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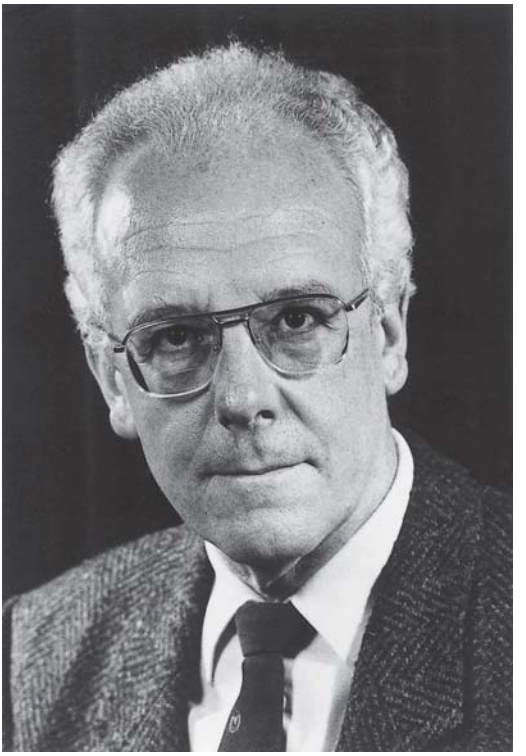

Curriculum vitae

1930 Hans Mohr was born on a farm in the Black Forst/Germany

1949 Graduation from a German Gymnasium under French supervision

1950 Undergraduate student at the University of Tübingen/Germany: Philosophy or science?

1953 Graduate student in biology with Professor Erwin Bünning

1955 Submission of a Ph. D. thesis to the Faculty of Sciences at Tübingen University

1956 Postdoctoral research fellow at the Plant Industry Station at Beltsville, Md., U.S.A.

1957 Married to Dr. Iba Kraut, brilliant biochemist and wonderful partner

1959 Habilitation at Tübingen University

1960 Professor of Biology, University of Freiburg; Visiting Professor, University of Massachusetts

1966 Member of the German Academy of Sciences (Leopoldina)

1982 Member of the Heidelberg Academy of Sciences and Humanities

1982 Honorary Editor of the International Journal of Plant Biology, Planta

1992 Director at the Governmental Insitute of Technolgoy Assessment in Stuttgart

1992 Member of the presidency of Leopoldina

1992 Member of the 'Innovationsbeirat' (State Government, Baden-Württemberg)

1995 Member of the 'Technologiebeirat' (Federal Government, Bonn)

1997 Retirement

2000 Honorary Member of the German Botanical Society

2002 Member of the University Council, University of Konstanz

Many honours, including honorary doctorates, the Cothenius medal in gold, the Max Born medal and the Bundesverdienstkreuz, 1st class

Author/Editor of 18 books and approximately 400 articles

A Life History Between Science and Philosophy

Hans Mohr

1 Philosophy or Science?

When I graduated from an old-fashioned German Gymnasium under French regime my interests were divided between science (physics) and philosophy, with an intuitive preference for the latter. However, by the end of my first semester at Tübingen University I realized that I needed a more solid education in science to study that branch of philosophy I was particularly interested in, namely epistemology. By that time I considered philosophy as primarily an epistemological subject.

Epistemology investigates the origin, nature, methods and limits of human knowledge. Since in the modern world the sciences had become the major source of positive knowledge, a deepened introduction to the basic sciences was obviously a prerequisite for any career in epistemology.

Moreover, I was dissatisfied with the prevailing German academic tradition of teaching philosophy as a history of philosophical thoughts. My deep interest in modern fields, such as modern logic and analytical philosophy, was hardly met. As far as the leading philosophical fashions of the time were concerned, neither Heidegger's existentialism or fundamental ontology nor the late Husserl's transcendental phenomenology attracted me.

Fortunately, some of the famous science professors in Tübingen had strong philosophical minds: Walter Kossel in physics, Max Hartmann in natural philosophy and Erwin Bünning in botany. Bünning, who by that time had established the concept of the physiological clock, had just published a superb treatise on *Theoretische Grundfragen der Physiologie* (Bünning 1949) which I studied with keen interest. Moreover, I enjoyed reading a well-thumbed copy of A.J. Ayer's brilliant book of 1936 *Language, Truth and Logic*. This ideally accessible, lucidly written work stabilized my plans to become a real scientist before considering any career in philosophy. Ayer, the genuine philosopher, had argued convincingly: "If you want a philosopher to be constructive..., then I think you've got to marry him to a scientist." At the end of *Language, Truth and Logic*, Ayer saw the future of

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philosophy only in its being the logic of science. In retrospect, I gratefully acknowledge that Bünning and Ayer put me on the right track.

Equipped with a stipend of the Studienstiftung des Deutschen Volkes, I studied physics and biology. At the graduate level, I preferred biology even though quantum physics and thermodynamics remained favorite topics. Fortunately Erwin Bünning accepted me as candidate for a doctorate in 1953. He was a great mentor and a fine person.

2 Early Steps in My Scientific Work

2.1 Towards Phytochrome

The action spectrum of a photobiological response represents, with certain assumptions, the absorbance spectrum of the effective absorbing substance (photoreceptor). Bünning wanted me to identify by means of action spectroscopy the photoreceptor involved in the germination of fern spores. After some preliminary studies I chose the spores of the common male fern, *Dryopteris filix-mas*, for the following reasons:

- These spores never germinate in complete darkness.
- The light requirement can be satisfied by a short light treatment of the fully imbibed spores. That is, germination can be 'induced' by light. If the spores are placed in darkness after the light treatment, complete germination takes place.
- In the Botanical Garden in Tübingen I detected a population of cloned *Dryopteris* sporophytes. They had been derived in the 1930s from a single rhizome by the late Prof. Lehmann, who was interested in the appearance of somatic mutations. From this clone I collected the most homogenous spore population you can imagine.
- The spore material could easily be germinated and inspected on a thin agar medium. I have only very rarely observed contaminations within the time span required for germination.

As far as my experimental equipment was concerned I was equally lucky: interference filters had just become available, and I, together with my friend G. Schoser, could construct an interference filter monochromator unit for photobiological purposes. This type of irradiation device has had decisive advantages compared with prism- or grating-equipped monochromators. Measurement of the photon flux of the monochromatic light beams posed a problem since photocells turned out to be a poor choice. However, Bünning provided the money to buy an expensive bolometer, and Kossel offered me an extremely sensitive thermopile which I could use over night

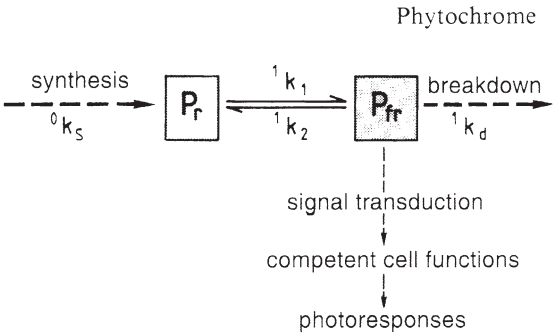

Fig. 1. Scheme of the phytochrome system. Explanation: phytochrome appears in two forms, *Pr* and *Pfr*. Without light only P_r, the physiologically inactive form, is made. Under the influence of light P_r changes into P_{fr}, the physiologically active form. The photoconversion P_r–P_{fr} is photoreversible; it follows first-order kinetics $^1k_1$, $^1k_2$ in both directions. The signal induced by light is passed on from P_{fr} (signal transduction) and received by cell functions competent for this signal, e.g. by promoter regions of competent genes. Specificity of photoresponses is determined by the spatial and temporal competence pattern for P_{fr}. Light (P_{fr}) has no influence on development of this competence. Phytochrome is a predominantly hydrophilic chromoprotein which is easily isolated from the cell. The absorption maximum of P_r is 665 nm in vitro, i.e. in the red (R); that of P_{fr} is 730 nm in the far-red (FR). (Mohr and Schopfer 1995)

(since it was needed in the Physics Department during the day). In fact, with the help of my girlfriend Iba (who fortunately agreed to marry me later), I could produce and measure with high precision all types of monochromatic beams which I needed for my work. The result was worth the effort: I was able to elaborate a very precise action spectrum, and we found the 'reversible red/far-red photoreactive system', which was later named 'phytochrome' (Mohr 1956).

In the meantime, however, the reversible red/far-red photoreactive system had been discovered and described by the Beltsville research group in studies on light-induced seed germination. A modern version of the phytochrome system is reproduced in Fig. 1.

Even though I was only second, I received the Research Prize of the University – the first time in my life I owned 2,000 Marks – and, more important in the long run, I was invited by H.A. Borthwick to join the Beltsville group as a postdoctoral research fellow.

2.2 The Beltsville Group

The discovery of the reversible red/far-red control of plant growth and development and the subsequent in vivo identification and isolation of the

photoreceptor pigment phytochrome constitutes one of the great achievements in modern biology (Sage 1992). It was primarily a group of investigators at the Plant Industry Station, Beltsville, Maryland, USA, headed by the botanist H.A. Borthwick and the physical chemist S.B. Hendricks, who made the basic discoveries and developed a theoretical framework on which the progress in the field of (molecular) plant development has been largely based.

I joined the Beltsville group in mid-1956. The mode of cooperation at the Plant Industry Station opened my eyes to the benefits of teamwork, and the wisdom, humility and helpfulness of the two senior scientists was an unforgettable experience which has been a constant inspiration throughout my research career.

2.3 Photomorphogenesis

Photomorphogenesis (Mohr 1972) has remained the major theme of my scientific efforts after my return to Germany, following Bünning's advice to try for habilitation, by that time a prerequisite for an academic career in Germany. By 'photomorphogenesis', we designate the fact that light controls growth and differentiation (and therewith development) of a plant independently of photosynthesis. In order to grasp the full importance of this phenomenon we must recall that the specific development of any living system depends on its particular genetic information and on its environment. In the case of higher plants, the most important environmental factor is light. Of course, light does not carry any specific information with regard to plant development. Rather, light – operating via photoreceptor molecules – must be regarded as an elective factor which influences the manner in which those genes that are contained in the particular organism are being used. In this sense, the study of photomorphogenesis (Fig. 2) became central to a worldwide program to investigate the influence of the environment on the development of higher organisms, including man. I contributed to this latter aspect with a book chapter in *Freiburger Vorlesungen zur Biologie des Menschen* (Mohr 1979a).

3 My Academic Career – A Short Story

I stayed at Tübingen University only for a little while. In February 1960, some months before my 30th birthday, I was offered the traditional chair for botany at the University of Freiburg to succeed Professor Friedrich Oehlkers, an eminent cytogeneticist.

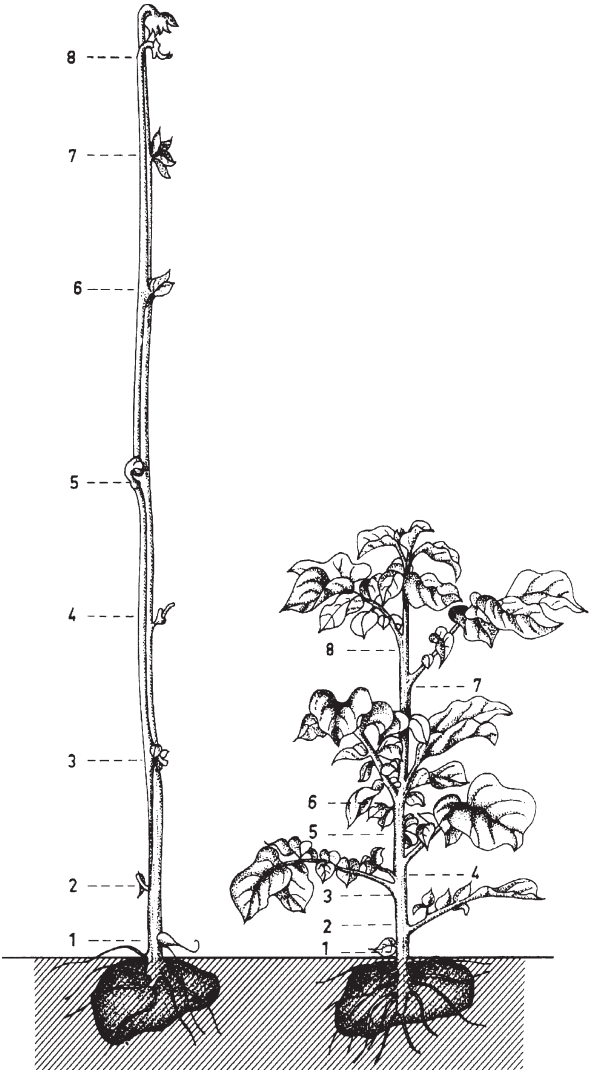

Fig. 2. Both potato plants (*Solanum tuberosum*) are genetically identical. *Left* An etiolated plant grown in darkness; *right* the normal light-grown plant. Scotomorphogenesis (etiolation) is characteristic of development of plants under light-deficient conditions; the alternative development in light is called photomorphogenesis. It is noteworthy that light affects the expression of patterns, the specification of which is light independent. In the present case, patterns of leaf arrangement (called phyllotactic patterns) are precisely the same in etiolated plants as in light-grown plants. However, development from leaf primordia to leaves takes place only in the light. Etiolation is an adaptive response of plants, because as long as the plant is grown in the dark, the limited supply of storage substances is predominantly invested in production (growth) of the shoot axis. This is the most likely way of ensuring that the plumule reaches the light before reserves are depleted. This scotomorphogenesis may be interpreted as a strategy for survival. Photomorphogenesis, on the other hand, is the suitable strategy for development in light (affluence strategy). (Mohr 1972)

To make the right choice was not easy, since I had planned firmly to return to the United States after habilitation, at least for a couple of years. Eventually, my wife and I decided to accept the position (Professor and Department Head) in Freiburg. An important factor at that time was that the administration agreed that I could spend at reasonable intervals a couple of months at American institutions to maintain close personal contacts with my colleagues in research and teaching.

Freiburg University turned out to be an excellent place. Once we had established a new faculty and moved into new buildings, the plant biology department was ready for top research and new kinds of teaching. In 1968, we were chosen by the Deutsche Forschungsgemeinschaft to become a center of excellence (SFB). This implied that we could count on sufficient support provided that we could meet the strict requirements in 3-year intervals.

During the political turmoils in the period 1968–1972, my wife and I reconsidered emigration to the USA. However, since 1972, I have had no doubts that Freiburg was the place where I wanted to work and to live. Only in 1991 did I accept an offer by the State Government of Baden-Württemberg to become a director at the newly established Institute for Technology Assessment in Stuttgart. This meant, in early 1992, the final departure from the laboratory and from regular academic teaching.

4 Some of my Research Topics in Freiburg

4.1 Photosensors in Photomorphogenesis

In order to react optimally to the light conditions in their environment, higher plants require various sensor pigments. Based on molecular physics, you can predict that phytochrome alone is not sufficient to measure all the relevant solar spectrum (290–800 nm) with the required accuracy. Today, it is known that three types of photosensors are involved in the process of photomorphogenesis in higher plants: phytochromes (> 520 nm; red/far-red), cryptochromes (340–520 nm; blue/UV-A) and the UV-B photosensor (290–350 nm).

We have tried over the years to understand at the physiological level the mode of coaction of the photosensors in bringing about photomorphogenesis, including control of gene expression. It can be seen from an early diagram (Fig. 3; Mohr 1987) how we felt the three photosensors worked together. It appeared in all cases that phytochrome (P_{fr}) is the effector proper whereas the blue/UV-A and the UV-B photoreceptors (together with phytochrome) determine the plant's responsiveness to P_{fr}. Even though in

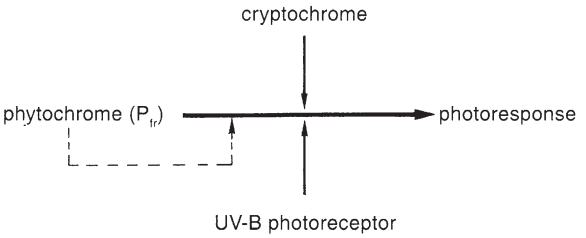

Fig. 3. Schematic of cooperation between phytochrome and the blue/UV-absorbing photosensors. Light absorption in cryptochrome and the UV-B photoreceptor determines the sensitivity of a photoresponse towards P_{fr}. *Dashed line* indicates that light absorbed by phytochrome can also increase the efficiency of P_{fr} or, expressed differently, it can increase the sensitivity of plants towards P_{fr}. (Mohr 1987)

the meantime the experimental approaches have become 'molecular' rather than 'physiological', the basic message contained in Fig. 3 has remained: in addition to the transduction chain triggered by P_{fr} and influencing responsive promoters by direct contact with transcription factors, "extensive cross-talk between signaling cascades downstream of multiple photoreceptors has become apparent..." (somewhat confusing, I admit, but this is the tribute of our field to becoming 'molecular') (Frankhauser and Staiger 2002).

4.2 Multiple Effects of Phytochrome

Obviously, P_{fr} has multiple effects at the organ level (Fig. 2). Multiple effects of P_{fr} can also be demonstrated at the cell and tissue level (Fig. 4). Subepidermal cells of mustard hypocotyls synthesize large amounts of anthocyanin under the influence of P_{fr}. Other cell layers of the axis do not form anthocyanin, even though they all react to P_{fr} with respect to their longitudinal growth. Some epidermal cells (trichoblasts) grow under the influence of P_{fr} into long hairs, but do not form anthocyanin, etc. The obvious multiple effect of P_{fr} at the level of tissues and cells can only be explained by the assumption that cells are differently competent for P_{fr} and that this pattern of competence exists before active P_{fr} is first formed. Epidermal trichoblasts of mustard hypocotyls (see Fig. 4) react differently to P_{fr}: on the one hand, they grow into long hairs, whilst on the other hand, their longitudinal growth is inhibited. Subepidermal cells show a corresponding pattern, i.e. one may say that they react positively by the synthesis of anthocyanin to P_{fr}, whilst they react negatively to P_{fr} with respect to their growth. We must inevitably assume specifically competent cell functions.

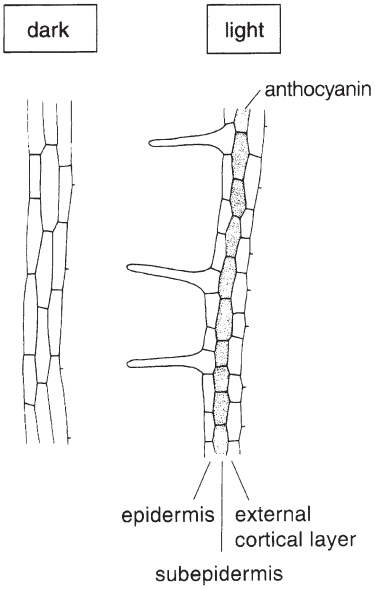

Fig. 4. Drawings representing the three outer cell layers of a mustard seedling hypocotyl in longitudinal section. *Left* Dark-grown seedling; *right* seedling kept for 24 h in light. (Mohr 1972)

4.3 Control of Gene Expression by Phytochrome

In 1966, we reported the induction of enzyme synthesis by phytochrome (Durst and Mohr 1966). Unexpectedly, the scientific community responded quite reluctantly. When I gave a seminar on the subject at Beltsville (October 1966) I could not convince colleagues that they should join us in investigating photomorphogenesis in terms of control of gene expression. Though readily accepted in Germany, the gene regulation hypothesis faced an icy reception in the USA. I received ironic (insulting?) comments throughout my lecture tour, even by some prominent colleagues who only a few years later enthusiastically joined the crowd once molecular physiology had become popular, and nobody any longer opposed the concept that phytochrome operates on development via control of gene expression. In principle, I was not very concerned because I knew that I was right, and I made precise plans while travelling in the USA to substantiate the gene regulation hypothesis after my return to the Freiburg laboratory. It worked!

A first step was to demonstrate that within the same tissue – we had chosen mustard seedling cotyledons where cell number and DNA content remained constant during the experimental period – phytochrome (P_{fr}) could simultaneously induce (Dittes et al. 1971) and repress (Oelze-Karow et al. 1970) enzyme synthesis while syntheses of some marker enzymes of the basic metabolism were not affected at all (Karow and Mohr 1967).

Unfortunately we were not able in the late 1960s to elucidate the nature of the signal transduction cascade from the cytosol to – what we assumed – competent promoters.

Our studies of nuclear-encoded chloroplast enzymes have finally demonstrated that phytochrome in fact regulates gene transcription (Schuster and Mohr 1990). However, we did not suggest that gene expression is controlled only at the transcriptional level. Rather I pointed out: "Full gene expression means the appearance of a final direct gene product – a protein – active at its physiological site of action... In principle, there are many steps between the initiation of transcription and the accumulation of the gene product at its functional location where gene expression could be regulated." As an example, in the case of nitrite reductase phytochrome produces the mRNA, whereas in order to make the enzyme out of the mRNA you need nitrate (Schuster and Mohr 1990). So you have a beautiful two-step control, transcriptional as well as post-transcriptional, which we could take apart.

4.4 Nitrate Assimilation and the 'Plastid Factor'

In 1982, I was elected member of the venerable (and well-endowed) Heidelberger Akademie der Wissenschaften. From 1986 onwards, the Academy financed a research unit in Freiburg to study the formation of the apparatus of nitrate/ammonium assimilation during the development of chloroplasts. The final goal of the research was to breed plants with an improved potential to assimilate nitrate (Mohr and Neininger 1994).

Since the research unit attracted a couple of excellent graduate students we could establish within a few years a consistent model for the formation of the apparatus of nitrate assimilation during the development of chloroplasts (Mohr 1990a). A fascinating result of this research may be mentioned briefly: the plastid factor (Oelmüller and Mohr 1986). Research from different angles (defect mutants, photo-oxidative damage of plastids) led to the conclusion that there is a plastid signal which acts as a transcription factor on nuclear genes. This signal (plastid factor) informs genes in the nucleus, which code for plastid proteins, that plastids are receptive to their protein products (Fig. 5). If the signal is missing, for example as a consequence of photo-oxidative damage to the plastids, transcription of nuclear genes coding for plastid proteins is blocked. In this case phytochrome is ineffective as an inducer of transcription. The plastid factor, the molecular nature of which is still unknown, is thus at a higher level of the regulation of transcription than is phytochrome (and nitrate) (Rajasekhar and Mohr 1986). The gene expression of typical cytosolic enzymes is not affected by

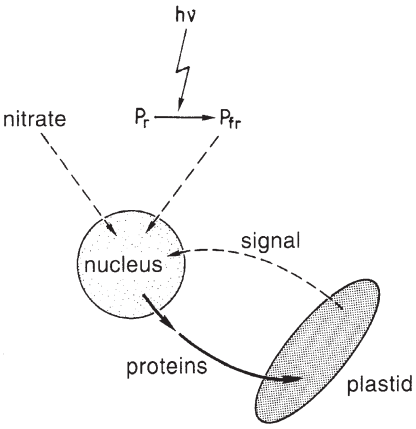

Fig. 5. Schematic showing the significance of plastid factor (*signal*) for expression of nuclear genes coding for plastid proteins. The plastid factor can be interpreted as an unspecific transcription factor without which neither light (via phytochrome) nor nitrate can become effective at the level of transcription. (Mohr and Schopfer 1995)

the lack of plastid factor. Under experimental conditions where, for example, SSU-mRNA and LHCII-apoprotein-mRNA disappear completely, synthesis of representative cytosolic, mitochondrial and glyoxysomal enzymes proceeds normally (Oelmüller and Mohr 1986).

5 A Textbook on Plant Physiology

In the 1960s a modern textbook of plant physiology was urgently needed to support teaching and to improve learning. Erwin Bünning persuaded me in the mid-1960s to publish my lectures on plant physiology which I had delivered in Freiburg and in part abroad. The original version of the textbook was written in German (Mohr 1969). Later, once the text was well established and Peter Schopfer had agreed to join me as an author, new editions as well as English (Mohr and Schopfer 1995) and Japanese translations followed.

To write a textbook is very different from preparing lecture notes! Expressed differently: to transform lecture notes into a coherent, consistent and balanced text requires an enormous concentration, in particular if the only time during the week left over for this task was from Friday night to Sunday afternoon. To achieve this goal you need stable health and a tolerant family. Fortunately, I had both.

The text was readily accepted by the students – and even by most of my colleagues. This was by no means a matter of course, since I left no doubt in my 'concepts of physiology' that physiology is not something like immature biochemistry but a science of its own, namely the science of organismic regulatory and control processes (Mohr 1988). Moreover, in my view,

physiology is a quantitative (or exact) science. By analogy with physics the aim of physiology is to elaborate general statements (laws).

This was not my personal hybris! Physiologists have always wished to postulate at least some statements with the same authority and validity as our colleagues in physics. The recent successes in biochemistry and molecular biology have significantly reduced the self-confidence of physiologists and even, at times, produced a kind of neurosis, leading to the statement "that physiology has moved to the periphery of the problems." I am still convinced that my view of physiology as sketched above is right, but I am no more convinced that the present generation of physiologists can prevent what I called some years ago "the molecular collapse of quantitative physiology." Of course, I appreciate and enjoy the amazing discoveries made in molecular plant biology during the last 15 years, but the limits to reductionism may not be ignored (Mohr 1989). A very important challenge in the next decades will be constructing an interface between genomics and whole plant and animal physiology (Melvin 2003).

6 Steps in my Philosophical Thinking

I do not claim to be a professional philosopher of science. Rather, I consider myself a natural scientist with a profound interest in the nature of scientific thought and in the significance – including the cultural significance – of science. Since nobody can afford time to follow up every interesting idea, I had to select philosophical problems with a high probability of a pay-off for a practicing natural scientist. As a consequence, my 'philosophy', including my 'political philosophy', has remained closely connected with the progress of the sciences.

6.1 Structure and Significance of Science

The discoveries of science had a profound effect on man's philosophy, ethics and spiritual beliefs. I had planned for many years to organize my ideas on this subject matter. The opportunity of writing a treatise was made possible by a Visiting Professorship granted to me by the University of Massachusetts during the autumn term of 1975. The published text is based on a series of 15 lectures that I delivered at the University. I am still grateful to the students, and to my colleagues and friends at the University, for the cordial reception, continuous interest and constructive criticism. It was the positive response of my class and the fascinating intellectual climate at

Amherst, Maas., that encouraged me to revise the lectures for print (Mohr 1977a).

I dedicated the book to Erwin Bünning and to Walter Kossel. As I mentioned above, Bünning's book *Theoretische Grundfragen der Physiologie* was a major determinant in my decision to become a biologist (Bünning 1949). The late Walter Kossel introduced me to physics. He was not only a great physicist, but also a fascinating philosopher and an admirable personality. I had some bad feelings when I submitted the final text for print. I could only hope that the professional philosophers would forgive me if my treatise did not always respect the conventional division of labor between science and philosophy. I fully agreed with David Hull who had just criticized some noted scientists who tried their hands at 'philosophizing': "Just as scientists are entitled to established standards of competence for their undertakings, philosophers have a right to expect at least minimal competence in theirs" (Hull 1975). On the other hand, I felt that it was legitimate to base a reflection about 'structure and significance of science' primarily on the self-understanding of the practicing scientist. My deep-rooted respect for philosophy in toto and for epistemology in particular would hopefully prevent me from becoming chauvinistic in favor of the scientific world view.

The influential Anglo-Saxon schools in the philosophy of science have generally equated philosophy with epistemology, treating ethics as not properly part of academic philosophy. Since I was not obliged to any philosophical school, but looked at the problems from the point of view of a practicing scientist, I did not follow the tendency of excluding anything from consideration that might raise moral problems. Rather, I intended to emphasize this aspect. Moreover, I took the liberty of looking at some traditionally epistemological problems, such as empiricism and rationalism, from the point of view of scientific knowledge.

Another point was that by this time (1975) most philosophers of science, in particular within the dominant positivist school, took the Comtean view of physics as the paradigmatic science and of biology as a relatively immature and secondary study. Even as an enthusiastic biologist who was proud of his trade, I could not ignore this tendency since there is some truth in it.

While there is no principal difference between physics and biology, the general approach in both fields and the nature of physical and biological theories and laws obviously differ to a considerable extent. I often referred to physics rather than to biology not only for the sake of simplicity, clarity and brevity, but also for the reason that physics has a far wider scope than biology. Physics deals with the properties of all matter whereas biology is only concerned with living systems or with ecosystems in which living

systems play the major part. All living systems are physical objects, but only a very small number of physical objects are considered to be living systems.

In the treatise I have often used the term 'responsibility'. This term implies, and I did emphasize this at the very beginning, that we are responsible for our acts. Indeed, I presume that moral responsibility is part of human nature, irrespective of the century-long discussion on determination, free will and moral responsibility. Determination to a scientist conveys the general proposition that every event has a cause. Whether this general proposition is true is a difficult question to decide, but it is certainly assumed to be true by most scientists. Otherwise science, in particular prediction, explanation and purposive action, would not be possible. On the other hand, we presume that we are responsible for our acts. It is implied as a matter of course that moral responsibility is an integral part of human nature. Indeed, we all believe that moral responsibility is real.

Since moral responsibility implies free will and self-determination (in the sense that we can create de novo determinants for our conduct and thus break causal continuity), the very serious and difficult question arises of whether moral responsibility (which implies free will) is compatible with our scientific knowledge, which plainly says that the concept of a breach in causal continuity is not acceptable. From the point of view of science, the reality of free will cannot be conceded. On the other hand, as human beings, we depend on the belief that at least some of our actions (called 'willed actions') are preceded by deliberation and choice and that our choice can be influenced by consideration of consequences.

Of course, I could not solve the paradoxes of free will (Stent 2002), but a thorough description of the paradoxes turned out to be a great advantage when I analysed – later in the book – the principle of causality and the structure of teleological action.

6.2 Epistemology and Evolution

Einstein once stated that for him the most unintelligible thing about the world is that it is intelligible. Why can we use the axioms and theorems of Euclidian geometry to reason about the physical world (Mohr 1977b)? Why is it legitimate to apply to a wheel (a physical object) the mathematical formula derived for a circle:

$$c = 2\pi r$$

As you all know, the use of diagrams is not essential to geometry. Geometrical reasoning per se is purely abstract. If diagrams are introduced it is only

as an aid to our reason. In any case, a circle and a wheel are totally different things, but nevertheless the wheel obeys the formula obtained for the circle.

I have written here another formula, derived by Gauss, for a purely mathematical relationship between two variables:

$$y = \frac{1}{\sigma\sqrt{2\pi}} \cdot e^{-(x-\bar{x})^2/2\sigma^2}$$

Why is it possible to describe and treat the frequency distribution in biological populations with the help of this relationship, e.g. the frequency distribution of intelligence test scores in a human population? In brief: why is mathematics, a purely deductive system of axioms and theorems, applicable to nature? Galileo stated in 1623 that "nature is written in mathematical language" (and this phrase has been repeated and followed by scientists ever since), but he could not give any naturalistic explanation why this is so.

We may extend our question to the whole of logic (I consider mathematics to be part of logic). Why can we rely on syllogistic reasoning? It is probably that the principle of the syllogism was formulated not before but long after the usefulness and validity of syllogistic reasoning was discovered by man. Logic is the theory of deductive argument, not its source. Why does the real world obey logic? Wittgenstein (in his early phase) was very concerned about this question. As he puts it, our justification for holding that the world could not conceivably disobey the laws of logic is simply that we could not say of an illogical world how it would look. This is obviously not a good argument. Rather, it is a sign of perplexity and ignorance.

Or remember Ayer in *Language, Truth and Logic* (Ayer 1936): His second class of propositions were the formal propositions of mathematics and logic, and they were held to be tautologies. Ayer thought of them (as did Wittgenstein) "as being merely rearrangements of symbols which did not make any statement about the world" (Magee 1971). As Ayer pointed out:

The empirist does encounter difficulty...in connection with the truths of formal logic and mathematics. For whereas a scientific generalization is readily admitted to be fallible, the truths of mathematics and logic appear to be necessary and certain to everyone. But if empiricism is correct, no proposition which has a factual content can be necessary or certain. Accordingly, the empirist must deal with the truths of logic and mathematics in one of the two following ways: he must say either that they are not necessary truths, in which case he must account for the universal conviction that they are; or he must say that they have no factual content, and then he must explain how a proposition which is empty of all factual content can be true, useful, and surprising. If neither of these courses proves satisfactory, we shall be obliged to give way to rationalism. We shall be obliged to admit that there

is some truth about the world which we can know independently of experience; that there are some properties which we can ascribe to all objects, even though we cannot conceivably observe that all objects have them. And we shall have to accept it as a mysterious inexplicable fact that our thought has this power to reveal to us authoritatively the nature of objects which we have never observed. (Magee 1971)

We know today that the fact Ayer is referring to is neither mysterious nor inexplicable. Ayer (and nearly all philosophers so far) did not take into account that experience has been accumulated and preserved as genetic information during biological evolution. From the point of view of the individual, this inherited foreknowledge about the structure of the world has the character of synthetic judgements a priori; from the point of view of evolution, however, the same statements must be regarded as synthetic judgements a posteriori, based on experience.

From the standpoint of the individual, a synthetic judgement about the world that we can know independently of experience is a synthetic judgement a priori in a strict sense. However, from the point of view of evolution, the same judgement is a synthetic judgement a posteriori; it is based on experience, namely on the experience of our phylogeny, which is preserved and stored in the genetic information, in the peculiar nucleotide sequence of the genetic DNA we have inherited from our parents. Kant's dictum that, although there can be no doubt that all our knowledge begins with experience, it does not follow that it all arises out of experience, can no more be maintained. The fact is that we combine in our individual life two kinds of experiences: the genetically inherited experience of our ancestors and the experience we have made in our personal life, including the experience transmitted to us by cultural tradition and social imitation. This is, in brief, the message of what has been called evolutionary epistemology (Vollmer 1975).

Having introduced this new branch of epistemology, I want to return to Ayer (and to Kant). Ayer (1936) writes in *Language, Truth and Logic*:

...the admission that there were some facts about the world which could be known independently of experience would be incompatible with our fundamental contention that a sentence says nothing unless it is empirically verifiable...the fundamental tenet of rationalism is that thought is an independent source of knowledge, and is moreover a more trustworthy source of knowledge than experience; indeed some rationalists have gone so far as to say that thought is the only source of knowledge. And the ground for this view is simply that the only necessary truths about the world which are known to us are known through thought and not through experience....