chemistry, and in fitting one part of the story to another.

The book is not everything, however. It is short; sometimes it teases rather than satisfies. There is little mention in it of the people who have done the molecular unraveling; Asimov chooses brevity and the plain facts instead. Its last chapter, on the future and social implications, is just hurried.

Two lesser quibbles. Its typography is unfortunately poor: small type in narrow columns. Its illustration is undistinguished; and one would like to see each explanatory drawing fitted into the text where it belongs, rather than having to seek "Figure 23."

In attractive typography and in beauty and clarity of illustration, *The Human Body* is everything that—pity—*The Genetic Code* is not. It is a popular physiology at a simpler level than *The Genetic Code*; any intelligent reader might enjoy it; a junior high school student could understand it. It omits the nervous system;—this will be covered in a companion volume on the human brain.

As a science writer and a nonscientist, I hope more and more young scientists will soon join the Asimovs. John Fischer of *Harper's* recently quoted Loren Eiseley—who, according to Fischer, "wrote in secret, almost as a vice, for nearly 15 years"—as saying: "If I had let any of my colleagues know that I wrote for a general audience, or what they called a popular audience, it would have ruined me academically, and I would never have gotten ahead in my chosen profession." In these days!

VICTOR COHN
Minneapolis Star Tribune,
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BIOLOGICAL AND MEDICAL SCIENCES

Toward a Modern Synthesis of Evolutionary Thought

Can the result of biochemical investigation provide significant insight into evolutionary processes?

Lynn H. Throckmorton and John L. Hubby

More than 20 years ago the largely independent investigations of systematists, mathematical biologists, and geneticists combined to produce the dynamic, synthetic approach to evolution. The power of this modern synthesis rested primarily upon the fact that it was founded broadly on many of the basic scientific disciplines. During the years since its inception, the Modern Synthesis and its sibling, the New Systematics, have made profound contributions to biological thought. Here, as has happened so often in the history of biology, conceptualization in one area has reached a culmination at almost precisely the time that new approaches, new methods, and new concepts were developing in other, apparently unrelated, areas. The study of evolution is again at a stage for transition. Recent advances in physiological genetics, comparative biochemistry, and developmental biology are providing wider insights and powerful tools which may potentially allow studies of evolutionary processes to be carried to even deeper levels. The modern synthesis of the early 1940's is no longer a truly modern synthesis in these formative years of the 60's. One of biology's fundamental disciplines, biochemistry, is missing. Two recent contributions to biological literature, Ernst Mayr's **Animal Species and Evolution** (Harvard University Press, Cambridge, Mass., 1963. 813 pp. Illus. $11.95) and Vernon Ingram's **The Hemoglobins in Genetics and Evolution** (Columbia University Press, New York, 1963. 192 pp. Illus. $6), lead us to hope that this deficiency will not persist indefinitely.

Major advances are often heralded by the appearance of a lucid, thorough, and authoritative summation of the current status of a field of study. This should be particularly true in a field as complex as the study of evolution, and we are indeed fortunate that Mayr's superb resynthesis appears at such an opportune time. As a leading spokesman, both for the Modern Synthesis and for the New Systematics, Ernst Mayr is uniquely suited for the task of documenting and evaluating our progress toward an understanding of evolutionary processes. Realizing that evolutionary biology has become too vast a field to be covered in a single volume, he has restricted his discussion to only those aspects that involve the species. Basically, he has taken concepts from developmental and population genetics and utilized these theoretical considerations to evaluate and interpret a massive amount of data from a wide variety of disciplines. Quite rightly, he does not develop the mathematical bases for population genetic theory or document the experimental evidence from developmental genetics. These areas are well covered in the recent literature. However, and this is one of the outstanding features of his work, he does document and discuss the pertinent information available from the areas of systematics, ecology, evolutionary genetics, and behavior. The coverage, while encyclopedic, is far from a mere catalog of existing data. A presentation of new concepts is combined with a discussion of those replaced, new ideas are defended as older ones are refuted, and the needed exploitation of current avenues of approach is emphasized while future potentialities are suggested. The documentation required to substantiate or support each assertion, conclusion, or argument is smoothly interwoven with the discussion, and the result is an eminently readable and thoroughly absorbing description of one of the most fascinating areas of biological investigation.

It is virtually impossible to do justice to a work of this scope and detail in

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the space available for a review. We can only offer a brief consideration of major areas and themes, and for the remainder assure the reader that Mayr has provided discussions of almost every topic of significance to the student of animal speciation. *Animal Species and Evolution* is composed of 20 chapters organized to cover six major areas. The impact of population thinking on our present understanding of species problems and evolutionary processes provides the unifying theme throughout. As Mayr so clearly states, "It cannot be emphasized too strongly that the population is ultimately the key to every evolutionary problem. . . . It is the . . . temporary incarnation and visible manifestation of the gene pool . . . the proving ground of new genes and of novel gene combinations . . . [and] interactions of the genes in a gene pool provide a degree of integration that permits the population to act as a major unit of evolution. . . ."

In the first section, on the characteristics of species, he covers species concepts, the occurrence and significance of sibling species, the biological properties of species, and isolating mechanisms. The discussion of species concepts and their application is noteworthy, and his defense of the species as a nonarbitrary unit will certainly be welcomed by all but the most extreme of the extremists. Recognizing that lack of information, incompleteness of speciation, and asexuality all pose certain difficulties to the application of a species concept, Mayr points out that difficult cases are infrequent in most groups and that "the biological species concept, even where it has to be based on inference, nearly always permits the delimitation of a sounder taxonomic species than does the morphological concept." He concludes that, since the species is a reproductive community, since it interacts as an ecological unit with other species, and since it is an expression of an integrated gene pool, the biological species is a far more meaningful unit than the random aggregate of individuals, the typological species.

In the next three areas, the structure and genetics of populations, the population structure and variation of species, and the multiplication of species, he develops his thesis that natural selection operates on the phenotype and that developmental and genetic homeostasis combine to conserve phenotypic uniformity at both the individual and population levels. The interaction of genes and the high rates of gene flow between demes result in a tight cohesion of the gene pool which must be disrupted if speciation is to occur. The similiarity of sibling species is offered as proof of the view that complete reconstitution of the genotype can occur without effect on the visible phenotype. The "remarkable phenotypic uniformity of most species . . . in spite of a great deal of variation in populations . . . forces [us] to conclude that there must be a selective premium on phenotypic uniformity and that optimal fitness is closely correlated with one particular phenotype." The fact that "natural selection favors phenotypes, not genes or genotypes . . . and that the phenotype determines fitness, is the reason for the extraordinary evolutionary importance of the developmental processes that shape the phenotype. . . . Any improvements in the 'epigenotype,' any genes that buffer development better against fluctuation of the environment . . . will contribute to fitness." Developmental homeostatic devices, though hypothetical, are thus considered to be of prime importance in contributing to the internal cohesion of the gene pool.

Prerequisite for Speciation

Mayr then points out that "both pleiotropy and polygeny contribute to the genetic cohesion of the population. Pleiotropy contributes because each gene through its manifold effects on development enters into a teamwork with numerous other genes. The replacement of one gene by another in a gene complex may affect numerous interactions of the genotype and lead to an upset of stability which can be compensated only gradually. Polygeny contributes because selection pressure for or against any aspect of the phenotype will affect all the genes that polygenically add to this character. A chain reaction of gene substitutions may result, the resistance to which is determined by the magnitude and the nature of the correlated pleiotropic manifestations of the genes involved. . . . With recombination producing in every generation new assortments of genes . . . which in turn have to form well-balanced and fully viable phenotypes, it is evident that the integration has to extend beyond the level of the individual. There must be harmony among all the genes of which a local gene pool is composed. This gives the local population its cohesion and makes it a significant level of integration. . . . This internal cohesion of the gene pool is an immensely conservative force. It serves as a powerful brake on all forces that attempt to change the contents of the gene pool and makes it well-nigh impossible to create discontinuities within the gene pool." For these reasons Mayr believes that geographic isolation is a prerequisite for the formation of discontinuities in the gene pool—that is, for speciation. He concludes that "nearly all the potential modes of speciation . . . suggested in the past are improbable and that the reputed instances [for example, of sympatric speciation] are quite consistent with the theory of geographic speciation. . . ."

Units of Evolution

The next section, on the species in transpecific evolution, is a discussion of the origin of new types, the invasion of new adaptive zones, the emergence of evolutionary novelties, and the genetics and epigenetics of transpecific evolution. He draws from all his previous discussions to illustrate the thesis that "The species are the real units of evolution . . . and speciation, the production of new gene complexes capable of ecological shifts, is the method by which evolution advances . . . adaptations, specializations, and regressions . . . are really not separable from the progression of entities that display these trends, the species."

With one of the best, and shortest, statements concerning man's evolution, Mayr concludes his book. The utilization of population concepts and the emphasis on man as a polytypic species not only bring human evolution into a realistic perspective but also demonstrate the real unity of evolutionary concepts as these are derived from investigations of other animal systems.

All will find Mayr's discussions stimulating, many will find them completely acceptable, and some will wish to take issue with certain of his conclusions. In his preface Mayr writes, "Interpretation is necessarily subjective. . . . To take an unequivocal stand . . . is of greater heuristic value and far more likely to stimulate constructive criticism than to evade the issue." Most of our criticisms center on the more extreme statements of Mayr's views. As a case in point, Mayr relies heavily on the *reality* of developmental homeostatic mechanisms as support for many assertions and conclusions about the nature of species and of speciation mechanisms. As illustrations of this we cite the following: "Degree of morphological similarity in sibling species is an indication not of genetic similarity, but rather of developmental homeostasis" (p. 58). "Each individual gene substitution during the origin of these [sibling] species was somehow compensated for and prevented from affecting the end product of development, the phenotype" (p. 280). "The case of sibling species proves that little of the genetic variation penetrates into the phenotype in the presence of strong homeostatic devices" (p. 304).

Alternative Possibilities

It must be recognized that there are possibilities alternative to those suggested by Mayr. The simplest and most obvious of these is that, because of their mode of action, there are many genes which will not, and cannot, be expressed in the visible phenotype. Thus, the morphological similarities of sibling species may well represent, in large measure, true genetic identity. Even granting extensive genetic reorganization between species, there may be a relatively large section of the genotype that contributes primarily to physiological and biochemical processes unrelated to gross morphology, and adaptation, in many instances, may be best served through reorganization of this section of the gene pool. Indeed, when one recognizes how meager are the data that support the hypothesis of developmental homeostasis as Mayr conceives it, the existence of sibling species may be considered as real and direct evidence against it.

Apparently Mayr excludes this possibility because "each gene serves as a modifier for many, if not most, other gene loci" (p. 220). From this it follows that any reasonable amount of gene substitution will produce a chain reaction that results in the total reconstitution of the genotype. Thus, a totally different genetic basis would exist for the morphology of the individual. However, it is certainly not an established fact that the nature of gene actions and interactions is of the type that he postulates. Indeed, much of the evidence now being marshalled about the regulation and control of gene activity could lead one to precisely opposite conclusions. The immediate problem, then, is to demonstrate where, in the broad spectrum between total interaction and complete independence of genetic elements, the truth lies. If total interaction is proved to be a reality (and this can best be done by some biochemical approach), then discussions such as Mayr's will be provided with a solid foundation. If it is not, many of Mayr's conclusions will need to be reevaluated. For example, if total interaction does not exist, then various regulative devices might not operate to produce the powerful cohesion within the gene pool which is said to make geographic isolation necessary for the production of discontinuities within the gene pool.

Considerations such as these, together with recognition of the importance of the phenotype and the significance of developmental processes in its production, lead us to conclude that biochemical information can provide insights that will be critical to the understanding of evolutionary processes at the population level. This conclusion is quite at variance with a statement made by Mayr: "The nature of the functional mechanisms of physiological interactions are only of minor interest to the evolutionist, whose main concern is the viability of the ultimate product, the phenotype" (p. 295).

The biochemical approach, and indeed a quite different viewpoint, is documented in Vernon Ingram's book, *The Hemoglobins in Genetics and Evolution.* Based on a series of six Jesup lectures given at Columbia University in March of 1962, this small, very readable book illustrates quite convincingly the power of the physiological and biochemical approaches to the study of evolution. The rigor of chemical methods—for example, as Sanger applied these methods to the study of insulin—has been exploited by Ingram and others, and the results of some of these studies provide the material upon which the book is based. Because it is oriented toward a general audience the book begins with a brief description of current ideas concerning the genetic control of protein synthesis. The second chapter is devoted to a discussion of the experimental results of investigations of the mechanisms by which hemoglobin is synthesized. Brief consideration is given to the possible universality of protein synthesizing systems, and the remainder of the chapter is devoted to a description of the architecture of the hemoglobin molecule and to a consideration of the ways in which the various peptide components are arranged in the different hemoglobin variants.

Gene Flow or Identical Mutations

The third chapter is a discussion of some of these variants and their genetic implications, in terms of peptide structure and in terms of their distributions in populations. Reading Ingram's descriptions and discussions immediately impresses one with the wide variety of problems that are amenable to investigation by the use of these techniques. Some of the fascinating potentialities for this type of investigation are illustrated in his discussion of the hemoglobins D. In this instance a variant protein, present at a frequency of 1.8 percent in the Punjab, is found in isolated families in North Carolina, Chicago, and Portugal. Ingram is inclined to favor, as an interpretation of this distribution, not repeated origin through identical mutations, but rather the contribution(s) of a "passing stranger" from the Punjab. It is quite obvious that the results of this kind of analysis could make fundamental contributions to such problems as the repeatability of mutations, the amount of gene flow between populations, and the genetic structure of populations. Another rather different problem was approached in an investigation to ascertain how many "hidden" mutations would be found in a population of individuals who appeared to have "normal" hemoglobin. Within a sample of 120 individuals, investigation of 45 percent of the molecule revealed no differences. Such a study again demonstrates the applicability of these methods towards the solution of problems of fundamental significance in the formation of evolution theory—in this instance, the problem of the amount of genetic variability concealed at a single gene locus in a population.

Chapters 4 and 5 constitute an account of some of the thinking about, and investigation into, the fundamental problems of gene action. The discussion ranges from considerations of the quantitative control of protein synthesis to the nature of the processes which "turn on" and "turn off" genes. It is quite apparent that the answers which may ultimately derive from such studies will provide much-needed information about the actions and interactions of genes. In a final chapter, Ingram presents an absorbing discourse on the evolution of the hemoglobins. Utilizing two postulates, one concerned with the nature of mutation and the action of natural selection, the other derived from the concept of "repeats," he provides a scheme according to which all of the polypeptide chains of hemoglobin-like molecules among the vertebrates, including myoglobin, are derived ultimately from a single basic unit, presumably a single ancestral gene locus. His scheme seems all the more plausible when one realizes that, as Ingram points out, the alpha chains of the human and the gorilla differ from each other by no more than two amino acid residues. Again this suggests intriguing potentialities. We may be closer than we recognize to an unequivocal demonstration of the genetic basis for homologous phenotypes.

From these two books then, both stimulating in their own ways, directions in current thinking and investigation become apparent. Mayr's book documents the culmination of the classic approach to evolution and, at the same time, recognizes the significance of physiological processes for an understanding of evolutionary phenomena. It thus foreshadows a future reliance of evolutionary biologists on the results from biochemical investigations. Ingram's discussion of the hemoglobins illustrates the activity of biochemistry as a maturing partner in the investigation of evolutionary problems. Together they point the way toward a more modern synthesis.

New World Primates

Primates. Comparative anatomy and taxonomy. vol. 3, *Pithecoidea. Platyrrhini (Families Hapalidae and Callimiconidae)*; vol. 4, *Cebidae*, pt. A; vol. 5, *Cebidae*, pt. B. W. C. Osman Hill. Edinburgh University Press, Edinburgh, Scotland; Interscience (Wiley), New York (vol. 3, 376 pp., 1957, $17.50; vol. 4, 523 pp., 1960, $27.50; vol. 5, 537 pp., 1962, $32). Illus.

With these three volumes, published while he was still prosector to the London Zoological Society, Hill extends his massive monograph to cover the New World Primates. The two earlier volumes in the series dealt with the prosimians: the first, on the lemuroids and lorisoids, was published in 1953 [reviewed in *Science* **119**, 558 (1954) by B. Patterson, and by myself in *J. Mammal.* **35**, 601 (1954)]; the second on the tarsioids, in 1955 [reviewed in *Science* **123**, 944 (1956)]. These latest three volumes introduce the simians and treat in detail the marmosets (volume 3), the smaller cebid monkeys (volume 4), and the large cebids with highly specialized prehensile tails (volume 5). According to a recent announcement, four or five more volumes will be needed to complete the work.

This is an enormous labor for one author; Hill attempts to cover all living and extinct primates in virtually their total biology, not only the comparative anatomy and taxonomy promised by the subtitle but also reproduction, development, behavior, paleontology, and their general natural history. No previous work by a single author approaches it in scope and detail. It is not surprising, then, that this survey is of very uneven quality, sometimes inaccurate, often disappointingly inadequate, but a unique and generally useful contribution.

The first section of volume 3 is a chapter that introduces the higher primates (that is, those beyond the prosimians covered in the preceding volumes) which Hill terms the Pithecoidea. This term was proposed by Pocock and championed by Wood Jones. It has been widely used and is clearly preferable to its commonest rival, Anthropoidea (which, in its adjectival form, anthropoid, has so curiously come to signify un-manlike and at the same time un-monkeylike). Fortunately the choice is purely one of names, not one of concepts of relationship. There is, of course, the question as to the validity of this linking of groups that quite certainly evolved independently from Early Tertiary prosimians in the Old and New Worlds. It would be better, in my opinion, to omit this artificial linkage and simply to elevate the Platyrrhini and Catarrhini to subordinal rank. One would expect to find in this chapter, which surveys monkeys, apes, and man, a discussion of the parallelism that is so well illustrated in these two groups, but this theme is not developed.

The second section of volume 3 is a 39-page chapter on the Platyrrhini in general. This is unique in the literature on primates, since most writers, struck with the basic cleavage of the group into marmosets and cebid monkeys, have treated these separately, with only very brief remarks on their common features. In the 19th century this would have seemed more justifiable; Thomas Huxley, indeed, took the extreme view of their separateness and elevated them to an independent rank, the Arctopithecini, coordinate with the New World monkeys and the Old World pithecoids. With the discovery of *Callimico* (described in 1904, but unappreciated until 1911), which shares the commonly used diagnostic characters of both groups, this cleavage seemed to have disappeared and either one or three families seemed called for. Hill had chosen to rank them in a separate family, and they are so treated in the text. But, after he received a specimen of this rare animal, he realized that it is clearly a tamarin, and he notes this in the preface. This explains the discrepancy between the volume's title on both its spine and dust jacket, which indicate only the Hapalidae, and that on the title page, which strangely was not changed and continues to list the family Callimiconidae.

The remainder of volume 3 is devoted to the marmosets. The taxonomy of primates is a notorious mess, and the plight of the platyrrhines is especially bad—but marmoset classification is the absolute nadir. Unfortunately, these volumes compound the confusion, even though they provide a very useful synopsis. The plague of names begins before one chooses a volume from the shelves. Volumes 1 and 2 are identified on their spines as treating the Strepsirhini and the Haplorhini. If he is to grasp that the second volume will yield information on monkeys, the reader must understand a term and concept that has been widely rejected and much criticized by reviewers of the earlier volumes. Then he must realize that the marmosets are considered in volume 3 under the name Hapalidae, a name which has been invalid for more than half a century. *Callithrix* has been universally adopted as the official name for the common marmoset not only by American workers, as Hill implies, but by most of the world's great museums, including the British Museum, and it is used in nearly all current literature, including the London Zoo's own *Zoological Record*.

Of all the possible classifications of marmosets, Hill has chosen the most fragmenting. He divides the marmosets into nine genera (including *Callimico*). This certainly is excessive splitting. Some of them surely deserve no more than subgeneric status, as Hill admits, and the distinctions between *Tamarin* and *Tamarinus* and between *Hapale* (= *Callithrix*) and *Mico* are too trivial even for that. (To add to the difficulty two marmoset names have been