

# Epilogue

The investigation initiated by the nineteenth-century chemists to explain photosynthesis came to a preliminary conclusion around 1960, when a sophisticated, molecular-level model of the mechanism was developed. The problem—how to explain the light-driven production of carbohydrates and oxygen from carbon dioxide and water in green plants—had troubled scientists for more than a century. The solution included an intricate cyclic path, the prerequisites of which, namely, reducing equivalents and chemically usable energy in the form of adenosine triphosphate (ATP), were produced during the course of two photochemical reactions operating in series and dependent on two different pigment systems.

The story of how this solution was reached was described in this book with an emphasis placed on the internal dynamics of the modelling process; and it was suggested that several recurrent heuristic strategies can be identified that characterise the methodology of the researchers under study. It may be worthwhile to summarise some of the central features that emerged and might be of wider applicability. The modelling of a complex mechanism, such as photosynthetic carbon dioxide assimilation, was presented as being a collective enterprise. The functional decomposition of the mechanism, a widespread strategy in dealing with complexity as we know from William Bechtel and Robert Richardson, was correlated to the division of labour between several research groups, which *cooperated informally* with one another.<sup>1</sup> No central agency organised this process; rather, the different groups defined their own contributions to the overall project depending on their research interests and skills. Most scientists specialised in certain experimental techniques and applied them to a limited range of issues within photosynthesis research, at the same time keeping a close eye on the (complementary) work of other researchers in the field. The more complex the issue turned out to be, the more subgoals were identified (corresponding to functional subunits of the mechanism) and the more diversified the community became.

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<sup>1</sup> Starting in the 1950s, the locations of the different processes also were considered, although it was not yet part of the primary focus of research (differing from the elucidation of other biological mechanisms, as studied by, e.g., Bechtel and Richardson).

Decomposition of the mechanism into functional units—the *modularisation* of the process, as it is referred to in this study—helped individual researchers to focus on one specific aspect or partial process of photosynthesis, while the rest of the mechanism was left untouched. Alternatively, people imported the conception of one subprocess from the literature, while working on the rest. Early on in photosynthesis research, for example, the synthesis of carbohydrates from formaldehyde was treated as such a module: it was accepted as a self-sufficient element, which most researchers integrated into their various models of the first stages of the mechanism. The most extreme example of modularisation, which eventually resulted in the construction of two distinct partial models of photosynthesis, involved the separation of the “dark” reactions of photosynthesis from the “light” reactions. Although these two partial processes were closely interrelated, and known to depend on each other, from about 1940 they were no longer studied as a single unit. This conceptual separation coincided with a disciplinary separation: while the “dark” reactions became the domain of *biochemistry*, the “light” reactions developed into one of the favourite research themes of *biophysics*.

The integration of experimental results into an explanatory model that adhered to accepted theory, remained a challenge. One of the most important heuristic strategies to meet this task was identified in this study as the *transfer of causal knowledge* from one field to another. This is, in effect, very similar to what Lindley Darden referred to as schema instantiation; although, it might concern only much smaller items than full schemata. The strategy is interpreted here as the tentative classification of a new situation as being similar to a type of situation that had already been elucidated. This was particularly useful in cases where it was impossible to undertake difference tests to find out more details about the involved causally relevant factors, mainly because of the lack of appropriate methods—such as in nineteenth-century chemistry, when hardly anything was known about photosynthesis except for the identity of the raw materials and the end products. The chemists, hence, started from what they knew about the reaction paths of the raw materials *in vitro* and tried to transfer these interaction patterns to the mechanism of photosynthesis. This strategy continued to be an extremely powerful tool, for example in elucidating the course of the dark reactions of photosynthesis around 1950: by then, intermediate compounds were identified by means of radiotracers and paper chromatography; but how these compounds interacted, had to be inferred from the body of knowledge assembled in other systems.

This type of reasoning is sometimes referred to as “reasoning by analogy” and enjoys a rather bad reputation among philosophers, due to the fact that it is obviously fallible. At the same time, it is a widespread heuristic move in scientific practice. If phenomena are observed, the underlying mechanisms of which are known in similar contexts, one might suppose that a very similar mechanism would satisfactorily explain the problem at hand. In photosynthesis research, either only a couple of factors and their interaction were transferred from one epistemic context to another or even full modules of the mechanism under study. It was frequently accompanied or followed up closely by a phase of empirical investigation in order to ascertain whether the assumed explanation did, in fact, hold. Yet, even if this empirical search did not go

anywhere, scientists sometimes retained the tentatively transferred elements if their theoretical foundation and the explanatory value was persuasive enough. The long-held belief in the accuracy of the formaldehyde model of photosynthesis (which was exclusively based on the knowledge gained in artificial systems), despite the failure of scientists to demonstrate that formaldehyde was formed in plants, is a case in point.

Beyond conceptual knowledge of the mechanism, other elements of knowledge were also transferred to photosynthesis research, including new explanatory approaches, theoretical notions of a general nature or the application of new methods and instruments. Frequently, it was not the photosynthesis researchers themselves, who actively sought to import knowledge from other fields to photosynthesis studies when they found themselves in an impasse (although there were exceptions, such as the intensive search of the literature for potential chemical intermediates of photosynthesis that Martin Kamen and Sam Ruben undertook when they started their tracer studies). Rather, new pieces of knowledge were imported mostly by scientists who were experts in other areas (such as atomic physics, physiology and radiation chemistry), who had diverged from their original path of research to make a quick contribution to photosynthesis studies: *research opportunists*, as they were called in this book, in a somewhat provocative choice of term. Some of them returned to their original specialty, while others—unexpectedly for themselves—stayed in the field.

Finally, it was repeatedly emphasised that the group of photosynthesis researchers, as a whole, usually pursued a range of different modelling options concurrently. This *pluralism of alternatives* is particularly prominent in phases of high uncertainty, such as, for instance, the nineteenth-century search for a chemical pathway or the attempts to determine the maximum quantum yield of the process. Whenever important issues were at stake, while the available knowledge was meagre, a premature restriction of alternative options, in the light of what appeared promising at the time, was judged to be unwise. This strategy was applied to fundamentally diverging options (such as the chlorophyll complex model versus models including the photosynthetic unit concept) as well as to “local” alternatives (such as whether 2-phosphoglyceric acid (2-PGA) or 3-PGA was the first product of thermochemical carbon dioxide reduction). This implies that at no point there was one “winning” model, not even in 1960; it were always families of different model variants that were being discussed. The debate about the origin of photosynthetic oxygen provides a fine example of the persistent pursuit of alternatives. From the early nineteenth century onwards and well into the 1930s, the standard notion was that the oxygen originated from the carbon dioxide. However, researchers also explored the possibility that the oxygen might have, in fact, originated from the water. Not many scientists had much faith in the latter hypothesis, but it was still a viable option that they could not afford to ignore. In the end, it proved correct; but, to this day, the possibility has not been excluded that some of the photosynthetic oxygen might still result directly from carbon dioxide reduction.

How were these different options pursued? It is little surprising, although intricate in detail, that existing model suggestions were constantly modified in the light of new experimental findings or theoretical developments (although in photosynthesis

research the latter initiated far less frequently a process of reconsideration than new empirical results). Researchers might add factors to the model, replace or redefine earlier ones or revise full sequences; construe alternative pathways to produce an effect or insert intermediate functional modules that had so far been neglected, and so on. Recall, for example, Robert Emerson and William Arnold's 1932 finding that in photosynthesis only one molecule of oxygen was produced per couple of thousand molecules of chlorophyll. At the time, the standard model included the assumption that oxygen was produced by the direct interaction of chlorophyll molecules with the molecules of carbon dioxide, in a one-to-one relationship, which was clearly in conflict with the new data. The community reacted in a number of ways. At first, most of the scientists seriously doubted the validity of the data. James Franck, for example, was convinced for a long time that Emerson and Arnold had not stimulated the system to operate at its maximum efficiency. Others, including Emerson himself, tried to account for the data by introducing new factors to the standard model—such as the suggestion that an enzyme which was only present in very low concentrations might be involved in oxygen evolution. And a third, more radical group, notably headed by Hans Gaffron and Kurt Wohl, postulated that fundamental changes concerning the action of chlorophyll be made to the standard model. They proposed that, instead of one chlorophyll molecule acting on one molecule of carbon dioxide, thousands of light-absorbing molecules might be “cooperating” in photosynthesis. All these alternatives were pursued, although Franck's and Emerson's more conservative approaches were strongly favoured. Gaffron and Wohl's modification implied that a previously unheard-of mechanism operated in photosynthesis; so that, although the assumption would have explained the data, most scientists considered their idea ill-founded. Nobody was able to imagine how this cooperative mechanism might function. The situation only changed when the concept of energy resonance transfer was brought up and applied to photosynthesis studies.

This reluctance on the part of researchers to revise or drop long-held model assumptions, that is, a certain *epistemic inertia*, was widespread in the episode under study. As a rule, scientists tended to respond to new data or revised theoretical knowledge by trying to modify and expand the existing models as moderately as possible. It was only when these efforts constantly failed that the group abandoned certain model families. This dropping of a model variant from the stage was, more often than not, a rather unspectacular event: nobody stopped to “falsify” the hypotheses in question, such as, for example, the existence of a complex binding of carbon dioxide to chlorophyll, which had been part of the generally accepted knowledge from 1870 until far in the 1930s. Researchers simply chose to spend their time on more productive issues, even if they were not aware of the difficulty, in fact impossibility, to prove a particular causal hypothesis implied in the mechanism definitively wrong. Take the maximum quantum yield controversy, neither Emerson nor anyone else was able to demonstrate the irrelevance of the eccentric experimental conditions that Otto Warburg and Dean Burk had advanced. Alternative pathways, incompletely understood module composition, imperfectly realised set-up and so on, could always have had an effect. All Emerson could do (and did, as far as he was able to) was to demonstrate the relevance of certain conditions for certain results and then draw

inferences as to why these results of Warburg's did not reflect the maximum quantum yield of actual photosynthesis. If this proved impossible, if none of the alternatives to a contested part of the mechanism could positively be established (as was the case in the search for formaldehyde), the only option open to researchers was to wait until either the question had lost its relevance or new methods emerged. This point was reached when Kamen and Ruben used their new radioactive tracer technique to look for formaldehyde. They were as unable to find formaldehyde as their predecessors, but they found a lot of other compounds that opened up the path to more promising model alternatives.

Having so far reflected on the epistemological side of the modelling process, it needs to be underlined that the modelling of the photosynthesis mechanism was an enterprise that hinged on the mastering of experimental practice. This can most clearly be demonstrated by the fact that photosynthesis researchers spent so much time and energy on algae culturing. The more experiments they carried out using algal cells, the more intricate details they discovered about the complex metabolic reactions of these organisms. The physiological state of the algae turned out to be one of the most decisive influencing factors on the cells' photosynthetic performance. From the 1930s onwards, most researchers chose to work with a standard strain of *Chlorella* which Emerson had originally introduced to the field; and the exchange of information on experimental organisms and recipes for culturing media made up a large part of the correspondence of the actors. It is very likely that chemists such as Melvin Calvin, biophysicists such as Louis N. M. Duysens and even plant physiologists of later generations were no longer familiar with the reasons for the choice of species (*Chlorella* or *Scenedesmus*), or of specific algae cultivation techniques. They continued with established tradition not only because they trusted their predecessors' skills and decisions but also to ensure that their results could be compared with earlier findings. In this sense, experimental organisms such as *Chlorella* really did "incorporate" experimental knowledge: they were needed to satisfy the constant conditions of the experimental set-up; although, perhaps, nobody knew exactly which of their many properties influenced the mechanism in what ways. The same held true for other aspects of experimental practice. The importance of tacit knowledge is impressively demonstrated by the fact that the actors often sought to solve controversies by conducting experiments together: there might always be aspects of the know-how of an experimenter that are crucial to the outcome of the experiment; yet, they might be so self-evident to the experimenter herself that it does not even occur to her to explain these details—unless, of course, a controversy arises.

The difficulties of experimental practice and the need to master the pertinent methods explain why scientists were so conservative, not only in their support of model hypotheses but also in terms of research techniques and explanatory approaches: Warburg and many others investigated *Chlorella* cells manometrically in certain media for most of their working lives. The fact that researchers jumped from one theme or field to another, as Warburg did, was clearly prompted by the strategy to exploit the technique's possibilities in as many disciplines as possible. And Warburg, in particular, was a very successful advocate of the technique's advantages. Many of

the central figures in twentieth-century photosynthesis research had learned manometry while they were fellows or members of Warburg's institute; and upon leaving they brought this technique to other places. Searching for kinetic information by manometrically measuring the process soon replaced the mainly stoichiometrically guided (and largely unsuccessful) hunt for chemical intermediates. And once the choice of technique had been made, and some standard experiments carried out with it, researchers kept to it—not the least, as to be able to compare experimental outcomes.

Yet, having emphasised the power of heuristics, methods and strategies, one must not forget that a great many of the paths thus pursued led nowhere. Warburg is a marvellous example of a protagonist whose models and hypotheses soon proved untenable, although his methods and techniques were of lasting impact. On the other hand, there were unexpected discoveries that no heuristic rule could have foreseen—for example, when Emerson set out to investigate the influence of blue light on the gas exchange of *Chlorella* cells and found instead the enhancement effect on photosynthetic efficiency. In some phases, research activity was high and methodically uncontroversial, while the actors felt they were conceptually stuck. This was the case, for example, in the 1930s, when existing model alternatives were continuously worked on, without the scientists having any idea as to where the different paths would eventually lead (if anywhere). There were experimental findings that failed to arouse the conceptional interest they would have deserved, such as the red drop of photosynthesis that Emerson and Lewis had come across in 1943; whereas there were instances of explanatory breakthroughs that were discarded as empty speculation, such as the suggestion of the photosynthetic unit by Gaffron and Wohl in 1936. The aim of this book was not to construct another grand narrative of discovery. The aim was to bring exactly those intricate details to the fore that undermine the very idea of such a narrative, that is, present the highly diverse approaches to elucidating the mechanism of photosynthesis, only some of which were to last; and to try and identify some recurrent heuristic strategies that scientists utilised when they were confronted with the inherent complexity of their subject matter: plants in light and darkness.

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