latter genus and *Gigantopithecus* form the Ramapithecinae. But are ramapithecines ancestral (or most closely related) to all great apes and humans, only to orangs, or to humans alone? Kay and Simons carefully review the morphology and the arguments, coming out strongly for the last alternative and suggesting that the group be formally included in Hominidae, which thus would have an antiquity of some 16 million years.

The views of phylogeny presented by Greenfield and by Zihlman and Lowenstein are based on the 5- to 8-million-year divergence between human and African ape ancestors suggested by the "molecular clock" hypothesis, which is here once more supported by Cronin and rejected by Goodman, Baba, and Darga. Zihlman and Lowenstein, and also Cronin, continue to push their "model" of the late Miocene common ancestor as similar to a living pygmy chimpanzee, but this appears to have no clear predictive or explanatory value and is based on poor understanding of current paleontological hypotheses; it is obfuscatory rather than illuminating, as also implied here by de Bonis. Boaz takes a middle road, averaging fossil and "clock" dates to obtain divergence times; he also considers the role of various *Australopithecus* species in human evolution, a matter examined carefully by White, Johanson, and Kimbel in a paper reprinted from the *South African Journal of Science*. This reprinting was not necessary here, but at least is acknowledged as such, as opposed to the chapter by Wolpoff, which is presented as original although it is identical to his article in *Current Anthropology* of late 1982, where it was accompanied by useful commentaries. Such double publishing is out of place in paleoanthropology, where the number of original papers is rising exponentially.

Ciochon concludes the volume with a wide-ranging overview, often providing better summaries of each paper than did the individual authors; he also offers a number of subgroup cladograms and an overall consensus version, as well as some useful tabulations of data gleaned from the morphological contributions. Both editors are to be congratulated for their efforts to standardize the papers without losing individual style; there are few inconsistencies, even between chapters, and even fewer printing errors. The four indexes (author, subject, taxon, and specimen) are incredibly complete and accurate. Two of the most interesting points to come out of the work as a whole are the extent of the use of at least some cladistic analysis by modern paleoanthropologists and the amount of homoplasy and convergence this approach has revealed among catarrhines. Twenty years ago, *Classification and Human Evolution* (S. L. Washburn, Ed.) provided a major impetus to reorient paleoanthropology with the inclusion of primate behavioral and molecular data and more rigorous systematics. The present work is less of a watershed than a stocktaking, but it certainly follows in that tradition and will serve as a point of reference in studies of Miocene hominoids for the next generation.

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An Approach to Epidemiology

The Population Dynamics of Infectious Diseases. Theory and Applications. ROY M. ANDERSON, Ed. Chapman and Hall, London, 1982 (U.S. distributor, Methuen, New York). xii, 368 pp., illus. $39.95. Population and Community Biology.

Population Biology of Infectious Diseases. R. M. ANDERSON and R. M. MAY, Eds. Springer-Verlag, New York, 1982. viii, 316 pp., illus. $18. Dahlem Workshop Reports, Life Sciences Research Report 25. From a workshop, Berlin, March 1982.

Parasites kill over 20 million people and debilitate a hundred times that many annually. Although we know enough about most of these pathogens to treat infected individuals, medicine has done little to bring about disease control at a community or population level in most of the world. These two books mark a resurgence of interest in the application of mathematical analyses based on ecological and evolutionary theory to the problems of disease transmission and control. Both volumes can be read with profit by biologists and applied mathematicians in addition to epidemiologists and public health workers.

The Population Dynamics of Infectious Diseases provides detailed discussions of recent work on parasite ecology and disease dynamics. Roy Anderson, Branko Cvjetanović, Klaus Dietz, Robert May, and seven others describe the transmission of viruses and bacteria, worms (hook-, round-, and tape-), insect-transmitted diseases (malaria, onchocerciasis), and snail-transmitted diseases (schistosomiasis, fascioliasis). The book's great strength is that the mathematical models are all strongly linked to biological data. This is worth noting; a survey of 75 epidemiological models published from 1974 through 1978 showed only five that contained actual data. The literature was full of elegant theories in search of diseases, and hubris was the modeler's disease. Cognizant of the fact that models have yet to lead to the successful control of any major disease and of allegations by non-numerate workers that models are just seductive alternatives to understanding, Anderson has provided a collection of authoritative essays that have both pedagogical and operational utility. Mathematical details are kept to a minimum, and the book is full of ideas and clear statements about unsolved problems.

In a final cautionary chapter David Bradley asks whether models have any advantage over less precise intuitive approaches to understanding and controlling infectious disease. He concludes that, despite problems in the past with oversimplified and overambitious models, the models of malaria and schistosomiasis have been invaluable in teaching and research. This book is full of other model-derived insights that have led to improved vector control and explain why a vaccination program may actually increase the prevalence of a disease among adults, why culling foxes won't control rabies, why removing pump handles may not stop a cholera outbreak, and why the interplay between individual immunity and herd immunity can have consequences that are far from obvious.

Population Biology of Infectious Diseases provides a very readable overview of our knowledge of the impact of infectious diseases, and the transmission, control, and evolution of animal parasites. The report of a Dahlem workshop, the book comprises nine background papers and discussion reports. The latter provide a stimulating and critical evaluation of what population biology might contribute to the control of disease. Throughout, the emphasis is on general principles; complex parasitological and medical terminology are kept to a minimum. The multidisciplinary audience this book deserves will appreciate the useful glossary and index and photographs of the 40 internationally recognized conferees.

There are excellent background papers on the impact of infectious diseases on animal and human populations, on the natural history of transmission, and on

problems encountered with various control techniques. Population biologists have been preoccupied with predator-prey and competitive interactions, so it is not surprising that the conferees disagreed on whether pathogens regulate their host populations. It is also clear that very little is known about the regulation of parasite populations themselves. Dietz reviews the use of different types of mathematical models for parasite transmission, and Anderson explores the concept of an infection's (or parasite's) basic reproductive rate, an extremely useful variable in predicting the success of a disease control technique. A. C. Allison reviews the coevolution of human hemoglobins and malaria parasites and argues that parasite evolution is typically from virulent to commensal. The conferees doubted that this was a necessary progression and noted that the rabbit and myxoma virus have evolved intermediate relationships repeatedly. In fact, host-parasite systems are most likely to have unstable equilibria, coadaptational limit cycles, and permanent dynamical behavior. Finally, W. D. Hamilton proposed that parasitism is responsible for sex, for meiosis, for all Mendelian variation, and for real species—guilds of genotypes committed to the free exchange of biochemical technology for parasite exclusion. The conferees were not completely convinced and suggested a number of tests for Hamilton's hypotheses.

The conferees agreed that existing models of host-parasite interaction have three weaknesses. First, they fail to allow for the spatial and temporal heterogeneity found in nature. Transmission equations rarely credit the asymptomatic Typhoid Mary and the promiscuous superspreaders of venereal disease any differently from the rest of us. Second, most models fail to allow for the complex interactions between various parasites within an individual and between parasites and malnutrition. Third, present models are rooted in ecology and lack the necessary genetic basis. This is their most serious weakness, because it is increasingly clear that there is considerable genetically controlled variation in compatibility between parasites, their vectors, and their final hosts. Unfortunately, the mechanisms of genetic regulation of host-parasite compatibility are generally unknown, and, for now, the theorists may be excused their simplifying assumption that all mosquitoes, snails, trypanosomes, and people are created equal.

These books come at a time when infectious diseases have never been so prevalent, when parasites and their vectors are being moved and mixed with increasingly serious consequences, and when both are rapidly evolving resistance to drugs and pesticides. They demonstrate both the great need for robust models of infectious disease epidemiology and the strengths of an analytical approach that is strongly linked to the real world. Yet, by drawing attention to the inadequacies of reductionism and to numerous unsolved problems in parasitology, the editors admit that attempts to produce a Newtonian epidemiology have failed. Therein lies the importance of these two volumes—the challenge to join in the development of a Darwinian epidemiology. Anderson and May have succeeded in clearly defining the significant contributions that population biology might make to controlling the great neglected diseases of mankind.

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Reproductive Tactics

Mate Choice in Plants. Tactics, Mechanisms, and Consequences. MARY F. WILLSON and NANCY BURLEY. Princeton University Press, Princeton, N.J., 1983. xii, 252 pp., illus. $35; paper, $12.50. Monographs in Population Biology, 19.

Mating patterns in plants have been prime subjects of evolutionary thought for decades. Patterns of mating have been characterized from pollen and seed dispersal patterns and from genotype distributions within and among families. The prime purpose has been to determine the extent of inbreeding and assortative mating in natural populations. Recently, there has been considerable interest in the cost of mating and how it may be optimized. The parental investment that a plant makes during one reproductive session and the allocation of that investment to different functions may be under strong control to maximize individual fitness. If plants can deploy parental investment in an adaptive manner, might they not also be able to choose their mates, as this too would enhance their individual fitnesses?

This volume presents a series of arguments and hypotheses that mate choice is made before and after fertilization by females and that males compete for mates. The volume is an interpretation of a number of pre- and post-zygotic processes and phenomena in terms of mate choice and sexual selection. The authors' objectives are to explore the potential role of mate choice in influencing the reproductive biology of higher plants and to suggest some mechanisms by which mate choice may be accomplished. They have been successful in their advocacy of sexual selection through skill in argumentation and in the use of data from the literature, while recognizing the paucity of supporting evidence. In a sense, the book is an exercise in the subjunctive, about what might be, if . . . then. . . . The conceptual framework is formulated with regard to sexual selection in animals. The assumptions that plants have the ability to discriminate among an array of pollen donors, that donors possess mechanisms rendering themselves discriminable by pollen recipients, and that plants act upon such discrimination for the most part remain to be validated.

The authors contend that reproductive success in females is resource-limited rather than pollen-limited, whereas male reproductive success is more often limited by the number of mates than by resources. This sets the stage for female choice and male-male competition. Female choice may be exercised prior to fertilization through differential acceptance of pollen based upon its self-incompatibility, vigor, and contribution to the progeny. Female choice may be exercised after fertilization through selective seed and fruit abortion. Male-male competition is through the duration of pollen availability, flower number, pollinator attraction, and differential pollen grain germination and pollen tube growth. The exposition of these general points is accompanied by data and a discussion of subordinate hypotheses and their interrelationships.

This volume provides a new perspective on plant reproductive biology and attempts to explain and unite many previously unrelated aspects of reproduction such as delayed fertilization, pollen tube growth rates, double fertilization, and seed abortion. Traditionally, pollination, pollen-pistil compatibility, and fruit and seed development have been treated as separate matters. The volume also contains a substantial amount of synthesized information on plant reproductive biology that is of considerable interest regardless of its relationship to mate choice. Given the challenges and questions raised in this book, it will provoke critical thinking and experimentation on a fascinating subject.

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