25 March 1977, Volume 195, Number 4284 SCIENCE

The Emergence of Ecology as a New Integrative Discipline

Ecology must combine holism with reductionism if applications are to benefit society.

Eugene P. Odum

It is self-evident that science should not only be reductionist in the sense of seeking to understand phenomena by detailed study of smaller and smaller components, but also synthetic and holistic in the sense of seeking to understand large components as functional wholes. A human being, for example, is not only a hierarchal system composed of organs, cells, enzyme systems, and genes as subsystems, but is also a component of supraindividual hierarchal systems such as populations, cultural systems, and ecosystems. Science and technology during the past half century have been so preoccupied with reductionism that supraindividual systems have suffered benign neglect. We are abysmally ignorant of the ecosystems of which we are dependent parts. As a result, today we have only half a science of man. It is perhaps this situation, as much as any other, that contributes to the current public dissatisfaction with the scientist who has become so specialized that he is unable to respond to the larger-scale problems that now require attention. There is a rich literature on hierarchal theory and philosophy which deserves to be read by today's specialists (*1*). As expressed by Novikoff (*2*), there is both continuity and discontinuity in the evolution of the universe. Development may be viewed as continuous because it is never-ending, but also discontinuous because it passes through a series of different levels of organization.

An important consequence of hierarchal organization is that as components, or subsets, are combined to produce larger functional wholes, new properties emerge that were not present or not evident at the next level below. Fiebleman (*3*) has theorized that at least one new property emerges with each new integrative level of organization. Whatever the emergent rate, we can conclude that results at any one level aid the study of the next level in a set but never completely explain the phenomena occurring at that higher level, which itself must be studied to complete the picture. The old folk wisdom about "the forest being more than just a collection of trees" is indeed the first working principle for ecology. For example, intensive research at the cell level has established a firm basis for the future cure and prevention of cancer at the organism level, and perhaps for genetic engineering at the population level, should we ever choose to experiment in this direction. However, cell-level science will contribute very little to the well-being or survival of human civilization if our understanding of supraindividual levels of organization is so inadequate that we can find no solutions to population overgrowth, social disorder, pollution, and other forms of societal and environmental cancer. This is not to say that we abandon reductionist science, since a great deal of good for mankind has resulted from this approach, and some of our current short-range problems can perhaps be solved by this approach alone. Rather, the time has come to give equal time, and equal research and development funding, to the higher levels of biological organization in the hierarchal sequence. It is in the properties of the large-scale, integrated systems that hold solutions to most of the long-range problems of society. Again, Novikoff (*2*) expressed it well when he wrote, ". . . [E]qually essential for the purposes of scientific analysis are both the isolation of parts of a whole and their integration into the structure of the whole. . . . The consideration of one to the exclusion of the other acts to retard the development of biological and sociological sciences."

The New Ecology

The rise of what I have previously called the "new ecology" (*4*) is—in part, at least—a response to the need for greater attention to holism in science and technology. Since the word "ecology" is derived from the Greek root *oikos* meaning "house," it is an appropriate designation for the study of the biosphere in which we live. However, until quite recently, ecology as an academic subject had a much more limited scope than the name indicated. When I first came to the University of Georgia as a young instructor in 1940, my suggestion that a course in ecology be included in a core curriculum for majors received an exceedingly cold reception. My colleagues of those days confused ecology with natural history and voiced the opinion that no new ideas or principles were likely to be revealed in an ecology course that had not already been covered in courses in taxonomy, evolution, physiology, and other subjects considered to be more basic. As a partial result of this rebuff I decided to write a textbook that would emphasize unique principles that emerge at the supraindividual levels of organization. The first edition of *Fundamentals of Ecology*

The author is Callaway Distinguished Professor of Ecology and director of the Institute of Ecology at the University of Georgia, Athens 30601. This article is based on an address given when the Prix de l'Institut de la Vie was awarded jointly to the author and his brother, Dr. Howard T. Odum, in Paris on 18 June 1975.

(5), written in collaboration with my brother, Howard T. Odum, and published in 1953, was revolutionary in two respects: (i) principles were presented in a whole-to-part progression with consideration of the ecosystem level as the first rather than the last chapter, and (ii) energy was selected as the common denominator for integrating biotic and physical components into functional wholes. As the book passed through two more editions and was translated into other languages, these approaches and viewpoints became generally accepted, not only by professionals, but by the public at large. As the environment-awareness movement began to emerge in 1968, some professional ecologists actually resented the public's use of "their" word, but we welcomed it as a long overdue recognition of holistic concepts. Although "ecology" is frequently misused as a synonym for "environment," popularization of the subject is having the beneficial effect of focusing attention on man as a part of, rather than apart from, his natural surroundings.

A joint research study on a coral reef by my brother and me in 1954 (6) can perhaps serve as an illustration of how ecosystem-level study can reveal emergent properties which tend to be missed in piecemeal study. At Eniwetok Atoll we measured the metabolism of the intact reef by monitoring oxygen changes in the water flow. We also did a detailed trophic analysis as a means of charting major energy flows, and were able to construct an energy budget for the whole system. It became evident from the latter that corals and associated algae were much more closely linked metabolically than had previously been supposed, and that the inflow of nutrients and animal food from surrounding ocean waters was inadequate to support the reef if corals and other major components were functioning as independent populations. We theorized that the observed high rate of primary production for the reef as a whole was an emergent property resulting from symbiotic linkages that maintain efficient energy exchange and nutrient recycling between plant and animal components. Our work created considerable controversy and stimulated a number of investigations. Teams of researchers with expertise in chemistry, microbiology, invertebrate zoology, and other fields descended onto the reefs, but remained loosely united in their interest in testing directly or indirectly basic hypotheses about the reef as an ecosystem. Some theories were verified, others refuted, with the result that today there is a rather good understanding of coral-algal relationships and mineral cycling mechanisms in reef systems (7). We like to think that setting up radical but testable hypotheses at the beginning had much to do with this progress. Scientists work together best when motivated by some common idea, even if—or perhaps, especially if—that idea is controversial.

Do these coral reef discoveries have any significance for urban industrial man? Perhaps they do. The Pacific coral reef, as a kind of oasis in a desert, can stand as an object lesson for man who must now learn that mutualism between autotrophic and heterotrophic components, and between producers and consumers in the societal realm, coupled with efficient recycling of materials and use of energy, are the keys to maintaining prosperity in a world of limited resources.

Since the study of ecosystems is best carried out by teams of investigators who are united in their objective of seeking to discover the emergent properties of the whole but have different skills and secondary interests, I realized early that it would be necessary to establish some kind of organization to promote such teamwork. At the University of Georgia we established the Institute of Ecology for this purpose and, with the help of outside financial support, we carry out long-term studies. The Sapelo Research Foundation has provided continuous support that enabled us to mount an unhurried study of the Georgia salt marsh estuaries. A long-term contract with the Atomic Energy Commission (now the Energy Research and Development Administration) has provided a similar opportunity for population and ecosystem-level study of terrestrial and freshwater environments on a large area set aside for atomic research along the Savannah River, an area recently designated as the nation's first national environmental research park (8).

The complex of Georgia salt marshes and estuarine channels belongs to a general class of ecosystems which we have designated fluctuating water-level ecosystems. They are pulse-stabilized by tidal flows which act as energy subsidies that enhance productivity as much as ten times over that which would be achieved without this natural use of tidal power. Because we could document the work potential and, therefore, the value of these estuaries, our findings have been widely used as a basis for formulating laws and other measures to protect the U.S. coastal zone from insidious alterations (9). This work, along with parallel investigations of other natural landscapes, has led to the recognition of an important class of ecological systems which from the holistic viewpoint may be termed subsidized, solar-powered ecosystems (10). Human agriculture belongs to this class. We have much to learn from natural systems of this sort since most of our agroecosystems lack stability and tend to behave in a boom-and-bust manner, perhaps because we do not yet understand the network of feedback energy flows necessary to maintain continuous high productivity.

While much of the work at the Savannah River area has of necessity involved piecemeal studies on the effect and environmental fate of radionuclide and thermal discharges from atomic reactors, we did at the onset select ecosystem development as our central or unifying focus. The locale provided an unusual opportunity to observe and experiment with the process of natural ecological succession, and to study the impact of artificial reforestation as well, because hundreds of fields were taken out of cultivation when the atomic energy facilities were constructed in 1952. We theorized that new systems properties emerge in the course of ecological development, and that it is these properties that largely account for the species and growth form changes that occur (11). The idea that there is a holistic strategy for ecosystem development remains controversial. An alternate theory that species aggregations do not interact as a whole, and that ecological succession can be adequately explained on the basis of competitive exclusion and other species-level processes, has also been vigorously promoted (12). Again, controversy is welcome since disagreement on the "big ideas" is certain not only to generate useful knowledge, but to promote the art and science of both the experimental and analytical approaches.

The somewhat disappointing performance of the U.S. effort is the International Biological Program (IBP) can, in hindsight perhaps, be attributed to the fact that unifying theories or concepts were not set up for testing on the onset. Hundreds of investigators with widely different training and expertise were funded and were expected to work together as a team without a clearly defined common denominator (13). The biome program as a major part of the U.S. effort under the IBP was conceived in a holistic vein, and the idea of studying the totality of major solar-powered natural ecosystems such as grasslands, forests, deserts, tundras, and so forth was a uniquely American concept. But in practice there was a shortfall of integration. For example, in the grassland studies, which received the first and largest funding, there was never any "grassland theory" for the reductionists to rally around. A prodigious effort by a handful of systems ecologists did manage to link some of the fragmented data into something approaching an ecosystem-level model, but even the most sophisticated mathematical models cannot compensate for inadequate planning, uncoordinated data gathering, or, most of all, the lack of central theme.

The new ecology, then, is not an interdiscipline, but a new integrative discipline that deals with the supra-individual levels of organization, an arena that is little touched by other disciplines as currently bounded—that is, by disciplines with boundaries established and strongly reinforced by professional societies and departments or curriculums in universities. Among academic subjects, ecology stands out as being one of the few dedicated to holism. But I do not mean to imply that ecology is emerging by default; other disciplines, including perhaps even economics, as I will note later, are striving to climb upward on the hierarchal ladder.

The Link with Social Sciences

From another context, the new ecology links the natural and the social sciences (*14*). In the bottom of the Great Depression of the 1930's sociologists began to shift from the dictum that the proper study of man is man (alone) to the idea that the proper study is man in environment. For example, my father, the late Howard W. Odum, directed a major effort within the Institute for Research in Social Sciences at the University of North Carolina toward development of the concept of regionalism, which he viewed as an approach to the study of society based on the recognition of distinct differences in both cultural and natural attributes of different areas, which, nevertheless, are interdependent (*15*). Regional study of social science was widely misinterpreted in those days as being merely an inventory device designed to upgrade "backward" regions so they would contribute to, rather than detract from, the total economy of the nation. Rather, Howard W. Odum envisioned the real goal as the integration of regions, and he hoped that the concept would provide an antidote to divisive sectionalism, which was then spawning bitter economic and political warfare between sections of the nation. To a remarkable extent the philosophy of regionalism did help smooth social and economic transitions in the Southeast, but as a major theory of sociology the concept stalled because there was no appropriate linkage with natural science (applied ecology had not yet emerged to this level of thinking) and because statistical methods of the day were totally inadequate to cope with the mountains of data collected by social science researchers. Now, advances in systems science and electronic data processing promise to alleviate the data processing problem, and we have the new ecology as an improved link with the rest of science.

At the national level, I believe, the current effort to mount a program of research and management for the coastal zone may be the first major test of whether we are yet ready to combine the best of reductionist and synthesis science as a basis for rational decisions. Experience in mounting team research at the ecosystem level suggests that one or more major theories or paradigms that can be tested (and refuted, if possible) must provide a focus if the coastal zone effort—which of necessity must involve local, state, regional, and federal groups—is to be a truly scientific enterprise and not just another series of expensive and frustrating inventories. The tidal subsidy theory and the concept of regionalism stand as two unifying focuses for productive team research in this area.

Since the kind of sectional conflicts which for so long hampered our national development are now appearing on a truly frightening scale in the confrontations between so-called "advanced" and "backward" nations, even a partial success at coastal zone management could have a favorable global impact by demonstrating that action based on holistic values and properties is a viable alternative to development on the basis of competitive exclusion alone.

Technological and Environmental Impact Assessments

The need to raise thinking and action to the ecosystem level is especially evident as the practices of technology assessment and environmental impact analysis assume increasingly important roles in decision-making, especially with regard to public works and energy and industrial development. As a member of the advisory committee of the Office of Technology Assessment (OTA) established by Congress, I can vouch for the fact that there is a serious dichotomy of thinking between those who urge that OTA restrict its work to piecemeal assessment of new technology on the grounds that greater precision can be achieved in this manner, and those who argue for broadening the studies to include environmental, social, and economic aspects on the grounds that a holistic level of assessment is more realistic (*16*). The point is that the questions and answers can be quite different depending on the level of assessment. For example, a thoroughly competent study restricted to the technical performance of a fission nuclear reactor could well show that this method of power generation is reasonably safe. Since technologists have stressed safety as *the* limiting factor and the public has logically followed in making safety *the* issue, then a favorable technology assessment of the safety problem would become a powerful signal for government and industry to launch a massive development of this form of atomic energy. Yet a total assessment that includes economic and environmental components (and covers the whole chain of events from mining to waste disposal) might show that as a first-generation attempt to utilize atomic power the light-water fission reactor is badly flawed technology, and thus not yet ready to play a major role in power production, especially where alternatives are available (*17*).

In the pages of *Science* the writing of environmental impact statements, as required by the National Environmental Policy Act, has been denounced as a "boondoggle" (*18*) and defended as a necessary step in the right direction (*19*). In my opinion, most impact statements, as now almost mass produced, are inadequate because they focus on the wrong level—often, for example, on the species or factor level when the questions and decisions clearly involve the ecosystem level. In other words the practice of environmental impact assessment is not so much bad or inadequate applied science as it is wrong-level applied science, a viewpoint that has not been emphasized in published discussion on the subject. For example, most would agree that important chemical factors such as oxygen concentration and basic biological characteristics such as species composition should be included in a baseline assessment of a body of water. However, a table of dissolved oxygen measurements and a long list of species present, as often included in current impact statements, provide little useful information for assessing the impact of a projected perturbation such as a thermal discharge from a power plant. With little, if any, additional effort in terms of time and money, one can increase the useful information content manyfold by assessing more functional and integrative properties that relate to oxygen and species. By measuring dissolved oxygen over diurnal cycles, the balance between the two major metabolic processes, photosynthesis and respiration, can be determined; systems-level information of this sort is usable in judging the potential impact of a procedure that might change the temperature of the water, alter the input of organic matter, and so forth. Likewise, arranging species data into a diversity profile reveals how numbers and kinds interact and gives a clue as to the developmental status of the community, thus providing a far better basis for impact assessment than would a mere list of species. Accordingly, environmental impact assessment, as well as technology assessment in general, should move from mere component analysis, wherein factors and organisms are treated as if they were independent entities, to more holistic approaches wherein interactive, integrative, and emergent properties are also included. The "new ecology," of course, must provide the basic theory for this necessary evolution in practice. In the meantime, there is much to be said for a procedure that combines a few carefully selected systems-level properties that monitor the performance of the whole, with selected "red flag" components such as a game species or a toxic substance that, in themselves, have direct importance to the general public (*20*).

Economics and Ecology

The ultimate in a holistic approach to preparing environmental impact statements must involve integration of economic and environmental values. In the real world monetary values are always going to weigh heavily in any decision regarding man's use of his environment. Regrettably, environmental and economic assessments usually are made by different teams or individuals. Not only do these teams rarely communicate with one another, but each also tends to restrict evaluation to its own preconceived narrow world of the natural or man-made environment, respectively, ignoring the fact that it is the interaction between these systems that is of paramount importance. Environmental and economic assessors should work together, or at least the results of study by different groups of specialists should be integrated. There are ways to scale economic and ecologic values which at first might seem incapable of comparison. For example, where alternate choices are involved one can set up a numerical scaling system in which the maximum quantitative value for each component is set at 1 (or 100), and all other values scaled accordingly. These scaled values can then be weighted according to a Delphi or other technique based on consensus of knowledgeable assessors (*21*). Another approach involves using energy as a common denominator for man and nature (*22*).

If subjects were organized according to the literal derivation of their names, then ecology and economics would be companion disciplines since the words are derived from the same Greek root, with ecology translating as "the study of the house" and economics as "the management of the house." The disciplines remain poles apart on college campuses as well as in the minds of the general public as long as each restricts itself to only a part of the house, nature's and man's part, respectively. As ecologists have begun to take an interest in the man-made environment a few economists, notably Kenneth Boulding, Nicholas Georgescu-Roegan, William Nordhouse, James Tobin, and Herman Daley, have begun talking about an emerging "new economics" that is more attuned to natural laws and that includes a more equitable valuation of the natural environment (*23*).

A closer liaison between ecology and economics makes good sense because in so many cases actions which benefit the general environment also benefit the general economy in the long term. It is in the short term, especially the 2- to 4-year electoral cycle of political action, where the most recalcitrant conflicts occur. Take, for example, strip-mining for coal or other earthbound resources. In the short-term view government should encourage and subsidize rapid exploitation of the resource and place few, if any, restrictions on strip-mining on the theory that the national economy would quickly benefit from a substitution of domestic coal for imported oil. In the long-term view just the opposite would be indicated, namely, that careful, well-planned mining, including mandatory land rehabilitation, is in the best interest of both the economy and the environment. Land valuable for food production, recreation, and life support would be preserved or restored. The steady, moderate production of coal would ensure that energy conservation would be pursued while air pollution and other threats to health would be less likely to get out of hand. New industry and towns would have a long life in contrast to local booms and busts that generally accompany unrestricted mining. Water, which is required in huge quantities to use or process coal, would be less likely to be squandered. Otherwise, dry-country cities such as Los Angeles and Phoenix might have to use all the newfound energy to obtain water, with a probability of net economic loss. As the ecologist might say, it is the secondary impacts that will get you if you do not consider the whole. Best of all, the long-range scenario would ensure that the nation has coal long after the easily obtainable Mideast oil is gone, thus making us less dependent and more secure in terms of national defense.

Politics and Ecology

Finally, there is yet another divided world, the scientific and the politico-legal spheres of action, where holistic thinking might help. In a recent editorial in *Science* Gerald Edelman expresses pessimism that these two disciplines will ever intersect, and states that we are left with "two extreme ideological positions—scientism and anti-scientism" (*24*). As long as students and practitioners of both disciplines insist on fragmenting their subjects, rigidly adhering to their own way of thinking and calling each other derogatory names, adversary interaction will continue to predominate. I am much more optimistic about the integration of these spheres because I have found that a meeting of minds in study panels and public commissions begins with the general acceptance of the idea that large-scale problems and issues might have common denominators that could be assessed along with the more narrowly defined scientific, political, or legal aspects. If hierarchal theory is indeed applicable, then the way to deal with large-scale complexity is to search for overriding simplicity. Sometimes, it appears, this turns out to be old-fashioned common sense. As noted, the dichotomy inherent in short and long time spans imposes a major stumbling block in acting on common sense judgment.

In summary, going beyond reductionism to holism is now mandated if science and society are to mesh for mutual benefit. To achieve a truly holistic or ecosystematic approach, not only ecology, but other disciplines in the natural, social, and political sciences as well must emerge to new hitherto unrecognized and unresearched levels of thinking and action.

References and Notes

1. See especially *Beyond Reductionism*, A. Koestler and J. R. Smythies, Eds. (Hutchinson, London, 1969); *Hierarchical Structures* L. L. Whyte, A. G. Wilson, D. Wilson, Eds. (Elsevier, New York 1969); *Hierarchy Theory*, H. H. Pattee, Ed. (Braziller, New York, 1973).
2. A. B. Novikoff, *Science* **101**, 209 (1945).
3. J. K. Feibleman, *Br. J. Philos. Sci.* **5**, 154 (1954).
4. E. P. Odum, *Bioscience* **14**, 14 (1964). The ecosystematic emphasis of the "new ecology" owes much to the work of C. Juday, R. L. Lindeman, and G. E. Hutchinson in the 1940's.
5. E. P. Odum and H. T. Odum, *Fundamentals of Ecology* (Saunders, Philadelphia, ed. 1, 1953); *ibid.*, ed. 2 (1959); E. P. Odum, *ibid.*, ed. 3 (1971).
6. H. T. Odum and E. P. Odum, *Ecol. Monogr.* **25**, 291 (1955).
7. R. E. Johannes *et al.*, *Bioscience* **22**, 541 (1972); *Proceedings, Second International Symposium on Coral Reefs* (Great Barrier Reef Committee, Brisbane, Australia, 1974), vol. 1.
8. *National Environmental Research Park: Savannah River Plant, Aiken, South Carolina* (available from Energy Research and Development Administration, Washington, D.C.)
9. Between 1968 and 1971 Georgia and most other coastal states enacted marshland or estuarine zone protective laws. Estuarine values are discussed by J. G. Gosselink, E. P. Odum, and R. M. Pope [*The Value of the Tidal Marsh* (Center for Wetland Resources, Louisiana State Univ. Press, Baton Rouge, 1974); available from author on request].
10. In terms of source and level of energy the world's ecosystems can be conveniently classified as solar-powered, subsidized solar-powered, and fuel-powered (urban-industrial).
11. E. P. Odum, *Science* **164**, 262 (1969).
12. W. H. Drury and C. T. Nisbet, *J. Arnold Arbor. Harv. Univ.* **54**, 331 (1973); H. S. Horn, *Annu. Rev. Ecol. Syst.* **5**, 25 (1974); *Sci. Am.* **232**, 90 (November 1975).
13. R. Mitchell, R. A. Mayer, J. Downhomer, *Science* **192**, 859 (1976); P. M. Boffey, *ibid.* **193**, 866 (1976).
14. E. P. Odum, *Ecology: The Link Between the Natural and the Social Sciences* (Holt, Rinehart & Winston, New York, ed. 2, 1975).
15. H. W. Odum, *Southern Regions of the United States* (Univ. of North Carolina Press, Chapel Hill, 1936); ——— and H. E. Moore, *American Regionalism* (Holt, New York, 1938).
16. In making a preliminary assessment of the work of the Office of Technology Assessment, C. A. Decker [*J. Int. Soc. Technol. Assess.* **1** (No. 2), 5 (1975)] labels these alternatives as the "disjoint" approach and the "integrated" approach. See also D. Shapley, *Science* **180**, 392 (1973); *ibid.*, p. 1264.
17. I emphasize that I am not taking sides in the nuclear power debate. I am convinced, however, that assessment cannot be made piecemeal and that a truly total assessment is yet to be made.
18. D. W. Schindler, *Science* **192**, 509 (1976).
19. R. W. Peterson, *ibid.* **193**, 193 (1976).
20. Such a "hybrid" procedure is discussed by E. P. Odum and J. L. Cooley in *Biological Evaluation of Environmental Impact* (Council for Environmental Quality, Washington, D.C., in press).
21. This procedure was used in an evaluation of highway alternatives [E. P. Odum, G. A. Bramlet, A. Ike, J. R. Champlin, J. C. Cieman, H. H. Shugart, *Transportation Research Record No. 561* (Transportation Research Board, National Academy of Sciences, Washington, D.C. 1976), pp. 57–67].
22. This approach was used in (9); see also H. T. Odum and E. C. Odum, *The Energy Basis for Man and Nature* (McGraw-Hill, New York, 1976).
23. See especially N. Georgescu-Roegen, *The Entropy Law and the Economic Process* (Harvard Univ. Press, Cambridge, Mass., 1971).
24. G. M. Edelman, *Science* **192**, 99 (1976).

Functional Specificity of Thymus-Dependent Lymphocytes

A relationship between the specificity of T lymphocytes and their functions is proposed.

William E. Paul and Baruj Benacerraf

Two principal classes of lymphocytes, the thymus-independent (B) and the thymus-dependent (T) lymphocytes, participate with macrophages in the reactions and interactions that constitute the immune response. The specificity of the B lymphocytes is well understood, largely because these cells and their progeny secrete specific antibody molecules. The antigen-combining sites of antibodies are identical to the combining sites of the surface receptors of the B lymphocytes that were responsible for their secretion (*1*). Since the range of specific chemical configurations against which antibodies can be made is very large (*2*), the variation in B cell receptors must be equally extensive.

By contrast, information on the specificity of T lymphocyte receptors has been limited to the results of functional analyses (*3*). That is, T cell receptors have been studied by determining which substances would initiate a given response and which would not, because, until very recently, no antigen-specific T cell products were available. Even now, the analysis of specific T lymphocyte factors has just begun, and only very limited specificity data have yet been obtained.

Nevertheless, as a consequence of functional analysis of T lymphocyte receptors, we are now aware of the restricted range of specificity of these cells, particularly when compared with B cells. This restriction of the specificity of T lymphocytes must directly reflect the types of functions which these cells mediate: (i) the recognition of histocompatibility antigens (*4*), and (ii) the regulatory and surveillance functions of the immune response (*5*). In mediating these functions, the T cell takes part in precise types of interactions with other cells, and hence the T lymphocyte is required to recognize the surface markers of the cell with which it interacts.

In this article, we relate the specificity restrictions of T lymphocytes to these functional characteristics. We also attempt to draw some conclusions concerning the nature of the T lymphocyte receptors and the mechanism by which T cells exert their regulatory functions from our knowledge of (i) these specificity restrictions and of (ii) the genetic control of T lymphocyte functions.

Specificity of T Lymphocyte–Mediated Responses

Against thymus-dependent antigens. The concept of the restricted nature of the range of specific responses that T lymphocytes can mount was first developed as a result of studies of delayed hypersensitivity and contact reactivity (*6*). These T lymphocyte–dependent phenomena and their in vitro counterparts—namely, antigen-stimulated lymphocyte proliferation (*7*) and production of migration inhibition factor (MIF) (*8*)—develop principally in response to immunization with protein and polypeptide antigens. By contrast, immunization with polysaccharides (*9*) or with multivalent haptens (*9*) fails, in most instances, to initiate a state of delayed hypersensitivity, and cells from animals immunized with these materials do not express in vitro correlates of delayed hypersensitivity.

Dr. Paul is chief of the Laboratory of Immunology, National Institute of Allergy and Infectious Diseases, Bethesda, Maryland 20014. Dr. Benacerraf is Fabyan Professor of comparative pathology and chairman of the Department of Pathology, Harvard Medical School, Boston, Massachusetts.