

Book Reviews

Evolution above the Species Level.

Bernhard Rensch. Columbia University Press, New York, 1960. xvii + 419 pp. Illus. \$10.

The origin of higher categories is one of the basic and to some, at least, one of the most perplexing problems in evolution. The idea that species and higher groups have not evolved in quite distinctive ways but rather that the latter have also arisen by normal speciation, albeit under special circumstances, is now accepted by most biologists. First considered in the light of modern evolutionary mechanics by Huxley (1942), Mayr (1942), and Simpson (1944), this interpretation is now an important component of the synthetic theory.

During the last part of World War II, Bernhard Rensch of the University of Münster wrote a book, entitled *Neuere Probleme der Abstammungslehre, die transspezifische Evolution*, "with the intention of proving that very probably the major trends of evolution are brought about by the same factors that bring about race and species formation." Written without knowledge of the works of Huxley, Mayr, and Simpson, and published in 1947, Rensch's book complemented and supplemented them in a remarkable way. The second German edition, which was published in 1954, and which has recently been translated into English at the suggestion of Theodosius Dobzhansky, is an all encompassing work, considering nearly every aspect of evolutionary biology in the light of an enormous wealth of data. Apparently it was written with an impelling desire to demonstrate that "there is no reason to assume noncausal or autonomous processes in evolution." Variants of this phrase appear throughout the book, and in Rensch's opinion, at least, many professional biologists still need to be convinced.

The roles of mutation, recombination, fluctuations in population size, se-

lection, isolation, and hybridization and their interaction in producing the mechanism of infraspecific evolution are succinctly discussed in modern terms. Six types of races (rather than isolating mechanisms) are recognized: historical, geographical, ecological, physiological, genetic, and hybrid. Historical or successional races (and species) represent fragments of phyletic lineages and are, therefore, more difficult to delimit taxonomically than the contemporary ones. Although this point is implied in the discussion, it should perhaps receive greater emphasis. Rensch stresses the importance of geographic races as the antecedents of species, but there is now ample evidence that geographic isolation is not always required. Reproductive isolation, which would include ecological, physiological, genetic, and hybrid isolation, may lead to the origin of races and species from sympatric populations. Rensch does not deny this point, but he is not yet convinced that reproductive isolation (here used in the inclusive sense of Dobzhansky) may play a major role in race and species formation.

The chapter on undirected and trans-specific evolution emphasizes the "non-directedness" of evolution as well as "forced development" during phylogeny. The concept that organisms "try out" a wide variety of viable body forms and mechanisms, within the limits imposed by selection, has been considered in various ways by other authors. Involved here is the "opportunism" of Simpson or the "multiple evolutionary pathways" of Bock. By "forced development" Rensch means "directed selection acting upon the material provided by primary undirected variation." This effect of adaptively oriented selection is illustrated by a wide variety of examples from living organisms. Its implications are further explored in the chapter on anagenesis. Ecological, biomechanical, and physiological factors play an important role in the direction of evolution. The example cited dem-

onstrates that there must be a sequence of change involving these factors. At the end of this chapter there is a section on the "possible evolution of organisms on extraterrestrial bodies." It is concluded that the probability of life elsewhere in this galaxy is fairly high.

Rensch supports the now well-established fact that the absolute speed of evolution has varied greatly in different groups of animals. His data on the duration (in years) of various categories for a variety of animals support some fairly obvious generalizations, such as a longer duration for marine species and "lower" groups than for terrestrial ones. There is, in general, a geometric increase in the age of the higher categories. Although the factors affecting evolutionary rates are discussed, there is no consideration of the kinds of rates or of rates in numerical terms. This section is actually more concerned with duration than with evolutionary rate as the latter is currently defined.

The longest section of the book, and perhaps the most important one, is devoted to what Rensch calls "kladogenesis" or phylogenetic branching. This evolutionary pattern is divided into a series of phases labeled: explosive radiation, phase of specialization, and overspecialization or degeneration leading to extinction. Any analogy with individual ontogeny is regarded as meaningless. Explosive radiations commonly occur when groups first arise, but, as Simpson has also noted, they may occur at any time in the history of a group as a result of intensified selection or occupation of new or different niches, and they may involve any of the higher categories.

The phase of specialization (essentially what Simpson has called "intra-zonal" evolution) that frequently follows rapid radiation is mainly modification within a major adaptive zone, although Rensch does not use this term and his thesis is not developed in relation to the zone concept. It also should be noted here that the first two phases usually, but not invariably, occur in this order. Rensch's aim is to elucidate the ways in which changes of phyletic significance can occur in terms of evolutionary trends and orientation. He points out that this phase represents a slowing of radiation, mainly because most of the available niches were occupied during the first phase.

Following a brief, modern interpretation of irreversibility, which is particularly evident in this phase, there is a lengthy consideration of how mor-

phologic change can be brought about at the transspecific level. The effects of genes regulating differentiation may involve, more or less, the entire organism; consequently, alterations during ontogeny may be extensive and interrelated. Rensch's "constructive" genes are in this category, and their effect on hormone production and growth have important significance in phylogeny. As his numerous examples demonstrate, alterations in pleiotrophy, allometric shifts in proportion, modifications in the compensation of body material related to changes in proportion and mass, as well as biomechanical limitations particularly related to extremes of body size are factors affecting the organism as a whole. Within the restrictions imposed by selection, both mutations involving "constructive" genes, which will mostly influence the above factors, and those with more limited effects are considered to be important in supraspecific evolution.

Parallelism, another phenomenon characteristic of this phase, is the result of parallel selection and common genetic background—a conclusion generally agreed upon today—but it is also related directly to the adaptations of the ancestral group. Orthogenesis, also particularly related to the phase of specialization, is treated mainly in relation to phyletic increase (and decrease) in body and organ size. The extensive contributions of Rensch and his students on allometric growth provide important evidence here, as in the section discussed above. Increase in body size, particularly in mammals, has definite selective advantages such as greater developmental vigor, relative decrease in some organs to permit enlargement of others, and improvement in metabolism related to increase in cell number and to change in the mass-surface area relationship. Decrease in the size of the body may also be advantageous for flight or concealment. Decrease in organ size is mostly related to negative allometry and, in some cases, to compensation of body tissue.

Excessive growth ("overspecialization") is regarded as mainly an allometric phenomenon, although it may be due to "undirected" mutation not affected by selection, or a result of sexual selection. The retrospective aspect of overspecialization is perhaps implied but not discussed. Phyletic aging (will this term *never* die?) and extinction are not, as Rensch rightly points out, necessarily correlated. The former may in-

volve "deviation from the typical shape of the taxonomic group" or physiological factors, while the latter may also be mostly the result of competition or climatic change.

The effects of mutation on ontogeny are considered in relation to their phylogenetic implications. Archallaxis refers to alteration early in ontogeny, while coenogeneses are early deviations or adaptations which are not apparent in the adult. Deviations also occur at intermediate stages or later (anabolic) which may disappear or be evident in some way in the adult. Stages may also be omitted or shifted to an earlier phase of ontogeny. Fetalization (proterogenesis) is known to have a role in phylogeny. All these alterations may have adaptive value, and they seem to be involved in the origin of new structural types.

The evidence from neontology cited above certainly favors, if it does not prove, the role of random mutation and selection in the origin of new character complexes which, even in retrospect, define a new higher category. As Rensch points out, the well-documented higher category transitions in the fossil record, and even the incompletely recorded ones, are consistent with this conclusion.

Progressive evolution from lower to higher levels of organization is here called anagenesis. This increasing complexity, which is typically accompanied by a progressively greater division of labor (rationalization), is one aspect of Simpson's phyletic evolution (the other being random, reversible change), but it may also occur in his "splitting" mode and, when it involves a shift in adaptive zone, lead to his quantum evolution. But even so regarded, with its "definable evolutionary direction" (Simpson), anagenesis is a phenomenon of great interest. Rensch stresses increased complexity, greater division of labor, increased simplification of structure and function, increased plasticity of the same, and finally increased freedom from or domination of the environment as the main factors of anagenesis. Improvement of the nervous system is a special but important part of this picture. Evolutionary trends are implicit in Rensch's discussion, trends usually involving the entire organism and guided by selection. This is also evident in his consideration of human evolution—for example, in the development of upright posture and the elaboration of the forebrain.

Having dealt at length with evolutionary progress, the author turns briefly to the origin of life and its explanation in terms of evolutionary principles. The origin of self-duplication in the primordial nucleoproteins is compared with mutation, because this unique faculty may have first appeared, by chance, in a few molecules of these complex proteins, and selection may have been involved in the establishment of this new kind of matter.

Autogenesis is rejected in favor of ectogenesis (causalistic, guided by environmental factors). Not satisfied, however, with the implications of ectogenesis, Rensch proposes the term *biogenomogenesis* to signify that the "regularities ('laws') of evolution . . . are the result of vastly complicated causal reactions." Perhaps a plea should be entered here for synthesis in terminology!

The most original and surely the most controversial chapter in this book deals with the evolution of the phenomena of consciousness. There can be no argument with Rensch's desire to find a material basis for consciousness, or to favor the evolution of behavioral processes along with somatic evolution. Some may be disturbed by the attempt to project various attributes of consciousness from the human level down the evolutionary ladder to "lower" levels, instead of working up from the "bottom." Some may also object to a postulated gradual evolution of the behavioral process, without the recognition of definable levels of behavior with their evolutionary implications. Parts of this chapter seem unduly obscure to a non-psychologist (and to at least one comparative psychologist). Clarification, and perhaps simplification, would be helpful in a future edition.

In the introduction to his book, Rensch points out that the literature pertaining to evolution is so vast that "this desirable universality of knowledge can only rarely be obtained." Different backgrounds produce differences of opinion. The author is optimistic about this, however, because the contributions of the past two decades on supraspecific evolution have increasingly demonstrated a similarity of interpretation, regardless of the fields involved. His moderate pessimism in the conclusion that many biologists will not accept the essential role of randomness in progressive evolution or the evolution of behavior along with somatic evolution seems rather unnecessary for this day and age. Randomness in this

context is identified with our inability to analyze completely what is really going on in the extraordinarily complicated processes of evolution.

This is an extremely stimulating book, partly because of the wealth of evidence that has been brought to bear on all aspects of evolution and partly because of the way that Rensch interprets this evidence. As Dobzhansky points out, this is indeed a most important contribution to the grand synthesis.

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Louis Agassiz. A life in science. Edward Lurie. University of Chicago Press, Chicago, Ill., 1960. 449 pp. Illus. \$7.50.

The name Agassiz is familiar to those living in the neighborhood of Cambridge, Mass., because of the Agassiz Museum of Harvard University. Agassiz is a name that is also known to some of those who work at the great Marine Biological Laboratory at Woods Hole, because that laboratory is, in part, an outgrowth of a small teaching and research station that was founded on Penikese Island by Louis Agassiz. But most biologists remember Louis Agassiz primarily as an old-fashioned member of their profession, as one who could not accept or even understand Charles Darwin's theory of evolution.

Thus, Louis Agassiz is neatly labeled and pigeonholed. Perhaps this stereotyping of our precursors is necessary, that is, if we are to remember them at all; for they steadily grow more numerous, and their very numbers now insure that many worthy men will be forgotten. Some few, however, may be remembered through the fact that they have been abstracted until they are little more than proper nouns and thus their names have become serviceable in the taxonomy of scientific ideas. We have always found it convenient to attach the name of some past scientist to a discovery or to an attitude or, even, to some past event. That this treatment of our predecessors is less than just we readily admit, and so we can welcome the labors of a biographer who rescues a scientist who has been reduced to little more than a mnemonic device, and who restores him to full human status. This is just what Edward

Lurie has done in writing this remarkably complete, authoritative, and interesting biography.

Louis Agassiz reads almost as if it were a picaresque novel, but a picaresque novel in reverse, because the hero was in no way a picaroon. In fact, he was the very opposite; he lived a life of exemplary virtue, and he excelled in just those qualities that we find today in many of our scientific leaders. As a youth he was a model of industry; he led in his studies and soon mastered the classical learning that was available to him in the Collège de Bienne in his native Switzerland. But this was not enough. He wanted to become a naturalist, and without the entire approval of his family, he extended his studies and his field researches. Even as a boy he revealed both his ambition and his determination. He decided to become the greatest naturalist of his generation, and he determined that no person, no hardship, and no obstacle should deter him.

He was remarkably well equipped for his chosen career. He learned easily and quickly, and he retained great masses of facts almost automatically and without effort. He also understood what he learned and he could organize his knowledge and recognize the underlying principles in his accumulated data, as he showed when he classified the fishes of the world and when he devised his theory of continental glaciers. It would be an understatement to describe his personality as winning, because he routinely charmed all with whom he came in contact. (His personal difficulties were limited to a few of his students and to a couple of his colleagues who had been his intimate associates for some years, and perhaps he also had difficulties with his first wife.) Almost automatically he observed Cabell's great law of living, "Thou shalt not offend against the notions of thy neighbors." But Agassiz was in no way a hypocrite; his notions *were* the notions of the academic world in which he lived, only he expressed his ideas a little better than most.

Early in life Agassiz exhibited a characteristic that we are only now beginning to appreciate fully—he was always able to raise money. When his father's resources for financing his extended education in Germany proved insufficient, he found a maternal uncle whom he persuaded to take over. His teachers were also uniformly helpful. Later, in France, Cuvier did his part and made it possible for Agassiz to re-

main a while in Paris. Baron Alexander von Humbolt contributed to Agassiz from his personal funds and used his political influence to get Agassiz grants from the Prussian state. Later, at Harvard, Agassiz routinely and conscientiously ignored all budget limitations and overspent his funds almost as a matter of principle, but he was always able to raise enough money to cover the deficits. He could always rehabilitate his own personal finances by giving a few public lectures. Such talents we can appreciate.

It is not the purpose here to outline either the character of Agassiz or the events of his life, but only to call attention to some of the aspects of his biography that Lurie has presented so interestingly. Agassiz' was a complex personality, and some of his attributes and actions seem very modern and up to date. He definitely preferred opportunities for advancing his standing as a scientist to mere academic status, as he demonstrated when he declined a professorship at Heidelberg because his research and publications were going on so well where he was. But he was also an expert academic politician, a quality he demonstrated when he joined a small group, who called themselves the "Lazzaroni" and who were instrumental in establishing the National Academy of Sciences. This group sought by combining their influence to control all academic appointments in the sciences in American universities. The Lazzaroni were, for a while, all powerful, and they placed their friends and supporters in many important chairs.

That Agassiz failed to become the greatest naturalist of his time was due to a development he could never quite understand. He was equipped with almost unlimited industriousness and ambition. He was exceptionally intelligent and attractive. As a youth, he worked with the leading scientists of his time, and they one and all liked him, admired him, and advanced his fortunes in every way they could. He had also prepared himself in the best of all possible ways. He had mastered *Naturphilosophie* in Germany but had also learned, by studying in France with the hard-headed and practical Cuvier, to prefer the factual to the speculative aspects of science. He had mastered and practically dominated ichthyology and was credited with establishing the glacial theory. For a time he dominated biology in America, all the while remaining a very potent force in Europe. He and his work