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Metamorphosis in Animals: The Transformations of the Individual and the Type

The transformations undergone by certain animals in the course of their lives have provided human expression with some of its oldest images. From time immemorial the metamorphosis of the caterpillar into a butterfly has served as a metaphor for intimations of higher being. And the same creature, in the quiescent pupa, the nympha or chrysalis, has provided a strict hieratic image of contemplation, of serene expectation of things to come, of the promise of resurrection.

It is scarcely possible to witness the transformations of a dragonfly without experiencing an assault of inner images pointing in the same direction as the meditations in which Jan Swammerdam for the first time reverently described the metamorphosis of the May flies as a "copy of human life." The first part of our discussion will deal with cyclic changes of this kind, all leading back to the same starting point, the egg.

The word "metamorphosis" with which we designate these changes of form is employed by biologists in several senses. Those of us who have a literary background are perhaps acquainted with the concept of metamorphosis employed by Goethe and still used by comparative morphology: the divergent forms successively embodying a fundamental type or blueprint. Goethe's discussion of the metamorphosis of plants treats of this kind of transformation; all theories of evolution deal with such metamorphoses, and accordingly seek to determine how one fundamental type develops from another.

Both possibilities of transformation have been discussed in so many variants at our Eranos Conference that a biologist may be justified, in his contribution, in considering them both from one standpoint. Consequently, the second part of our discussion will deal with the transformation of the type. If this lecture comes at the end of our Conference, it is not because I claim the last word. It is an end, because if the study of natural phenomena takes a complete view of its subject matter, it must lead us back to the beginning. Thus it stands at the end because our conferences are sustained by the spirit of encounter and correlation among all fields of knowledge.

I

We turn first of all to the strange transformation that certain animals undergo in the course of their lives; in these species an individual appears successively in a number of forms. The first form, and sometimes several of the early forms, may deviate so radically from the mature form as to obscure their membership in the same species or even genus: the early form "masks" the mature type and is consequently called a "larva." To follow the life development of the different forms of larvae is one of the main problems of zoology and it has not yet been fully solved. No one can say how many larvae are still considered by biologists as distinct species. Insects and crabs, worms, snails, mollusks, and echinoderms are the groups in which metamorphoses are most frequent. But among the vertebrates frogs and salamanders provide examples with which every child is familiar.

In this kind of metamorphosis the question of an animal's change of form is clearly brought home to us, and with it the question of the creature that undergoes the change and of the extent of its inner and outer transformation. For our discussion of the problem we choose the example of the butterfly—perhaps its familiarity will help to give us a stronger impression of the strangeness of the operations it effects. The study of the metamorphosis of insects and of the butterfly in particular has given us significant insights into the workings of these processes. And the research carried on in the last few years is so illuminating that there is every reason to favor this sector of animal life as a basis for a general exposition of the problem of metamorphosis.

A first question facing scientists was, in a general sense, clarified in the years from 1926 to 1940. It is this: at what stage of development can we ascertain the presence of the forms that will later mature? By interventions in the development of eggs, we are able to determine the time at which essential traits in the development of the various organs are fixated, in other words, when their development is determined. The irradiation of eggs with ultraviolet light offers the possibility of particularly minute observations: it produces localized injuries which tell us something about the place and time of appearance of the earliest rudiments of organs. At certain definite moments—the sensitive phases—in the earliest embryonic development we are able to produce injuries which do not at all disturb the formation of the larva but do appreciably affect the metamorphosis to the mature form. In flies, where many organs (proboscis, eyes, legs, wings) become visible only in the last act of development, it has been possible to show that these organs are all prefigured in the earliest germ development, in a form which cannot yet be distinguished under the microscope but which is nevertheless wholly or in large part established. The time in which this fixation occurs varies from one group of insects to another. In insects with complete metamorphosis, i.e., with larva, pupa, and mature form (= imago), the egg already contains the rudiments of all the organs that distinguish the three stages, and in addition all the equipment for the processes leading from one stage to the next. These experiments lead biologists to ask how the structure and development of these organs are prefigured in the submicroscopic structure of the germ. But here we shall merely mention the existence of this question, without discussing it, because it is one of the great riddles which biologists, chemists, virologists, and physicists are all trying to solve.

In any event, three radically different forms are prefigured in the egg of the butterfly. In the caterpillar stage certain organs function fully, but certain others that will develop in the imago are no more than little groups of cells that we call imaginal disks. Experiment reveals a complex mechanism by which the modifications of the various forms and the transformation from one to another are strictly regulated. But at the same time the study of the first processes of development shows us that the infinitesimal quantity of living substances constituting the egg creates these patterns and guides and regulates the events which will ultimately result in the minutely ordered sequence of the animal's future development. The discovery of this mechanism does not reduce the egg to a mosaic of patterns, functioning together like parts of a machine; rather, it leads us to view the mechanism of growth as a system "developing itself," a process embodying the whole specific nature of the living creature. This autonomous growth teaches us to look with suspicion on all comparisons between the organism and a machine: such comparisons have only the most limited validity, and in employing them we must remain fully aware that every living creature is very much more than a machine. None of the episodes of metamorphosis mysteriously prefigured in the seed is so striking as the sudden transformation of the caterpillar into a pupa or as the last act: the emergence and maturation of the butterfly. The common molts whereby the caterpillars grow from a few millimeters at the time they leave the egg to finger length or more—these castings off of skin are also transformations; they too require some of the processes that characterize the final metamorphosis. We shall have to touch on them in our discussion, but we shall concentrate on the last act of the caterpillar's life, the actual transformation.[1]

What change of mood takes place in a caterpillar that after a long, monotonous period of feeding on some plant—frequently one and only one particular plant—it should suddenly look around for an entirely different place favorable for pupation? What transformation takes place when this caterpillar turns into a quiescent chrysalis, in many cases previously spinning a delicate cocoon of the kind that provides us with natural silk fiber? What change of mood leads certain caterpillars suddenly to begin spinning a delicate but strong fiber belt from which the pupa will hang? And what, finally, leads the creature to cast off the pupal covering, spread its wings, and totally alter its mode of life to become a butterfly? We can say nothing of the inner processes that accompany these transformations, but let us at least bear in mind that these moods and changes of mood are important factors in the reality whose mechanism is in part disclosed by our biological experiments. We shall try to look into this process as far as the present state of our knowledge permits.

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[1] For details on these processes see: J. J. Bounhiol, "Recherches expérimentales sur le déterminisme de la Métamorphose chez les Lépidoptères," *Suppléments au Bulletin biologique de France et de Belgique* (Paris), XXIV (1938); O. Pflugfelder, *Entwicklungsphysiologie der Insekten* (Leipzig, 1952); B. Scharrer, "Hormones in Insects," in K. V. Thimann, ed., *The Action of Hormones in Plants and Invertebrates* (New York, 1952), Vol. I; and C. M. Williams, "Morphogenesis and the Metamorphosis of Insects," *The Harvey Lectures 1951–1952* (New York), Series 47 (1953). The most recent investigations are described in "Relazioni Tenute al Convegno sulla Neurosecrezione," *Pubblicazioni della Stazione Zoologica di Napoli*, Suppl. (Naples), XXIV (1954); [and also *Zweites internationales Symposium über Neurosekretion* (*Lund, 1957*), ed. W. Bargmann, B. Hanström, and B. and E. Scharrer (Berlin, Göttingen, and Heidelberg, 1958) —A.P. (1963)].

In the last two decades important new factors have been revealed by ingenious experimentation, and the butterflies have been investigated with particular thoroughness. These experiments have caused a decisive change in our thinking about the metamorphosis of insects. Only three decades ago it was generally agreed that insects produced no hormones, because at that time attempts to implant seminal glands disclosed no hormonal effect on the bodies of insects, whereas a very noticeable effect is produced in vertebrates. Today, observations of insects, despite the very different structure of the seminal glands in the two groups, disclose a complex process showing certain parallels with that which takes place in vertebrates. And this transformation in our knowledge is also in keeping with the subject of our Conference.

A number of experiments showed first of all that the brain of the insect exerted an indispensable influence on the entire metamorphosis. A caterpillar can be kept alive for a considerable time without a brain, but no metamorphosis occurs. At a certain moment—we shall have more to say of the time factor later on—this particular activity of the brain sets in: it produces, in the organism as a whole, a state of readiness for transformation. If isolated parts are subjected to this influence, they too undergo the transformation. But how does the insect brain induce such readiness?

The investigation of this mysterious process may be regarded as one of the most significant achievements of zoology in the last fifteen to twenty years. For it has led to the discovery that in the insect brain, along with the typical nerve cells, cell groups are at work whose function it is to form hormones, substances which are carried by the blood to the various scenes of their activity. Careful dissection of the brain has revealed, in the cerebrum of insects, two pairs of these cell groups, both of which are neurosecretory (see fig. on p. 302).

We also know that these hormones are transported along the nerve fibers to two little glands known as *corpora cardiaca*. It is not definitely known whether the brain hormones are modified in the *corpora cardiaca*, but we do know that they are not yet active at this point. It is their influence through the blood on another producer of hormones, the prothoracic gland—in the foremost of the three breast segments of the caterpillar—that first has far-reaching consequences. The excellent Pierre Lyonnet (1707–1789), a French lawyer of the eighteenth century, described this

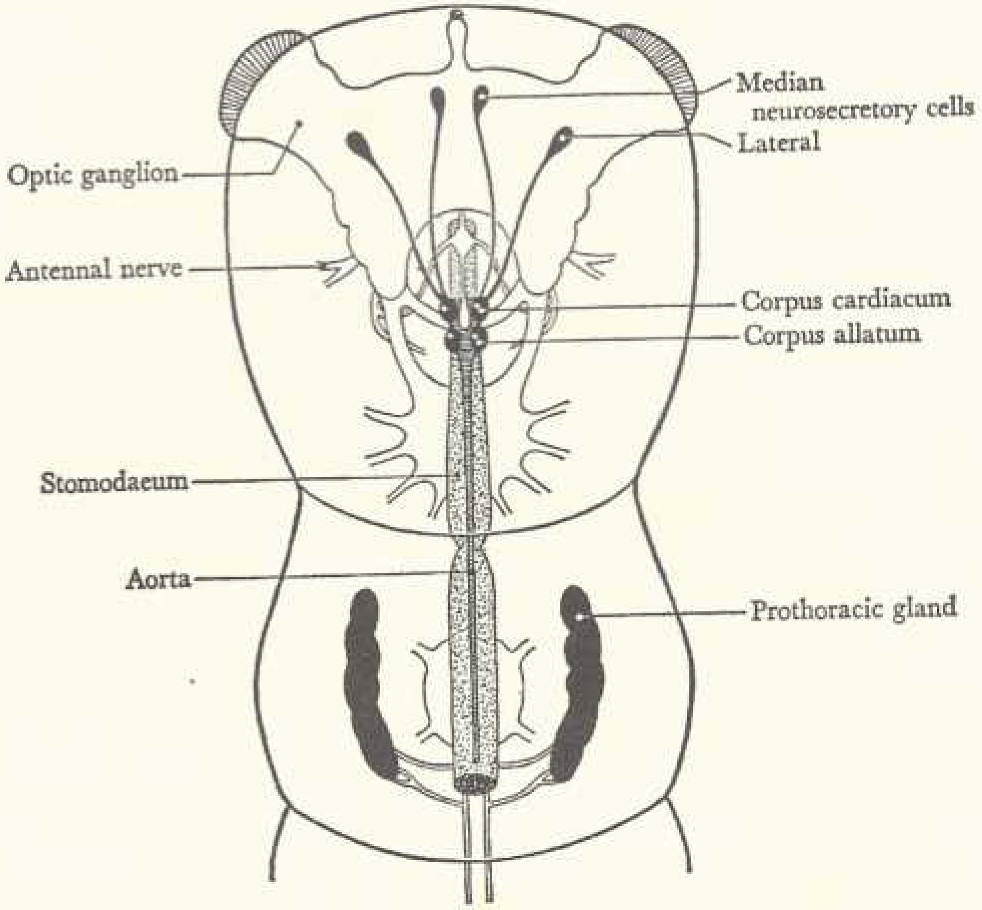

Diagram of the anterior part of an insect,
with the most important hormone glands

prothoracic gland in great detail in his *Traité de la Chenille qui ronge le bois des Saules*, one of the fruits of his industrious leisure. Two centuries were to pass before it became known that this seemingly unimportant group of cells is the producer of an essential substance. No metamorphosis can take place without this prothoracic gland or, in certain other insect groups, a corresponding gland that may be somewhat differently situated.

The brain substance which reaches the blood by way of the prothoracic glands stimulates these glands to secrete the actual hormone of metamorphosis which, distributed through the blood in minute quantities, is able to release in the most divergent organs the processes which, taken together, lead ultimately to pupation and transformation. In a drop of pupa blood containing the substances secreted by the prothoracic gland a group of germ cells can be made to develop into mature spermatozoa, whereas without this hormone the same group of cells in the same blood would have remained in a state of quiescence and matured no further. None of the many hormones in vertebrates produces this maturation of sperm cells that we meet with in insects. The prothoracic hormone is a very special substance.

In certain butterflies we observe still another reaction that shows how closely living creatures are wedded to their environment. In a large silk spinner, *Platysamia cecropia*, the caterpillar transforms itself into a pupa just as we should expect. But in order to develop any further, the pupa requires a period of rest at a cool temperature, a so-called diapause. Uncooled pupae never turn to butterflies. The cooled pupa, on the other hand, can be preserved for months at a temperature of approximately 40° Fahrenheit and be made to transform itself into a butterfly at any time. An experiment conducted at Harvard University by C. M. Williams, who has intensively investigated this species and its relatives, provides some highly significant information. The brain is removed from an uncooled pupa. Normally this pupa would be incapable of any further transformation. But now a brain is inserted which has previously been subjected to the requisite cooling in its original abode. Even in the uncooled pupa, the precooled brain suffices to release complete metamorphosis. In normal life hibernation brings about the necessary cooling and thus becomes a factor in promoting and regulating life. In technical terms, cooling makes the brain "competent" for metamorphosis, while the ensuing warmth creates an "active" brain. The outside brain does not have to be grafted in its proper anatomical place but merely has to be present, an indication that it merely supplies substances which act through the body fluid.

The joint action of the brain glands and of the prothoracic glands is only a part of the complicated process of metamorphosis. Still other participants are required. The brain with its neurosecretory cells (26 in all in C. M. Williams' specimen) and the prothoracic glands are always present in the caterpillar phase. What then prevents them from emitting their secretions at any chance moment in the life of the caterpillar? What prevents the young caterpillars from metamorphosing themselves at an early stage and producing smaller pupae and butterflies?

Delicate studies in experimental biology have resulted in the discovery of an important factor which prevents premature metamorphosis. Near the brain, at the front end of the insect's large dorsal basin, are two little glands, the *corpora allata*, often closely joined to the *corpora cardiaca*. In 1938 the French biologist J. J. Bounhiol demonstrated in Bordeaux that these *corpora allata*, despite their small size, perform an important function. They continuously pour into the insect's blood a substance which influences a number of metabolic processes and which, in particular, maintains the tissues in a youthful, larval state. Many kinds of insects were subjected to the experiment—here I shall not speak of the technical difficulties—with conclusive results: removal of the *corpora allata* induces metamorphosis. These two little glands secrete the substance which acts as a brake, normally postponing the last great event in the life of the insect from molt to molt. For this reason the *corpora allata* have also been called "juvenile glands" or "status quo glands," and their secretion has been termed a rejuvenation hormone. The term accounts no doubt for the secret interest which many scientists and still more laymen take in this mysterious substance.

Under the influence of the juvenile hormone of the *corpora allata* the larval stage of insects can be extended for a long period: we are all familiar with the flights of cockchafers, which occur at intervals of three or four years, indicating that this period is the life span of the larva. The stag beetle lives as a larva for five years; some of the large dragonflies spend several years in the larval phase. An American variety of cicada (*Magicicada septemdecim*) has a larval period of seventeen years, to which the American Indians attach a special significance. A southern variety of the same species spends thirteen years in the larva. The larvae of these cicadas live in the ground. In the last stage they build a little earthen tower four to six inches in height, a hollow finger of earth, at the tip of which the larva turns into a nympha. At the base of the tower a hole remains open, through which the nympha later leaves to climb a tree where it turns into a fully winged insect having a life span of only about one month.

Our knowledge of the juvenile hormone raises a new question. Who sets the alarm clock to mark the moment when the "rejuvenation" should stop? Who gives orders that hormone production should stop at the right moment, so enabling the substances that make for metamorphosis to do their work? We do not fully know. The question is still controversial. In some insects the inhibiting effect of the *corpora allata* in the larva diminishes from molt to molt—the braking factor is thus reduced by stages. In others—the butterflies, for example—it stops suddenly after the caterpillar's last molt; there are certain indications that the *corpora allata* themselves resorb the rejuvenating substances which are still circulating in the blood and in the final phase make them completely ineffectual.

As soon as the rejuvenating substances cease to circulate, the hormones of the prothoracic gland gain the upper hand and the final metamorphosis sets in. With metamorphosis the prothoracic glands have done their work and are done away with. The *corpora allata*, on the other hand, grow considerably and assuredly have other functions in the imago, but of these we still know very little. Insects have still other glands to which biologists attribute an importance for metamorphosis. But their function is uncertain and I mention them only to avoid making things look too simple.

Thus we know of certain reagents known as hormones, small quantities of which induce and govern essential developments in the life of the insect. Perhaps it will be worth our while to reflect for a moment on the action of hormones, for it is only by considering the part they play in the general process of development that we can gain even a limited and provisional idea of the mystery we call the organism.

A point of particular interest is that the secretions of the hormone glands are not specific or only slightly so: the hormone of the prothoracic gland of a fly acts like that of a butterfly; *corpora allata* of entirely different origin produce the typical reaction in almost all insects.

This brings us to a first important insight: the hormone glands are very general action systems; they are widely distributed and interchangeable. The reaction characteristic of each insect—the formation of the butterfly's wings with their specific patterns, that of the fly's proboscis, the special leg structure that distinguishes a mole cricket from a green grasshopper, all the colors and forms that characterize each particular species of insect—these "specific" characteristics are not brought about by hormones. They result from hereditary reaction patterns in the tissues, which are in every case endowed with form potentialities peculiar to the species. The hormones are necessary as intermediaries; without them the potentiality cannot be realized, but they do not create it.

The living substance of the species prepares the way for all this at an early stage of development. To each part of the body it assigns its possibilities of growth, to each nerve center its modes of response. It also provides the hormone centers, and in all these embryonic preparations it regulates the sequence of stages, the transformations that culminate in the final metamorphosis.

Consequently biologists do not, in this connection, speak merely of cause and effect. The prothoracic hormone is not the cause of metamorphosis, any more than the secretion of the *corpora allata* causes the inhibition of metamorphosis. The reaction norms of this or that organ might, just as well as metamorphosis, be said to be the "cause" of metamorphosis or inhibition. Both ideas are false: hormone and reaction norms go hand in hand, both spring from the formative processes of a germ cell. As systems of action and reaction, they are parts of a larger system, which already in the germ cell is attuned to transformation in time.

Thus the preparation of all the mechanisms of transformation begins in the germ cell. In some insects, flies for example, this early preparation includes the setting aside of new germ cells, so that, even before the individual for which the egg is destined begins the course of his life, provision is made for the next generation. If the plasma of the species begins at so early a stage to prepare the way for the end of the individual and the coming of a new generation, you will readily understand how a biologist may incline to agree with the mystics that the end is in the beginning, the beginning in the end.

The example of the butterfly does more than acquaint us with important new findings of research; the study of transformation in an animal group so remote from man does more than enrich our view of nature. I have described this case in some detail because, despite the strangeness of its whole mechanism, so different from ours, the transformations of the butterfly present a mysterious parallel to our own. For one thing, they too are subject to the supraindividual laws of the species. Let us give this question a moment's attention.

Our course of development is also determined in the egg; many of our patterns are pre-established; the structure of those actions and reactions which bring about the changes characteristic of the ages of life and determine the various constitutions and temperaments is laid down in advance. Let us consider just a few of the most important correspondences on which our observation of the metamorphosis of butterflies throws light.

To the co-operation of brain hormones and prothoracic glands corresponds, in the vertebrate, a mechanism that has been investigated in detail only in the last few years. Neurosecretory cell groups in the midbrain of the vertebrates produce hormones, which move through the extensions of these cells and collect in a particular part of the brain, the hypophysis, which is formed from the nervous system in the embryo. To a certain extent this neurohypophysis performs the same function as the *corpora cardiaca* in insects. From it the stored-up hormones pour into the blood, through which they reach other workshops, the adrenal glands for example, in which further reactions are touched off. Among the processes guided by the neurohypophysis, one of the most certain seems to be the influence on the body's water economy. Another probable effect of the neurosecretory cells in the midbrain has been revealed by experiments with birds. The path of the hormone channels to the neurohypophysis is surrounded by the fine veins of a special cerebral circulatory system, which perhaps leads the hormones via the blood channels to the main part of the hypophysis, the anterior lobe, whence in turn they exert their special effects, for example on the seminal glands.

In making this comparison, let us not forget that in some cases—in men as in the higher mammals—the thymus serves as a special organ of rejuvenation and that its change of function and structure at the time of sexual maturity brings about an important hormonal change. It is probable that we shall discover still other substitutions of this kind, and synergisms as well.

These parallels are also manifested in the human habitus, which can show certain signs of metamorphosis, though they are far less conspicuous than in insects.

If we wish to account for the profound changes of mood that occur in the vertebrates, including man, we shall have to find out more about the way in which the neurosecretory centers act as intermediaries between the hormone glands and the nervous system. It is quite safe to suppose that the affects and many unconscious processes are governed by the orchestration of these factors.

The presence of a similar preformed system of excitation in insects shows us that the mechanisms underlying changes of mood and related changes of behavior are very much alike in radically divergent types of animal.

Now I should like to give you an idea of how closely the hereditary orchestration of the hormone glands and the reaction mechanism of the tissues can be reflected in an animal's outward appearance. The changes in the plumage of birds may give us an idea of this.

At the nestling stage the plumage of the laughing gull (*Larus ridibundus*) is a protective dun color; the change to the normal plumage of the young gull is a kind of metamorphosis. The dress of the young bird, which is very different also from that of the old ones, is heavily sprinkled with brown and lacks any conspicuous head markings. But the tip of the tail is black, while the bill and feet are grayish green and flesh-colored.

The first mating dress has a new feature: the head is a deep brownish black, mixed with little white feathers, and there is some white around the eye. There is still a good deal of brown at the top of the wings, an indication of youth. The tail retains its black tip. This, along with the hood, is characteristic of the laughing gull breeding for the first time.

Only in the second year, as a sign of full maturity, is the magnificent gull gray of the wings attained; the tail now becomes pure white, the head a deep dark brown bordering on black, the feet and bill an intense red.

All the stages of life are clearly marked by the habitus; the bird's outward appearance communicates its changes of stage to the other members of the species, who are enabled by hereditary predisposition to interpret this script, and also to scientists, who have deciphered it by painstaking effort.

And still another change of inner stage is reflected in the bird's dress. Each summer, year after year, the plumage is modified after the mating period; the dark hood vanishes and the head is marked only by a few sparse spots of black. Thus the period of sexual quiescence is outwardly distinguished from the mating period.

I have designedly chosen this simple case of a native European bird in order to dispel the idea that metamorphosis is always an impressive, dramatic affair. But in this unassuming yet significant form the phenomenon is widespread and deserves more attention than is usually accorded it. The colors and forms which make up these patterns are far from being superficial and meaningless; on the contrary, all form and function are tied up with an animal's specific essence. The surface no less than the individual function of a given inner organ reflects the essence and meaning of the whole. In some of the highest animal groups, particularly in those with the most highly developed vision, such as the birds, the manifestation of inner changes in outward appearance is particularly pronounced. And these transformations are not mere epiphenomena, they are not irrelevant surface occurrences; they are interpreted, "recognized" by other members of the species whose behavior they determine. Not only does an inner transformation in the individual correspond to the change in dress and behavior; no, every member of the species is equipped with the means of recognizing the changes in the appearance of its fellows and of acting accordingly.

The plumage is not the only outward manifestation that changes with the inner state; in birds, the song, the call, also becomes a means of communication no less varied than the change of dress and gives eloquent expression not only to momentary changes of mood but also to the great rhythms of life. We have all noticed how the sound of the woods changes with the seasons, even though no birds may be in sight: how lively the forest is in May, in the spring, when even the invisible inhabitants bear witness to their life in songs and calls, and how different in late summer, how strange this silence reflecting the metamorphosis of the hidden songbirds. Song is existence—in it the bird discloses its life, following the moods of the moment far more closely than is possible in the more constant medium of dress.

Our discovery of animal metamorphoses raises the question of their meaning and purpose. And though the scientist's first task is to investigate the what and the how, still, when it comes to the study of living things, he cannot evade the question of meaning. The question "Why? To what end?" arises inescapably, though it is often hard to know when the question is permissible and when it exceeds the limits of scientific knowledge.

A first purpose of metamorphosis is the conservation of life. This aspect of the question is perfectly compatible with scientific statement, and a wide field of inquiry, known as ecology, is devoted to such problems among others.

In the lives of many animals, change of form is related to a radical change of environment. This is most particularly true of innumerable creatures of the ocean, whose larvae swim or float in the open sea. Few genuine metamorphoses take place in fresh water—and this is a problem in itself. On closer scrutiny, we find that freely moving larvae with distinct forms are particularly frequent in species which in their definitive form are confined to one spot or are at least highly immobile. The starfish and sea urchins, the snails and shellfish, the worms that live in sand or in reeds, are all confined to one spot; and all of them have free-floating larva forms. Undoubtedly the purpose of these pelagic stages is to diffuse the species with the help of favorable ocean currents. One is reminded of the way in which plants, which must also live in one place, scatter their seeds. Here, then, metamorphosis is important for the conservation of the species.

Equally clear is the purpose of metamorphosis among the many parasites whose change of form is connected with a change of host and helps the animal to prepare itself for the next stage in its complicated life.

We find similar factors of conservation in examining the metamorphoses of insects. But here it is the mature forms which diffuse the species. The larvae are often restricted to a small feeding ground; they live in a single plant, in the ground where travel is difficult, in a narrowly circumscribed area at the bottom of a brook, or, in the case of fly maggots, in an animal cadaver. In all these cases it is the mature winged form that enables the insect to conquer new realms, which are often reached by long flights. The more mobile the flying form, the farther the species, which as a larva is often restricted to a very small area, can extend its range. Anyone who sees a dragonfly resting far from the water is a witness to the mysterious process by which insects diffuse their species, often crossing seas and mountain ranges.

The ecological interpretation of metamorphosis involves only one aspect. If we consider the distribution of metamorphoses in the animal world, another important set of facts opens up to us. Complete, deep-seated metamorphosis, such as that of the sea urchins or insects, is limited to the simpler forms of organism—it occurs in none of the higher types.

Insects and crustaceans are the highest of the invertebrates disclosing genuine metamorphosis. The highest type of invertebrate, the cephalopod, shows only scant traces of metamorphosis, involving chiefly the proportions of the tentacles and the form of the fins. If we classify the vertebrates according to the development of their nervous systems, we again find the most conspicuous metamorphosis in the lowest groups: the lancelet (*Amphioxus*) shows a spectacular metamorphosis, while that of the lampreys, frogs, and salamanders is very considerable. The fishes with highly developed nervous systems, the sharks, rays, and bony fishes, have no true metamorphosis; only a few deep-sea varieties—the eels, for example—have a conspicuous one, and here again what changes do occur are largely changes of proportion and color, never of basic structure. None of the large groups of land animals, neither the reptiles nor the birds nor the mammals, shows a true metamorphosis.

This strange distribution of complete metamorphosis calls our attention to a hierarchical order. Not only are the animals around us embedded in special environments to whose conditions they are adapted; they are also centers of an activity of their own, experiencing their environment in their own way. But this rich inner life and the resulting relations to the world are apportioned very unequally among the animal groups—so much so that all scientific systems more or less admittedly base their classification of the large groups on a system of relations with the environment. To be sure, our insight into these distinctions has been considerably reduced in the last hundred years by the predominance of utilitarian conceptions; today we are trying to regain and increase it by the use of objective methods and to formulate our statements on the subject with greater precision.

Complete metamorphosis seems incompatible with the highest levels of animal life—that is the first and most general conclusion of a comparative survey. By full metamorphosis we mean a change of structure involving essential changes in behavior, in the functioning of the nervous system and the sensory organs—a metamorphosis, in other words, such as that which takes place in a pupal stage. The extraordinary transformation of a pluteus into a sea urchin is also of this kind.

The restriction of full metamorphosis to the lower levels of animal life also involves many problems. Of these we shall consider only one: the significance of the individual.

To biologists the perishable individual is primarily an interchangeable representative of the enduring species. And the discovery of the primary character of the supraindividual has given this point of view still greater currency. Consequently, even the astonishing mechanisms for the preservation and defense of the individual tend to be regarded too exclusively as mere parts of a larger system working toward conservation of the species. When, for example, a biologist applies the term "hypertelic" to phenomena which obviously serve some purpose beyond conservation of the species, it is evident that he regards the survival of the species as the one and only *telos* and looks upon any hypertelic feature as a mere nail in the animal's coffin, as a symptom of degeneration.

Thus it is imperative that we begin once more to view the relation between the collective and the individual as a complementary, reciprocal relationship, and that we cease to disregard the evolution of the individual. It seems to me that in furthering this point of view a biologist can make a not unimportant contribution to the discussion of the problems with which our Conference is concerned.

At this point we must counter a possible misunderstanding, the notion that complete metamorphosis precludes individuality. Individuality is an attribute of all living things, and the more closely we observe, the more evident become the signs of individual differences. The investigations of von Frisch and his students on bees are gradually leading us to abandon our original notion of insect behavior as a relatively invariable sequence of instinctual reactions and to recognize striking individual variations.

The presence or absence of a genuine, complete metamorphosis will have to be considered in the light of the relation between the species and the individual. As long as the conservation of the species has precedence over the formation of individuals, metamorphosis remains a satisfactory mode of development, providing an excellent solution to certain problems and allowing of extreme variation in the form of the larva and mature animal. But as the "centrality" of the individual becomes more pronounced, it increasingly precludes the possibility of genuine metamorphosis and makes for the retention of a single specific form.

The highest forms of individuality, such as we observe among the higher vertebrates, do not occur in those animals that undergo metamorphosis. We have said that an individual factor is demonstrable even with metamorphosis—but it would be a mistake to suppose that minute observation of butterflies and bees, termites and wasps, discloses increasingly subtle differences, ultimately confronting us with a kind of miniature human being. Even the closest observation reveals only as much individuality as is possible within certain limits of variability—and all complex organisms have such limits.

The attainment of higher degrees of inwardness, of a richer structuring of the world through the experience of the individual, is a phenomenon of a special kind which has often been noted by biologists trying to understand the evolutionary process. This phenomenon is what has been called "elevation," as opposed to mere "specialization" (Franz, 1935). What Sewertzoff (1931) designated as "aramorphosis" refers to an intensification of all the functions as opposed to an "idioadaptation" which seems to refer one-sidedly to definite environmental conditions.[2] In our own studies on cerebralization we have dealt with the same problems, trying to arrive at objective definitions of this "elevation" or "aramorphosis" by investigation and measurement of the highest nerve centers.

[2] Victor Franz, *Der biologische Fortschritt* (Jena, 1935); A. N. Sewertzoff, *Morphologische Gesetzmässigkeiten der Evolution* (Jena, 1931).

The highest degrees of elevation known to us, the most complex aramorphosis, the most intense cerebralization—all are accompanied by an emphasis on the individual and hence by a particular "life value" which far exceeds any pure conservation or transformation of the species.

II

In investigating cyclic metamorphoses, such as that of the butterfly, biologists work within the clearly recognizable life spans of individuals. Difficult as some of the technical and theoretical problems may be, the frame of reference within which these investigations move is perfectly clear: with the discovery of the interrelation between action systems and reaction systems, with the reduction of these organs and functions to their genesis in the germ cell, a scientific solution has been found to a number of important problems.

But biologists are working on still another problem relating to transformation, which presents far greater difficulties: to explain the hidden processes which cause variations in the fixed life cycles of a species and so produce new forms. The countless documents of paleontology and comparative morphology demand such an investigation. The biologists who are carrying on this work in our time investigate all manner of new biological forms, even though what is new about them may be ever so unimpressive. This concern with what is totally new creates a great basic difficulty which does not arise in connection with the problem of cyclic metamorphoses: in the investigation of evolution there is no self-contained system of reference by which to interpret the results of experiment—as every physiologist does (often unconsciously but with perfect justification)—it is not possible to relate our experimental data to a *known* totality. We can only refer them back to the inherited substance of the genus or species in which the change has been produced. We can only prove that there has been a deviation from what was formerly present. But there is no sign to lead the scientific intelligence forward into the future. Is the change aimless, accidental, without direction? Does it follow rules of change which we shall be able only in the distant future to formulate on the basis of a whole sequence of changes? Most experimental biologists set down the "mutations" which we actually observe as accidental and undirected. But in judging this interpretation we must proceed with the utmost caution, bearing in mind that it is difficult, if not impossible, to draw conclusions relating to the future. A good deal of sterile discussion would be avoided if more attention were paid to this fundamental difference between the study of evolution and descriptive physiology.

In view of this difficulty facing the experimental study of evolution, it strikes me as exceedingly important to define the system of reference within which one is operating. In studying extinct animal species and comparing them with existing forms, one must conclude with the present unless we are dealing with wholly extinct groups. Thus a comparison with the groups to which we ourselves belong cannot encompass the remote future of the human race. But the study of large extinct series of organisms, or even of groups reaching into the present, permits us to include the latest and the earliest forms in a single system of reference and so to draw inferences concerning relationships that are necessarily hidden from the experimental scientist. Here I wish to speak about one aspect of such investigation in order to illustrate the second important meaning attaching to the word "transformation" in biology.

Transformation of types—metamorphosis of living forms. The question raised by these phenomena is equally obscure, and the phenomena themselves are just as puzzling and significant whether we turn our attention to the flowering plants or the vertebrates, or limit ourselves to a far smaller and more homogeneous group such as the birds, or concern ourselves with the insects, corals, snails, or mollusks, in whose shells such fantastic possibilities of formation are realized.

Here we shall concentrate on the evolution of the mammals. We ourselves are a part of it, and the problems involved encompass the problem of our own development.

Starting from geological facts, we establish a chronological relation between the evolution of the mammals and the other orders of biological development known to us from the insights we have gained into the organisms of earlier periods.

The time with which we are dealing amounts to some three hundred million years and embraces three long periods, punctuated by two great transformations which are among the central problems of evolution. In the course of these three hundred million years a vast number of very diverse evolutionary processes took place. One chain of development produced the horse, others of a very different kind culminated in the elephant, the whale, the deer, the antelope, or the giraffe. We must at least bear this multiplicity in mind, though in the following we shall consider only a single direction of transformation.

The first period began with the Triassic age and probably ended with the last Cretaceous age. This is the period in which the first, most primordial type of mammal lived on earth. Here we shall simply observe that there was such a period. At that time there were many forms of archaic mammal; among them the group that forms a true placenta and that we call Eutheria is of particular importance to us.

The second period began with the Tertiary and came to its climax in the middle of it, roughly in the Miocene. Now there developed a higher type of mammal, again extremely varied in form and mode of life. Isolated groups have survived from both periods, few from among the early Eutheria, many from the higher stage, among which the deer, antelope, elephant, horse, seal, whale, dolphin, long-tailed monkey, baboon, and anthropoid ape must be included.

In the middle of the Tertiary, if not before, occurred the transformation that is of particular importance to us. It was then that the Hominidae made their appearance, forms close to our human type, with which perhaps our own mode of existence began.

Here, of course, I shall only try to give the most general picture of the three periods and two transformations. My purpose in so doing is to throw some light on the origin of our form of existence and so illustrate the questions involved in the biological study of transformation by an example that is particularly close to us.

Let us first take a look at the archaic, basic type with which our picture begins. Here we shall disregard the duckbills and echidnas (the egg-laying mammals) as well as the marsupials, for these animals have evolved in very peculiar ways and can supply only very indirect information about the transformations with which we are concerned. The archaic representatives of the large group of Eutheria were relatively small in stature. Martens, squirrels, shrews, and porcupines give us a general idea of these oldest Eutheria.

The development of the higher brain centers is slight; as a means of orientation the sense of smell is dominant, though the eyes and ears may play a considerable role. For this reason we call this stage macrosmatic.[3] Employing a recently elaborated method of codifying brain development on the basis of the cerebral cortex, we find in these archaic mammals indices running from 1.7 to approximately 5—figures which take on meaning only when compared with our figures for higher stages. These early mammals were not very long-lived (three to ten years seem to be the limits), but they achieved sexual maturity at an early age, bore litters of five to ten—perhaps more—and seem to have all had brief gestation periods, roughly from five to six weeks. The young were helpless, naked nestlings—there was generally some sort of nest construction, often lined with some of the mother's hair for warmth. The brain development at the moment of birth was so slight that this central organ had to increase in volume by roughly seven to tenfold, sometimes more, a circumstance which made the infant quite helpless. The young developed quickly to maturity. Though with numerous variations, this was the basic pattern.

Another characteristic of these primordial mammals is related to the short gestation period. At birth the eyes and ears were undeveloped and for many days still in need of the liquid medium previously provided by the womb, the primordial water of the sheltered beginnings. This was provided by a temporary envelope. The eyelids grew together; the ear lobes bent forward and grew into the skin; the walls of the outer acoustic duct grew together. Protected by these envelopes the organs of sight and hearing developed their mature form. The close relation between these envelopes and early birth is attested by the marsupials, which have gestation periods of only eight to ten days and whose eyes and ears are similarly sealed in the early stages.[4]

The second stage in the development of the mammals discloses a number of new traits. Body size increases, some giant forms occur. The brain centers are considerably more complex; optic and acoustic orientation become far more important than in the archaic period; in some groups—the apes for

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[3] For further details and documentation see my *Biologische Fragmente zu einer Lehre vom Menschen* (2nd edn., Basel, 1951); and "Die allgemeine biologische Bedeutung der Cerebralisations-Studien," *Bulletin der Schweizerischen Akademie der Medizinischen Wissenschaften* (Basel), VIII (1952). See also K. Wirz, "Studien über die Cerebralisation: Zur quantitativen Bestimmung der Rangordnung bei Saugetieren," *Acta Anatomica* (Basel), IX (1950); and "Ontogenese und Cerebralisation bei Eutheria," *Acta Anatomica* (Basel), XX (1954).

[4] R. Weber, "Transitorische Verschlüsse von Fernsinnesorganen in der Embryonalperiode bei Amnioten," *Revue Suisse de Zoologie* (Geneva), LVII (1950).

example—the sense of smell is appreciably blunted; the whales go furthest in this microsmatic development. The cortical indices run roughly from 8 or 10 to 70 (compared with 1.7 to 5 in the first stage). Longevity increases with body size, twenty to thirty years becomes a common life span and members of some groups often live to be forty—the enormous life spans attributed to elephants are a mere indulgence of the human imagination; actually the age of fifty is seldom exceeded and then by no more than two or three years. Twenty-five to thirty years may be regarded as average longevity at this stage.

There is also a significant transformation in the mode of reproduction. Sexual maturity is postponed to the second or third year, sometimes until still later. Only one or two young are born at a time. The infant is much closer to the adult state than at the archaic stage: in behavior and proportions the young animal is a small replica of its parents. The brain has developed considerably: its volume doubles or at most triples by maturity; sometimes—as in camels and horses—it increases only by roughly one half. These young animals leave the nest at a very early age, a state of affairs characteristic of the higher mammals. Where the infant, as among the apes, clings to the mother and lets itself be carried, it takes an active part in the proceedings and is not merely held by the parent. This highly developed state at birth is the result of a prolonged period of gestation, many weeks longer than in the archaic forms, in some groups exceeding a year, in the sperm whales sixteen months, in the elephants twenty-two months. During this time the infant achieves the full sensory development of the adult, the posture characteristic of the species, the hereditary modes of social behavior, and full mobility. All these characteristics grow and mature in the shelter of the womb. Still another new development is that in many groups blood loss in childbearing is either reduced to a minimum or ceases altogether, thanks to a particular form and function of the connection between mother and young: this stage is attained by the whales and the higher hoofed animals and, among the primates, by the lemurs. The fact that the true apes, even at this higher stage, retain the original placenta with loss of blood at birth presents a problem in itself.

Our account of this second stage in the development of the mammals has been static—but each of the characteristics we have mentioned raises the question of change, of transformation.

We have spoken of increased body size and stressed the greater longevity.

What unknown transformations in the organization of the basic substance, the specific plasma, does this imply? How much regrouping and modification in the relations of the transformation systems that regulate the life of a mammal? We know that this transformation affects the reaction systems of the organs more than the action systems of the hormone glands, which always produce relatively unspecific agents. The change in the orchestration of the sense organs by which the animal experiences its environment gives us an idea of the mysterious and far-reaching processes involved in the mammal's development to a higher stage: apart from a number of structural changes, there is a general broadening of the animal's social and ecological relations. The new stage brings with it a more pronounced individual form; the individual gathers and utilizes more experience over a longer period of time, and this is reflected in the life of the group. This increase of experience is of course closely connected with the transformations that determine increased growth and longevity. Thus the new stage is not characterized by a mere accumulation of isolated physiological traits. And it is only when we consider the whole texture of new possibilities that we begin to suspect the magnitude of the problems raised by such transformations. Whether the transformation was effected in many small steps or in larger, more sudden metamorphoses, we do not know—nor do we know whether or not the transformations are of the same kind as those that are observed in experiments today, whether or not they resemble the mutations studied in genetics. From time to time research in comparative morphology opens up a rift through which we perceive a phenomenon that seems to represent a part of these far-reaching processes. We know today, for example, that the body began to change in form and increase in size at a stage of relatively low brain development, and that larger brain volumes were attained much later in the development of the higher mammals.[5] We have also learned that in most groups of mammals the new mode of reproduction, characterized by reduction in the number of young, prolonged gestation, mobility at birth, came first, and that only after this mode of reproduction was fully established did the process of brain transformation set in. This precedence of the transformation in body form, mode of growth, and mode of development over the increase in brain volume has also been

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[5] T. Edinger, "Die Paläoneurologie am Beginn einer neuen Phase," *Experientia* (Basel), VI (1950), 250–258; and "Paleoneurology versus Comparative Brain Anatomy," *Confinia Neurologica* (Basel), IX (Goldstein Anniversary-Number) (1949).

demonstrated in birds. Here, it may be presumed, we have hit on a significant rule governing the evolution of higher animal forms—we prefer to speak of a "rule," for in view of the wealth of possibilities we shall do well to be cautious in speaking of "laws."

Another phenomenon worth noting is that for a few days or weeks during gestation the eyelids and ears of all mammals at this second stage form the envelopes characteristic of the first stage. The embryo seems to be preparing for an archaic, early birth with the old protective mechanisms. These mechanisms of the early stage are embedded by heredity in the germ cell of every higher type of mammal, and the corresponding processes take place in the embryo—while the prolonged gestation period of the higher stage is fixed by heredity in the maternal organism. This repetition of protective structures connected with early birth is one of the most impressive indications of the profound kinship of all mammals. To the scientist it is a functionally meaningless sign indicating the occurrence of an archaic period in the uterus and hence also marking the moment at which the embryo enters on a new phase. Now the eyelids and ears open, and in the dark peace of the uterus there begins the period which the archaic mammal would have spent in the sheltered world of the nest or under its mother's protection. As indications of transition, these phenomena are of the utmost significance for our knowledge of the mammals' order of rank. They bear witness to the reality of transformations from stage to stage, regardless of how we picture these transformations.

And now the third stage—that of the Hominidae. It is with this stage that we are most especially concerned, and even if we take a definitely biological view in surveying the three stages, the special nature of man is evident. But whereas we possess a large number of documents—fossil evidence—for some groups of the first two stages, those pertaining to the Hominidae are still relatively rare.

Thus we know little about the early geological stages. At the end of the Tertiary and somewhat later we have the Australopithecus of South Africa, a presumably erect hominid with a relatively small brain volume of 700 cubic centimeters. The more we study these hominids, the more human they seem: it is not without reason that a new name has recently been given them, Australanthropus instead of the original name that meant "southern ape." Only recently the prehominid, Oreopithecus, was discovered in Tuscany, a prehuman type from the Miocene—proof that these early forms of our race also lived on European soil.[6] We do not yet know the size of the earliest hominids. The Australopithecus of the late Tertiary was approximately as large as the present dwarf races of mankind.

In our biological comparison we must utilize all paleontological documents as completely as possible. But narrow limits are imposed on this work, and we learn relatively little from fossil finds, because the hominids were noteworthy for their lack of physical specialization. It is probable that even at early stages this type was distinguished from others only by behavior, experience of the world, and social forms, none of which can be read from fossil remains.

But in any case a biological comparison must be based on a species that is known to us. Thus we take man of the historical period as our type. This is the only way of figuring out what transformations must have taken place in the course of the mysterious process through which man became man. Having defined our type according to the best scientific method, we compare the paleontological material with it. This is the only way in which we can evaluate this material and determine to what extent it supplies a record of our development.

The first important fact resulting from comparison with the two preceding stages is a further prolongation of the life of the individual. The average longevity is now twice that of the higher mammals: sixty to seventy years instead of thirty to forty-five. We shall content ourselves with this statistical observation, but it should be noted that we are still looking for an explanation of it. We know of no special orchestration of the hormone glands that might explain why human beings have a longer life span than the higher mammals. Since the secretions of the hormone glands are largely similar in the most divergent vertebrates, the increased longevity is probably a product of the reaction systems and hence ultimately of the germ plasma and its hereditary factors. Whether the increased nerve mass in our brain has anything to do with it, we do not know. Our neopallium index of 170 is more than three times that of the anthropoid apes and more than twice that of the elephants. The paleontological findings suggest that also in the development of man, the new body form—in this case erect posture—preceded the higher brain development, that the rule we have noted in connection with the birds and lower mammals also applies to man.

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[6] J. Hürzeler, "Zur systematischen Stellung von Oreopithecus," *Verhandlungen der Naturforschenden Gesellschaft in Basel* (Basel), LXV (1954), 88–95.

Particularly significant are the transformations in mode of growth. Sometimes we obtain a better understanding of the reality by setting up a fiction as a basis of comparison. The fiction we choose here is a human type that is also in every respect a higher mammal of the second stage. The comparative biology of the higher mammals provides ample material from which to construct a fiction of this kind.

The extraordinary brain development in itself requires a period of gestation far longer than that of the anthropoid apes. Since all the higher mammals are born in the posture typical of their species, the newborn animal-man should also, at birth, be capable of standing erect, endowed with the neuromuscular maturity of a foal or calf, a small macaque or baboon, a dolphin or a newborn whale. Taken together, these circumstances should call for a period of human pregnancy extending from twenty to twenty-two months.

It is a strange fact that the human mode of development accords precisely with this requirement. Since the work published by E. von Lange in 1903,[7] it has been widely recognized that our development in the first year after birth is fetal, and further light was thrown on the matter in 1922 by the American biologist Scammon.[8] Our growth processes follow the laws of fetal development up to the moment corresponding to the birth of our fictitious animal-man. In reality our period of development breaks down into two radically different parts. The long gestation that is theoretically required is passed in two media: the first half, in the womb, makes possible the maturation of inherited dispositions; the second half, thanks to early birth, is situated in the richer environment of group life, in a social uterus as it were, where development becomes a synthesis of maturation, experience, and adaptation to the life of the community. This fusion of growth and learning is the special secret of the human stage. The fiction of the animal-man throws a bright light on our astonishing mode of development which is not, as has sometimes been thought, a mere prolongation and slowing down of the animal mode. Our human life has a richly articulated basic melody, a pervading theme which is varied in the life of each individual. The part of it which may be evaluated as fetal, since it occurs before man

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[7] "Die Gesetzmässigkeiten im Längenwachstum des Menschen," *Jahrbuch für Kinderheilkunde*, n.s., LVII (1903).

[8] R. E. Scammon, "On the Time and Mode of Transition from the Fetal to the Postnatal Phase of Growth in Man," abstract in *Anatomical Record*, XXIII (1922): 1, 34.

acquires his specific posture and language, is sharply divided into a purely maternal and a richer social period. The ensuing period up to full maturity is once again divided into stages which have no counterpart in the development of the higher mammals, the most specific of these being the late acceleration of growth at the age of puberty. In the first part of our lecture we have mentioned a few of the organic factors that regulate the stages in our development, which we compared with the metamorphoses of insects. But we have also learned that these hormonal organs are of a very general nature and do not account for specifically human features, that their organization and orchestration are governed by specific structures which we must assume to be situated in the plasma, with its hereditary fabric of cell nuclei, though thus far we have no definite knowledge of the specific factor that produces man's prolonged life span and characteristic transformations.

The early period of development peculiar to our form of existence is closely related to the specific nature of man. For man is unique in the fact that though the apparatus with which he experiences his environment is largely laid down by heredity, the free combination of hereditary material with subsequent impressions plays an enormous part in his actual experience. A good deal of light is thrown on the mystery of what has been called our openness to the world by our form of development, for all the essential forms of human behavior have their roots in the social uterine period with its special mode of development accompanied by learning. Upright posture, language, intelligent action—these three specific human attributes develop from open predispositions in the course of maturation; the social group—chiefly the mother but under normal circumstances the entire environment, social as well as natural—contributes to their formation. All this is connected with the special nature of our infant state, which only the dullest observer can identify with the nestling stage of the archaic mammals. The human embryo first passes through an archaic phase, in which the gates of the senses are sealed off, a phase oriented toward early birth. In the second to fifth month this phase is completed. Then the human embryo enters its second phase: that of the higher mammal; once again the gates of the senses open, as though the infant were already born. In this period the neuromuscular apparatus matures quickly. It is not for nothing that neurologists have likened the state of our nervous system at birth to that of a foal rather than that of a lion or bear cub. So far, man seems to be developing according to our model. But the blueprint does not call for completion of this second phase; it is diverted into a third. The growth of the hind extremities begins to lag, so that they are no longer than the arms at the time of birth. The human child comes into the world in its unique position, turning its eyes to its mother in its helplessness as no other higher mammal does in the act of suckling. The peculiarities of our newborn babe can only be meaningfully explained as a birth into the "social uterus."

If I were asked what fact accessible to biological investigation marked the most significant transformation in the development of man, I should speak of the connection between our openness to the world and freedom of decision and the twin phases of our early development, and most particularly of the special character of the first year of man's life, which I have designated as the period of the social uterus.

The transformation from an animal embedded in its environment, from a creature whose reactions to a relatively few predetermined things are fixed by heredity into a being open to the world, master of his experience, and able to choose his social forms and means of communication: this is the one great step in the development of man. The rest—the transformation in the human germ of the experiential mechanism, from hereditary structures with little capacity for receiving impressions into specifically human "open" systems, which take on their characteristic structure only in confrontation with the environment, and which even then remain subject to change to a degree that varies with the individual—is complementary. The special character of creative individuals is in part determined by this childlike openness. And the constant need of completion that is manifested in religious sentiments is another aspect of this human openness; we find it symbolized in the image of the open wound or of the flower awaiting fulfillment. With what biologically identifiable particulars of our human structure this specific openness is connected, we do not know. But whether it proves to be localized in the cerebral cortex or elsewhere in the brain, there is no doubt that its special nature derives from specific predispositions embedded in the human plasma.

Paleontological investigation has situated the events that make up the genesis of man roughly in the middle of the Tertiary, perhaps some twenty million years before our historical era.

Comparative biology, for its part, has begun to describe the great typological stages that characterize the transformation leading to man. This comparative research is today tending toward a new point of view. Formerly, biology was generally concerned with establishing the characteristics that we share with higher animals related to us in form. Where this method was employed, it was necessary to forget or disregard everything that is specifically human, though it was this very factor whose origins were to be explained. The contrary procedure, which consists in investigating only the distinguishing features, in order to stress our special position, is just as one-sided, for it disregards the many essential traits that we share with the animals. Both these methods set artificial boundaries; both speak of a something called "man," but in both cases it is a lifeless, intellectual fiction.

In our attempts at comparison we try to describe the whole life form at every stage. In this way we arrive at descriptions that take account both of the parallels and of the differences, and thus show what must actually have happened at every stage of development. The exposition is static. But by emphasizing the contrasts between stages, it calls attention to the facts that an investigation of the dynamic aspects of human development must try to explain.

Our comparative studies make it clear that the investigation of fossils touches on only one aspect of the problem of transformation. I believe that it is one of the great tasks of biology to open up the whole range of the problem.

Only then are we made aware of such unanswered questions as these: Was what we have termed the human stage attained in *one* vast process of development? Or was it realized in many separate steps? Are such steps comparable to those which experimental scientists call mutations; are they small transformations accumulating over millions of years? Or are these experimentally induced transformations merely one type of transformation among many others of which we thus far have no experimental knowledge?

To these questions we have no definite answers, despite the very positive statements of certain students of evolution. For in choosing among possible hypotheses and solutions in biology, men are not guided entirely by objective evidence; another important factor is their whole personal mode of experiencing the world, and this includes religious needs, aesthetic evaluations, historical knowledge, theoretical views of all kinds, dominant moods, critical encounters and experiences, intuitive powers and the general cultural situation which affects our conscious attitudes and, to a still greater degree, our unconscious ones.

The richer becomes our experience of the specific nature of the human mode of existence and its special possibilities—particularly our insight into the prefigured structure of the finished human individual—the more mysterious and obscure becomes the problem of origins.

But all of us here are working together to obtain such insight into the prefigured structures. Perhaps our survey has thrown some light on the magnitude of the problem of origins seen in its biological aspect. I trust we have made it clear that our attitude is not one of easy, comfortable agnosticism. Nothing is gained by insisting that we know nothing; the essential is that we seek, by rigorous and untiring research, to know what is within the limits of our knowledge. It is only the widest knowledge that can confer some insight into the vastness of what remains hidden, that can enable us to peer into the darkness which hides what we do not yet know, and this encompasses not only today's scientific problems, but also the dark sphere of eternal mystery. At the end of every quest, even when it is crowned by discovery, the biologist, too, peers into the darkness that one of our lecturers has termed *lumineuses ténèbres*. There lies the zone of silence where discourse has its limits. In the course of our conscious effort, we come to the point where, with the Zen master, we find it better to raise a finger than to say anything whatsoever.