

will prove to be the most important key to understanding social organization of natural groups of monkeys, and that its study will well repay the rather formidable practical problems involved in maintaining any really long-term study." The widespread acceptance and

application of this idea will mark the beginning of a new era of primate studies.

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## Historical Zoogeography

**Evolution, Mammals, and Southern Continents.** ALLEN KEAST, FRANK C. ERK, and BENTLEY GLASS, Eds. State University of New York Press, Albany, 1972. 544 pp., illus. Cloth, \$17.50; microfiche, \$12.50.

A little over a century ago J. Wagner (remembered today for his description of the earliest known bird, *Archaeopteryx*) pinpointed a mountain in northeast Turkey, Büyük Agri Dag, as the site from which the mammals radiated. Wagner regarded this twin-peaked mountain, known today as Mount Ararat, as the final resting-place of Noah's ark.

Historical biogeography has come a long way since Wagner's time. By the middle of the present century P. J. Darlington (*Zoogeography: The Geographical Distribution of Animals*, Wiley, 1957) was able to formulate a general theory accounting for the origin and dispersal of vertebrates on a global scale. He suggested that the major vertebrate groups, including mammals, had originated in the "Old World tropics" and that successful groups dispersed from there: to Australia, to Africa, to Eurasia, and thence across the Bering land bridge into North and subsequently South America. Ancient relics on the other hand would survive at the "ends of the earth," having been replaced by more advanced forms at their center of origin. This widely accepted hypothesis was based on a model of the world as changing endlessly in detail but fixed in its main pattern of land and climates. Following W. D. Matthew and G. G. Simpson, Darlington rejected Alfred Wegener's hypothesis that the continents had moved with respect to one another.

The revolutionary development of plate tectonics theory during the past 15 years now renders static global models, and evolutionary schemes based upon them, obsolete. Hypotheses that visualized the radiation of most verte-

brate groups from the "Old World tropics" and the survival of relics in the geographic cul-de-sacs of Africa, Australia, and South America are now undergoing extensive revision.

This collection of review articles on the evolution of mammals on the southern continents is one of the first volumes on historical biogeography to appear since continental drift became a fact of paleogeography. Containing generally excellent essays on fossil and contemporary mammals of three continents, the book will be useful to vertebrate zoologists and others interested in the interaction of organic evolution and paleogeography. Although earlier versions of these essays were published separately in the *Quarterly Review of Biology* (September 1968 through June 1969, December 1971) the collection is worth reviewing here as it confronts the major problems of historical and evolutionary biogeography.

Biologists have long been intrigued by the concentration of primitive mammals in the three widely separated southern continents. These strikingly different (except for the cosmopolitan rodents and bats) faunas display remarkable structural and ecological convergence. Australia is characterized by marsupials and egg-laying monotremes; South America by a mixture of placentals and marsupials; and Africa by placentals only. The six descriptive essays on the fossil and contemporary mammal faunas of these continents constitute the most valuable portion of this book. The major fossil localities and their faunas are reviewed authoritatively; patterns of radiation, distribution, ecology, and evolution are described family by family. The text is enhanced by numerous illustrations of living and extinct forms and by extensive bibliographies. The indexes are excellent.

H. B. S. Cooke describes the fossil

mammals of Africa and their paleoenvironments. He shows that, far from being a refuge for the survival of archaic forms, the continent has been an important center of mammalian evolution. Several successful groups, including man, have dispersed to other parts of the world. The contemporary mammals of Africa are reviewed from systematic and regional viewpoints by R. C. Bigalke.

The peculiar character of the Australian mammal fauna was aptly summed up by Darwin when (lying on a sunny river bank in 1836 and reflecting on the Paradox, as the platypus was then called) he wrote: "An unbeliever in everything beyond his own reason might exclaim 'Surely two distinct creators must have been at work. . ..'" Keast capably summarizes our knowledge of this fauna, about whose phylogeny and late Cenozoic history we have learned much in the past decade, but about whose early history we still know nothing. Far from being "living fossils," the Australian marsupials are actively evolving and speciating.

The two chapters on South American mammals are outstanding, and are especially instructive because their authors disagree on several issues. B. Patterson and R. Pascual, writing about the fossil faunas, hold that the original Mesozoic stocks (marsupials, edentates, ungulates) and the early Tertiary immigrants (rodents and primates related to African groups) arrived by island-hopping from North America. P. Hershkovitz, in contrast, raises the possibility that the primitive marsupials originated on Gondwanaland and moved between the then-joined Australian-Antarctic continent and South America by way of the Scotia Arc. As for the rodents and primates, he suggests their probable derivation directly from Africa as the South American and African plates rifted apart. A third controversy concerns the onset of the large-scale faunal interchange between North and South America that has traditionally been linked to the appearance of the Panamanian land bridge toward the end of the Pliocene. Although these issues cannot be settled yet, Patterson and Pascual rightly note that there is little fossil evidence to support Hershkovitz's more speculative views on the fauna's history.

Mammals arose about 200 million years ago, at a time when the Mesozo-

ic supercontinents were breaking up. Keast reviews a range of fascinating problems in his chapter on the significance of continental drift for evolution on the continents and islands of the

Southern Hemisphere. He discusses a wealth of biological data in the light of the Dietz-Holden paleogeographic reconstructions. He contends that some of the paleontological and biogeographic

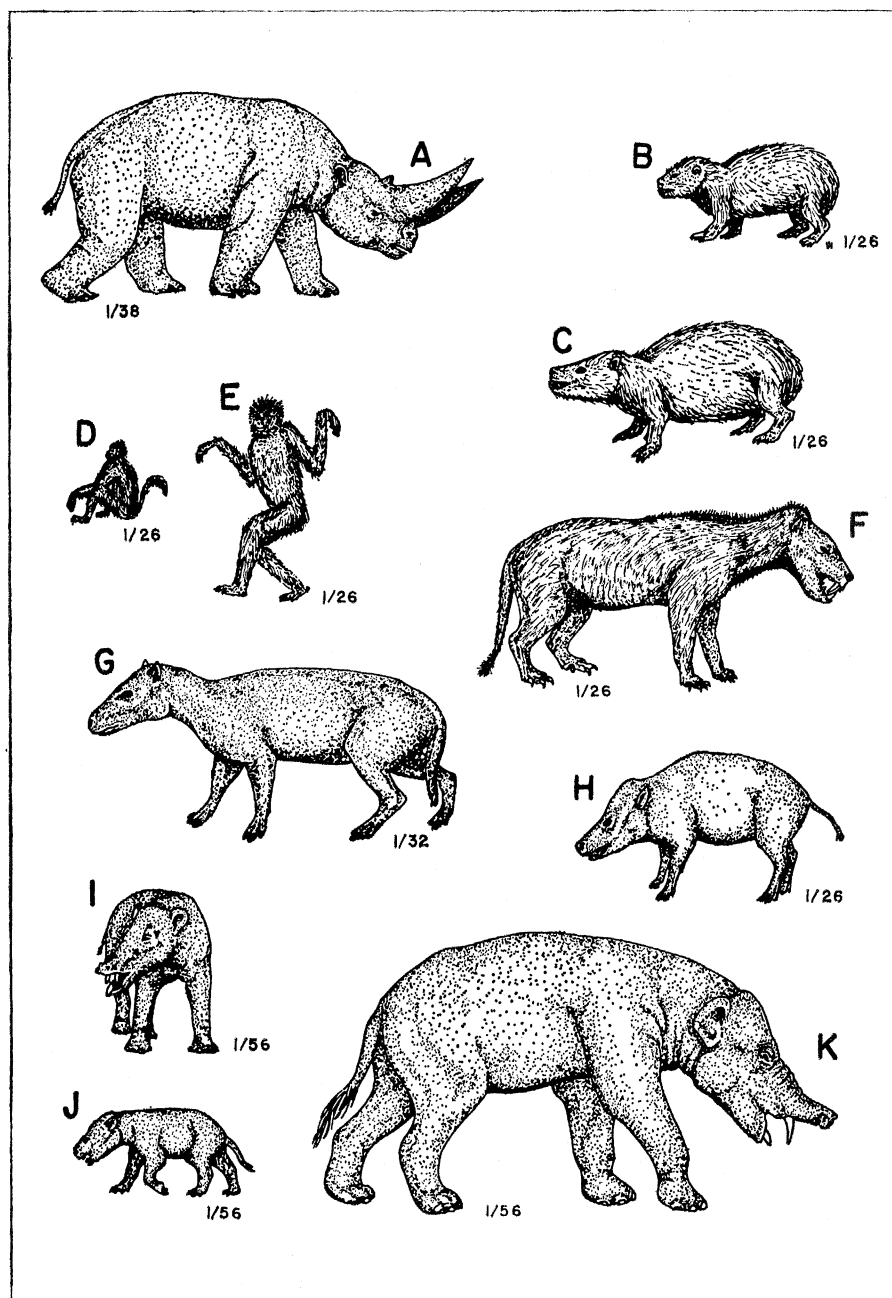
data are inconsistent with the whole notion of drift. In interpreting such data in this manner (and in doing so he has undoubtedly been influenced by 50 years of precedent) he appears unaware that the biological record is now irrelevant to the question of whether or not drift occurred. Distribution patterns, whether of fossils like *Lystrosaurus* or of modern marsupials and leptodactyloid frogs, are no longer of much use in establishing paleogeographic patterns. Biogeographers must be prepared to follow the lead of the geophysicists and geologists until the details of paleogeography and paleoecology are reestablished on a dynamic global model. Historical biogeography is now in a period of continuous revision, and it is not surprising that some aspects of Keast's account are already out of date. The reader will nevertheless find his article a valuable introductory source, and his conclusions are certainly provocative (p. 69):

The new data on continental drift are of little or no significance yet, in helping to explain or interpret early patterns of mammalian distribution in the southern continents. They do nothing to shake earlier convictions [of Simpson and Darlington] that both South America and Africa obtained their Tertiary faunas from the north. Only in the case of Australia do they necessitate rethinking.

My main criticism of this volume is that many readers will be unable to judge the validity of this conclusion or the contrary conclusions reached by others. In the absence of comparable accounts of the mammals of North America, Eurasia, or India it is difficult to assess the detailed arguments. Regrettably, in the ten years since the inception of this collection at the XVI International Congress of Zoology, the editors failed to see the necessity of treating patterns on a global scale. We have received a fine jigsaw puzzle, but some of the pieces have been withheld.

My second criticism is minor. In a volume with so many editors I was surprised to note that two contributors use metric units, three use English units, and one employs a combination of the two systems.

Finally, I draw the reader's attention to some outstanding problems of evolutionary biology well illustrated by the mammals of the southern continents: the concept of faunal dominance and the associated processes of competition, replacement, and enrichment; the relationship between area, isolation, climate, and evolution; the concept of faunal balance; and the relationship be-



Reconstructions of major morphological types of Oligocene mammals in Africa. A, *Arsinoitherium* (Embrithopoda); despite appearances it is not related to the modern rhinoceroses, but may be related to the hyracoids; it disappeared during the Oligocene. B and C, *Saghatherium* and *Megalohyrax*, hyracoids which formed a dominant element of the Oligocene fauna and are represented today by the hyraxes. D and E, *Parapithecus* and *Propithecus*, two of the oldest known anthropoid primates. F, *Hyaenodon*, a representative of an extinct group of carnivorous animals, the creodonts. G and H, *Bothriodon* and *Mixtotherium*, extinct artiodactyls. I and K, *Phiomia* and *Palaeomastodon*, early proboscideans. J, *Moeritherium*, a relative of the early proboscideans. These are members of the first known Tertiary terrestrial mammal fauna (consisting of some 73 species) from Africa. The African fauna at this time was largely endemic. Of the forms represented here A through E and I through K probably arose in and were confined to Africa. F through H, which have been found also in Europe and North America, were probably immigrants from the north. Numbers represent approximate reductions. [From H. B. S. Cooke's chapter in *Evolution, Mammals, and Southern Continents*]

tween environmental changes and speciation on a global scale. Understanding of these phenomena, so ably developed for simple island situations by E. O. Wilson and the late Robert MacArthur, is still too simplistic to cope with the complexities of continents. Given that one of the most difficult tasks facing biogeographers is the application of the principles of population genetics and evolutionary ecology to these great historical problems, this volume will provide the creative with countless ideas.

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## Phytogeography Reactivated

**Taxonomy, Phytogeography and Evolution.** A conference, Manchester, England, Sept. 1971. D. H. VALENTINE, Ed. Academic Press, New York, 1972. xii, 432 pp., illus. \$22.

**Floristics and Paleofloristics of Asia and Eastern North America.** Proceedings of symposia, Seattle, Wash., and Corvallis, Ore., Aug. 1969. ALAN GRAHAM, Ed. Elsevier, New York, 1972. xii, 278 pp., illus. \$25.

For many decades of this century the field of plant geography has been somnolent if not moribund. Cain's excellent and dynamic *Foundations of Plant Geography* published in 1944 was succeeded by a few retrograde, specialized texts that did little to stimulate or define the discipline. However, the recent revival of concern with continental drift and the effects of paleobotanical heterodoxies have assisted in a substantial revival of interest in phytogeography. The field now is clearly concerned with dynamics, explanation, and fresh perspectives that go well beyond the rather sterile listings of where plants grow.

The 25 papers contained in *Taxonomy, Phytogeography and Evolution* deal with aspects of such general topics as major geographical disjunctions in relation to evolution and migration, endemism, and "geographical" evolution in genera and families of special interest (in this case, the Gesneriaceae, *Epilobium*, *Nothofagus*, *Alchemilla*, and the Combretaceae) and with a series of "special topics" such as the migration of weeds, the history and ecology of continental European plants, floristic connections between portions of Britain and France, and computational methods in the study of plant

distributions. Unfortunately, virtually no attention is given to the important contributions of physiological ecology, phytochemistry, or paleobotany to our understanding of past and present plant distributions. Despite the arbitrary segregation of the papers according to various section headings, two prominent themes emerge. One is a concern with the mode of origin of major disjunctions, such as those that exist between Eurasian and North American forests (J. Kornaš), North America, Japan, and the Himalayas (H. Hara), the Restionaceae of Africa, Australia, and South America (D. Cutler), American amphitropical deserts (O. T. Solbrig), and the cool temperate floras of the Southern Hemisphere (D. M. Moore). The other is a preoccupation with insular floras, evidenced by the discussions of the Canary Islands (D. Bramwell), Crete (W. Greuter), Hawaii (G. Gillett), Caribbean Islands (B. Morley), New Zealand (P. H. Raven), and the Aegean (A. Strid). Even the European mountains (C. Favarger), West African mountains (J. K. Morton), and California (H. Lewis) fall into this "island" category.

Many of the contributions are reviews of the work of the individual contributors and their students and as such are of restricted novelty or scope. Solbrig's paper is of special interest because it presents the background and future plans for a multidisciplinary study of American amphitropical desert disjunctions, and is particularly valuable because of the methodological précis given in it. Moore's extensive discussion of Southern Hemisphere floras goes far beyond phenomenology in describing various distributional patterns that recur in diverse genera and interprets these in the light of the biological characteristics of various taxa and the geological and climatic history of the large region concerned. Bramwell argues convincingly that the endemic flora of the Canary Islands is an old one and that the woody habit of many endemic genera is relict and not derived, as it is in the Hawaiian flora.

The papers that constitute this book do not hang together particularly well, and in fact a general theme to the book is not clearly evident. A concluding synthesis and final interpretative chapter would have been of great value to the general reader and perhaps would have more solidly legitimized the title of the book.

*Floristics and Paleofloristics of Asia*

and *Eastern North America* is perhaps more successful because of its more restricted sphere of coverage and the greater strength and mutual complementation of the major papers that it contains, though a few of the contributions are of only minor interest. Recognition of the strong floristic affinities between eastern Asia and eastern North America goes back as far as the middle of the 18th century, but it is Asa Gray who is generally credited with bringing these affinities to the attention of biologists. Gray's two short papers—reprinted in this volume—provide the theme and historical inspiration for this collection of papers.

Graham introduces the origin and the history of the recognition of the floristic affinities between eastern Asia and eastern North America and discusses the errors of interpretation that have been introduced into paleobotanical studies by misidentifications and incorrect age determinations, and further reflects his skepticism of the Geoflora concept by stating that the Mixed Mesophytic forest and its Cenozoic history are "too complex to be adequately expressed by a single floristic theory." Wolfe, in his interpretation of Alaskan Tertiary floras, goes even further in his statement that the "confusion of the fundamental concepts of vegetation and flora has confused the history of the Mixed Mesophytic forest" and that this confusion is inherent in the concept of the Arcto-Tertiary Geoflora.

Evaluation of the extensive paleobotanical information given for Alaska, the Rocky Mountains, and Japan, of the neobotanical information given concerning the phytogeography of northeastern Asia, and of the American-Asian affinities among flowering plants, ferns, bryophytes, and lichens leads to the inevitable conclusion that the origin of the strong floristic affinities between Asia and North America is *not* as well understood as one might assume from much of the literature on the subject. As Graham points out, "rather than providing a final explanatory statement for a classic pattern of disjunct distributions, the data challenges the validity of many established and accepted concepts."

The overall flavor of this second book is strongly partisan, however, and one suspects that the Geoflorists will be heard from again.

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