfortunes that befall all flesh: injuries and diseases. Amazingly, dinosaur bones sometimes record the traces of such maladies, and we devote a chapter to the osteological evidence of dinosaurian injuries and illnesses. This field of study has become an area of paleontology in its own right, paleopathology.

The idea that dinosaurs may have been more like modern birds and mammals than like living reptiles in many features of their biology has its roots in the work of none other than Richard Owen, who gave the Dinosauria their name. As E. D. Cope wrote in 1868: "If he [Cope's "*Laelaps*"] were warm-blooded, as Prof. Owen supposes the Dinosauria to have been, he undoubtedly had more expression than his modern reptilian prototypes possess. He no doubt had the usual activity and vivacity which distinguishes the warm-blooded from the cold-blooded vertebrates." In his first attempt to revise the taxonomy of dinosaur footprints of the Connecticut Valley, R. S. Lull (1904: 475) invoked the idea of warm-blooded dinosaurs as a way to eliminate the possibility that dinosaurs might have had the indeterminate growth typical of reptiles. If dinosaurs, like birds and mammals, grew to a fixed size and then stopped growing, then the ichnologist might not have to face the possibility that footprints of a wide range of sizes could have been made by members of the same species of dinosaur.

Although other paleontologists, such as Richard Owen and L. S. Russell, also considered the possibility of warm-blooded dinosaurs from time to time, it was the work of John H. Ostrom, John R. Horner, and Robert T. Bakker from the 1960s to the 1980s that really put dinosaur physiology on the front burner of paleontological attention. Bakker and Horner in particular were such dynamic and engaging advocates of warm-blooded dinosaurs that the idea received wide attention in the popular media, most notably the movie *Jurassic Park*.

A full examination of the various arguments about dinosaur physiology would require a book in itself. We have chosen to limit coverage in this book to some of the stronger and/or more recently proposed arguments for and against the hypothesis of warm-blooded dinosaurs; the chapters dealing with this topic thus constitute a mini-section within our overall section on dinosaur biology (see the accompanying box for some of our thoughts, though).

We end this section by looking at the dinosaurs that got away: dinosaur footprints. Every dinosaur skeleton represents a tragedy for its erstwhile

Some Irreverent Thoughts about Dinosaur Metabolic Physiology: Jurisphagous Food Consumption Rates of *Tyrannosaurus rex*

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It is agreed by all living humans that the highlight of the movie *Jurassic Park* (Universal Studios, 1993) was the consumption of the lawyer by the true hero of the movie, *Tyrannosaurus rex*. This brings up an obvious question: How many lawyers would it take to properly feed a captive *T. rex?* Fortunately science has now progressed to the point where this important question can be answered—and plans made accordingly.

Two pieces of information are needed:

(A) The food requirements of a *T. rex* for one year

(B) The food value of one lawyer

Following the way that it was portrayed in *Jurassic Park,* let us first assume that our *T. rex* is endothermic. Let us also assume that our tyrannosaur weighs 10,000 pounds (4540 kg)—perhaps a bit on the light side (Farlow et al. 1995), but close enough.

Farlow (1990; see Farlow 1976 for details about the data used) published an equation relating the food consumption rate (in watts, or joules/second; that is, the amount of food energy needed per unit time) to body mass (in kilograms) in living endotherms (mammals and birds):

$$\text{consumption rate} = 10.96 \times \text{body mass}^{0.70}$$

For a 4540-kilogram *T. rex,* the equation predicts an average food consumption rate of 3978.8 joules/second. Because we are interested in the time span of one year, we must now multiply this result by 3.1536×10^7, which is the number of seconds in one year (that is, 60 seconds/minute × 60 minutes/hour × 24 hours/day × 365 days/year—unless you are watching golf on TV, in which case this number is much higher), to give us the tyrannosaur's energy needs in joules/year. This results in a big number: 1.2547×10^{11} joules/year.

This gives us the first part of what we need to know in order to begin rounding up enough lawyers to keep our dinosaur content. We must now calculate the energy value of one lawyer.

There are three components of the food value, in joules, of one lawyer: (1) the energy value (in joules) of 1 kilogram of lawyer flesh; (2) the number of kilograms (mass) in our sacrificial lawyer; (3) the digestive percentage, or assimilation efficiency, of a carnivore digesting meat—in the present case, this is the percentage of the lawyer that actually has food value. (We assume that clothing, briefcase, cellular phone, and pocket organizer have no energy value, and so these components of an operational lawyer will be ignored in our calculations.)

We assume that the energy value

occupant—the skeleton would not be there in the rocks had the creature not come to an often untimely end. Footprints, in contrast, were made by living animals going about their business. They may therefore be able to provide us information about dinosaur biology that would be hard to discern from a fossilized carcass.

Two chapters, then, consider the study of dinosaur footprints. Chapter 36 emphasizes the extent to which it is possible to identify footprint makers, the nomenclature applied to dinosaur tracks, and what trackways tell us about dinosaur locomotion. Chapter 37 focuses on the geologic circumstances under which dinosaur footprints are preserved, and on what of lawyer meat, like that of other animals, is 7×10^6 joules/kilogram (Peters 1983). We further assume that our lawyer weighs 150 pounds, or 68.1 kilograms.

The assimilation efficiency of carnivores eating meat is about 90 percent (Golley 1960; this is much higher than for herbivores feeding on high-fiber forage—as presumably was the case for most herbivorous dinosaurs; see Tiffney, chap. 25 of this volume).

The energy value of a single lawyer can now be calculated as

$$68.1 \text{ kg} \times (7 \times 10^6 \text{ joules/kg}) \times 0.9 = 4.2903 \times 10^8 \text{ joules}$$

By dividing the yearly energy requirements of our *T. rex* by the energy value of a single lawyer, we get the yearly lawyer consumption that our dinosaur would need:

$$(1.2547 \times 10^{11} \text{ joules/year})/(4.2903 \times 10^8 \text{ joules/lawyer}) = 292 \text{ lawyers/year}$$

The calculations are the same if we assume that our tyrannosaur was an ectotherm, except that we must use an equation relating food consumption rate to body mass in reptiles and amphibians (Farlow 1990; same units as for endotherms):

$$\text{consumption rate} = 0.84 \times \text{mass}^{0.84}$$

For a 4540-kilogram *T. rex,* this equation predicts a feeding rate of 991.3 watts, which works out to 73 lawyers per year.

We can see, then, that genetically resurrected tyrannosaurs would have a far greater predatory impact on the lawyer population if they were endotherms than if they were ectotherms. This is perhaps a good reason for hoping that dinosaurs will turn out to have been endotherms.

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these trace fossils may be telling us about when and where particular kinds of dinosaurs lived.

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