Environments of the Geologic Past

The naive and mischievous notion that biology is reducible to chemistry is held by many chemists, a few biologists, and an inordinate number of college deans. It has begun to put ecologists, even more than most biologists, on the defensive. Knowing that the systems they study are infinitely more complex than any molecule or cell, and at least as interesting, ecologists are not prepared to abandon them because they are difficult, but they are uncomfortably aware that decades of empirical research in ecology have been guided by extremely little in the way of theory. Their special vocabulary of biomes and ecads is an ideal medium for intramural polemics, but serves ecologists badly in the corridors of molecular architecture. Moreover, their platitudinous principles, cast in terms of the integrity of the ecosystem, care of the human habitat, and so on, sound like twaddle to the unconverted. Being unaggressive backwoodsy types for the most part, ecologists have tended to meet the challenge of molecular biology by retreating into hurt silence.

If they are uneasy about their honor in their own departments, ecologists can take heart at learning how their work is regarded in other quarters. In the social sciences, for which biology is basic but insufficient, ecology is the perennial source of new ideas, and the discipline is in some danger of being smothered by affectionate sociologists and psychiatrists. In humanistic scholarship, literary and artistic styles and the "thrust" of history are spoken of as aspects of the "ecology of mind." And, in the earth sciences, across the whole spectrum from geochemistry to meteorology and oceanography, there is little doubt that the ecology of the past is the wave of the future. Better than most people, geologists understand the difference between history and antiquarianism, and there is nothing nostalgic about this interest in paleoecology. In stratigraphy, for example, the classical or evolutionary work being largely finished, the problems of correlation that remain are ecological problems, involving the interpretation of facies formed in contemporary but different environments. As a result, with their habitual concern with the present as the key to the past, geologists are finding ecology too important to be left to ecologists, and are plunging (some of them literally, in wet suits) into modern habitats with new tools and fresh viewpoints.

To judge from this symposium volume, **Approaches to Paleoecology** (Wiley, New York, 1964. 440 pp. $12.50), edited by John Imbrie and Norman Newell, paleoecology is not only a lively, fashionable, and increasingly rigorous science, but it is also a rapidly growing collection of techniques and insights, of direct, practical importance to geologists in their daily work, including the finding of oil. Some of the most valuable of these insights are borrowed from molecular biology and microbiology, thus attesting to the breadth of paleoecology (and to the absurdity of the split within academic biology). Such biogeochemical matters receive little attention in this book, which has some excellent carbonate mineralogy but is otherwise more conventionally organized around animal ecology as practiced by stratigraphers. The omission of chemical approaches is forgivable, however, if the book is seen as a companion volume to *Researches in Geochemistry* (1959), edited by Philip Abelson and also published by Wiley.

The symposium on which the book is based was arranged by the Paleontological Society at its 1961 meeting in Cincinnati, Ohio. Few symposia are so deserving of hard covers. Some of the early chapters, such as J. W. Durham's on biogeography, have the customary tantalizing quality, but the majority have obviously been thoroughly reworked, under editorial prodding, and now represent substantial original contributions and reviews. Ancient environments as such are treated only incidentally, the emphasis throughout being on the methodology to be used in inferring former environments from hard and variably altered rocks, and from the fossils that some of them still contain. Biological approaches (seven chapters, by E. R. Trueman, O. L. Bandy, Björn Kurtén, R. G. Johnson, J. A. Shotwell, W. R. Walton, and E. G. Purdy) are mainly confined to animals, individually and as members of populations and communities. A pair of chapters examines the indicator value of structures, those produced by physical agencies (E. D. McKee) and by animals (Adolf Seilacher), in sedimentary rocks. The kinds and degrees of bias imposed on the fossil record by postdepositional alteration (diagenesis) are considered in five chapters, two of them by R. G. C. Bathurst, the others by P. K. Weyl, K. E. Chave, and R. C. Murray, respectively. Finally, one of the editors (J. W. Imbrie) discusses statistical approaches, but the factor-analytic model he has chosen for exposition is excessively empirical and cumbersome and will probably not gain many adherents.

Behind the history of every sedimentary rock there lurks an ecosystem, but what one sees first is an environment of deposition, followed by alteration. Modern ecologists are not unfamiliar with environments of deposition, or with oxidative decomposition, but alteration of fossils in solid rock is outside their province, and may even offend their sense of fair play. Paleoecologists are especially concerned with the milder, room-temperature-and-connate-water kinds of diagenesis, and find them to be pervasive but subtle in their effects. Although brief discussions of silicification and pyritization are given in Bathurst's review chapter, the focus in this book is on carbonates.

Replacement of other carbonate minerals by dolomite is a major annoyance to paleontologists, so Murray's studies are encouraging in one respect; he finds that dolomite commonly grows by replacing pre-existing carbonate, rather than as cement between older crystals. Thus, the original fabric of the rock, including the carbonate fossils, is not necessarily lost. The limestones discussed by Murray are mainly Paleozoic, and have been dolomitized at the expense of calcite, the source of the added magnesium being unspecified.

By contrast, in the Carboniferous and younger limestones considered by Bathurst, aragonite and high-magnesium calcite have been changed to nearly pure calcite, low in magnesium. High temperatures appear to be ruled out by the field relations, and the change of aragonite to calcite is therefore not a simple inversion, but must result from solution and replacement. As Weyl shows in his chapter, classical solution chemistry is inadequate to deal with these problems on the requisite scales of time and space. From their diverse viewpoints, all the authors point to percolating waters, loaded with ions of varying mobility, as the agents of diagenesis in limestones. Moreover, Chave's observations on skeletal durability, like Bathurst's and Murray's on crystallography, imply the disappearance of huge quantities of shell. Initially composed of impure calcite and the more soluble aragonite, much shelly material may now be found only as magnesium atoms in dolomite.

In a different petrographic realm, the idea that the mud fraction of greywackes may result from recrystallization, and not from original deposition in the deep ocean, has equally hair-raising implications. It is not the loss of the carbonate fossils, or of the original fabric of the sediments, that makes these possibilities so disturbing; it is the insidious redistribution of chemical constituents, supposedly locked for all time in well-formed crystals. Migration of ions in recent deep-sea sediments has made nonsense of several elegant theories of geochemical balance, and of dating. It now appears that histories of the salinity of the oceans, of the chemical architecture of skeletons, and of temperatures inferred from O^{18}/O^{16} ratios in carbonates, will have to reckon with migration of ions in solid rock.

Turning to environments of deposition, and the animals that lived or died in them, a modern ecologist is bound to notice a distinctly old-fashioned outlook in some of these chapters. It is a source of great strength, as well as of some weakness. As shown particularly by Trueman's refreshing discussion, older ideas of functional morphology are still valid; ecologists can learn much by simply looking at animals, before mentally decomposing them into fluxes of organic carbon. From the depth of the pallial sinus of a bivalve mollusc, or the height of the test of a heart urchin, Trueman can say something about the depth of burrowing, the nature of the food, and the particle size of the substratum. Hinge ligaments of bivalves vary remarkably in arrangement and mechanical strength, but, as the variations are only part of a cluster of adaptations for burrowing or attachment, their simple correlation with habitat is weak. Trueman also discusses recent studies of gas-regulatory liquid in the chambers of *Sepia* and *Nautilus*, studies which throw light on the buoyancy and posture of extinct cephalopods.

The special flavor of paleoecology is best illustrated by Seilacher's ingenious chapter on *palichnology*, the study of fossil tracks, wiggles, and burrows. Even the second most obvious question about a track—"Which way did he go?"—is not always easy to answer, nor is the answer trivial for animals that may have walked the backslope of a coral reef or rested on the flank of a geosyncline. Seilacher notes that fossil traces cannot be redeposited, but belong indubitably to the environments where they are now found; moreover, they bring us as close as we are likely to get to the behavior of extinct animals. Together with current markings, often legible in the same beds, tracks can show the orientation of sessile suspension-feeders into the current, or the retarded steps of a trilobite walking upstream; five-rayed resting places of Triassic brittle-stars show how the animals kept pace, while remaining buried, with the deposition of several inches of sand; abundant tracks and burrows show that some black shales were not formed under euxinic ("Black Sea") conditions. Such data are of great value in the interpretation of deep-sea deposits, especially where rapid but erratic deposition by turbidity currents has made ordinary fossils scarce. Subsidence to abyssal depths between one bed and the next is inferred from the loss of the shallow resting traces and deep protective burrows characteristic of shallow water, and the substitution of intricate grazing tracks made by specialized deposit-feeders. Clearly, palichnology has come a long way from the time when the best "lithographica" were made by undergraduates at Wurzburg. Nevertheless, the reconstruction of biocoenoses from the "quantitative ichnospectrum," or the proportions of different kinds of traces, rests on some fairly antiquated assumptions about present-day ecology, such as the one that "deep-sea animals gain little by hiding in the sediment" (p. 313).

Modern ecology owes a great debt to autecological studies like Trueman's and Seilacher's, but it tends nowadays to leave functional morphology to the physiologists, and to concentrate on more abstract, generalizable systems such as populations and communities. It is in this area of greatest theoretical interest that paleoecology seems weakest and most primitive. With the conspicuous exception of Kurtén's chapter, ancient populations are not considered in this book. The social psychology of extinct animals might seem to be lost beyond all conjecture, yet Kurtén's beautiful researches on the Pleistocene cave bear have shown how elementary statistics on age and sex composition of fossils can lead from considerations of differential juvenile mortality and selection as related to population density to inferences about family size, sexual behavior, and rates of inter-deme migration. Few invertebrates approach the cave bear in psychosocial complexity, and their populations should be easier to study, but although Kurtén discusses population dynamics of Silurian ostracods and modern prawns, the usefulness of age distributions seems not yet to be widely appreciated.

Perhaps because most marine paleoecologists were geologists first, "mortality" for them is still largely a matter of diagenesis and redistribution before burial. It is useful, and sobering, to know that only about 30 percent of modern benthic species and individuals have fossilizable parts, and that 39 percent of the stations in Tomales Bay have completely dissimilar life and death assemblages of molluscs. But before one can reconcile these data of Johnson with his conclusion that "the benthic marine community today is the most preservable community on earth" (p. 120), one must remember that numerical and biomass data from modern seas give only the preservable standing crop.

Any such conclusion is premature without some knowledge of productivity, including the rate at which fossils are generated. In a sea-bottom community this problem is most easily approached by examining age structures of mollusc populations. Again, in Purdy's chapter, Maine data on the *numbers* of deposit-feeding pelecypods lead to a nearly meaningless debate about whether clay-sized material alone, or clay plus organic matter, "limits the density" of molluscs. Fundamental studies of *Gemma* and *Mya* populations, on competition between them

over time, and on their rates of fossilization, were published for a nearby clam flat in 1959 by Bradley and Cooke, but this work is not cited by Purdy or by Johnson.

The central problem of paleoecology, one that is approachable only through historical data, would appear to be the evolution of stable community structure. Hedgpeth discusses it in a brilliant introductory chapter, but he has found no takers, at least not in this symposium, for his suggestion that changing specific diversity over time be studied by the methods of Lotka and MacArthur. Shotwell's huge collections of late-Tertiary mammal bones may be appropriate for the purpose, but his crude quantitative methods (not discussed in his chapter) accept the diversity of a "savanna" or "woodland" community as if it were something given a priori, rather than a parameter to be estimated from biased samples.

Collections of foraminiferans are ideally suited for analysis of specific diversity and community organization, but the treatment of these problems by the experts, Walton and Bandy, leaves much to be desired. The longest chapter in the book is Walton's report on the foraminiferal ecology of the Gulf of Mexico, which is based on 950 samples of recent sediments. "Faunal variability" (diversity) is defined as the number of ranked species (pelagic and benthic, living and dead) whose cumulative percentage in the sample is 95, and "dominance" is the percentage abundance of the commonest species. Not surprisingly, the fewer the species, the higher the percentage of the dominant, but this relation is used only to establish some fuzzy "depth zones," which are complex functions of salinity, bottom type, increasing ratios of pelagic to benthic species in deeper water, and the size and specimen density of the samples. The same mixture of environmental factors and statistical artifacts enters in the recognition of "depth" and "geographic" facies from maps of the percentage abundance of species or genera. Walton does not discuss the relation of diversity to sample size, the misleading nature of percentages, or the ways in which closely similar data are treated by students of diatoms, soil arthropods, or pollen. Underlying his splendidly arbitrary approach, of course, is the geologist's stubborn belief that depth of water *ought* to be an environmental parameter, regardless of what ecologists say. Its justification is that it works, at least as applied to foraminiferal zones of "transgression" and "regression" in the Oligocene Anahuac formation of Texas. One ventures to doubt that it will work outside the Gulf province, just as one doubts the generality of Bandy's observation that species of *Virgulina* are smaller in deeper water while those of *Cyclammina* are larger.

A group of organisms held together, like moths at a light, by common responses to physical environment is not a community, but an aggregation. Ironically, the term *Biocoenosis* was invented for a marine assemblage that is much of this sort. Little community structure of an interesting kind is to be expected where waves and currents reshuffle water masses, substrata, and organisms with impartial thoroughness. Compared to a soil or a lake, or even to a coral reef, sea-bottom communities in temperate seas have little more organization than insects in amber. Hence, when Johnson concludes that "many, if not most, of the species in level bottom communities appear to be quite independent of one another" (p. 128), he states no more than the truth, but he also explains why problems of organization are not prominent in the thinking of paleoecologists. Their slowness to make use of population dynamics, however, is not so easy to account for.

The sedimentary record being what it is, geologists' bias toward shallow-water marine ecology will undoubtedly continue. They have already made many outstanding contributions, most of which are referred to in this book but cannot be discussed in this review. Paleoecologists are being steadily recruited from geology, bringing to ecology the freedom from old prejudices and the strong motivation of the autodidact, as well, naturally, as some of the blind spots. As more of them move from level sea bottoms to coral reefs, while a few take up grasslands, forests, and lakes, they will encounter ecological organization for themselves. When they do, we can expect fundamental and exciting contributions to the history of biological order, of a kind that no biologist can make. Meanwhile, their youthful enthusiasm for his subject gladdens the heart of an elderly ecologist, weary and grown hypercritical, no doubt, from long discourse with deans.

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Physics

Atomic Collision Processes. Proceedings of the Third International Conference. M. R. C. McDowell, Ed. North-Holland, Amsterdam; Interscience (Wiley), New York, 1964. xvi + 1165 pp. Illus. $38.50.

This large volume contains the papers presented at the Third International Conference on the Physics of Electronic and Atomic Collisions, which was held at University College, London, from 22 to 26 July 1963. The first two conferences in the series were held in New York (in 1958) and in Boulder, Colorado (in 1961), and the fourth is scheduled for Quebec in August 1965. The present volume marks the first appearance in print of the full proceedings of one of these conferences, and also reflects the growth of interest and participation in these meetings which resulted in the presentation of a more select group of papers at the London meeting.

The 140 papers have been divided into 12 sections: slow electron scattering by atoms, resonances, polarization of radiation emitted on electron impact, excitation and ionization of atoms by electron impact, further theory (mainly electron-atom collisions), electron-molecule collisions, recombination, negative ions, photo-processes, inelastic heavy-particle collisions, elastic heavy-particle collisions, and collisions with molecules and other topics. Of these nine were invited review papers by Massey, Heddle and Seaton, C. A. McDowell, Bates, Biondi, Dalgarno, Bailey and Hughes, Bernstein, and Patel. Both theoretical and experimental papers are presented in all of the sections, with theory predominant in the first six sections which cover collisions of electrons with atomic systems, while most of the papers on heavy-particle collisions are experimental. This perhaps reflects the greater difficulties associated with the theory of the mutual scattering of composite systems as opposed to the somewhat more tractable theory of an electron impinging upon a composite system.

In addition to the formal program, there were discussion sessions on theoretical and on experimental problems, and these have been recorded in the proceedings. The discussions of theoretical problems were based on a set of conference papers that were chosen to illustrate a number of different ap-