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THEORY CONSTRUCTION IN BIOLOGY THE CASE OF THE ORIGIN OF LIFE¹

1. INTRODUCTION

Questions of origin have traditionally posed special problems in philosophy and in science. The problem whether questions of origin constitute legitimate objects of investigation, has been debated within different frameworks of thinking about the natural world. For example, within the context of the mechanical philosophy, the properties displayed by any living organism were commonly regarded as the necessary outcome of the properties and disposition of its parts, in accordance with universal laws of matter in motion. But how did an organism come to have just *these* parts and just *this* arrangement of parts? This was a question on a different level and was held to be concerned with the motives and purposes of the divine Creator of the Universe, with final causes in the strongest sense.

God may have produced the world and its contents (including living organisms) according to the principles of mechanics, but the precise way in which the Creator executed this mechanical production would have been guided by a preconceived plan, towards a preconceived end. Questions about the reasons why God chose one plan rather than another, why God chose to endow any living species with its particular organisational form rather than some other, were kept outside the bounds of the mechanical philosophy; there was

¹ Earlier formulations of the ideas expressed here were presented by myself at philosophical seminars and conferences in London, Dübrovnik, Cambridge and Mexico. This paper has benefited considerably from the discussion on all these occasions. Particular thanks for long-term critical encouragement are due to Gail Fleischaker, Heinz Post, Avinash Puri, Wim van der Steen and Reza Tavakol. They should in no way be held responsible for the claims made in this paper, nor for the way in which I have knitted the whole story together.

no place here for teleological explanations in terms of final causes. Thus, questions about origin were excluded.

It was still possible, however, to explain the organism formally as a product of design, to take its overall organisation as given and treat this organisation as a formal cause that conditions the organism's mechanistic operations. The most elaborate justification of this position was given by Kant in his "Critique of teleological judgement", published in 1790. According to Kant, our understanding is so constituted that we have no way of explaining natural phenomena except in terms of mechanical causes. This is a subjective property of our understanding and does not mean that all of nature is objectively such that it can be explained in this way. In those cases where we judge objects of our experience to be subject to purposive relations, over and above causal relations in the mechanistic sense, we may legitimately conceive of the whole object as an idea that is causally prior to its constituent parts. This idea would have guided the production of the real object, much as a work of art is produced by a painter or sculptor.

Confronted with apparently self-organising natural objects, such as living organisms, Kant argued that the same strategy is appropriate. Here we may think in terms of 'natural purpose' and introduce ideal *formal* causes into our explanatory schemes. This, in very rough outline, is how Kant justified the use of teleological explanation in terms of formal causes in biology². On the other hand, while we could legitimately presuppose the prior existence of some 'blueprint', we had no means of access to the (non-human) understanding that, hypothetically, had the idea of it. Hence, questions about the origins of the forms of organisms were beyond the domain of human understanding or judgement.

With respect to perspectives on the living world, a crucial turning point came with the Darwinian theory of evolution. The emulation of Darwin's explanatory strategies led to the abandonment of thinking in terms of natural (or divine) purpose in favour of historical explanations in terms of the concepts of variation, adaptation and natural selection: of all possible structures that variation might produce, only those that were better adapted to their specific environments than their competitors would survive long enough to produce offspring.

² Lest I be accused of hubris, it is of course impossible to represent Kant's intricate argument adequately in two brief paragraphs. My sole aim here is to draw attention to the facts that not all teleology involves final causes, that in Kant's case in particular, final causes played no role in the explanation of natural phenomena, that Kant was concerned with the explanation (not the ontological status) of living organisms and that his solution was an idealist one. An excellent and detailed analysis of Kant's critical teleology is presented by McLaughlin (1990).

The particular forms of living species came to be seen as the result of causal mechanisms operating in natural selection; teleological notions could henceforth be dispensed with, at least in principle.

Of course, the Darwinian theory of evolution (or any of its subsequent formulations) did not in itself provide an explanation of how particular species, let alone the first living organisms on Earth, might have come into being. It was within the Darwinian framework, however, that questions about biological origins, including the origin of life on Earth, became a matter of serious scientific concern. Nevertheless, the fact that theories about biological origins were, and are, formulated does not mean automatically that they are adequate from a methodological point of view. Do the theories yield explanations that conform to reasonable philosophical criteria of what constitutes good scientific procedure? To answer this question, it is necessary to have some agreement about what these reasonable philosophical criteria might be.

2. LOGICAL POSITIVISM AND ITS LEGACY

Strong methodological criteria were laid down within the framework of logical positivism (or its variant, logical empiricism), which has had such a powerful hold on 20th-century philosophy of science and on science itself, especially physics. The logical positivist ideal was one of a substantively unified science, with theory reduction as the proper form of unification, theories as interconnected sets of universal laws of nature (plus boundary conditions, etc.) and explanations conforming to Hempel and Oppenheim's covering-law model. This ideal has proved to be utopian: in practice, most of physics and virtually all of biology have always fallen far short of its standards, as is now widely recognised by philosophers of science³. However, no clear consensus has emerged yet about the question whether the positivist enterprise should be jettisoned entirely, or whether some or all of the principles it incorporates should merely be weakened.

For the sake of argument, let us assume for the moment that the *aim* of unification along positivist lines is worth striving for at least. The biological sciences as they are now would then immediately be in serious trouble. Are there *any* biological theories that consist of interconnected sets of universal laws of

³ The early critiques of, especially, Thomas Kuhn (1962; 1970) and Paul Feyerabend (1975) have spawned an enormous literature, much of it hostile towards any attempts to capture 'scientific method'. Among more recent works in philosophy of science that take methodological issues seriously without assuming the existence of some transcendental method, and that expose problems in the logical positivist/logical empiricist position from different perspectives, are those by Cartwright (1983), Chalmers (1990), Garfinkel (1981) and Hacking (1983).

nature? Does biology now have any *universal* laws, even if we relax the demand for 'universality' by restricting it to the terrestrial domain? Can we point to any cases of successful theory reduction (in the sense of strict logical deducibility), either within the biological sciences or between the biological and the physical sciences? Do typical explanations in the biological sciences conform to the covering-law model?

None of these questions can be answered unequivocally in the affirmative⁴. Is biology then so immature, even backward? This would be a surprising conclusion, given the flourishing state of research in the biological sciences, the vast sums of money that are allocated for this research, and the inroads that it has made in the practices of medicine, agriculture, and so on. There does not seem to be any reason to assume *a priori* that biological scientists are peculiarly lacking in methodological sensitivity or work in a theoretical vacuum, nor that those organisations that fund biological research would be prepared to subsidise the scientific equivalent of playground activities.

It should be said straight away that it is not obvious that the physical sciences as a whole fare significantly better. True, in theoretical physics there are more laws that are treated as being universally valid, there are more theories with neat mathematical formalisms, and more explanations can be constructed so as to fit the covering-law model. This is not surprising, given that most philosophers of science, especially those of a positivist bent, received their initial inspiration from (theoretical) physics and have sought to instantiate their methodological principles mostly with examples from physics.

But it has turned out not to be a straightforward matter to reduce thermodynamics to statistical mechanics, for example, without introducing *ad hoc* assumptions⁵. It is not a straightforward matter to produce a realistic model grounded in dynamics of, say, a laser or a waterfall without tinkering with all kind of approximations⁶. And just try and explain with logical rigour from the formalism of quantum mechanics why glass is transparent!

Physical theory typically rests on a great deal of abstraction and idealisation; it deals with point masses, ideal gases, frictionless systems, and so on. This is one of its strengths if generalisation and unification are the primary aims – but at a price. Derivations from the formalism, when given a physical interpreta-

⁴ For a discussion of these questions, see van der Steen & Kamminga (1991). The primary focus of the paper is on the role of laws of nature in biology, but it also addresses problems concerning reductionism and deductive-nomological explanation in the biological sciences, precisely because the three issues are interrelated at the methodological level.

⁵ See, for example, Garfinkel's discussion of this case (Garfinkel 1981, ch. 2).

⁶ See, for example, Cartwright (1983, especially ch. 8).

tion, have to be stretched and strained in order to be brought into relation to the structure and behaviour of real systems of even modest complexity. (This problem applies especially in those cases where the formalism of the theory is mathematically intractable, that is, in the case of virtually all fundamental theories of modern physics.)

It is standard procedure to use models in these cases, but these models rarely stand in clear-cut deductive relationships to the theories that inspired them⁷. Moreover, the most successful models in physics have little to say about the natural world, as pointed out by Alan Chalmers:

While physical science has proved to be extremely effective for dealing with artificially contrived, technological situations, its capability for dealing with the natural world is limited outside some aspects of astronomy. This is exemplified by the notorious unpredictability of weather forecasts or, more seriously, by the inadequacies in our appreciation of the environmental impact of our technological intervention in the natural world (Chalmers 1990, p. 36).

The biological sciences have, thus far, shown a greater concern with the real and the natural, which happens to be complex and variable, thus limiting possibilities for generalisation and formalisation.

It could be argued (and often is) that any methodological differences between the biological and the physical sciences may be a matter of degree, rather than of principle, resulting primarily from the relative complexity of biological systems and the environments with which they interact. But the vast majority of real physical systems is also complex and, in this respect, there is no clear difference between the objects that the physical and the biological sciences deal with. The distinction in practice is that, in physical theory, differences and complexities have traditionally been 'idealised' away as much as possible, while the biological sciences have tended to emphasise the idiosyncrasies and complexities of real biological systems. Both in the classical taxonomic and in the modern evolutionary traditions, differences are at least as important as similarities. It *does* matter to survival that green plants can syn-

⁷ A useful review of the role and construction of models in physics, especially in the case of mathematically intractable theories, is given by Redhead (1980); Cartwright's critical remarks about the relations between real situation, model and theory should be read in conjunction (see note 6). It should not be thought that problems of modelling are confined to difficult areas such as quantum mechanics: it used to be standard practice in classical dynamics to remove mathematical non-linearities artificially (for reasons of tractability); the recent reintroduction of non-linearities has shown up potentially profound consequences for the construction and testing of theories and models (see Tavakol 1991).

thesise carbohydrates from carbon dioxide and water while human beings cannot, or that fish have gills and cats do not – and so on.

To avoid misunderstanding, I do not wish to imply here that there is anything reprehensible about abstraction or idealisation as such, nor that it is confined to physics. Biologists, too, ignore certain differences when they make generalisations and they, too, perform controlled experiments in contrived ('unnatural') settings. And, of course, physicists do study natural phenomena (such as light) and do not ignore *all* differences. (For example, it *does* matter that electrons have a negative charge and neutrons do not.) Proper abstraction or idealisation depends on the nature of the investigation and is a matter of skill, both in the physical and the biological sciences. What I do claim is that, as a matter of historical fact, the use of mathematical tools and the ideal of axiomatisation along the lines of Euclidean geometry have encouraged abstraction and idealisation in theoretical physics to an extent that has not proved fruitful in the biological sciences. It has also made the formal relations between 'fundamental' theory and real phenomena problematic in large areas of physics. Whether we are dealing here with issues of principle or historically contingent matters is not my prime concern. What I wish to stress is that differences in priority are not necessarily indicative of differences in methodological adequacy.

The possibility should be considered, then, that in its concern with the real and the natural, biology has different priorities that have methodological consequences. In particular, the special aims of biologists may be consequential for the patterns of explanation that are used in the biological sciences. Indeed, there is a widespread intuition that there *is* something special about biological explanation. Given that this intuition is by no means confined to cryptovitalists on the one hand or hardline positivists on the other, the question deserves some exploration.

3. THE AIMS AND STRUCTURE OF BIOLOGICAL EXPLANATION

An examination of the patterns of biological explanation can be undertaken from two different perspectives that will turn out to be interrelated. We can ask *what* biologists seek to explain, in other words, what kinds of question they typically aim to answer; or we can ask *how* biologists explain, in other words, what kinds of explanation they typically offer. A successful explanation must, of course, address the question that is being asked and what is being asked depends on what is taken as given⁸. As a general rule, each biological ques-

⁸ The general approach to explanation here, in terms of presuppositions and contrast spaces, follows that of Garfinkel (1981, ch. 1). As far as I am aware, its general conse-

tion can be given four different interpretations, depending on what is presupposed, and each interpretation of the question will require a different kind of explanation.

Consider the question why haemoglobin binds oxygen in the blood. (1) If it is taken as given that oxygen is bound by *something* in the blood, the point at issue would be why it is haemoglobin, rather than some other molecule, that binds oxygen. The explanation would be given in terms of the structure of the haemoglobin molecule, notably the structure of the haem group with its iron atoms. (2) If it is taken as given that haemoglobin is responsible for the transport of oxygen in the blood, then the question would concern the nature of the binding process (rather than some other form of transport) and the explanation would be given in terms of a description of the binding mechanism and the conditions under which haemoglobin binds and releases oxygen.

Thus far, there is nothing peculiarly biological about this example. Explanations in terms of structures (the what) and in terms of mechanisms (the how) are common throughout science. In these cases, incidentally, a reductionist methodology seems perfectly appropriate.

The possibilities have not yet been exhausted, however. (3) If it is taken as given that haemoglobin in the blood does *something*, why is it its property of binding oxygen, rather than some other property, that should interest us? The explanation here would be given in terms of the effect that oxygen transport to the tissues has in maintaining the integrity of the whole system (i.e. the body) of which haemoglobin is a part. (4) If, finally, it is taken as given that haemoglobin binds oxygen in the blood, it can still be asked why such a molecule as haemoglobin, with the particular structure and properties it has, came to be part of the body as a whole at all. In this case, an explanation (or, more usually, an explanation sketch) would typically be offered in terms of the selective advantage that was conferred on organisms that have haemoglobin in their blood over any competitors with less efficient oxygen-binding capacity.

The last two categories are concerned with function, though in different ways. In one case, we are interested in the contribution(s) that a particular item makes to the system of which it is a part (its systemic function). In the other, interest is focused on the selective value that the same item has had in the evolutionary history of the species where that item is encountered (its evolutionary or historic function). While these two uses of the notion of function are separable in principle, they are in practice inextricably linked in mod-

quences for explanation in biology have not been explored systematically before. (It should be pointed out that, although Garfinkel's book is subtitled "Rethinking the questions of social theory", much of the discussion is concerned with and relevant to scientific explanation in general, not just explanation in the social sciences.)

ern biology. The interlinkage results from a rejection of teleology in favour of evolutionary thinking, not from logical necessity.

Staying with the same example, not every effect that haemoglobin has is properly designated its function. For example, haemoglobin causes our blood to be red, but this property of haemoglobin is not normally called its function. It is precisely because we can tell some story about the selective value that haemoglobin as an oxygen carrier (rather than as a red pigment) might have had for our ancestors that we talk of systemic function at all⁹. Conversely, insight into the contributions that haemoglobin makes to maintaining the body in a living state (i.e. its systemic function) is required before we can construct any reasonable explanation about its possible selective value in the evolutionary history of our species.

Hence, we may get two different forms of functional explanation (one in terms of some cause-effect relationship and the other in terms of adaptation in the past), but in each case tacit reference is made to the other. In fact, this interrelatedness applies to all four forms of explanation outlined above. These are not mutually exclusive, but complementary and, at least collectively, biologists typically aim to offer explanations in answer to each of the four interpretations of the question we started with. This makes the overall structure of biological explanation very complex.

To see how tightly interconnected the different types of explanation are, consider the following relationships: reference to haemoglobin structure is made when the mechanism whereby it binds and releases oxygen is explained. Reference to this mechanism is made when the systemic function of haemoglobin is explained and this systemic function will be referred to in attempts to explain historically why haemoglobin should have had adaptive value. Finally, this historic function is referred to when an explanation is given of why a protein with the specific structure of haemoglobin exists in the body. This interrelatedness means that the four types of explanation must, in each case, show overall coherence. This coherence, however, consists in an intertwining, not in a clear-cut deductive (or reductive) relationship.

⁹ What I take to be the same point is made by Mitchell (1989) in her analysis of the explanatory character of function ascriptions, inspired by (but going significantly beyond) Wright's etiological model (see Wright 1976). She concludes that consequences, in order to be designated as functions, must be features which play a significant role in (natural) selection. (As she also argues, this position does *not* entail a commitment to viewing natural selection as an optimising process directed towards some ultimate goal; selection need not even provide the optimal solution to some particular environmental problem, but only the best possible option accessible at the time, given the available variants.)

4. ORIGINS AND HISTORY

In many areas of biology, research strategies are aimed primarily at providing explanations in terms of structures, mechanisms and systemic functions. The historic, evolutionary issues then only play a tacit role in the background. They do not, however, disappear altogether, because of the interrelatedness of explanations concerning evolutionary and systemic functions¹⁰. Appeals to the notion of adaptation or selective advantage in the abstract, when there is talk of systemic function, would amount to a lapse into teleology. Evolutionary theory provides the escape route, but it must be used in a concrete way, not just pointed at.

In some fields historic explanation plays a central role in theory construction, evolutionary biology being one of them. Another is the field of the origin of life, which of course connects up with evolutionary biology (or at least, it should do, if we want to maintain coherence in the biological sciences as they stand).

Several factors are involved in the construction of any form of historical explanation¹¹. First, it involves the identification of past causes to explain present (or at least more recent) effects. Secondly, the reasoning typically goes abductively from present conditions to past conditions and these past conditions, plus connecting laws, are then used to explain present effects. Thirdly, and this is important, the primary explanatory work is almost invariably done by antecedent conditions rather than laws, the laws in the explanans playing only a supportive role. Finally, the explanation as a whole typically consists of a causal narrative history (as distinct from mere chronology and from the classic covering-law model).

Historical explanations should meet several conditions of adequacy.

(1) The etiological plausibility of the past causal conditions must be established, by providing independent evidence that the postulated past cause can produce the relevant effect under *some* conditions. (For example, if we propose that most of the oxygen in the atmosphere now is derived from the pho-

¹⁰ A closely related point is made by Sarkar (1998), who also spells out in detail the consequences for explanatory reductionism.

¹¹ The discussion of historical explanation here only gives a brief outline of the conclusions of a lengthy analysis presented by Meyer (1990). Having characterised historical explanation and the conditions of adequacy that it should meet, Meyer went on to show that the explanatory strategy underlying Oparin's theory of the origin of life on Earth exemplifies his model of historical explanation. Moreover, he argues that subsequent criticisms of Oparin's theory have usually centred on alleged violations of the historical or etiological plausibility condition. In other words, the nature of the criticism serves to reinforce the general methodology adopted by Oparin.

tosynthetic activities of green plants and blue-green algae, it must be established that photosynthesis by these organisms does indeed produce oxygen).

(2) The historical plausibility of the past causal conditions must be established, if possible by means of several independent lines of argument that lead to the same conclusion. (For example, the fossil record may establish that the biomass of green plants and blue-green algae was sufficient to produce the appropriate amount of oxygen; and analysis of minerals in rocks of different ages may establish that an increase in the atmosphere's oxygen levels coincided with an increase in plant biomass).

(3) Alternative hypotheses should be excluded by establishing their etiological and/or historical implausibility. (For example, calculations of oxygen release during volcanic eruptions and of the amount of volcanic activity in geological history may establish that volcanic activity can account only for a tiny fraction of the total amount of oxygen present in the atmosphere now.)

In practice, full causal narrative histories may be very difficult to come by, because of difficulties in obtaining all the evidence required to meet the above conditions. We would, typically, get explanation sketches rather than full explanations. Nevertheless, there does not seem to be anything 'unscientific' (to use a positivist term) about attempts to construct causal narrative histories. Hence, there do not seem to be any good reasons for excluding historical questions from science as a matter of principle, however difficult they may be to answer in practice. A confrontation with the practical problematic of historical explanation is the price we have to pay for avoiding the problems inherent in idealist teleology.

It could, of course, be argued that questions of origin still pose problems that go beyond those of historical explanation in general. *Some* questions of origin are perceived by us as concerning particularly radical historical breaks, for example the origin of the universe, the origin of life and the origin of human consciousness. But (leaving aside the tricky case of the origin of the universe) are there really matters of principle at stake here? We have reasonable explanation sketches of the origins of our solar system, of the origins of the eukaryotic cell and of the origins of capitalism, to name but a few. (All these explanations are, of course, open to revision). It is not obvious that a different methodology is needed in those areas where we, from our anthropocentric perspective, tend to see the historical breaks as particularly significant.

5. WHAT SHOULD A THEORY OF THE ORIGIN OF LIFE LOOK LIKE?

Everything that has been stated thus far with respect to biological explanation provides us with clues about the kind of questions that any theory of the origin of life on Earth should address. A brief sketch follows.

The first question that confronts the scientist enquiring into the question of the origin of life on Earth concerns the properties that primitive organisms should have had for us to recognise them as living beings. This question need not be interpreted in the metaphysical sense of 'what is Life?', but can most profitably be approached purely operationally, along the lines proposed by Gail Raney Fleischaker¹². If we look at what organisms in general do in their concrete settings, a set of minimal criteria can be abstracted that we may expect to apply to any living organism. These criteria will be concerned not only with the internal structure, organisation and operations of organisms, but also with their interactions with their respective environments¹³.

In our current framework of biological theory, evolutionary continuity between the first living organisms on Earth and all extant life on the planet is assumed. This implies that the first living organisms took part in the evolutionary process, in other words, they had descendants unlike themselves. This raises questions about the order in which different properties of living organisms evolved during the early history of life on Earth. Answers to such questions will depend strongly on the particular set of minimal criteria that is adopted in relation to the first question. (For example, which property is taken to be more primitive: metabolic integrity in the midst of material exchange between organism and environment, or the capacity for reasonably faithful, but not error-free, replication?¹⁴) The answers should also be consistent with the historical 'record', as revealed for example by comparative taxonomic studies.

The third set of questions concerns the physicochemical conditions of the environment at successive stages in geological history, both globally and locally (in relation to specific habitats). Physical, chemical, geological and, except for the earliest stages, biological theory will all have an input here and the answers on offer must again be consistent with whatever historical records are

¹² See especially Fleischaker (1988 and 1990).

¹³ There is an important sense in which organism and environment actively co-determine each other, as argued by Levins and Lewontin in their classical contribution, "The organism as the subject and object of evolution" (Levins & Lewontin 1985, ch. 3).

¹⁴ For a historical account of the tensions between these two positions, see Kammaing (1986). That these tensions continue is clear from the writings by proponents of 'genetic priority' (for example Cairns-Smith 1985; Küppers 1990) and by proponents of 'metabolic priority' (for example Dyson 1985; Fleischaker 1990).

available (for example with knowledge about the mineral composition of ancient rocks).

Finally, the question must be addressed what the mechanisms were that brought about the origin and development of systems with the properties defined in answer to the first two sets of questions, under the conditions defined in answer to the third. Besides a multi-faceted theoretical input, experimental simulation also plays an important role here, in order to test the plausibility of these mechanisms. (As regards testability, we do not of course have the means at our disposal to rerun the whole, or even just the early, evolutionary history of terrestrial life in the laboratory. It is, however, common practice in this field to test the hypothetically crucial stages of transition by means of simulation experiments whenever possible.)

The construction of a full causal narrative history will involve establishing the etiological and historical plausibility of all phases of transition that are held to be crucial in any particular theory of the origin and early development of life on Earth. At each stage, explanations in terms of structures, functions and mechanisms should at the very least be sketched in, and explanations should be offered about the specific selection pressures that might have been responsible for novel properties being preserved (at least for a while) during the course of evolution. The overall narrative needs to be internally consistent and coherent with all background theories that connect with it.

If these conditions are fulfilled, even in outline, then that is a major achievement not to be scoffed at. The resulting theoretical structure may be complex, even precarious in its dependence on so many other theories that are open to revision or refutation, but the explanatory strategy does not obviously violate any methodological principles that play a useful role in science as we know it. It is not to be expected that we shall ever construct a theory of the origin of life on Earth that can be axiomatised neatly. What we can reasonably expect (because examples exist already!) is to gain qualitative insights into the early history of life on Earth.

6. CONCLUSIONS

The methodology outlined above is not only theoretically appropriate to investigations about the origin of life on Earth, it has in fact been applied in this field at least since Oparin¹⁵. Indeed, the principles it rests on were present, in

¹⁵ As mentioned in note 11, Meyer (1990) argues this point in detail. My only reservation about Meyer's treatment is that he underestimates the extent to which principles of historical explanation were introduced in this field well before Oparin, albeit in much less well articulated form (see Kamminga 1991).

rudimentary form, already in the 19th-century writings of biologists such as Pflüger.

But does this methodology still reflect the values inherent in the logical positivist ideal, albeit in a weaker form? It could be argued, for example, that explanatory coherence, which I do demand, is simply the poor woman's unification through reduction. Unification, especially at the explanatory level, is certainly worth striving for in science; and reduction, even if it applies only locally, is one means of achieving unification. (It is not the only means.) However, the intricacies of biological explanation, especially when the historical dimension is taken seriously (as it should be), pose severe constraints on possibilities for theory reduction¹⁶.

The dominant explanatory import of antecedent conditions also limits the usefulness of theory reduction. Perhaps some mathematical physicist (or a supercomputer) in the future will provide a description of the amoeba in terms of the Schrödinger equation¹⁷, but that will not automatically yield novel insight into the biologically interesting properties, let alone the evolutionary origins, of the amoeba. Would it be heresy to suggest that biologists *rightly* give higher priority to questions about the biological properties and evolutionary origins of the amoeba than to the formal derivation of its description from the Schrödinger equation?

Finally, there is the question of the methodological maturity of biology as compared with the physical sciences. If the aims of biology are different from those in (theoretical) physics, then the methodologies appropriate to achieving these respective aims may also differ. In that case, the fact that biology does not live up to the standards thought to be appropriate for physics tells us very little. I have argued that the aims of biology *are* different and that explanatory strategies differ as a result.

In addition, I have already hinted that there is a trade-off between abstraction and generalisation on the one hand and realism on the other, that in its very concern with real, natural systems, biology tends to come up with theories that are only locally valid and that provide qualitative rather than quantitative insights. This trade-off between generalisation and realism was captured nicely by Richard Levins in a short paper on modelling in population ecology way back in 1966. Ironically, now that non-linear modelling is becoming more and more pervasive, physical scientists are also beginning to appreciate the value of qualitative insights into real systems (such as the weather), rather

¹⁶ For a cogent discussion of this issue, I again refer to Sarkar (1998).

¹⁷ This would be a remarkable achievement, given that the Schrödinger equation has thus far been solved *exactly* only for the hydrogen atom.

than quantitative predictions deduced in a stepwise manner from some mathematical formalism applied to contrived situations¹⁸. In the case of non-linear systems, the links between formal deducibility and explanatory efficacy are now perceived to be highly problematic, even in classical dynamics. Perhaps philosophers of science will take note and come to appreciate that early twentieth century mathematical physics is not the only possible source for the methodological standards they prescribe.

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¹⁸ See, for example, Tavakol (1987). This new awareness is one of the positive results of the 'chaos revolution'. What is less clear at this stage is the extent to which this 'revolution' has yielded significant novel insights into natural systems (as distinct from 'systems' of mathematical equations). For a cautionary account, see Kamminga (1990).

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