eral organization of the Cephalopoda by the same authors. Next follows a series of chapters on the anatomy, physiology, and function of cephalopod organ systems: locomotion and buoyancy, the skin, the nervous system, sense organs, neurosecretion and endocrine organs, the digestive system, development of blood and coelomic systems, respiration and circulation, the coelom and coelomic cavities, the excretory system, genital organs, reproduction, and life history. The book concludes with chapters on embryology, predators, parasites, geographical distribution, fisheries, migration and vertical distribution, systematics, and, finally, evolution. Several of these last chapters are translations and revisions of previously published works brought up to date by their authors. These include the chapters on parasites, condensed from Hochberg's 1983 review, and on evolution, expanded from Teichert's presentation in *The Mollusca* (vol. 12, 1988).

Even though some chapters were completed nearly 20 years ago, they are saved from being obsolete by updated summaries and bibliographies. I recommend that users of this work begin each chapter with the summary at the end, examine the illustrations, scan the bibliography, then read the body of the chapter. The inconvenience of this procedure will soon be overshadowed by recognition of the comprehensiveness of the text and the value of the illustrations.

There comes a realization that this wonderful treatise will be a starting place, the first work to be consulted by generalists and specialists alike, for the current generation and far into the next century.

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Horse Sense

The Evolution of Perissodactyls. DONALD R. PROTHERO and ROBERT B. SCHOCH, Eds. Clarendon (Oxford University Press), New York, 1989. x, 537 pp., illus. $70. Oxford Monographs on Geology and Geophysics, no. 15. Based on a workshop, Edmonton, Alberta, Aug. 1985.

In his 1807 *System of Nature*, William Turton thought rhinoceroses belonged in the order Bruta (with elephants, sea cows, armadillos, and the platypus), horses and tapirs in the order Belluae (with hippos and hogs), and hyraxes in the order Glires (with rodents and rabbits). It took Cuvier, de Blainville, and Owen to confederate rhinos, horses, tapirs, hyraxes, and a herd of extinct relatives as the Perissodactyla, the mammalian order of odd-toed ungulates. Almost 150 years later, we learn from *The Evolution of Perissodactyls* that the genealogy and legitimacy of this confederacy are still in contention.

This volume is a thorough, perhaps invaluable, compendium of perissodactyl systematics and evolution. One of the first contentions it tackles is the relationship of hyraxes, the conies of Old Testament lore. Proverbs describes their ecology: "The conies are a feeble folk, yet make their houses in the rock"; and Deuteronomy comments on their affinities: "The camel and the hare and the coney chew the cud but divide not the hoof." This biblical synapomorphy may yet tempt a systematist investigating hyraxes.

If camels were designed by committee, hyraxes were designed by camels. They resemble a cross between a rhinoceros and a rodent, and the resulting smorgasbord of morphological traits has generated a dyspeptic taxonomy: hyraxes have been linked to elephants and sea cows, to horses, rhinos, and tapirs, and to rodents and rabbits, with recent opinion polarized around a hyrax–perissodactyl or a hyrax–tethythere (sea cows, elephants, desmostylians) clade. M. S. Fischer's even-handed treatment of this phylogenetic wrangle tries to neutralize the dyspepsia.

Favoring the hyracoid-tethythere relationship are a number of shared similarities in the skull, feet, placenta, and molecular properties. The rub is to deduce whether these similarities are due to convergence or common descent—a puzzle common to all schools of systematics interested in deciphering phylogeny. Fischer makes the case that the hyrax-tethythere resemblances are convergent and the molecular data untrustworthy. It is comical but depressing to read that when some of the molecular data (eye lens protein alpha-crystallin) are not varnished by "*a priori* cladistic assumptions" the most parsimonious tree makes sister groups of marsupials and chickens, and of pangolins and bears and implies that Cetacea, Carnivora, Rodentia, and Lagomorpha are not monophyletic groups. Is Deuteronomy any worse? Fischer defends a hyracoid–perissodactyl clade, citing similarities in the dentition, hoof structure, carotid circulation, and Eustachian sac morphology. T. Rasmussen's survey of the fossil hyracoids (19 genera and 53 species in two families) reveals extensive radiations and bygone diversity, but the earliest known hyraxes (middle Eocene, Africa) are too derived to illuminate their ancestry.

Fifteen of the remaining chapters are straightforward, often comprehensive, systematic reviews and cladistic analyses of unquestioned perissodactyls: *Hyracotherium* and other primitive Eocene forms; palaeotheres; tapiroids; rhinocerotoids; amynodonts; indricotheres; chalicotheres; and brontotheres.

J. J. Hooker's exhaustive analysis of early perissodactyls yielded a cladistic nightmare: 50 equally parsimonious trees, each with 262 steps and a consistency index of 0.382, namely, a bushel of homoplasy. After permitting a few palatable reversals, Hooker achieved an unresolved trichotomy between the Titanotheriomorpha (lambdotheriines, brontotheriines), the Moropomorpha (chalicotheres, tapiroids, rhinocerotoids), and the Hippomorpha (equids, palaeotheres, pachynolophoids). The editors should have warned Hooker about using phenacodont condylarths as the ancestral morphotype for perissodactyls in chapter 6 (p. 86). That ancestry was sabotaged back in chapter 3 with the cogent description by McKenna *et al.* of *Radinskya yupingae*, a primitive herbivore from the late Paleocene of China that seems to be a more suitable progenitor.

Seven chapters cover equid evolution: the phylogeny of the family; the species and biogeographic history of *Hipparion* horses; variation in Recent versus fossil horses; and the extinct species of *Equus*. R. L. Evander's phylogenetic tree of equid evolution involves 18 species and is bushier than the "classic" orthogenetic story line. His analysis, however, deliberately excludes temporal variation in fossil horses—"a [paleontological] species is thus the state of a lineage at one instant in time" (p. 109)—and conveniently sidesteps the problem (and process) of anagenetic change.

This issue harkens to J. A. Hopson's (chapter 1) indictment of aspects of the cladistic approach to systematics. When faced with a dense fossil record of continuous anagenetic change in derived features in stratigraphically sequential populations, cladistic analysis is tempted "to ignore such complex continua among taxa" or "implicitly deny their existence" or "oversimplify complex distributions in the interest of clear cut results" (p. 9).

The summary chapter by the editors on perissodactyl evolution (plus new classification) is useful, but occasionally drifts into polemic. The hypothesis of hyraxes as perissodactyls is just that, not fact—as is the case (so far) with the "new," radically revised Eocene-Oligocene time scale and correlations that put the Duchesnean in the middle Eocene.

The Evolution of Perissodactyls, by virtue of its sheer scope and detail, is now the paleontological reference on the systematics, fossil record, and radiations of odd-toed ungulates and hyraxes. It is flawed by the lack of an index, which is inexcusable in a reference

work, and by the sloppy execution and reproduction of some figures, especially the range charts.

There are also needless flights of ideological fervor. Chapter 1 (Hopson) dedicates the volume to Leonard B. Radinsky, a vertebrate paleontologist at the University of Chicago who contributed extensively to our knowledge of perissodactyl evolution and systematics, and who died tragically of cancer in 1985 at the age of 48. But dedications wilt quickly under doctrinaire attitudes. In swiping at past errors, some of the contributors appear to divide systematists into Swiftian houyhnhnms (that is, themselves) and yahoos (that is, others), tossing into "others" Radinsky, R. E. Sloan, L. Van Valen, G. G. Simpson, and other paleontologists who happen to have published on perissodactyl systematics in the dark days before cladistics. These authors forgot that: (i) cladistics will not deliver us from error; and (ii) respect for historical context is one prerequisite for accurate history and intelligent criticism. Schoch tells us that "until recently there has been little, if any, concern among investigators, as to whether these groups [five superfamilies of perissodactyls] were natural." Really. Odd, then, that most of the perissodactyl groups and subgroups put together by the yahoos stand up fairly well to the gauntlet of systematic and cladistic analyses in this volume.

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A Death in the Pleistocene

Frozen Fauna of the Mammoth Steppe. The Story of Blue Babe. R. DALE GUTHRIE. University of Chicago Press, Chicago, 1990. xiv, 323 pp., illus. $40; paper, $16.95.

"The Story of Blue Babe" is about a bison bull that was killed 36,000 years ago by an Alaskan lion, and then, during the past decade, was reborn as the first complete frozen mummy exhibited in North America. This story, from the moment we spy the forelegs in the placer mine above Pearl Creek to the final stretching of the skin, when the lion's carnassial tooth fragment appears, is a true detective thriller, replete with astonishing clues (for example, the bison's blue color) that are gradually gleaned from the beast and the surrounding silts.

Yet it is the larger story of the frozen fauna of the mammoth steppe, cleverly woven around the inner tale of Blue Babe, that the author really strives to get across. For a quarter century Guthrie, a mammalian paleontologist at the University of Alaska, has pursued this subject. In 1966 he introduced the term "Mammoth Steppe" to characterize the cold, dry, grassy plain that supported the Pleistocene megafauna including horses, mammoths, and abundant bison. In this book, he expands and defends that characterization. He reanalyzes the late Pleistocene pollen evidence from Alaska, thus carrying the battle to the palynologists, some of whom have challenged the central concept of extensive Pleistocene grass cover. The late Pleistocene biota of the far north extended far beyond Beringia (that is, the exposed area of the sea and adjacent parts of Alaska and Siberia), reaching from the Yukon westward across most of Eurasia into the British Isles. As Guthrie notes, reconstructions of late Pleistocene ecosystems are not simply questions of "how to paint a large panel of stage scenery." They lie at the root of current urgent concerns about where global change is going to lead civilization as we know it. As Guthrie further states, "The pulls and tugs of ideas in this debate involve fundamental questions of ecological theory, for example, how species and communities react to different climatic changes."

Another area of significant new theory concerns the ethology of horned ungulates. Guthrie deduces not only from the case of Blue Babe, but also from Mousterian cave paintings of steppe bison (which he clearly demonstrates had the same color, hair, horns and hump as "Blue Babe"), that these bison fiercely attacked their predators, including humans. He also develops diverse clues (including the "missing hump") that intraspecific contests between horned males could be lethal. As he now sees it, ungulate ethologists of the 1960s (including himself) placed undue emphasis on ritualized defensive aspects of agonistic behavior and tended to ignore the specially adapted offensive structures that most horned and antlered ungulates use to injure, or even kill, their rivals.

This book is a wonderful tour de force, indicating the incredible range of detective work that a good paleontologist can accomplish over a period of two sabbaticals. It is also a well-told and well-illustrated tale for professional and amateur alike. The book is dedicated to two Russian and two Finnish paleontologists who have been Guthrie's

"The necropsy. Blue Babe was taken out of the freezer, and we began to carefully clean the carcass, looking for clues to the bison's death and mode of preservation." [From *Frozen Fauna of the Mammoth Steppe*; photo by Don Borchardt; Institute of Arctic Biology, University of Alaska]