Hominoid Phylogeny

New Interpretations of Ape and Human Ancestry. Russell L. Ciochon and Robert S. Corruccini, Eds. Plenum, New York, 1983. xxiv, 888 pp., illus. $95. Advances in Primatology. Based on a symposium, Florence, July 1980.

In recent years, research on the origin of the human lineage has mushroomed. New fossils have been recovered across the Old World, and previously known ones have been reanalyzed with new techniques and outlooks. These studies have combined with expanding investigations of the molecular biology of living primates and the burgeoning fossil record of early humans to bring the ape-human divergence into sharper focus. Four major hypotheses are emphasized in this volume by most of the protagonists in the theoretical debate, as well as by a group of supporting players with important grist for the model mill. Some of the papers were first prepared for a symposium in 1980, and many review (and extend) prior work of their authors, but with two exceptions all contain novel and sometimes innovative results. In terms of vital statistics, 37 contributors (of whom six are represented twice) prepared 30 chapters, grouped into eight sections.

Bernor provides a carefully reasoned survey of the chronology and zoogeography of the Eurasian and North African Miocene, that time interval from 24 to 5 million years ago which is of central importance to the emergence of the human clade. He presents valuable tabulations of the relative and chronometrically calibrated ages of all fossil sites mentioned in the volume, ranges of the hominoid (ape and human) taxa, and maps of the mega-ecology of successive phases of the Miocene; his own main contribution is the documentation of six to eight bioprovinces or regions of local continuity and partial environmental isolation, with notes on the dispersal of hominoids among them.

Most workers today follow molecular (and some morphological) data in linking the African apes and humans and the orangutan in two major clades, but major uncertainty exists as to whether any early fossils pertain solely to the former. Somewhat surprisingly, Kluge's cladistic analysis of a wide variety of data, including "karyomolecular" features, suggests the older view that the great apes may have shared a common ancestry after the divergence of humans. Kluge also rejects out of hand the idea that *Pongo* is the sister taxon to *Homo*.

The paleontological papers are of three main kinds: description of specific fossils (especially from the Indo-Pakistani Siwaliks); discussion of specific groups or morphological systems; and broader taxonomic or ecological surveys. In the first category is the fine article by Walker and Pickford, who not only describe but carefully illustrate newly recovered portions of a known individual of the Early Miocene Kenyan *Proconsul africanus*. They conclude that this pivotal (that is, morphologically well-known) taxon had shoulder, foot, and part of the elbow quite like those of living apes, combined with more conservative wrist, hand, and thigh; the pelvis and trunk, site of many hominoid modifications, are as yet unknown. Moreover, a new foot of contemporaneous *P. nyanzae* is shown to be an isometrically scaled-up version of *P. africanus*, although body weights may have been 40 and 12 kilograms. Morbeck and Rose concentrate on Hungarian and Siwalik postcrania, respectively, agreeing that these two samples represented species more "advanced" toward modern hominoids than other Miocene forms. Fleagle's review of Oligocene and Early Miocene postcrania is broader, emphasizing the distinctiveness of Old World monkeys and the platyrrhine-like morphology of early catarrhines; his pictorial phylogeny of the anthropoid elbow is especially well done. Some of the same points are made in his paper with Kay on the Oligocene *Propliopithecus* and "*Aegyptopithecus*," which are considered close to the common ancestry of all modern Old World anthropoids but placed within the Hominoidea nonetheless.

Ward and Pilbeam analyze Miocene through modern hominoid nasomaxillary midline anatomy, confirming a threefold division: a conservative pattern like that of Old World monkeys and gibbons in Early Miocene African and some mid-Miocene European fossils; a *Pongo*-like pattern in *Sivapithecus*; and the *Homo*-like condition in *Australopithecus* and African apes (it is intriguing that Schwartz [*Primates* **24**, 231 (1982)] derived a *Homo-Pongo* clade from essentially similar data). According to Ward and Pilbeam, *Pongo* and *Sivapithecus* also share (with *Australopithecus* and *Homo*) rotated upper canine roots, thick molar enamel (moderate in the living species), and robust maxillae. Enamel thickness has recently been thought to increase in one or more lineages through the Miocene and Pliocene before decreasing in Pleistocene *Homo* and *Pongo*, but Ward and Pilbeam now suggest that it was at least moderately thick in the last common ancestor of all living hominoids. They conclude that *Ramapithecus*, long thought to be the Miocene human ancestor, is best ranked as a subgenus of orang-like *Sivapithecus*, from which they differentiate it only in degree of alveolar process invasion by the maxillary sinus and size (I would agree taxonomically, but add mandibular corpus and symphysis proportions to its distinctions).

Gantt discusses enamel thickness (and prism conformation) more intensively but less clearly, suggesting from single specimens that *Proconsul* had enamel as thick as *Sivapithecus* of equal molar size. But if *Sivapithecus* were megadont (had very large molars for its body size), as suggested by Pilbeam and accepted by Andrews, it would have had much thicker enamel than *Proconsul* compared to body weight. Pickford argues that thin-enameled *Proconsul* inhabited both wet and dry forests, whereas possibly allochthonous later thick-enameled African "sivapiths" entered newly available woodland zones. Andrews shows that Eurasian *Sivapithecus* also lived in woodlands, some of which show indications of strong seasonality, as found among no living primates except a few macaques. He suggests an average body size of 30 to 40 kilograms (if megadont), a mixed herbivorous diet with low fruit or leaf content (possibly based on underground storage organs common in woodlands), and a partly terrestrial, though by no means cursorial, locomotor habit.

Kay and Simons survey all Eurasian Miocene hominoids in detail, revising taxonomy to place some populations previously called *Ramapithecus* into the conservative *Dryopithecus* and others into known species of *Sivapithecus*; the 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.

ERIC DELSON
Department of Anthropology, Lehman College, City University of New York, Bronx, New York 10468, and Department of Vertebrate Paleontology, American Museum of Natural History, New York 10024

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