In the light of these tremendous standards, Hölldobler and Wilson sometimes put perhaps too much emphasis on worker ants' being like preprogrammed machine parts designed by colony-level selection to serve their colony in its role as a superorganism. Though it is timely to revive Wheeler's superorganism model of the ant colony, because in many cases adaptations that promote gene replication and survival exist only at the colony level, generalization can be misleading. Much very recent work is also beginning to show that in many ant species workers are themselves reproductive and that workers, sometimes in a continuous conflict with the queen, may largely determine their society's life history and sex allocation. At this stage we simply do not know how subtle is the decision-making of individual workers, particularly reproductive ones in small societies, yet Hölldobler and Wilson repeatedly comment that ants have small brains. This emphasis on the simplicity of individuals hardly seems parsimonious, as elsewhere, for example, Hölldobler and Wilson document the wonderful navigation skills of foragers of the desert ant *Cataglyphis* (which can learn and form cognitive maps) as shown by the pioneering work of Rüdiger Wehner and his colleagues. If individual foragers can have such processing power, it is surely not a good working assumption to suppose that all ants are stereotyped simpletons in other roles. Such issues as the intelligence of the individual colony member or the collective intelligence of the colony may be the stuff of future revolutions in the study of social insects.

"A solitary forager of the desert ant *Cataglyphis bicolor*." The genus *Cataglyphis* "represents the extreme [foraging strategy] of solitary hunting combined with solitary retrieval." Workers of *C. bicolor* "make about 5 to 10 forays each day.... The foragers "tend to persist in only one or a very few directions for their lifetime, if for no other reason than that travel outside the nest is very dangerous and life is short. Most of the workers are soon picked off by spiders and robber flies, in spite of their ability to run ... up to a meter per second.... Yet the system is so efficient that the average forager retrieves a food weight during her lifetime 15 to 20 times greater than her own body weight." [From *the Ants*; photograph by R. Wehner]

At all events, even those who may be critical of some passages in *The Ants* will nevertheless find insight and inspiration in this beautifully written book. Like Wheeler's epic, it will inspire many new generations of students with its blend of scholarship, enthusiasm, and unabashed delight. This book will convert many a young biologist, or even chemist, physicist, and mathematician, into a myrmecophile—that is (to quote from the book's extensive and invaluable glossary), into an organism that spends at least part of its life cycle with ant colonies. Given that there may be 20,000 species of ants on this planet and that of the 8800 species so far described only a tiny fraction have been studied in any detail, Hölldobler and Wilson's elegant invitation to "Go to the ant— ... consider her ways and be wise" (Proverbs, chapter 6) should not be resisted.

NIGEL R. FRANKS
School of Biological Sciences, University of Bath, Bath BA2 7AY, United Kingdom

Cephalopodologie

Traité de Zoologie. Anatomie, Systématique, Biologie. PIERRE P. GRASSE, Ed. Tome 5, fascicule 4, Cephalopodes. KATHARINA MANGOLD, Ed. Masson, Paris, 1989. 804 pp. F1100.

Comprehensive reference works frequently require a number of years to compile, are eagerly awaited by specialists, and once published gradually come into general use by researchers, educators, and students. The volumes of *The Invertebrates* inaugurated by Libbie Hyman in 1940 provide an excellent example of such a history, as does the classic *Traité de Zoologie* directed by Pierre P. Grassé.

Among works of such lengthy gestation the present installment of the *Traité* surely holds the world record. In the 1930s the eminent Swiss zoologist Adolf Naef was selected to write the volume on the Cephalopoda, on the strength of his classic monographs on the phylogeny, evolution, morphology, and embryology of these advanced invertebrates published in the preceding decade. Naef began the project in 1939, but the events of history, teaching and family responsibilities, and ill health conspired to limit the results to an accumulation of notes, which he submitted before his death in 1949 to Grassé. Grassé asked Adolf Portmann of the Institute of Zoology in Basel, who was not a cephalopod specialist, to complete the work using Naef's notes. Believing Naef's work to be outdated, Portmann abandoned the notes and wrote a 200-page manuscript, which he submitted in 1954. Because the recently submitted gastropod and bivalve manuscripts ran to 4600 pages, Grassé required that the cephalopod section be increased to 400, a task the displeased Portmann was unwilling to undertake until the early 1960s. The resurgence of research on cephalopods then prompted Portmann to enlist Katharina Mangold, a former student and established cephalopod specialist at Laboratoire Arago, Banyuls-sur-Mer, France, to incorporate the new literature into the manuscript. By the time one section was updated, preceding ones had become obsolete, and, as the objective of the *Traité* was to be "comprehensive," the project became locked in a cycle of updates. Around 1970 Portmann asked Mangold to be a full coauthor, and in 1974 when Portmann became ill Anna Bidder from Cambridge agreed to join the effort. During the next few years the aid of other specialists was engaged. Finally, the now huge manuscript was submitted in February 1981, nearly an order of magnitude larger than was demanded by Grassé 27 years earlier. Additional material was added in proof in 1985, and the latest literature was added in 1987. The long gestation terminated successfully in late 1989.

One can justifiably ask if a work 50 years in the making can be worth the wait. In the case of *Cephalopodes* the response is a resounding "Oui!" Nothing comparable to it exists in the cephalopod literature. The cephalopod volume scheduled for *The Invertebrates* has not been completed and perhaps never will be published, and the quantity and diversity of knowledge being accumulated on cephalopods make it unlikely that such a detailed and comprehensive one-volume work can ever again be assembled. The long developmental period moreover enabled the book to evolve, in keeping with the evolution of the field, from concentration on systematics and morphology to include material on biology and behavior, and the expansion of authorship enhances and enriches the results.

The French is straightforward, easily understood; sentences are not convoluted, and much of the terminology will be familiar to those acquainted with the literature in English. Somewhat disconcerting to the first-time user of the volume will be the location of the table of contents in the French manner on the very last pages of the book and the inclusion of page numbers there only in parentheses in the listings of the subsections of the chapters.

A short introductory chapter by Mangold, Bidder, and Portmann is followed by a detailed, well-illustrated chapter on the gen-

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.

CLYDE F. E. ROPER
Department of Invertebrate Zoology, National Museum of Natural History, Washington, DC 20560

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