

THE EVOLUTION OF THE ARTIODACTYLS

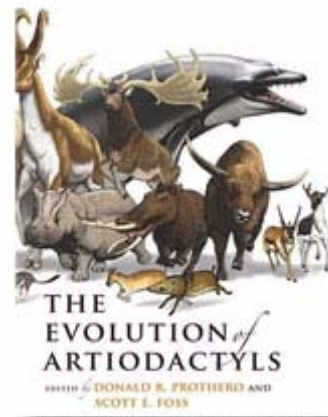
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Donald R. Prothero and Scott E. Foss (Editors)
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The discovery in molecular phylogenies of mammals that cetaceans were nested within the Artiodactyla (Graur and Higgins 1994) created a tempest in the teapot of mammalian paleontology that has still not abated. In the frenzied rush to reconcile the DNA evidence with the (at the time) dramatically different interpretation from morphological data, huge strides have been made in understanding the evolution of the Artiodactyla, as well as the early evolutionary history of whales. The problems raised by this fundamental reorganization of the evolutionary relationships within this diverse mammalian order will keep paleontologists busy for a generation or more, in spite of the increasing numbers of specialists working on these problems. Revised phylogenies taking into account molecular evidence and including cetaceans have brought into question some of the most widely-accepted and morphologically consistent groups within artiodactyls, including suiforms and ruminants.

With a continually evolving evolutionary and taxonomic framework, summaries of the current state of knowledge within the Artiodactyla are invariably out of date before they are even published. Janis et al. (1998) published the most recent relatively complete account of artiodactyl systematics (focused on the Tertiary of North America) unfortunately in the middle of the scramble to reconcile paleontological and morphological data with the increasingly well-supported molecular topology. With the blinding array of recent papers

on the paleontological evidence for cetartiodactyl phylogeny, a novel synthesis is merited to help make sense of all the changes that have arisen from our revised understanding of the relationships of this most diverse group of large mammals.



Don Prothero and Scott Foss have undertaken this synthesis on a global scale, through the entire history of the Artiodactyla. The resulting volume is a very thorough, scholarly account of the entire tapestry of artiodactyl evolution. Almost every chapter poses several new research questions that have arisen from the increased scrutiny to which artiodactyl systematics have been subjected. The result is an inspiring and exciting account of current knowledge set in the context of future research directions and evolving understanding of macroevolutionary and paleoecological processes. The far-reaching ramifications of the addition of cetaceans to the Artiodactyla are apparent in the numbers of chapters that cite the same problem nodes in the cladogram as they affect the need for research within different families of artio-

dactyls. The book is a series of contributed papers by a variety of specialists, mostly focused on individual families of artiodactyls, although there are also a few chapters lumping multiple families of morphologically similar and phylogenetically muddy species. There are also 2 chapters on the molecular systematics of artiodactyls and the position of Cetacea within the Artiodactyla, as well as an account of the evolution of paleoecology within the order. The primary aim seems to be a summary of the current taxonomic status of fossil and living artiodactyls. A few chapters undertake some minor revision, but most are compilations of work published elsewhere, pointing out problem taxa and areas of uncertainty. Nowhere else could you find a more complete and up-to-date account of artiodactyl systematics, a particularly timely resource in light of the active research in this area. All of the chapters highlight critical taxonomic problems and most of them summarize the current status of genera and species within each of the families. The chapter by Janis provides a particularly interesting summary of major paleoecological milestones in the evolution of artiodactyls. This chapter emphasizes some macroevolutionary problems of general relevance to mammalian paleontologists, even those who, like myself, rarely work with animals the size of artiodactyls. For those without the time or interest to read the entire book, Prothero and Foss provide a summary chapter that highlights the problems of general interest raised in each chapter.

This is an excellent resource for the student of mammal taxonomy; it offers both a single source for current systematic status of the major groups of artiodactyls as well as a variety of ideas for research projects that will resolve critical problems in artiodactyl phylogeny. The global scope and comprehensive taxonomic and temporal coverage yields a source of information that would otherwise be extremely difficult and time-consuming to collect. Unfortunately, it suffers from a number of the problems common to many such edited volumes written by a large group of authors. The chapters are often wildly different in depth, format, and focus of coverage. Some, such as the chapter by Theodor et al. on early artiodactyls or that of Foss on Helohyidae, have complete lists of occurrences, figures of most of the major taxa, and a taxonomic placement for each of the species. Others, such as Groves' chapter on the Cervidae, do not even offer a list of species, and many others have no list of occurrences, making it difficult to determine which occurrences they regard as belonging to which

taxa. This is particularly critical given the number of revisions to which artiodactyl families have been subjected. It is this lack of completeness in some families that prevents this book from providing the sort of complete resource for artiodactyl systematics that one might have hoped it could offer. There is also a confusing lack of consistency in the allocation of space to different taxa. It is understandable that the early artiodactyls would require 27 pages in the book, given their diversity and taxonomic controversy. It is a bit confusing, however, that there are 10 pages devoted to the Entelodontidae (7 genera) and 21 to the Giraffidae (31 species, 3 extant) but only 8 to the Cervidae, the second most diverse family in the Artiodactyla and only 14 to the Bovidae, the most diverse artiodactyl family. The allocation of a separate chapter to the Agrichoeridae while lumping the rest of oreodonts into a single chapter is a bit confusing, especially considering that the Agrichoeridae (18 species) encompass only two named genera. There is no chapter at all for the systematics of cetaceans, in spite of the fact that all the authors acknowledge the place of whales within the artiodactyl order. Even where the depth of coverage is similar between chapters, there is no consistent format for the presentation of information, so it can be difficult to find comparable information for different groups; sometimes the diagnosis is presented under its own heading, but sometimes it is integrated into the discussion of the taxonomic problems in the clade, and hence must be culled from the text. Some clades have formal definitions, while others do not. A more difficult problem to remedy editorially is the mosaic of cladistic and traditional systematic methods employed by the authors of various chapters. There is a range from pure cladistic, parsimony analyses to likelihood-based phylogenetics to traditional descriptive systematics and even some quasi-phenetics. This array of methods is, of course, a result of the differing approaches of the various authors, but the use of terminology is not consistent between them. The term "cladogram" has a very specific meaning to a phylogenetic systematist, but it is used here in a variety of senses, including as applied to an untested phylogenetic hypothesis generated from traditional systematics. There are also a number of chapters that fail to explain their methods, or to present lists of characters or character matrices to support what seem to be cladistically generated cladograms. These flaws, however, while frustrating to one using the book for research purposes, do not change the fact that this book is the first

complete synthesis of systematics in this order of mammals.

Prothero and Foss have produced a critical resource for those working on the problem of artiodactyl phylogenetics, and even offer some points of interest to mammalian systematists and paleoecologists in general. This volume summarizes in a single book what would otherwise be dispersed across the systematic literature. This work also emphasizes the continuing need for systematic studies of artiodactyl clades, as, in spite of hundreds of years of taxonomic studies, fundamental problems remain in understanding the relationships

of these groups. Some of the critical themes running through multiple chapters include the need to understand the relationships among the apparently paraphyletic "Suiformes," the critical question of how camels and oreodonts relate to other selenodont artiodactyls, and the call to tackle taxonomic problems created by early monographs on diverse fossil artiodactyls such as oreodonts and horned ruminants. Continuing research into these areas will be greatly aided by this resource, and will produce results critical to our understanding of the origins of modern large mammal diversity.