A Biogeographic Event

The Great American Biotic Interchange. FRANCIS G. STEHLI and S. DAVID WEBB, Eds. Plenum, New York, 1985. xviii, 532 pp., illus. $75. Topics in Geobiology, vol. 4.

As generally portrayed, South America's biogeographic history unfolded on a grand scale. In the Late Mesozoic, this huge landmass severed its connection with the rest of Gondwanaland and became an isolated biological reserve. Despite minor contamination by foreign invaders and some leakage of its resident biota, South America, for the next 90 million years or so, maintained its own peculiar evolutionary history. This phase abruptly ended some 3 million years ago, when a slender anastomosis of land between Central America and northern South America promoted one of the most dramatic biotic exchanges ever recorded. The North American component of this exchange then brought havoc to much of South America's resident mammal fauna, forcing the extinction of many lineages.

This story, however dramatic, belies a complexity of events documented with extraordinary thoroughness. When biogeography flourished in the 18th and 19th centuries, South America was one of its favorite subjects. It therefore seems appropriate that the biogeography of South America and its relationship with the Caribbean and Central American regions should be in the limelight during the current renaissance of historical biogeography. This compendium on the biotic exchange between South and North America is a remarkable demonstration of the sweeping eclecticism of the new biogeography. It shows how far we have come in refining a great history and how this refinement depends on many different avenues in the natural sciences.

The book also shows how complicated a problem in historical biogeography can get. This discipline must surely epitomize our frustration with the maze of relationships presented by the natural world. The editors' goal is to describe with precision the Late Cenozoic Pan-American exchange in systematic, ecologic, paleontologic, and geologic dimensions and to uncover, with comparable precision, its causes and effects. Even within the context of historical biogeography, their objective is daunting. Most of our recent success in historical biogeography has involved description of higher-order patterns. These patterns relate the isolation of major faunas and floras to a very general history of continental breakup and drift. The subsequent events of interchange between continents, at times when barriers are broken down, offer more elusive problems. Analysis of them requires a sharply focused picture of the timing of the interchange, its environmental constraints, and the potentials for dispersal of the organisms in question.

The editors admit that their success in resolving such a picture is mixed. Yet the book demonstrates, with admirable honesty, where concrete results drift into speculation. Perhaps the most fundamental achievement is in depicting the event itself against the history of the New World biota. The question is posed, how "great" was the great American biotic interchange? Was it truly a unique event or merely the most recent, if somewhat exaggerated, peak in a long-term cycle of biotic exchange? The answer is clear. This interchange far exceeds the intensity of earlier ones. In an exhaustive review, Larry Marshall describes the major reason for our confidence in this view. This is the astonishing improvement in our knowledge of the fossil history and geological time scale for South America, an improvement largely due to the energetic efforts over the last decade of Marshall and his North American coworkers, as well as the research of resident paleontologists in South America. Marshall follows G. G. Simpson in dividing South America's history of mammals into several phases. The last of these phases—stratum 3 in Simpson's terms—was initiated by the sudden appearance, about 3 Ma (megaannum or millions of years before present), of cricetid rodents and procyonids and was followed, at around 2.5 Ma, by the explosive introduction of the Panamanian travelers.

It is also clear, as Webb emphasizes, that the legions of invaders from both the south and the north about 2.5 Ma are easily distinguished from the heralds of interchange dating back to 8 or 9 Ma. However, the precise timing of the Panamanian rush hour remains an intriguing problem. The preferred date is, lo and behold, largely determined by the fossil occurrences of the mammals themselves. Independent lines of evidence do not fall so neatly into place. Excellent reviews (Smith, Donnelly, Gose) of the relevant geology show certain irreconcilable differences but converge on a fuzzy estimate of between 10 and 5 Ma for the closure between Central and South America. Moreover, invertebrate marine faunas, as discussed by Jones and Hasson, also suggest a somewhat earlier closure of 10 to 5 Ma, whereas the marine microfossils indicate a 3.5 Ma connection. Some resolution is provided by the consideration of sea level changes by Savin and Douglas. These authors describe a notable emergence of the land connection slightly earlier (3 Ma) than the Panamanian exchange, although their analysis also discloses ephemeral emergences of the isthmus at earlier times.

Related to the problem of timing is the environmental setting for the great exchange. It is thought that the major forces of invasion are represented by mammals adapted to savannah or semiarid habitats. This requires a dramatic conversion of such habitats in the Panamanian region to the dense tropical rain forests of today. Again, the fossil mammals provide self-fulfilling predictions. Their supposed semiarid adaptations provide the primary paleontological "evidence" for the existence of the savannah dispersal corridor. Documentation from pollen-bearing sediments or other independent sources has been poor. Nonetheless, astute chapters by B. B. Simpson and Neff and Mares remind us that Recent Central America and northern South America, although dominated by rain forests, display a pastiche of environments, some of which are semiarid and savannahlike. This mosaic of present-day environments, as well as the changing topography of the Panamanian bridge in geologic time, supports the possibility that this connection at the height of exchange offered somewhat drier conditions.

Perhaps the most puzzling questions have to do with the participants in the exchange. Why does the exchange have such a strong mammalian component? This impression seems partly to reflect less complete fossil records for other groups. The modern herpetofauna of North America clearly suggests a late invasion of many elements from the south (Vanzolini and Heyer). However, distributions of fossil reptiles and amphibians, as thoroughly reviewed by Estes and Baez, do not suggest broad-scale interchange in the past. Furthermore, it is largely data from the Recent biota that suggest the marked dispersal of birds (Vuilleumier) and fishes (Bussing) in the Late Cenozoic. Most problematic are distributions of plant groups that may have played a major role in the exchange but are poorly known for historical information (B. B. Simpson and Neff).

A second problem concerns the effects of the exchange. Modern work has dispelled the venerable notion that many of the long-term denizens of South America were driven to extinction by marauding legions from the north. Marshall, Cifelli, and Pasqual *et al.* stress that the extinction of many of the archaic lineages long preceded the invasion.

Yet the record clearly shows that the invasion was coincident with extinction of more modern residents of South America. By contrast, the impact of the southern dispersers on the North American faunas was certainly less important and enduring (Webb, Mares).

Why were the effects of this exchange so one-sided? Webb puts forth a form of the argument promoted by G. G. Simpson and other biogeographers. The northern invaders hail from a vast staging area, where the Holarctic continents were broadly joined in the Early Cenozoic. In this sense, the invaders were already well traveled. They were also adapted to a variety of temperate environments and to the more marked faunal mixing of the Northern Hemisphere. It was this legacy, and not some inherent biological superiority, that promoted their success in South America. Though plausible, this explanation smacks more of narrative than of a theory anchored by hard evidence. Indeed, the chance of a decisive explanation seems slight. However, it is only with the kind of lavish historical documentation assembled by Stehli and Webb that we can presume to consider these more challenging mysteries.

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Atmosphere Physics

Physical Meteorology. HENRY G. HOUGHTON. MIT Press, Cambridge, MA, 1985. x, 442 pp., illus. $37.50.

As Houghton points out in the preface to this book, "physical meteorology" is an inept term for a subdivision of meteorology, since all of meteorology involves the application of physical principles to the atmosphere. Early in the present century the term was introduced to designate the parts of meteorology not considered to be directly applicable to weather forecasting, which was then the principal focus of the subject. Though it has always been recognized that radiation from the sun is the prime source of the energy for atmospheric motions, explicit evaluation of its influence was not considered necessary, since it was thought that atmospheric behavior, as summarized on weather maps, implicitly included its role as well as that of the physical processes involved in the formation of clouds and precipitation.

The study of atmospheric behavior empirically using weather maps is called "synoptic meteorology." Prior to the availability of high-speed large-capacity computers, weather forecasting was carried out by the application of the rules obtained from this study to the movement of pressure and wind systems. The theoretical study of atmospheric flow patterns using the partial differential equations of motion is called "dynamic meteorology." The complexity and nonlinearity of these equations did not permit their integration even approximately before the development of high-speed computers with large memories. With the availability of computers of adequate speed and capacity, dynamic meteorology has largely replaced synoptic meteorology as the basis for weather forecasting. Thus synoptic and dynamic meteorology have been regarded as the central branches of meteorology. Other meteorological topics involving the direct application of the laws of physics are lumped into "physical meteorology."

Of these other aspects, Houghton has selected the transfer of radiation—shortwave from the sun and longer infrared from the earth and atmosphere—through the atmosphere and the physics of the formation of clouds and precipitation for most of his attention, devoting three chapters to each of these topics.

The atmosphere is commonly regarded as a mixture of gases, principally nitrogen and oxygen. In fact, in addition to gases it contains solid and liquid particles that, though they make up a very small proportion of its mass, play very important roles in the transfer of radiation and the formation of clouds and precipitation. To provide a basis for the treatment of these roles, Houghton presents in his first chapter a summary of the nature, methods of measurement, sizes, composition, and sources of particles in the atmosphere and in the second chapter a summary of scattering by molecules and by these larger particles. Finally, after the six chapters covering his major topics, he devotes one chapter each to optical phenomena in the atmosphere and atmospheric electricity.

In recent years several applications of meteorology have led to a great increase in interest in radiative processes in the atmosphere. These include studies of the possibility that carbon dioxide and other polyatomic trace gases added to the atmosphere by human activities may be affecting the earth's climate, the use of radiation measurements by satellites to infer the temperature and humidity distribution in the atmosphere as initial conditions in numerical weather prediction, and, most recently, studies of the possible influence that the introduction of smoke and dust in a nuclear war would have in producing a "nuclear winter." Similarly, interest in cloud physics was stimulated by attempts to increase precipitation, dissipate fog, reduce lightning, and otherwise modify the weather, by studies of the interaction of cloudiness and radiation in climatic modeling, and by investigations of the rainout and washout of pollutants to produce acid rain. In this book the fundamental physics for all of these applications is discussed.

The treatment throughout is clear and concise. In some places derivations are complete; in others they are only indicated, or results are given without deriviation. An extensive list of references, some 600 of them, guides the reader to fuller treatments of each topic.

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Brain Asymmetries

Cerebral Lateralization in Nonhuman Species. STANLEY D. GLICK, Ed. Academic Press, Orlando, FL, 1985. xiv, 287 pp., illus. $49.50. Behavioral Biology.

It has been widely believed that cerebral lateralization is uniquely human. Although animal asymmetries were not unknown, it seems to have been assumed that they were relatively isolated and unimportant, and irrelevant to the understanding of higher mental faculties. The explicit challenge of more recent research has been to demonstrate that cerebral asymmetries in other species are homologous to the well-documented asymmetries of the human brain.

In the preface to the volume under review, Glick asserts that several homologies do indeed exist. One candidate is the recently discovered left-hemispheric control of vocalizations in passerine birds, an asymmetry that at once evokes the left-cerebral dominance for speech in humans. Arnold and Bottjer's careful review suggests, however, that the parallels are not so straightforward as they seemed at first. Recent work by McCasland challenges the cerebral basis of the asymmetry, and there is little correlation across species between asymmetric neural control and either the complexity of the song or its dependence on learning. There is no evidence of asymmetry of vocal control, for instance, in that highly talkative and imitative bird, the parrot—although, oddly enough, most parrots are left-footed!

Seven of the 11 chapters are devoted primarily to asymmetries in rodents. Most of these are concerned with cerebral lateralization in the rat and suggest parallels between rat and human in the asymmetries of transmitter systems and in the influence of