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A Personal Introductory History of Ethology

by Konrad Lorenz
Austrian Academy of Science
Altenberg, Austria

Ethology, the comparative study of behavior, is easy to define: it is the discipline which applies, to the behavior of animals and humans, all those questions asked and those methodologies used as a matter of course in all the other branches of biology since Charles Darwin's time.

When one considers with what rapidity the ideas of evolution, and particularly the Darwinian concept of natural selection, caught on in almost all branches of biology, one searches for an explanation as to why these ideas were so tardily accepted by the disciplines of psychology and behavioral science. The main reason that biological thinking and especially comparative methods were prevented from penetrating the study of behavior was an ideological dispute between two prominent schools of psychology.

The bitterness with which this dispute was pursued was nourished, above all, by the diverse philosophies of the antagonists. The School of Purposive Psychology, represented primarily by William MacDougall and later by Edward Chase Tolman, postulated an extranatural factor: "instinct" was regarded as an *agens* or agency neither in need of nor accessible to a natural explanation. "We consider an instinct but we do not explain it," wrote Bierens de Haan as late as 1940. To this conception of instinct was also appended a belief in its infallibility. MacDougall (1923) rejected all mechanistic explanations of behavior. For example, he considered it a consequence of instinct when insects pressed forward purposively toward light; he conceded the possibility of a mechanistic explanation, through tropism, only in those cases where these animals, most unpurposively, flew into a burning lamp. According to MacDougall and his school, everything animals do is in pursuit of a purpose and this purpose is set by their extranatural and infallible instinct.

Those of the Behavioristic School of Psychology justifiably criticized the assumption of extranatural factors as unscientific. They demanded causal explanations. Through their methodology they sought to place themselves as much apart as possible from the purposive psychologists.

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Requests for reprints should be sent to Dr. Konrad Lorenz, Österreichische Akademie Der Wissenschaften, Abteilung 4, Tiersoziologie, A-3422 Altenberg, Adolf-Lorenz-Gasse 2, N.Ö.

They regarded the controlled experiment as the only legitimate source of knowledge. Empirical methods were to take the place of philosophical speculation.

With the exception of a certain lack of appreciation for simple observation, this program incorporated no methodological error, and yet it brought about an unfortunate consequence: all research interests were concentrated on those aspects of animal and human behavior which readily lent themselves to experimentation — and this led to explanatory monism.

A combination of William Wundt's (1922) association theory with the reflex theory (Reflexology) that was then dominating the fields of physiology and psychology, as well as with the findings of I.P. Pavlov, facilitated the abstraction of a behavior mechanism — the so-called conditioned reflex — the qualities of which marked it as ideal for experimental research.

At that time the corrective criticism made by the behaviorists concerning the opinions held by the purposive psychologists was salutary in every way. But, unobserved, a ruinous logical error crept into behavioristic thinking: because only learning processes could be examined experimentally and since all behavior must be examined experimentally, all behavior must be learned. This conclusion is not only logically false but also, factually, complete nonsense.

Knowing the views of those in the opposition, and having made a justifiable critique of those views, the purposive psychologists as well as the behaviorists were pushed into extreme positions which neither of them would otherwise have taken. While those of one group were imbued with a mystical veneration of "THE instinct" which was attributed to inborn excessive capacities, those of the other group denied the very existence of instincts. The purposive psychologists, who were quite aware of innate behavior patterns, regarded everything instinctive as inexplicable; they refused even to attempt a causal analysis. Those others who certainly would have been capable and ready to undertake such analytical research, denied the existence of anything inborn and dogmatically declared that all behavior was learned. The truly tragic aspect of this historical situation is that the purposive psychologists, particularly MacDougall himself, knew animals well and possessed a good, general knowledge of animal behavior, something which is still lacking among the behaviorists even today, because they regard simple observation as unnecessary, in fact, as "unscientific." Here, in this context, the truth of a statement of Faust's comes to mind: "What one does not know is exactly what one needs, and what one does know one cannot use."

This ideological dispute between these two schools of psychology was still being actively pursued when, completely unnoticed by both and independent of their influence, the scientific study of innate behavior patterns came into being. At the turn of the century Charles Otis Whitman (1898) and, a few years later, independently of him, Oskar Heinroth discovered the existence of patterns of movement, the similarities and differences of which, from species to species, from genus to genus, even from one large taxonomic group to another, are retained with just as much constancy and in exactly the same way as comparable physical characters. In other words, these patterns of movement are just as reliably characteristic of a particular group as are tooth and feather formation and such other proven distinguishing physical attributes used in comparative morphology. For this fact there can be no other explanation than that the similarities and dissimilarities of these coordinated movements are to be traced back to a common origin in an ancestral form which also already had, as its very own, these same movements in a primeval form. In short, the concept of homology can be applied to them.

These facts alone prove that these movements originate phylogenetically and are imbedded in the genome. It is just this that is overlooked by those students of behavior who would like to explain away every conceptual distinction between innate and acquired characteristics. When the African black duck (*Anas sparsa*) living on tropical rivers, the mallard living on our own lakes, the many species of wild ducks living on the ponds of zoos and the domesticated ducks living in the barnyards of our farms, in spite of the differences of their environments and despite all the possible influences of captivity, display courtship movements that are unmistakably similar in a countless number of characteristics, the program for these movements must be anchored in the genome in a manner exactly identical with that in which the program of morphological character is coded in the genes. If, after this identification, theories concerned with the problem of "nature versus nurture" continue to be published, this is explainable only through the assumption that authors of these theories are unaware of the discoveries made at the turn of the century, or that they have chosen to ignore them. That they do this was clear to me quite early. At Karl Bühler's institute there were always visiting American psychologists. I asked each and every one of them if the name, Charles Otis Whitman, meant anything to them. Not one of them knew the name.

The discovery that movement patterns are homologous is the Archimedean point from which ethology or the comparative study of behavior marks its origin. Paradoxically, even the work of authors who deny the essential difference between innate and acquired behavior mechanisms is built upon the same factual base.

I discovered for myself, independently of Whitman and Heinroth, that patterns of movement are homologous. When studying at the university under the Viennese anatomist, Ferdinand Hoschstetter, I had become thoroughly conversant with the methodology and procedure in phylogenetic comparison. It became immediately clear that the methods employed in comparative morphology were just as applicable to the behavior of the many species of fish and birds which I knew thoroughly. Soon after this I met Oskar Heinroth, and early in the 1930's both of us learned through communication with the American ornithologist, Margret

Morse Nice, that Charles Otis Whitman had come to essentially the same conclusions as Heinroth about ten years earlier. At the same time all this was happening, we met the most distinguished of Whitman's students, Wallace Craig.

Neither Whitman nor Heinroth ever expressed any views concerning the physiological nature of the homologous movement patterns which they had discovered. My own knowledge of the physiology of the central nervous system came from lectures and textbooks in which the Sherringtonian reflex theory was regarded as the last word and the incontestable truth. The expression, "reflex," evokes the vision of a simple, linear causal relationship between the incoming stimulus and the response given to it by the organism. In this simplicity lies the seductive effect of the concept: it is just as easy to understand as it is to teach.

Under Karl Bühler's tuition I gained enough knowledge of the two prominent schools of American psychology to feel myself qualified to criticize them on two fundamental points. The first was that the infallible, preternatural "instinct" in which the purposive psychologists believed simply did not exist; too often had I seen innate behavior patterns taking their course in completely blind and senseless sequences. The second criticism was that the point of view of the behaviorists, that all animal behavior is learned, was totally false.

I had published several short articles, based on my own observations, about the problem of the innate and homologous in motor patterns when my friend, Gustav Kramer, imposed himself on the course of these events by influencing the biologist, Max Hartmann, to invite me to give a lecture to the Kaiser-Wilhelm Society for the Advancement of Science (now the Max-Planck Society). Kramer was carrying out his intention of providing a setting for a discussion between Erich von Holst and myself. Kramer was von Holst's friend as well as mine, and he was well aware that the phenomena which I was observing in the motor patterns of intact animals were very closely related to those processes which von Holst was investigating experimentally at the neurophysiological level. Gustav Kramer believed that the congruity between von Holst's research results and mine would be that much more startling and convincing the longer we worked completely independent of one another; that is why he perpetuated this remarkable feat of extended reticence.

So then, in 1935, I gave my lecture at Harnack House in Berlin. Its theme was based on my article, "The Concept of Instinct Then and Now." There I made it clear that any animal is perfectly capable, through goal oriented and variable behavior, of striving toward a purpose, but that this purpose may not, as the purposive psychologists supposed, be equated with the achievement of the teleonomic function of behavior. The purpose toward which the animal, as subject, is striving, is simply a run-through or discharge of that kind of innate behavior which Wallace Craig (1918) designated as "consummatory action" and which we now call the drive-reducing consummatory act. Up to this point what I said then is more or less what I believe today.

But what I had to say about the physiological nature of fixed action patterns was influenced by doctrinaire bias. Led by MacDougall, the purposive psychologists had continued their battle against the reflex theory of the behaviorists and, quite rightly, had emphasized the spontaneity of animal behavior. "The healthy animal is up and doing," MacDougall (1923) had written. I was already thoroughly familiar with the writings of Wallace Craig and, through my own research, I was well acquainted with the phenomena of appetitive behavior and of threshold lowering for releasing stimuli — and I should have kept in mind a particular sentence of a letter Craig had sent shortly before, in which he had argued against the reflex concept: "It is obviously nonsense to speak of a re-action to a stimulus not yet received" (Craig, Note 1).

At that juncture mere common sense ought to have prompted me to ask the following question: innate motor patterns have, apparently, nothing to do with higher intellectual capacities; they are governed by central nervous processes which occur quite independently of external stimuli and they tend to be repeated rhythmically. Do we know of any other physiological processes which function in a similar way? The obvious answer would have been: Such motor patterns are very well known, particularly those of the vertebrate heart for which the stimulus producing organs are anatomically known and the physiology of which has been thoroughly studied.

I lacked the independence of mind and the self-assurance that would have been necessary to ask this question. My valid aversion toward the preternatural and inexplicable factors which the vitalists had summoned to interpret spontaneous behavior was so deep that I lapsed into the opposite error; I assumed that it would be a concession to the vitalistic purposive psychologists if I were to deviate from the conventional mechanistic concept of reflexes, and this concession I did not wish to make. During the course of that lecture I did cover completely, and with especial emphasis, all those characteristics and capacities of fixed action patterns which could not be accounted for by means of the chain reaction theory, yet, in my summary at the end, I still concluded that fixed action patterns depended on the linkage of unconditioned reflexes even if the cited phenomena of appetitive behavior, threshold lowering, and vacuum activity would require a supplementary hypothesis for clarification.

Sitting next to my wife in the last row of the auditorium was a young man who followed the lecture intently and who, during the exposition on spontaneity, kept muttering, "Menschenskind! That's right, that's right!" However, when I came to the concluding remarks described above, he covered his head and groaned, "Idiot." This man was Erich von Holst. After the lecture we were introduced to one another in the Harnack House restaurant and there it took him all of ten minutes to convince me forever that the reflex theory was indeed idiotic.

The moment one assumed that the processes of endogenous production and central nervous coordination of stimuli (discovered by von Holst), and not some linkage of reflexes, constitute the physiological bases of behavior patterns, all the phenomena that could not be fitted into the reflex theory, such as threshold lowering and vacuum activities, not only obtained an obvious explanation but became effects to be postulated on the basis of the new theory.

A consequence of this new physiological theory of the fixed motor pattern was the necessity to analyze further that particular behavioral system which Heinroth and I had called the "*arteigene Triebhandlung*" (literally, species-specific drive-activity) and which we had regarded as an elementary unit of behavior. Obviously, the mechanism which selectively responded to a certain stimulus situation must be physiologically different from the fixed motor pattern released. As long as the whole system was regarded as a chain of reflexes, there was no reason for conceptually separating, from the rest of the chain, the first link that set it going. But once one had recognized that the movement patterns resulted from stimuli endogenously produced and centrally coordinated and that, as long as they were not needed, they had to be held in check by some superordinated factor, the physiological apparatus which triggered their release emerged as a mechanism *sui generis* (of a special kind). These mechanisms that responded to selective stimuli, in a certain sense served as "filters" of afference, were clearly fundamentally different from those which produced stimuli and from the central coordination that was independent of all afference.

This dismantling of the concept of the "arteigene Triebhandlung" into its component parts signified a substantial step in the development of ethology. The step was taken in Leyden at a congress called together by Professor van der Klaauw. During discussions that lasted through the nights, Niko Tinbergen and I conceived the concept of the innate releasing mechanism (IRM), although it is no longer possible to determine by which one of us it was born. Its further elaboration and refinement, and the exploration of its physiological characteristics, especially its functional limitations, are all due to Niko Tinbergen's experiments.

Concurrent with the conceptualization of the IRM, the concept of the fixed action pattern or instinctive motor pattern was also narrowed and made more precise, and in exactly the way Charlotte Kogon had proposed as early as 1941 in her book, *The Instinctive as a Philosophical Problem*, a book which regrettably remained unknown to me until just recently. Subsequently, and up to the present, the concepts of IRM and of the fixed motor pattern have proved their worth; their utility in the most diverse kinds of flow diagrams make it probable that they are, in fact, functionally, if not also physiologically, identical mechanisms. For the visualization and presentation of hierarchically organized instincts they have been especially useful.

During the years that followed, ethology developed quickly, both in the results achieved and in the increasing number of researchers. A large store of data was laboriously assembled; many unique discoveries were made. If one chooses to criticize this period of felicitous research, it can be reproached for one-sidedness, even for a certain failure to think in terms of systems. This was inherent in an orientation that almost completely ignored learning processes; above all, the relationships and interrelationships that existed between the newly discovered inborn behavior mechanisms and the various forms of learning were barely touched. My modest contribution, which comprised a formulation of the "instinct-learning intercalation" concept, got no further than formulation; besides, the example on which the conceptualization was based, was false.

In 1953 a critical study appeared which had a behavioristic point of view but which did not come from a behaviorist. In his "A Critique of Konrad Lorenz's Theory of Instinctive Behavior," Daniel S. Lehrmann (1953) dismissed, on principle, the existence of innate movement patterns and, in so doing, supported his argument substantially by using a thesis of D.O. Hebb who had maintained that innate behavior is defined only through the exclusion of what is learned and, thus, as a concept was "nonvalid," that is, unusable. Drawing on the findings of Z.Y. Kuo (1932), Lehrmann also asserted that one could never know whether or not particular behavior patterns had been learned within the egg or *in utero*. Kuo had already recommended abandoning the conceptual separation of the innate and the acquired. All behavior, in his opinion, consisted of reactions to stimuli and these reflected the interaction between the organism and its environment. For Kuo, the theory of a pre-extant relationship between the organism and the conditions of its environment is no less questionable than the assumption of innate ideas.

My answer to Lehrmann's critique was short and forceful but at first, missed the most essential mark. The assertion that the innate in comparative studies of behavior is defined only through the exclusion of learning processes is entirely false: like morphological traits, innate behavior patterns are recognizable through the same systematic distribution of attributes; the concepts of innate and acquired are as well defined as genotype and phenotype. The reply to the theory that the bird within the egg or the mammal embryo within the uterus could there have learned behavior patterns which then "fit" its intended environment was formulated by my wife and was described with a single phrase: "indoor ski course." I wrote at the time that Lehrmann, in order to get around the concept of innate behavior patterns, was actually postulating the existence of an innate "schoolmarm."

My formulation of the concept of the innate "schoolmarm" was clearly intended as a *reductio ad absurdum*. What neither I nor my critics saw was that in just this teaching mechanism the real problem was lurking. It took me nearly ten years to think through to where, actually, the error of the criticism and the counter-criticism was located. The error was so very difficult to find because it had been committed in exactly the same way by both the extreme behaviorists and by the older ethologists. It was, as a matter of fact, incorrect to formulate the concepts of the innate and the acquired as disjunctive opposites; however, the mutuality and intersection of their conceptual contents were not to be found, as the "instinct opponents" supposed, in everything innate being learned. It now seemed that the very reverse might be the case, that is, everything learned must have as its foundation a phylogenetically provided program if, as it actually does, appropriate species-preserving behavior patterns were to be produced. Not only Oskar Heinroth and myself, but other older ethologists as well, had never given much concentrated thought to those phenomena which we quite summarily identified as learned or as determined through insight. We regarded them — if one wishes to describe our research methods somewhat uncharitably — as the rag bag for everything that lay outside our analytical interests.

So it happened that neither one of the older ethologists nor one of the "instinct opponents" posed the pertinent question about how it was possible that, whenever the organism modified its behavior through learning processes, the right process was learned, in other words, an adaptive improvement of its behavioral mechanisms was achieved. This omission seemed particularly crass on the part of Z.Y. Kuo who had so expressly disassociated himself from every predetermined connection between organism and environment but, at the same time, regarded it as axiomatic that all learning processes induced meaningful species-preserving modifications. As far as my knowledge goes, P.K. Anokhin (1961) was first among the theorists of learning to grasp the conditioned reflex as a feedback circuit in which it was not only the stimulus configuration arriving from the outside, but more especially the return notification reporting on the completion and the consequences of the conditioned behavior that provided an audit of the reflex's adaptiveness.

As in many other cases of erroneous reasoning, the behaviorists' exclusion of questions concerning the adaptive value of learned behavior may be traced to their emphatic antagonism to the School of Purposive Psychology. The latter's uninhibited commitment to behavior's extranatural purpose created in the behaviorists such antipathy to all concepts of purpose that, along with purposive teleology, they also resolutely refused to consider any species-preserving purposefulness, including teleonomy as defined by C. Pittendrigh (1958). This attitude, unfortunately, made them blind to all those things that could be understood only through a comprehension of evolutionary processes.

The innate "schoolmarm," which tells the organism whether its behavior is useful for or detrimental to species continuation, must be located in a feedback apparatus that reports success or failure to the mechanisms of the first phases of antecedent behavior. This realization came to me only slowly and independently of P.K. Anokhin (1961). Whenever a modification of an organ, as well as of a behavior pattern, proves to be adaptive to a particular environmental circumstance, this also proves incontrovertibly that information about this circumstance must have been "fed into" the organism. There are only two ways this can happen. The first is in the course of phylogenesis through mutation and/or new combinations of genetic factors and through natural selection. The second is through individual acquisition of information by the organism in the course of its ontogeny. "Innate" and "learned" are not each defined through an exclusion of the other but through the external environmental source of the pertinent information that is a prerequisite for every adaptive modification.

The bipartition, the "dichotomy" of behavior into the innate and the learned is misleading in two ways, but not in the sense maintained in the behavioristic argument. Neither through observation nor through experimentation has it been found to be even in the least probable, even still less a logical necessity, that every phylogenetically programmed behavior mechanism must be adaptively modifiable through learning. Quite the contrary, it is as much a fact of experience as it is logical to postulate that certain behavior elements — exactly those that serve as the built-in "schoolmarm" and conduct the learning processes along the correct route — are never modifiable through learning.

But, on the other hand, every "learned behavior" does contain phylogenetically acquired information to the extent that the basis of the teaching function of every "schoolmarm" is a physiological apparatus that evolved under the pressure of selection. Whoever denies this needs the assumption of a prestabilized harmony between the environment and the organism to explain the fact that learning — apart from some instructive failures — always reinforces teleonomic behavior and extinguishes unsuitable behavior. Whoever makes him or herself blind to the facts of evolution arrives inevitably at this assumption of a prestabilized harmony.

The search for the source of information which underlies adaptation has, since those earlier years, yielded significant results. I will mention only the research done by Jürgen Nicholai (1970) with whida birds (*Viduinae*) which demonstrated the intricate manner in which information can be "coded": essential parts of the adult bird's song have been learned by monitoring the begging tones and other tonal expressions of whichever species of host bird the whida was reared by.

Inquiry into the phylogenetic programming of the acquiring processes has proved to be important in many respects. Like imprinting, some acquiring processes are impressionable only during specific sensitive periods of ontogeny; a failure to perceive and meet their needs during those crucial periods in animals and humans can result in irremediable damage. Within cultural contexts the distinction between the innate and the acquired is also significant. Humans, too, and their behavior are not unlimitedly modifiable through learning and, thus, many inborn programs constitute human rights.

Oskar Heinroth (1930) wrote in the conclusion of his classical paper on waterfowl:

> I have, in this paper, drawn attention to the behavior used in social intercourse and

> this, especially in birds living in social communities, turns out to be quite amazingly similar to that of human beings, particularly in species in which the family — father, mother and children — remain together living in a close union as long as, for instance, geese do. The taxon of suropsidae [the branch formed by reptiles and birds] has here evolved emotions, habits and motivations very similar to those which we are wont to regard, in ourselves, as morally commendable as well as controlled by reason. The study of the ethology of higher animals (still a regrettably neglected field) will force us more and more to acknowledge that our behavior towards our families and towards strangers, in our courtship and the like, represents purely innate and much more primitive processes than we commonly tend to assume.

This early admonishment notwithstanding, ethology was curiously tardy in approaching the human being as a subject.

In the investigation of humans it is not easy to fulfill the primary task of ethology which is the analytical distinction of fixed motor patterns. No less a man than Charles Darwin pointed out the homology of some human and animal motor patterns. The homology was convincing, but solid proof still remained necessary.

Irenäus Eibl-Eibesfeldt (1956) was the first to afford this proof. He chose the same movements which Darwin had studied: those expressing emotions. For obvious reasons, the experiments involving social isolation that are generally used to prove a motor pattern to be independent of learning could not be used with humans, so Eibl fell back on the study of those unfortunates with whom an illness had already initiated this experiment in an equally cruel and effective manner: he studied children born deaf and blind. As he was able to demonstrate by means of film analyses, these children possessed a practically unchanged repertoire of facial expressions, although, living in permanent and absolute darkness and silence, they had never seen or heard these expressed by any fellow human.

As a second route of approach, Eibl-Eibesfeldt used the cross-cultural method to study the expression of emotions in humans. He observed and filmed representatives of as many cultures as he could, in standardized situations such as greeting or taking leave, quarreling, experiencing grief and enjoyment, courting and so on. The essential patterns of expressing emotions proved to be identical in all the cultures he was able to study, even when the patterns were subjected to minute analysis by means of slow motion films. What varied was only the control exerted by tradition: this affected a purely quantitative differentiation of expression.

The most important result of Eibl-Eibesfeldt's extensive and patient research can be stated in a single sentence. The motor patterns shown undiminished by deaf-and-blind children are identical to those that, through cross-cultural investigation, have been shown to be inaccessible to cultural change. In view of these incontrovertible results, it is a true scientific scandal when many authors still maintain that all human expression is culturally determined.

A strong support for human ethology has come from the unexpected area of linguistic studies; Noam Chomsky and his school have suggested that the structure of logical thought — which is identical to that of syntactic language — is anchored in a genetical program. The child does not learn to talk; the child learns only the vocabulary of the particular language of the culture tradition into which it happens to be born.

A surprising and important extension of ethological research was the application of the comparative method to the phenomena of human culture. In his book, *Kultur und Verhaltensforschung* published in 1970, Otto Koenig demonstrated that, in the development of human cultures, the historically induced, traditional similarities on one side and, on the other, resemblances caused by parallel adaptation — in other words, between homology and analogy — are interacting in very much the same manner as they do in the evolution of species. For an understanding of cultural history, the analysis of homology and analogy is obviously of the greatest importance.

As a later development of ethology, I should like to mention the consequences of my own sallies into the field of the theory of knowledge. When a stroke of chance shifted me onto the chair of Immanuel Kant in Königsberg, I was unavoidably forced to come to terms with Kantian epistemology. To anyone familiar with the facts of evolution, the question concerning what Kant himself would have thought of the a priori must obtrude itself. That is, what would he have thought about everything that is given us without previous experience, and must, indeed, be given to us in order to make experience possible at all, if he had known about evolution. From the viewpoint of the history of science, it is by no means astonishing that at least three people not only asked this very question at the same time, but also simultaneously and independently of one another found the same answer: Sir Karl Popper, Donald Campbell and I, myself.

It thus seems that the development of a science resembles that of a coral colony. The better it thrives and the faster it grows, the quicker its first beginnings; the vestiges of the founders and the contributions of the early discoverers become invisible through being overgrown by their own progeny. There is one drawback to the strategy of growth pursued by the coral tree. The polyps at the end of its branches have a much better chance of further development than those situated near the foundation. The ends go on growing faster and faster without considering the necessity for strengthening, in proportion, the base that has to carry the weight of the whole structure. Unlike an oak tree, the coral colony does nothing to solidify its support. In consequence of this, there is a lot of coral rubble detached from points of departure and this is either dead or, if still partly alive, growing in indeterminate directions and getting nowhere.

Having myself grown very near the point from which ethology, as a new branch of biological science, has taken its origin, it may seem presumptuous if I compare the present state of our science to a coral colony whose branches, by losing contact with their foundation, are producing quite a lot of rubble. However, there is no doubt that they do, and I am presumptuous enough to criticize this. My justification lies in the fact that really important discoveries, such as those made by Charles Otis Whitman, Oskar

Heinroth, Erich von Holst, Kenneth Roeder and of others, are being forgotten for reasons which are partly to be found in mere fashion and partly in ideological prejudices.

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