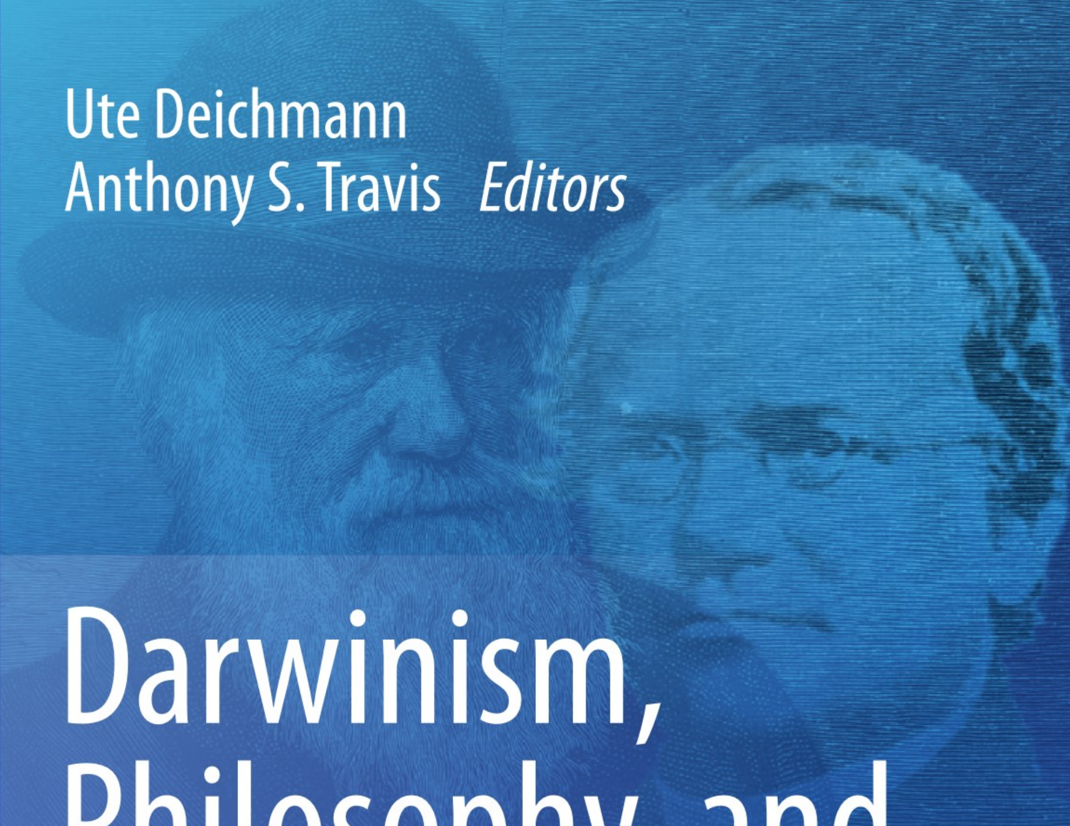
Ute Deichmann
Anthony S. Travis *Editors*



Darwinism, Philosophy, and Experimental Biology

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ARTICLE

Guest Editors' Introduction

Ute Deichmann · Anthony S. Travis

Throughout much of the twentieth century, evolutionary biology was largely separated from the experimental sub-disciplines of biology that were devoted to functional aspects of life. This is notwithstanding Theodosius Dobzhansky's famous dictum: "Nothing in biology makes sense except in the light of evolution" (1964, p. 449). His and similar statements obscure the fact that most of the great achievements in nineteenth and twentieth century biological sciences, such as those in experimental embryology, physiology, genetics, biochemistry, and molecular biology, were brought about without any engagement with evolutionary biology. The gap between the then largely descriptive and speculative evolutionary biology and these experimental fields was in fact manifest already in the late nineteenth century, when Wilhelm Roux, a student of Ernst Haeckel, founded experimental embryology (*Entwicklungsmechanik*) as an explicit countermove to Haeckel's evolutionary morphology. Roux rejected Haeckel's verdict that phylogeny was the sufficient cause of ontogeny, and that there was nothing else to explore in this matter.

At the turn of the twentieth century, the Darwinian theory of evolution by natural selection was strongly disputed among scientists. Its scientific value was frequently called into question, as expressed most fiercely by renowned British botanist and geneticist William Bateson (1902, p. v): "In the Study of Evolution progress had well-nigh stopped. The more vigorous, perhaps also the more prudent, had left the field of science to labour in others where the harvest is less precarious or the yield more immediate. Of those who remained some still struggled to push towards truth through the jungle of phenomena: most were content supinely to rest on the great clearing Darwin made long since." Bateson contrasted the study of evolution with the breakthrough made by Mendel: "Such was our state when 2 years ago it was suddenly discovered that an unknown man, Gregor Johann Mendel, had, alone, and unheeded, broken off from the rest—in the moment that Darwin was at work—and cut a way through."

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It was dissatisfaction with the descriptive and speculative approaches of evolutionary biology that led German-American physiologist Jacques Loeb to strongly promote biology as a purely experimental science: "In science we [can] only take things for proven when they are based on quantitative experiments and from this point of view ours [is] not the era of Darwin but the era of Pasteur."[1] This was his response to a group of Darwin scholars whose arguments he considered unscientific. He referred to the breakthroughs in experimental microbiology by French chemist and microbiologist Louis Pasteur, which led to the germ theory of infectious diseases and the first successful vaccine. Loeb's remarks reflected the then poor state of evolutionary biology, experimental biologists' resulting distancing from it, and their own rapid successes, without any connection to evolution, from the late nineteenth century.

The last decade of the century saw a refinement of Darwin's theory resulting in what was called neo-Darwinism (a term that later became mainly used for the next refinement of Darwinian Theory in the 1930s and 1940s). Based on August Weismann's germ plasm theory, and his earlier writings, some scientists, among them Alfred Russel Wallace, placed evolutionary theory exclusively on natural selection and attempted to rid it of unscientific connotations, in particular the Lamarckian idea of the inheritance of acquired characteristics, which were prevalent in Darwin's own works. Nevertheless, evolutionary biology remained to a large extent a descriptive and speculative enterprise.

In the years following the so-called rediscovery of Mendel's laws in 1900, theories of continuous variations and gradual evolution as originally put forward by Darwin and promoted by biometricians such as Karl Pearson became fiercely challenged by the growing number of Mendelian geneticists, and in particular by Bateson. They pointed to the discrete nature of genes, and—in their opinions—the resulting necessity to assume evolutionary leaps. It took almost three decades before the reconciliation between Mendelian genetics and natural selection was brought about by bio-mathematicians, most prominently Ronald A. Fisher, Sewall Wright, and J. B. S. Haldane. Some other biological fields such as ecology took up evolutionary questions. But it was only from the late twentieth century that questions of evolution began to play an increasing and fruitful role in various other areas of biology, in particular embryology and molecular genetics. Recent developments in evolutionary developmental biology challenge the dogmatic notion of the (second) neo-Darwinists according to which evolutionary change can only be gradual; a topic that is outside the scope of this issue (e.g. Davidson 2006; Laubichler 2009).

The six papers gathered here deal with the interaction of evolutionary theory and practice, as proposed by Darwin and the neo-Darwinians, with various areas of experimental biological research and with philosophy. They have been selected from contributions to the 2009 international workshop "Darwinism and Functional Biology, Other Sciences, and the Humanities," organised by the Jacques Loeb Centre for the History and Philosophy of the Life Sciences at Ben-Gurion University, Beer-Sheva, in collaboration with the Edelstein and Einstein centres at The Hebrew University of Jerusalem (30 March–1 April). The follow-up workshop of the Loeb Centre (8–9 June 2010), with its focus on evolutionary developmental biology and the notion of progress in biology, addresses developments and questions not dealt with here.

The first contribution, by Ulrich Charpa, analyses philosophical and historical connections and conflicts between, and within, nineteenth century evolutionism and microscopical research. Focusing on Darwin, Matthias Jakob Schleiden, William Whewell and

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[1] Jacques Loeb to E. G. Conklin, 9 January 1924, Library of Congress, Manuscript Department, Loeb Papers, file E. G. Conklin.

the “London Doctors,” Arthur Henfrey and Edwin Lankester, Charpa shows that there were deep methodological differences at the beginnings of evolutionist and microscopical biology that characterised their relationship as compatible but nevertheless unconnected domains until the mid-twentieth century. This was irrespective of special alliances across the two fields, as, for example, between Darwin and Schleiden, one of the founders of cell theory and methodologist of microscopical biology, who shared evolutionary convictions, and between Schleiden and Whewell, who despite disagreeing on the question of evolution, shared an adherence to Kantian philosophy of science.

Charpa’s main emphasis is on Schleiden, the author of the “Methodologische Einleitung” and his programme of microscopical research. This programme was based on a methodology which, in modern epistemological terms, can be characterised as reliabilist, personalist, and “collaboratist”. Good science was understood as a practice in which trained experts explore what was not hitherto visible. In contrast, Darwin designed a great explanatory programme relating to units of nature that were or at least had been (as fossils) *manifest*. In Darwin’s conception there were components analogous to fundamental laws, to the explanation of facts by such laws, and to the confirmation of lawlike assumptions based on independent classes of data. Microscopical research at that time could neither benefit from this “architecture” nor contribute to it. Meantime, Charpa concludes, the microscopists had their own agenda and their own philosophical frame.

The relationship between Darwin and Mendel is the topic of Ute Deichmann’s contribution. Unlike most studies dealing with this relationship, where the focus has been on the question of whether or not Mendel supported Darwin’s theory of evolution, Deichmann views Darwin from the perspective of Mendel, focusing not on evolutionary theory but on their approaches to heredity and variation. Small inherited variations were at the core of Darwin’s theory of organic evolution by means of natural selection, and one of his major concerns was to explain them. He even put forward a developmental theory of heredity (pangenesis) based on the assumption of the existence of material hereditary particles. However, because of its vagueness, lack of logical consistency, faithfulness to the widespread conceptions of blending and soft (Lamarckian) inheritance, and Darwin’s attempts to explain many complex phenomena at the same time without appropriate experimental and conceptual tools, this theory did not, and indeed could not, become a fruitful basis for future research in heredity. In contrast, Mendel’s approaches, despite the fact that features of his ideas were later not found to be tenable, proved highly successful for the development of modern genetics. Mendel took the study of the transmission of traits and its causes out of natural history. By reducing complexity to simple particulate models, thus rendering a quantitative analysis fruitful, he transformed the study of the transmission of traits into a scientific field of research which became the basis for what later was called genetics.

Darwin’s greatest accomplishment, the theory of evolution by natural selection, shows the success of naturalists’ methods. Deichmann suggests that the adoption of a more scientific methodology in the fields of inheritance and variation would not, as has been assumed, have necessarily prevented Darwin from proposing his fundamental theory. On the contrary, it might have made his proposition of natural selection more consistent and less diluted with pre-scientific notions and popular beliefs such as blending and soft inheritance.

Michel Morange’s contribution analyses the encounters between evolutionary biology on the one side, and biochemistry and molecular biology, i.e. fields of functional biology, on the other, at two different periods of time. During the twentieth century, evolutionary scenarios hardly played a role in functional biology, and, unlike present-day scenarios, did not generate research programmes. Morange compares two examples of these past scenarios with two from the present day ones. He chooses as early examples Jacques Monod's, Jeffries Wyman's, and Jean-Pierre Changeux's proposal of an evolutionary model to explain the particular properties of regulatory enzymes (1965), and Hans Krebs's suggestion of an evolutionary explanation for the emergence of metabolic cycles, in particular the cycle he discovered 50 years earlier (1981). The present day examples are taken, first, from a well-defined molecular engineering project, in which the nature of a coenzyme in the respiratory chain of the bacterium *E. coli* was changed, and, second, from analyses of mechanisms of protein folding, in which the selective roles of "nano-machines," protein complexes which assist the folding (e.g. chaperonins), are examined.

Raising the question as to why earlier attempts to include evolutionary approaches in functional biology, unlike the present-day situation, remained largely unfruitful, Morange analyses their major differences. According to him it is three major characteristics of present-day efforts which render it likely that encounters between evolutionary scenarios and functional biology are fruitful: An excellent description of the systems under study; a rigorous use of the evolutionary models; and the possibility to experimentally test the evolutionary scenarios. He suggests that if these criteria are not met, proposed evolutionary scenarios should be approached with considerable caution.

Susie Fisher examines the role of evolutionary questions in research related to the origin of viruses. She shows that despite the existence of powerful technologies such as computerised sequence data analysis and microarray assays, which allow molecular biologists today to explore cellular mechanisms and thus provide theorists with new opportunities to re-examine traditional Darwinian themes, Darwinian theory is conspicuously missing from the practice of virus research. In addition, 100 years of virus research has led biologists to view viruses as occupying a grey area between the living and the nonliving, and evolutionary biologists for most of the twentieth century to ignore them in their studies. Viruses were rarely considered from the same evolutionary standpoint as organisms. Thus despite the fact that by the 1930s virologists were aware of viral genotypic variation, the evolutionary implications of this variation were barely discussed, and other central Darwinian themes such as natural selection or evolutionary constraints were not employed in virus research.

Fisher shows that more recently there have been attempts to accommodate virus research within the "evolutionary synthesis." Today, some theories of cellular evolution do accord viruses and their enzymes a significant role in this process and also in major transitions in the evolution of life. Hence revisiting virus origin hypotheses may contribute to viruses becoming accepted as having always been vital members of the web of life, and thus worthy of being studied by evolutionary biologists. According to some researchers in the field, the mass of computerised data related to microbes and viruses that is now available even calls for a revolution in biological thought, in which basic notions, such as those of species, organisms, and evolution, might have to be revised. The conceptualisation of viruses and speculations on their origins demonstrate the intricate relationship of scientific technique, methodology and theory-making in the twentieth century. Nevertheless, Fisher concludes, this is clearly a case in which even a significant growth of scientific knowledge may not necessarily bring us any closer to understanding events that occurred almost 4 billion years ago.

Anthony S. Travis examines the contributions of the prominent English chemist Raphael Meldola to early neo-Darwinism. While the term "neo-Darwinism" is most often associated with a refinement of Darwinian theory starting in the 1930s, it is not always appreciated that a grouping of significant individuals in evolutionary studies with the same designation emerged during the 1880s. The first stirrings took place in the summer of 1883, when August Weismann publicly rejected Lamarckian influences and soon positioned himself as leader of the pure selectionists. Alfred Russel Wallace adopted this stance after reviewing proof sheets of Weismann's 1889 book. These neo-Darwinians were joined by Meldola, who had worked in an industry that adopted the most advanced and sophisticated theoretical concepts in chemistry. While Meldola's name often appears in historical accounts of the pioneers of evolutionary studies, it is invariably without explanation of his role. Travis's contribution delineates this aspect of Meldola's scientific endeavours. Encouraged to place his teenage interest in moths and butterflies on more scientific lines, he quickly appreciated the role of Lepidoptera as providing evidence for natural selection. Meldola was a keen correspondent of Darwin, who introduced him to the work of the Germans Fritz Müller and Weismann. Together, Meldola, Wallace, and Edward Bagnall Poulton remained faithful to neo-Darwinism even when it fell into decline due to the rejection of its notion of gradual change by the Mendelians and of natural selection by the neo-Lamarckians.

Meldola applied evolutionary thought effectively in other areas. He used social Darwinist terms to warn the British that their chemical industry would enter into terminal decline unless scientific education was improved. This reflected his own industrial experience, during which time he had witnessed "survival of the fittest" firms, and extinction of others that did not adapt to changing conditions. It no doubt encouraged him to be more ready to accept theories of selection than the many biologists who did not, because it was considered materialistic and anti-organicist. Meldola encouraged entomologists to adopt the ways of systematists among natural historians, with greater use of the philosophic faculty. The systematic thinker, armed with his data, and working from the tranquillity of an armchair at the fireside, was to be admired and emulated. It was far better to conjure up theories, and discard them, their purposes achieved when new and more appropriate theories appeared, than to concentrate on cabinet collections and wall displays. The emphasis on theory-led science was no doubt a result of Meldola's exposure to its success with chemistry; his strong bias towards theory was the result of the tremendous impact of the benzene ring concept in transforming academic and industrial organic chemistry.

Rony Armon surveys the biochemical studies and theories of Joseph Needham from 1922 to 1942. As already indicated in Travis's contribution, the theory of evolution by natural selection was far from gaining consensus, right from the publication of the *Origin* until the establishment of the neo-Darwinian "Synthesis" in the 1940s. Biologists invoked as alternatives e.g. the "Lamarckian" inheritance of acquired characters (as did Darwin himself). The "Synthesis" put Darwinism on the more solid ground of Mendelian heredity and statistics, and for decades became the cornerstone of evolutionary thought and research. Natural selection and genetic mutation were used to explain both the origin and diversity of life. Only recently has the equating of evolutionary theory with neo-Darwinian selection and mutation alone been challenged by researchers in evolutionary developmental biology.

With Needham, Armon presents an early case of an attempt to overcome the limitations of the neo-Darwinian approach in explaining the emerging of new mechanisms and functions in organic evolution. According to Armon, Needham's case is important for two reasons. First, because he pioneered the biochemical study of evolution and development. Second, despite the fact that, unlike many of his own generation, Needham was not anti-selectionist, his theories drew on the approaches of Herbert Spencer and Ernst Haeckel. He combined both approaches for the explanation in developmental terms, relying on principles of emergence, of how novel functions arise. Based on his analysis of Needham's case, Armon proposes that neo-Darwinism was simply not suitable for addressing this basic evolutionary question. As leading biologists suggest, selectionists predominantly deal with the question of why certain organisms and characteristics have been preserved rather than of how the characters, which eventually gave rise to these organisms, were produced. While historians and philosophers tend to explain the rejection of the Darwinian theory of evolution by natural selection as resulting mainly from social and cultural causes, Armon's account demonstrates that important explanatory issues may have been at stake as well.

The contributors are thanked for their readiness to relate their papers to the main theme of this special supplement and the timely way in which they have delivered their manuscripts and responded to referees' comments. The editors would like to express their thanks to Helmut Pulte and Gregor Schiemann, editors of *Journal for General Philosophy of Science*, for encouraging us to publish our papers in their Journal.

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ARTICLE

Darwin, Schleiden, Whewell, and the “London Doctors”: Evolutionism and Microscopical Research in the Nineteenth Century

Ulrich Charpa

Abstract This paper discusses some philosophical and historical connections between, and within, nineteenth century evolutionism and microscopical research. The principal actors are mainly Darwin, Schleiden, Whewell and the “London Doctors,” Arthur Henfrey and Edwin Lankester. I demonstrate that the apparent alliances—particularly Darwin/Schleiden (through evolutionism) and Schleiden/Whewell (through Kantian philosophy of science)—obscure the deep methodological differences between evolutionist and microscopical biology that lingered on until the mid-twentieth century. Through an understanding of the little known significance of Schleiden’s programme of microscopical research and by comparing certain features of his methodology to the activities of the “London Doctors,” we can identify the origin of this state of affairs. In addition, the outcome provides an insight into a critique of Buchdahl’s view on Schleiden’s philosophical conception.

Keywords Evolutionism · Microscopy · Reliabilism · Schleiden · Whewell · Darwin

1 Introduction

The emergence of nineteenth and twentieth century biology represents a highly complex phenomenon of which every narrative, focusing on particular ideas, methods, findings and heroes, falls far short. Let us take the following as a pertinent example: The three major achievements of nineteenth century biology were Darwin’s evolutionary theory, cell research as it has been methodologically framed by the German botanist Matthias Jakob Schleiden, and Mendel’s genetics. Even though all three approaches had their successors, the emergence of recent biology can be seen as the result of integrating the *explanation* of macrobiological phenomena (Darwin’s heritage), *quantified experimentation* (Mendel’s heritage) and microscopical as well as chemical *exploration* of organic units (Schleiden’s heritage).

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All three tendencies of biological research are well known. Even Schleiden, though the most neglected figure among the three, has received considerable attention from historians and philosophers of science within recent years. Relevant here is the fact that in the course of the past half century philosophers of science have proposed a variety of relations between the modern versions of the three approaches, especially reduction (Nagel 1961, Schaffner 1993), explanatory extension (Kitcher 1984), and bridging by establishing an intermediary field (Darden and Maull 1977). (The first of these views, the reductionist, has as its forerunner Schleiden's programme and as its basis the leading maxim of the unity of other sciences with physics.) In sharp contrast to the extensive philosophical debate on the systematic relations between Darwinism, Mendelianism and molecular biology (as the heirs of nineteenth century cell research), very little has been said about the historical relations between the three approaches at the time when they evolved, and about their factual connections, as well as their similarities and contrasts with regard to content.

What is well-established in the historiography of nineteenth century biology is the following:

- Mendel was a reader of Schleiden's methodological work (irrespective of the impact of this reading[1])
- Schleiden was an advocate of Darwin's evolutionism.
- the Cambridge scientist-philosopher Whewell, whose importance for Darwin's approach (especially the restrictions imposed on the presentation of his evolutionism and its elaboration) has been often emphasised, and Schleiden were both partisans of a Kantian philosophy of science.

This article will leave aside the relationship of Darwin and Schleiden to Mendel. It will focus, instead, on the connections between five contemporaries:

Matthias Schleiden (1804–1881),
Charles Darwin (1809–1882),
Edwin Lankester (1814–1874),
Arthur Henfrey (1819–1859),
William Whewell (1794–1866).

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[1] See Orel (1979). Schleiden's programme of microscopical research and Mendel's genetics were compatible and shared physicalist objectives in the long run. However, Schleiden's microscopy was *not* quantitive and did *not* include idealisation (see, especially, Mendel's substitution of real trait differences of degree [↑↓ wrinkled, ↑↓ tall etc.] by an ideal distinctness [± wrinkled, ± tall etc.]). What both researchers had in common was that (in contrast to Darwin's attitude) biological progress is based on *neglecting* the manifold of appearances in favour of dealing with a small number of selected phenomena. This is not the appropriate place to comment on Darwin's views on nature in general, but the fact that a respected historian (Richards 2002) finds good reasons to connect them to Humboldt's conception of *Kosmos* in the sense of "a harmoniously unified network of integrally related parts" (Richards 2002, p. 10) illuminates the difference to just focusing on cells and idealised peas.

In my opinion (to be presented in more detail in another paper), the roots of Mendel's analytic procedure are a) intuitive idealisation in traditional plant breeding; and b) the so-called analysis of phenomena in modern physics (or 'Galilean idealisation'). Cf. Falk (2007). Mendel's sources regarding the latter are to be found in the writings and practices of his teachers in physics (Doppler, Ettingshausen) and the younger Herschel, and *not* in botany (nor in that of Mendel's mentor Unger or of Schleiden, whose methodology Unger admired). A systematic comparison of Mendel's genetics to Darwin's concept of *gemmula* is given in Deichmann, this issue.

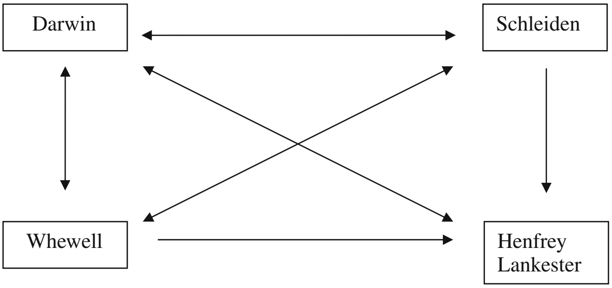

Fig. 1

And it will discuss:

- some historical details and features of Schleiden's and Whewell's philosophies of science with special regard to development and evolution.
- Darwin's reading of an early evolutionist essay by Schleiden.
- Schleiden's reading of Darwin's *The Origin of Species*.
- some aspects of the almost unknown story of the "London doctors," British partisans of Schleiden's microscopical programme, and their disinterest in evolutionism.
- the "reliabilist" component of Schleiden's views on scientific method and the related attitudes of the "London Doctors."

As this list suggests, the main emphasis will be on Schleiden, the author of the "Methodologische Einleitung." This also defines the usage of the term "methodology" here. In Schleiden's work, "methodology" refers: (a) to fundamental reflections on principles, to reasoning patterns, etc. (which constitute the smaller and mere programmatic part of Schleiden's text); and (b) to a set of, at first sight, philosophically modest ideas on the arrangement and on the technical as well as the personal preconditions of inquiry procedures in the domain of microscopical practice. As for (b), it constitutes by far the largest part of the "Einleitung", and these reflections are rooted in intuitions based on successful laboratory experiences. The contrast between the two meanings will play an important role with regard to the *philosophical* objective of this paper. I comment critically on a particular reading of Schleiden's writings and relate them to others' work, thereby highlighting aspects which are normally not taken into consideration if one speaks of "methodology"—at least if one is not acquainted with reliabilist orientations towards good scientific practice (see Sect. 5, below).

The *historical* objective is to shed some light on ten connections, which in fact differ somewhat regarding their relevance (Fig. 1):

2 Whewell, Schleiden, and the "Parallelising" Reading

Connecting and comparing Whewell's and Schleiden's views commends itself as an appropriate starting point. As stated in the foregoing, both were important authors in the formative years of nineteenth century biology; and both of their philosophies of science have been reviewed by Gerd Buchdahl, historian of scientific methodology and himself a Kantian thinker on science, as clearcut examples of Kantian philosophies of science.[2]

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[2] Buchdahl (1973/1989), Buchdahl (1971/1991). It was perhaps inevitable that Buchdahl in his Cambridge department would deal with Whewell. As for Schleiden, it was according to Buchdahl's own recollection

Before we consider the philosophical issue it is perhaps worth mentioning that the two authors were not totally unfamiliar with each other's work. But the familiarity as documented by citations and references is not at all balanced. Whewell's acquaintance with Schleiden's views is not even certain and at best must have been marginal. I will show that this imbalance is meaningful and draws our attention to interesting differences. But within what I refer to as the "parallelising" reception of the two this seems to be sufficiently explained by the nature and character of their writings and ambitions:

Both men were scientists-philosophers, just as were Herschel, Bernard, and Mach, but Schleiden was far from seeing himself as a relevant philosophical author. (Later, I attempt to demonstrate that Schleiden was an outstanding methodologist in the sense of (b) hidden behind a not very original philosophical mask (a)). In his explicit presentations he was a botanical expert making usage of the philosophies of Kant and of his personal mentor Fries and promoting the application of their philosophies to botany.[3] Schleiden was a very popular author in nineteenth century Germany and published numerous books and articles on various topics; but his most important contributions are botanical essays, and his major work is a book on his *own* discipline, the *Grundzüge der wissenschaftlichen Botanik*. This latter publication was devoted to a highly specialised topic in this field, microscopical cell research. In contrast, Whewell's most impressive writings include historical and philosophical reflections on science in *general*, dealing systematically with the different scientific domains and subdomains.[4] Indeed, Whewell, at Cambridge, was a scientific polymath, and among his several disciplinary expertises were astronomy and mineralogy. However, his expert contributions are not what a modern historian usually has in mind when paying tribute to this giant of Victorian science.

Buchdahl, to whom many historians and philosophers of sciences owe the "rediscovery" of Schleiden's and Whewell's philosophical works, sees the two approaches as examples of how philosophy of science should, in principle, be done at any particular time. This means primarily paying careful attention to the fundamental presuppositions of scientific work. To Buchdahl, both were not only authors anticipating the notion of "theory-ladenness" but they even formulated it much more precisely than did the influential twentieth century philosophers (Popper, Hanson and others). Intertwined with this appraisal Buchdahl saw them discussing the role of disciplinary matrixes more clearly than Thomas S. Kuhn in his *Structure of Scientific Revolution*, and even more thoroughly reflecting on the metaphysical and methodological preconditions of scientific research. Not to mention that their work—especially that of Schleiden—was relevant to actual scientific practice (something twentieth century philosophers of scientific method could hardly have imagined seriously). To Buchdahl, both approaches fit very well into his own view on how

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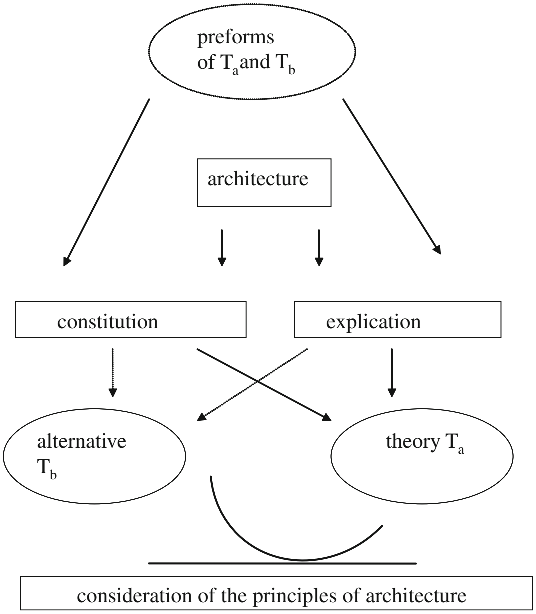
Footnote 2 continued
(private communication), a paragraph in Cassirer (1957, pp. 161–165) that attracted his attention. I mention this because it demonstrates that Buchdahl's Kantian/Friesian reading has already a neo-Kantian antecedent. As for the contents of Cassirer's discussion of Schleiden, suffice it to say that it is relatively short and focuses on the maxim of "Entwicklungsgeschichte." It is in all relevant aspects dominated by Buchdahl's article. Whewell is not mentioned by Cassirer in this context, nor in the latter's detailed investigation of post-Kantian systems (Cassirer 1923). Jahn (1991a) and Breidbach (1999) do not take Buchdahl's systematic reconstruction into consideration but follow Schleiden's own explicit attachments to Fries and Kant.

[3] See, especially, the writings collected in (Charpa 1989).

[4] See the edition, by (Buchdahl and Laudan 1967), of Whewell in German, Whewell (1840), with remarkable historical additions by the astronomer v. Littrow.

Fig. 2



science advances. In a simplified version his general view on scientific change would present itself as in Fig. 2.[5]

According to Buchdahl, science starts with primitive theories and progresses by the interplay of three components: The "constitution" component covers empirical data and their inductive or otherwise systematized role for a theory; the 'explication' component (of scientific progress) includes among other issues conceptual structures, their intelligibility, and conventions; and the "architectonic" component, to which is assigned control of the other two components and their interplay, primarily by determining the criteria of theory choice, as for example empirical adequacy, simplicity, coherence, type of explanatory arguments, etc. There is no a priori rule concerning the right "architectonic" preferences at all times. The criteria for control of scientific change are themselves changing, which to Buchdahl does not exclude progress. But, nevertheless, this is a position that neither Whewell nor Schleiden would have shared. In other respects, it is easy to see the extent to which Buchdahl's philosophy of science corresponds to certain features of Schleiden's and Whewell's approaches (Fig. 3):

The leading ideas (for Schleiden the leading maxims; Whewell was more ontologically oriented) correspond to Buchdahl's emphasis on the "architectonic" component. And this is how their "modernity" with regard to "theory-ladenness" and "disciplinary matrixes" is deeply rooted in a common conviction of Whewell, Schleiden and their twentieth century commentator on the relevance of balancing the criteria of theory-choice, in other words, reasoning, described in a Kantian manner as the activities of *Vernunft* and *Urteilskraft*. It should be added that both authors gave thought to development and evolution. This, at first sight, appears to guide us toward a deep similarity in the two approaches. But we shall see

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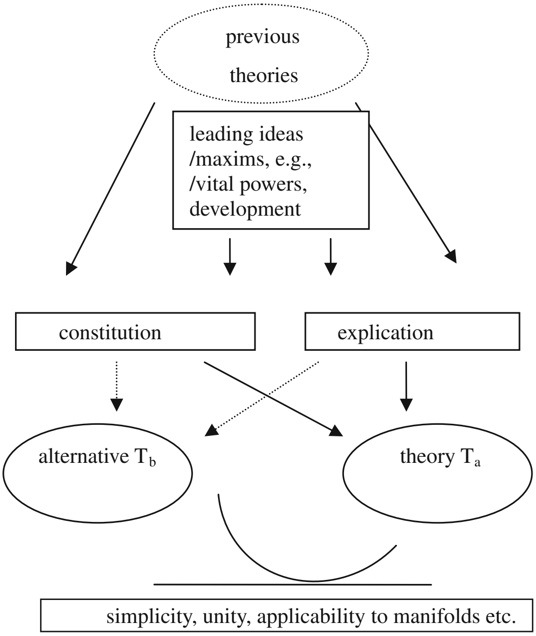
[5] A much more sophisticated reconstruction of Buchdahl's model of scientific progress is given by Jardine (2003). The main writings in this regard are Buchdahl (1969, 1970, 1992).

Fig. 3



that this is not the case and that by closer investigation we come across underlying major differences.

3 Some Historical Problems of the “Parallel-Perspective” and Some Irritating Addenda: Schleiden’s and Whewell’s Views on Development and Evolution

As mentioned earlier, Schleiden at first sight seems to have been more interested in Whewell’s position than the other way round. In the “Methodologische Einleitung” of the *Grundzüge* Schleiden refers to Whewell’s *History* and quotes Whewell’s comparison of the history of botany to that of astronomy.[6] In Schleiden’s *Schellings und Hegels Verhältnis zur Naturwissenschaft*, he relates his own criticism of romantic natural philosophy to Whewell’s defence of Newton against Hegel’s attacks.[7] To Schleiden’s close friend and philosophical consultant Ernst Friedrich Apelt, Whewell was “der erste Engländer, der in die Geheimnisse der kantischen Philosophie tiefer eingedrungen.”[8] As regards Whewell’s acquaintance with Schleiden’s views, cell research was widely discussed in the journals available to Whewell and to which he himself contributed, as for example, the *Edinburgh New Philosophical Journal*. In one of Whewell’s best known contexts of publication, the *Bridgewater Treatises*, we come across the reaction to Schleiden as “discoverer” and “observer” who “made the curious discovery that every vegetable cell is the result of a very minute body, or nucleus which he terms a cytoblast.”[9] Obviously, such relationships

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[6] Schleiden (1863, p. 8). Of minor importance is Schleiden’s discussion of Whewells’s observations on tides Schleiden (1865, p. 65).

[7] Schleiden (1843, p. 75, p. 83).

[8] Apelt (1854, p. 187).

[9] Roget (1840, p. 56).

to Whewell are very tenuous and do not touch the philosophy behind Schleiden's cell research. This fact is even more astonishing, if we take into account that

- Schleiden's two most influential books had been translated into English in Whewell's time.
- Whewell was a competent reader of German (he even translated Schiller) and was familiar with the teachings of Fries, who was Schleiden's philosophical mentor.[10]

This raises the question: Do Schleiden's references to Whewell show a philosophical impact? What we actually find is Schleiden's attempt to document the existence of an alliance against romantic natural philosophy, but nothing that has to do with Buchdahl's point: The parallelity in establishing the architectonic of science as a set of fundamental principles. Neither does Schleiden explicitly connect his project to Whewell's view on leading ideas; nor does Whewell ever utilise Schleiden's discussion of botany in his various panoramas of the sciences. This irritating fact seen within a "Buchdahlian" perspective does not necessarily mean that considering the "architectonic" level leads nowhere.

A good starting point for understanding the mutual disinterest of the two authors is just at that place where Buchdahl's reading of the texts establishes the parallelity, that is, Whewell's reference to Schleiden's teacher Fries in the *History*.[11] Whewell cited Schleiden's hero Fries with regard to zoological *classification*, when he discussed the number of natural groups: One aspect to take into consideration, as if it goes without saying, is that the basic idea as well as the main objective of biology is to outline the *order* of living beings. Insofar as Whewell dealt with the question of change in organic nature, he did so within this framework. In the first instance, biological change is merely ontogenesis, and the investigation of ontogenesis ought to be guided by the idea of vital powers. Vital powers are such powers that make a specific plant a specific plant in the process of growth.

To Whewell, if there should be biological change in the sense of phylogenesis, it was something we can think of in a speculative manner. Such an approach would be a part of *general history* and not of biology in its normal sense. In line with this, speculations about *phylogenesis* ought to be guided by the idea of *historical causation*. The adequate type of argument would be that of a historical explanation. Let us take the following example: One can, e.g. explain Caesar's success in Gallia by his strategic planning, the characteristics of the troops he commanded on one side and the capabilities of his antagonists on the other. One relevant point with historical explanation in this context is that Caesar, the Roman legions, and the Gallian tribes are or have been *manifest* beings. To understand the concept of historical causation one has to have in mind that to Whewell and many other nineteenth century philosphers events like Caesar's successes do not count as something that happened by chance. To them it came about by historical necessity and can be explained as almost lawlike, as for examples by the rules of military strategy. As for other scientific explanations, a causal historical explanation according to Whewell's philosophy could explain new and surprising phenomena, even prima facie counterexamples, and this faculty had its best explanation in the truth of the causal historical explanation proposed. If there were no laws of biological change available, the prospect of a biological historical explanation was obstructed.[12] Thus, in those cases in which scientists might have in mind

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[10] See below (footnote 11).

[11] Cf. Whewell (1837, vol. 3, book 16, chap. 7).

[12] This provides as least one rationale for Whewell's initial scepticism and later hostility towards the *Origin,* causing him to ban the book from the Library of Trinity College. See also Darwin's letter to Lyell, 4 January 1860, in F. Darwin (1887, p. 261).

something like the establishment of a science of phylogenetic change, they would have to start as the historians do: With well-defined entities that would have to be connected causally. In other words, if there should ever be "evolutionist" biology this project would depart from taxonomy, based on the idea of a well-defined (classified) organic world. It is exactly in the attitude towards taxonomy where Schleiden deviates from the philosophical position of his admired master Fries and even ignores Fries' explicit criticism.[13] And here we find the essential contrast between Schleiden and Whewell.[14]

To Schleiden organic nature is in a permanent process of change: ontogenesis and phylogenesis (*Maxime der Entwicklungsgeschichte*). As the problem with classification of hieracium, algae and other logically vague sets of biological entities shows, the project of taxonomy leads astray. The relevant research-guiding principle at all levels of biological investigation is that of focusing on cells. The cell is the unit of inquiry (*Maxime der Selbständigkeit der Pflanzenzelle*). In the long run, biological research approaches the "deeper" chemical and physical processes that cause the developing phenomena at the microscopical level. Cell research provides evidence of a continuum from single-cell-organisms to complex ones and transgresses the distinction between ontogenesis and phylogenesis. Both levels are in one go "temporalised." Whether this possibly indicates a history from the very first cells to modern men cannot yet be shown. It is entirely a matter of speculation. There is not yet a scientific history of the recent species, but if there should ever be one it would emerge from basic research on cells as units and not on species.

In summary, the comparison of the architectonic components of Schleiden's and Whewell's approaches gives an insight into fundamental differences: Whewell discusses the character of adequate *theorising* about evolution, providing causal explanations of existing and future empirical data. Schleiden focuses on *exploring* microscopical phenomena and organising them by temporalising. Causal explanations of organic phenomena belong within the context of future reductionist possibilities.

The result of the comparison can itself be made plausible if we look at the origin and status of the important fundamental principles in Schleiden's and Whewell's philosophies. Whewell's are found a posteriori, taught by historiography of science which itself is inspired by a priori reasoning. The principles are themselves eternal metaphysical ideas that become clear with the advancement of science. To Schleiden the general methodological principles (e.g. unity) were found by metaphysical reasoning a priori and this reasoning could be confirmed by history. This is not much different from Whewell's point of view. But the specific research guiding maxims of particular scientific disciplines are maxims generalised from empirical success. They are strategic rules helping to identify relevant empirical data—and not revealing the "real contents" of a vague fundamental idea (Whewell). Put more simply and with regard to biology, the cells and the processes which are involved in are not entities and properties "in mind" but something that can be *seen*. The maxims of orienting biological research at the unit of the cell and of *Entwicklungsgeschichte*, as well as the specific maxims for a successful handling of the microscope and the objects of observation (I will come back to their importance later), have their origins in Horkel's and Müller's laboratories, where Schleiden started his work.[15]

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[13] Cf. Fries' letter (Fries 1989) and Schleiden's reaction, affording Linné and others more respect, but ignoring Fries' insisting upon the priority of taxonomy.

[14] Cf. Charpa (1988).

[15] On the Berlin context see Jahn (1991a). The principle of *Entwicklungsgeschichte* varies the practices and opinions of Caspar Friedrich Wolff. It was this track, which Schleiden followed from 1837 on, that led to his cell-research. Cf. Mylott (2002, pp. 189–190).

4 Darwin, Whewell, and Schleiden

Before I compare Darwin's and Schleiden's views on evolution I will briefly recall the well-known role of the other "architecture" of science relevant to the formation of Darwin's thinking.[16] From Darwin's Cambridge years on, Darwin and Whewell were in a close contact, as extensively documented, e.g. in the Beagle report (1839). Whewell's anti-evolutionist demand for laws of change in his *Address to the Geological Society* during February 1839 are seen by historians of science as the challenge that provoked Darwin's selectionism and caused the long incubation period of Darwin's evolutionism. The early version of an evolutionist epistemology in *Descent of Man*, 1871 (Chap. 5), is considered to counter Whewell's "success argument" in favour of the non-human origin of the "fundamental ideas." One could speak of the impact of Whewells's philosophy as fertility ex negativo that inspired some improvements of a conception that it had disproved.

In contrast to the investigation of the Darwin/Whewell-connection, the relationship between Schleiden and Darwin has not yet drawn much attention from historians of science. One of the features both topics have in common is that their perspectives were supressed by the image of the giant Darwin, the prevailing view later on. To Schleiden (and the same applies to Whewell), Darwin was not an illustrious hero but someone who did competent work in a certain domain and (in contrast to Whewell's appraisal) had a brilliant idea.[17] Already in his early years as a botanist Schleiden had attentively noticed Darwin's report on the Beagle voyage.[18] As to evolutionism, in one or another form it was far from appearing sensationally in the context of German botany.[19] Already in 1860, when the first German edition of the *Origin* was published, Schleiden reacted promptly as a supporter of Darwin and the idea of the mutability of species.[20] Later on, his defences of the *Origin* caused a lot of difficulties and led to his leaving the University of Tartu. As to the awkward question of the ape-like precursors of man, which was at the centre of common interest, Schleiden saw a research-programme but not a given answer.[21] If one takes into consideration Schleiden's own radical thoughts about evolution (which will be reviewed with regard to the reception of Darwin), suggesting that recent organisms had emerged from primitive single- or mono-cells, there is no cause for controversy in working on the non-human prehistory of human beings. Schleiden considered Darwin's evolutionism as parallel to his own project of *Entwicklungsgeschichte* (ontogenesis with an open border to phylogenesis—as sketched above) as an admirable result of the competent work of a natural historian who had spent two decades collecting data on the macro-level and organising them according to his macro-principles.[22] This means that from Schleiden's methodological point of view (which is not the same as his private preference—he showed

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[16] Since Ruse (1975), Whewell's role (besides that of Herschel) has been discussed so extensively (e.g. Curtis 1987, Ruse 2000) that it is sometimes considered overdone, if not entirely exhausted (Hodge 2003, p. 68).

[17] "Darwin's Theorie ist sehr einfach und gleich fast dem Ei des Columbus. Er geht von verhältnißmäßig wenigen ganz bekannten Thatsachen aus, leitet daraus seine Schlüsse ab, oder entwickelt vielmehr nur das allgemeine Gesetz, welches in jenen Thatsachen schon liegt und stellt dann seine Ansicht mit solcher Sorgfalt und Umsicht, mit so großem Umfang von Kenntnissen gegen alle Einwendungen sicher, dass sich irgend Erhebliches schwerlich gegen dieselben noch vorbringen lassen wird." Schleiden (1863, p. 131).

[18] See first edition of the *Grundzüge*, Schleiden (1842, §190 et passim).

[19] Cf. Junker (1995).

[20] Cf. Schleiden (1860).

[21] Schleiden (1865, p. 265), on this episode see Scholz (2003).

[22] Schleiden (1863, p. 9).

a life-long interest in natural history), Darwin was an old-fashioned natural historian, far from gaining the deeper explanatory level of cellular phenomena, not to speak of the chemical-physical processes. But nevertheless in terms of the Schleiden-project Darwin presented himself as a highly interesting exemplar of an anachronistic natural historian, leaving behind the traditional classificatory agenda by relating his evolutionist explanatory patterns to species in a rough-and-ready-sense and/or populations.

If we turn our attention to Darwin's reception of Schleiden's work we find very few references: The three most relevant ones are to Schleiden's view on plant nutrition in *The Variation of Animals and Plants Under Domestication*[23]*;* another in *The Descent of Man* on "the celebrated botanist" and his remarks on rattle-snakes,[24] that had been published in an essay on Darwin's evolutionism in a popular German journal[25]; and the third as a five-page unpublished commentary on the English version of Schleiden's book *Die Pflanze und ihr Leben*.[26] Schleiden's book was first published in 1848. It was widely-read in his time and went through six German editions and several translations not only into English but also into Dutch, French and Swedish. The most interesting paragraphs with regard to evolutionism are to be found in Lecture XI which is entitled "The History of the Vegetable Kingdom". Here we find Schleiden's view on the prehistory of the contemporary organic world, described as follows:

> In some periods of […] gradual shaping out of the earth, the first germs of organic existence originated, through forces, which may indeed still be in action, but under conditions and co-operation of those various forces such as now longer appear possible on our earth. The ocean was probably the birth-place of these organisms, and their forms as yet very simple.[27]

He considers his view as belonging to the realm of "arbitrary speculation,"[28] but in fact it is merely hypothetical, and not at all arbitrary. Schleiden tries to give evidence as far as it is available. In this case it is the geological record:

> […] the first germs of life probably originated in water, and in agreement with this we find in the oldest stratified rocks, the Grauwacke, or as the English call them, the Silurian rocks, merely some few remains of species of Tangle, accompanied by sea animals, of which solitary representatives were already exhibited in the preceding Cambrian formation.[29]

As to the characteristics of the "first germs" these characteristics can be identified in the actual organic world as well:

> The simplest element of the whole vegetable world is the cell, a very simply constructed organism, the origin of which out of the peculiar association of carbonic acid and water, on the one hand, into gum or vegetable jelly, and of carbonic aid and ammonia on the other hand into protoplasma or albumen, is not so very widely removed from a possible explanation as the sudden origin of a vegetable germ with

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[23] Darwin (1868, pp. 271–272, 489–490).

[24] Darwin (1871, vol. 2, p. 30).

[25] Schleiden (1869).

[26] Darwin (ca, 1850), undated manuscript DAR 71, pp. 38–42, Cambridge University Library.

[27] Schleiden (1848b, pp. 277–278).

[28] Schleiden (1848b, p. 288).

[29] Schleiden (1848b), pp. 280–281).

> perfect definite power of development into a peculiar species of plant […] That the cell can vegetate as an independent plant, we know from the vegetable Creation at present around us, since many of the simplest plants, especially the *Waterplants,* consist of a single cell.[30]

Why were some ancient plants in the course of time preserved, while others disappeared, and new ones came into being? It had to do with the extent of adaptedness within processes of change of the surroundings:

> […] particular forms of plants of the previous epoch were preserved and continued over into the new order of things, while the most peculiar races sank with their soil, and partly died out, in consequence of the gradual essential alteration of the physical conditions. The arborescent Ferns, and the Calamites still existed but became more rare, while the *Cycadaceae* and Conifers developed in great abundance, and in numerous peculiar forms.[31]

The causes of variety

> appear to lie in the richness of the soil in readily soluble inorganic matters, which in the first place give rise to variations in the chemical processes of the plant, and thus to a greater or less deviation in the form.[32]

From mere variation to the formation of sub-species and a population that "becomes so permanent that we must describe it as species" took an enormous time-span; for the derivation from the original form of a plant to a stable and new type took not "centuries or tens of centuries", but "ten or a hundred thousand years."[33]

How did Darwin react to Schleiden's text? In particular, if one has in mind that it was the reading of Schleiden's *Die Pflanze und ihr Leben*—apart from Humboldt's *Ansichten*—that had paved the way of Ernst Haeckel (the outstanding German Darwinian who achieved 'habilitiert' with the help of Schleiden at Jena University) to biology.[34] We shall see that Darwin's discussion is surprisingly meagre, even if we take into account that speculative evolutionism was far from new or novel to him.

The manuscript relevant here is undated, but from around 1850 does not appear to be unreasonable. We know that the English edition of Schleiden's book appeared in 1848 and Darwin was in close contact with Schleiden's translators and partisans, the so-called "London Doctors," in order to facilitate the preparation of his work on *Cirripedia* (1851/1854), published by the *Ray Society* in 1851 and 1854 (we will come across this circle again with regard to Henfrey and Lankester). At that time, Darwin had already been clear about the principle of natural selection for more than a decade. In his correspondence he named this period as that of his "species-work," the years 1840–1854, spent collecting information connected with questions of speciation, variation, including domestication, etc.[35] Not by chance did Darwin recommend books such as Karl Friedrich von Gärtner's *Versuche und Beobachtungen über die Bastarderzeugung im Pflanzenreich* (1849) for translation to the *Ray Society*. This corresponds to his selective commentary on

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[30] Schleiden (1848b, p. 289).

[31] Schleiden (1848b, p. 283).

[32] Schleiden (1848b, p. 290).

[33] Schleiden (1848b, p. 291).

[34] See Haeckel's letter, dated March, 4 1861, printed in Uschmann (1954, pp. 57–58).

[35] Cf. Schweber (1985, p. 35).

Schleiden's evolutionist treatise. What Darwin picks up from the total text of "The History of the Vegetable Kingdom" is not much more than Schleiden's remarks on geography and nutrition, found in a foot-note on Alpine plants and their richness in form compared to the variety of forms at other places. The most extended passage of the manuscript relating to Lecture XI is the excerpted list of the names of the Alpine plants mentioned by Schleiden.

Darwin does not discuss Schleiden's

- principle of survival/non-survival due to external factors.
- idea of chemical causes of variance.
- idea of evolution as starting from simple cellular organisms (which reminds the reader of Darwin's famous "warm little pond").
- reflections on the time-spans needed for evolutionary processes (a problem that played an important role in Lord Kelvin's and other physicists' refutation of Darwinism).

Obviously, Darwin here acts like a natural historian collecting interesting exemplars of a certain type, without taking notice, or deliberately ignoring, anything that has nothing to do with his own theoretical ambitions. The best explanation for this is, in my opinion, that Schleiden's form of evolutionism simply did not promise any help for Darwin's own conception. The answer to the question of the origin of life, to all evolutionist authors, was dependent on a positive statement on the mutability of species. But as Howard E. Gruber has shown, to Darwin there were nevertheless two different problems, and during a long period he confined himself to work solely on the problem of the apparent gap between mere variety and the formation of a new species.[36] To Schleiden—as to most other evolutionists (one may think of Erasmus Darwin)—both issues were entangled.

In addition, Schleiden's evolutionist approach is "architectonically" built up quite differently: According to Schleiden, what was relevant in the evolutionary process from its beginning until the current state of organic life, was the world of cells and cellular processes. Thus, he would have surmised, survival and extinction, varying abundantly and staying unvaried, stabilisation of species and evolution to new species are things we can perhaps in a far future understand, scientifically, in the course of the improvement of our knowledge. In depth it all amounts to the chemical reconstruction of developmental reactions within the cells caused internally or by the chemical nature of the environment. What recommends itself in this context as a suitable unit of investigation is a simple form with short-time developmental processes, e.g. algae living in specific liquids, etc. Within the framework of Schleiden's project the chemistry of tigers and their nutrition is not a topic with which successful research can be linked to insights into the deeper causes of evolutionary change. Darwin, simply put, is looking for explanatory mechanisms that apply to tigers, sheep and complex plants and is sure of having found one. This difference between the units of consideration is behind Schleiden's friendly remark on Darwin's having found something like the "egg of Columbus" by systematizing what is already *within* the set of known facts.[37] The verae causae Darwin was hoping for could obviously not be Schleiden's chemical causes, which would in principle satisfy Whewell's conditions. But why not? Was that a matter of convenience, as one could speculate, because they were out of range for a generally interested natural historian, who was a "gentleman-naturalist," not a laboratory specialist? It is not that easy to provide an answer, especially if one recalls that Darwin had a strong interest in chemistry from his teenage years on and

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[36] Cf. Gruber (1985).

[37] See above (footnote 17).

that he was an enthusiastic reader of the works of Liebig and others, when dealing with agricultural chemistry.[38]

In my opinion the point at issue is quite different: Neither Schleiden nor Darwin had access to the chemical processes causing variation or even mutation. Chemistry was at too primitive a state of development, just on the point of adopting basic ideas of valency and structure. What to both was evident was that certain chemicals had certain effects on plants, for example there are links between the kind and mass of nutrition on the one hand and variation on the other, but this is far from knowledge about a chemical process as a vera causa. Such knowledge, had it existed, would conceivably, at least to the way of thinking at the time, have enabled the biologist, in every case he was interested in, to create new species or at least varieties by changing particular chemical conditions. What Darwin achieved was an ingenious explanatory systematisation of the available facts on the macro-level of populations and their members. Schleiden's project was the discovery of hitherto *unknown* facts at the micro-level. The distance between the two nineteenth century approaches and what a century later became known as "biochemistry" is enormous. However, there is a remarkable historical difference between the two conceptions regarding their dynamics: Darwinism, starting with Darwin's own attempt, had in a way to "wait" for its deeper biochemical reconstruction, in fact until the "Schleidenian" laboratory project was advanced enough, in our own time, to "see" not only cell-structures and dynamics but the molecules and molecular processes.

5 Henfrey, Lankester, Schleiden, and Darwin

> [To] Henfrey will always belong the credit of being the first Englishman to recognise the full significance of the movement [of German miscroscopical botany]. From that moment he unceasingly made known and diffused in this country the results of the German renaissance.[39]

This statement informs us about the position of Henfrey on the historical landscape described in the foregoing. But even this laudatory characterisation does not give sufficient credit to the worth and impact of his activities. There is not much known about his personal life. He underwent medical training in London, but never practised as a medical doctor. Instead he became lecturer and in his last years professor of botany at King's College. He was a prolific writer on botanical topics and one of the authors of the voluminous *Micrographic Dictionary* that included hundreds of articles reporting observational findings and advice, among them a detailed article on cell-research. Often, Henfrey's introductions refers to the "well known Schleiden"[40] and his proposals on working with the microscope. Darwin is cited once, on his travels, and the above mentioned work on *Cirripedia*.[41] In contrast, the name of William Whewell never occurs in the *Dictionary* (on this, one should perhaps allude to the fact that Herschel is noted only as the author of the article on Optics) and neither author is ever mentioned in Henfrey's *Elementary Course*[42]

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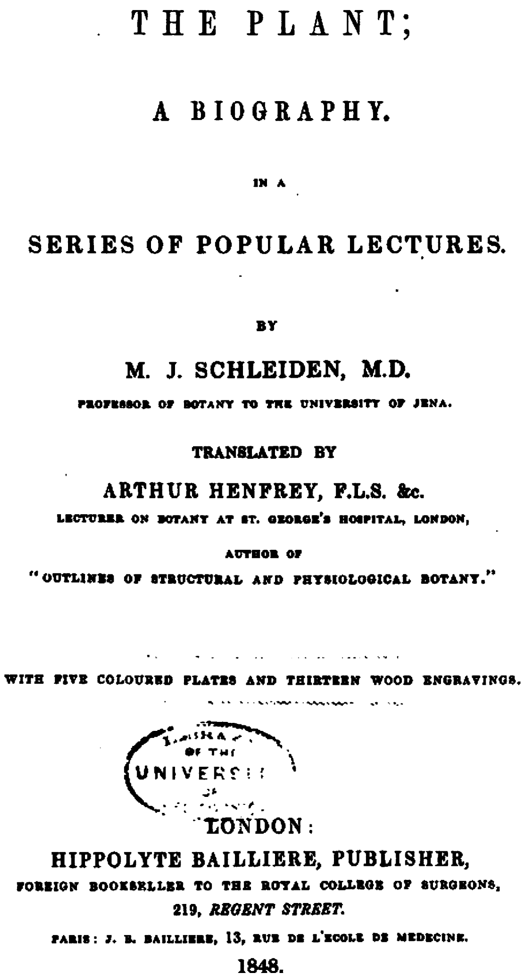
[38] Cf. Schweber (1985, pp. 39–47).

[39] Oliver (1913, p. 192).

[40] Griffith and Henfrey (1856, p. xv).

[41] Griffith and Henfrey (1856, pp. 46, 652).

[42] Henfrey (1858b).



THE PLANT;

A BIOGRAPHY.

IN A

SERIES OF POPULAR LECTURES.

BY

M. J. SCHLEIDEN, M.D.
PROFESSOR OF BOTANY TO THE UNIVERSITY OF JENA.

TRANSLATED BY

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"OUTLINES OF STRUCTURAL AND PHYSIOLOGICAL BOTANY."

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1848.

Fig. 4 (Schleiden 1848b)

(1858b), his *Introduction*[43] (1858a), or the *Outlines of Structural and Physiological Botany*,[44] a book which is full of *Schleidenia*.

What this indicates is nothing less than the fact that the movement Henfrey and his colleagues propagated was something quite separate from the Cambridge-philosophers and their "Newtonian" modelling of good science. Another tool for promoting the new microscopical project was *The Botanical Gazette*, a monthly journal appearing from 1849 on, one year after Henfrey had translated and published Schleiden's *Plant* (Fig. 4), and two years after his colleague and friend the physician and naturalist Edwin Lankester had done the same to Schleiden's *Grundzüge der wissenschaftlichen Botanik.*

Lankester was far more than a medical doctor. Having graduated from Heidelberg, he was a practising surgeon and health reformer. Some of his activities as a microscopist (he was the first president of the still extant *Royal Microscopical Society*) were

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[43] Henfrey (1858a).

[44] Henfrey (1847).

motivated by the necessity of examining the heavily contaminated drinking water of London in order to find the causes of cholera and other diseases.[45] Lankester was a close friend of Thomas H. Huxley, and befriended John Stevens Henslow, Darwin's tutor. But, as we shall see, these connections did not lead him to become interested in evolutionary hypotheses.

This allows us to take a closer look at some aspects of the way the two Schleiden-books were presented to, and received by, the British public. Lankester's translation of the *Grundzüge* starts with a surprising "explanation to the Public." He wrote:

> The second German edition of this work, of which the present volume is a translation, [[46]] was accompanied with a Methodological Introduction, intended as a development of those general principles of science, which are derived from the study of the observing mind and the observed external nature. As the discussion of these general principles occupies a considerable space in the original, and it was deemed desirable not to increase the bulk of the present work, this Introduction has been omitted.[47]

In a footnote Lankester adds:

> As general introductions on the principles involved in scientific inquiry, we have in our own language, two admirable works—Sir John Herschell's [sic!] [Preliminary, sic!] Discourse on the Study of Natural Philosophy, and Professor Whewell's Philosophy of the Inductive Sciences.[48]

This could at first sight be interpreted as a trivial preference for genuine English books on methodology. But this would be an inadequate explanation. The sloppiness of the citation, and the fact that Herschel's and Whewell's views differ in important respects, point to another direction, that of a particular *attitude* towards the "architectonic" component of science, at least with regard to botany. A random examination of some of Lankester's own books shows that—however admirable Lankester may have found Herschel's and Whewell's works—as an author he seems not to have paid any attention to them. His *Practical Physiology* (1872), *The Natural History of Dee Side and Braemar* (1855), *Half-Hours with the Microscope* (1860), and *Vegetable Physiology and Systematic Botany* (1865), never once make mention of Herschel's and Whewell's methodologies.

If we go back to Lankester's translation of the *Grundzüge*, the reader soon recognizes that not all the text of the "Methodological Introduction" is left out, but only a part. It is in Appendix D ("On the Use of the Microscope") that Lankester presents Schleiden's methodological considerations on microscopical research to the British reader. While these considerations contain a lot of prima facie "architectonic" elements, defining the

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[45] Cf. the contemporary satirical picture of the "Monster soup commonly called Thames Water," showing a woman with a microscope, alarmed by the dangerous looking living beings in a drop of polluted liquid, is reprinted in Porter (2001, p. 266).

[46] This is not exact. In contrast to his own presentation, Lankester's translation includes an Appendix C containing new passages from the 3rd German edition. The reason may have been that Schleiden here discusses, among other topics, the problem of cell formation and von Mohl's observation of the multiplication of cells by division, and not—as Schleiden in the beginning had erroneously assumed—by 'free' formation similar to growing crystals ("In conclusion, I will only observe, that from my own researches I must accede to these results of Mohl's in every respect", Schleiden (1849, p. 574).

[47] Schleiden (1849, p. iii).

[48] Schleiden (1849, p. iii).

conditions and criteria of good scientific research, they do not cover any other domain than that of microscopical work.

Before discussing the philosophical character of Schleiden's maxims relating to microscopy and their connection to Lankester's own picture of good scientific work, I draw attention to a curiosity in Henfrey's translation of Schleiden's *Pflanze,* to be found in Lecture XI on the "History of the Vegetable World" (related to Darwin's reading above). Schleiden's "Geschichte der Pflanzenwelt" ends with some not very inspiring words about the moral duty of humans to preserve nature. Without any plausible tie to this topic, Henfrey relates Schleiden's closing paragraph to the work of a British author who is announced as an object of admiration, just as in references to Herschel's and Whewell's books by Lankester. Henfrey inserts the following footnote: "See the admirable work of Dr. Prichard, 'The Natural History of Man;' comprising Inquiries […] London 1845." This addition at the bottom of the page closes the chapter where Schleiden presents his speculations about evolution. It is in a way an unobtrusive final commentary by the translator. A glance at Prichard's book shows it to be anything *but not at all* a work that illustrates Schleiden's position. To be sure, to a certain degree it focuses on the same topics as Schleiden's essay, change, variation and their relatedness to external factors. But Prichard's position is just the opposite:

> […] variations are possible only to a limited extent, and always with the preservation of a particular type, which is that of species. Each species has a definite or definable character.[49]

There is no evolution of species, not to mention of a history of the organic world with primitive cells, in the first chapter. In my opinion the interesting point here is not that Henfrey did not share Schleiden's evolutionism, but that he presents his own perspective in such a casual, almost offhand, manner. Darwin himself often quotes Henfrey in different contexts but never relates to him as an opponent, questioning the mutability of species and, as far as I can judge from Henfrey's publications, he never picks the topic up explicitly. To my mind, Henfrey's insertion has the same sort of rationale as Lankester's omission of parts of the "Methodologische Einleitung" and his odd hint to Herschel and Whewell. There were certain aspects of Schleiden's writings that they were apparently not very much interested in. But why did they enthusiastically spend so much time and effort in order to promote Schleiden's views on other issues? What were the "leading ideas" of the two "London Doctors," if they themselves had a "philosophy" at all?

An answer to this question is suggested by Lankester's and Henfrey's other activities. In 1844, Lankester and Henfrey cofounded the *Ray Society* with Lankester as the first secretary and Henfrey as the main editor of the volumes printed under the imprint of the society. The tremendous scientific importance they attributed to John Ray, the seventeenth century naturalist, is shown by the fact that one son of Edwin Lankester (more famous than his father[50]) received the name Edwin *Ray* Lankester, and was invariably referred to as E. Ray or just Ray Lankester. John Ray is famous for his taxonomical system that is seen as a major step towards modern classification. He was greatly admired by many other English scientists and naturalists in the nineteenth century.

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[49] Prichard (1855, p. 69).

[50] On John Ray as a model still of the next generation, and on E. Ray Lankester as adherent of the original Darwin/Wallace position, see Travis, this issue.

Fortunately, Edwin Lankester has provided information on how *he and his circle* envisaged Ray, and it is not primarily the taxonomist he presents in the *Memorials of John Ray*:

> The extent of the influence of the genius of Ray on the science of natural history is far greater than can be estimated by the number or size of the volumes he wrote, and is to be traced to his habit of acute observation of facts and the logical accuracy with which he arranged them. He made his knowledge of the structure and physiology of plants subservient to a great plan of their arrangement.[51]

The self-proclaimed admirers and heirs of John Ray, the "London doctors"—and this is obvious to every reader of their books—were not much interested in overall theorising, but in precise observation, the exploration of data, and stabilising and arranging such data. This matches perfectly with the British empirical tradition. And as for John Ray, he had no sympathy for the positions of the French rationalists, who were attracted by philosophies oriented at the ideal of theories with great explanatory and predictive power, such as Newtonian Mechanics. This converges perfectly with the "London Doctors'" disinterest in the hypothetic-deductive method and their disguised variant of "rational induction," as the Kantians had developed it. Consequently, they not only stayed away from Whewell's views and equally from Schleiden's insofar as these two authors shared an 'architecture' of hypothetical theorising and of theory-change in the sense of Buchdahl's model. But what part of Schleiden's views is left over?

6 The Microcopist's Methodology of Good Practice

The answer is simple. It is Schleiden, the pioneer of microscopical research, a scientist who did important work well before he subjected it to a Kantian-Friesian philosophy. And what the "London Doctors" were in need of was the methodological framework of Schleiden's research. This was in the narrow sense, far from fundamental reflections on matter, forces, laws and other general concepts, and whose relevance Schleiden emphasises in the "Methodologische Einleitung" over and over again but never made use of in his research practice. There exists something like a set of "sub-architecture" principles centred around the problem of how to use the microscope to the greatest advantage. It was exactly this part of the "Einleitung" that was translated as Appendix D to Lankester's English version.

Schleiden's main practice was in *exploration*, an approach we already find in Aristotle's biology, here refined by the new and evolving techniques of microscopy. And the central problems Schleiden, Henfrey and Lankester were facing were not those of gathering and formulating explanatory theories and confirming theories with data. What was demanded was nothing less than *obtaining* relevant data, *assuring* their reliability and *communicating* them with the help of drawings and making them accessible to others by conservation procedures.[52] The indispensable conditions of such activities were the capabilities of the microcopist himself.

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[51] Lankester (1846, preface, p. viii, ix).

[52] As for earlier examples of this of type of methodology, see the works of Jean Senebier and others on the "art of observation." Cf. Marx (1974) As is well known, mainstream twentieth century philosophy of science has classified such reflections and the entire discussion of *inquiry* as something related to the philosophically insignificant "context of discovery."

The precondition of good microscopical research is not an abstract idea, an “architecture,” but a competent *architect*, following maxims of the type “learn *a*, take into account *b* und do *c*, and if you are successful, integrate method and results into future learning.”[53] This is how researchers proceed from practice *a* to a superior practice *b*. It is easy to imagine that many trained practitioners will achieve more than just a few. Science is collaboration, with the tendency of improvement through increasing the number of competent explorers. This is why Lankester and Henfrey founded the *Microscopical Society* and Schleiden the *Physiologische Institut* (the first laboratory where students received familiarity with microscopical work[54]). And, moreover, this is why they collaborated and wrote introductory books and why something like the *Micrographic Dictionary* was published. It is illuminating to compare this to Darwin’s way of connecting his own work to others. As for Darwin, while he was a great networker, his work was seen to be nothing more than “the organisation of purpose for the creative person.”[55] Collaboration for Darwin meant providing the building blocks of his own “long argument.”[56] In that sense he was a loner. In sharp contrast, the microscopical project involved several participants, and, most importantly, was not linked to a particular explanatory thesis, but only to topics and methods.

The principles guiding microscopical research need not be philosophically derived. They are based on the experiences of laboratory observation and its success. And then as now they do not appear to present difficulties: On the contrary, we intuitively already obey their preliminary form in our every-day practice and experience,[57] using spectacles, if we are short-sighted, trying to be precise and not approximating, trying to save time and effort, leaving aside what is not to the point at issue, etc. The contrast of the efficiency orientation to that of natural historian’s culture of universal curiosity is obvious. Indeed, for instance, exotic materials may be inspiring; and if they are available one can draw on such objects in this or that way. But one need not travel to the jungle of Brazil or Malaysia in order to study cell-formation. As Lankester suggested to his young readers, the garden and indoors were all equally valuable locations for seeing with the microscope. Such apparently simple pedagogical advice matches and illustrates the London Doctors’ as well as Schleiden’s idea of *efficient* professional research.

As with Buchdahl’s “architectonic” component of theory-appraisal, employing standards of good practice can amount to conflicts, for example, between efficiency on one side and accuracy on the other. A competent researcher is capable of balancing such conflicts due to his laboratory experience (Figs. 5, 6, and 7). We need not discuss how to name this capability, but perhaps (while giving credit to Buchdahl, for letting me know that Schleiden ever lived) the Kantian term *Urteilskraft* would not be inappropriate.

The first step to successful microscopical work is training the “art of seeing,” that is, a tacit ability to observe, acquired by extensive practice (comparable to the modern doctor’s professional evaluation of X-ray, CT and MRI diagrams). Additionally one needs knowledge about the physical and physiological peculiarities of human vision to obtain insight into limitations of the researcher’s perception. The same caution holds for the

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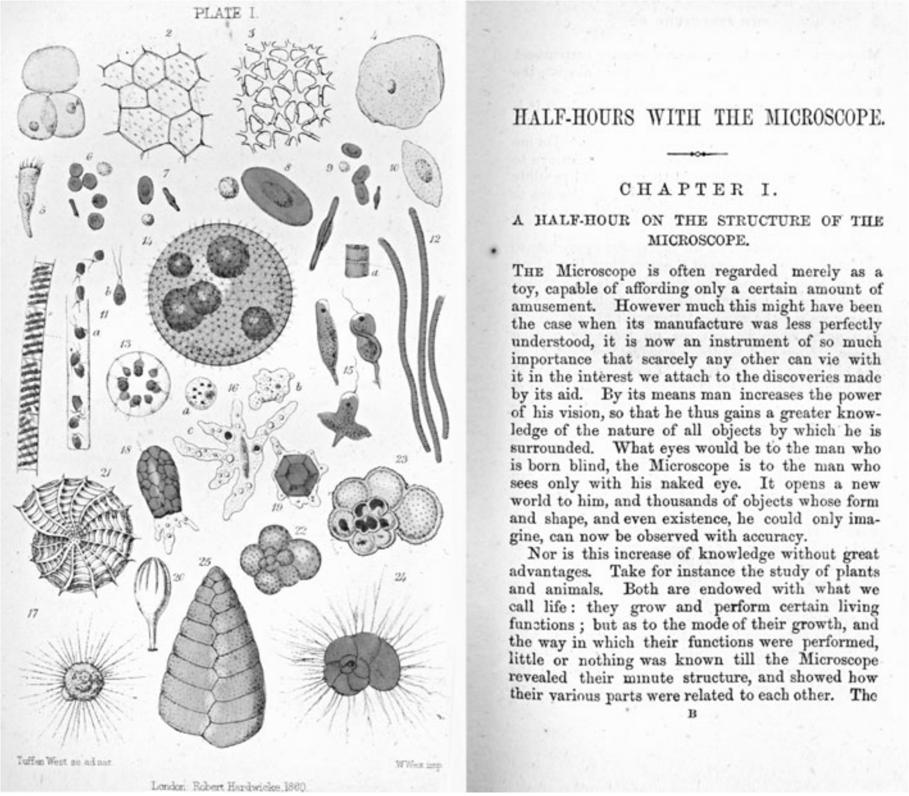
[53] To the best of my recall, it was at first Anne Mylott (Bloomington) who, in a discussion on her excellent dissertation thesis (Mylott 2002), tinkered with the idea that Schleiden’s *Grundzüge* could be more adequately read not as a philosophical treatise but as a manual of job instructions. cf. already (Mylott 1997).

[54] On this and other details of Schleiden’s life see Jahn and Schmidt (2005).

[55] Gruber (1985, p. 11). On Darwin’s interest at that time in general, see Hodge (2003).

[56] On this as a response to “Herschellian” demands see Hodge (1977).

[57] Cf. Goldman (1986), Thagard (1997), Charpa and Deichmann (2004), Charpa (2008).



HALF-HOURS WITH THE MICROSCOPE.

CHAPTER I.

A HALF-HOUR ON THE STRUCTURE OF THE MICROSCOPE.

THE Microscope is often regarded merely as a toy, capable of affording only a certain amount of amusement. However much this might have been the case when its manufacture was less perfectly understood, it is now an instrument of so much importance that scarcely any other can vie with it in the interest we attach to the discoveries made by its aid. By its means man increases the power of his vision, so that he thus gains a greater knowledge of the nature of all objects by which he is surrounded. What eyes would be to the man who is born blind, the Microscope is to the man who sees only with his naked eye. It opens a new world to him, and thousands of objects whose form and shape, and even existence, he could only imagine, can now be observed with accuracy.

Nor is this increase of knowledge without great advantages. Take for instance the study of plants and animals. Both are endowed with what we call life: they grow and perform certain living functions; but as to the mode of their growth, and the way in which their functions were performed, little or nothing was known till the Microscope revealed their minute structure, and showed how their various parts were related to each other. The

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Fig. 5 (Lankester 1860, plate 1 & p. 1)

specific character of the microscopic instruments, that have to be optimised and calibrated, and the preparation of objects to be observable, for example slicing, mounting, staining, preserving, and so on.

What the "London Doctors" and Schleiden had in common was an approach to scientific progress we can similarly identify in the writings of Claude Bernard, Helmholtz and others, that neither fits into the philosophical pattern of scientific advancement as theoretical progress nor to that of many historians of science as mere change of cultural activities.[58] The point at issue for Schleiden and the "London Doctors" was that good research in the life sciences is progressive insofar as it leads to *reliable* observations and *low-risk* (that means reliable as well) generalisations. Schleiden might have been more ambitious in his attempt to establish linkages to well confirmed existing theories than either Henfrey or Lankester. But to Schleiden, as with the "London Doctors," it is beyond any doubt that successful research is not a matter of hazardous hypotheses. It is a matter of well-informed professional *practice*. The development of this practice, right up to X-ray-photography and the electronic microscope in twentieth century science, and integrating

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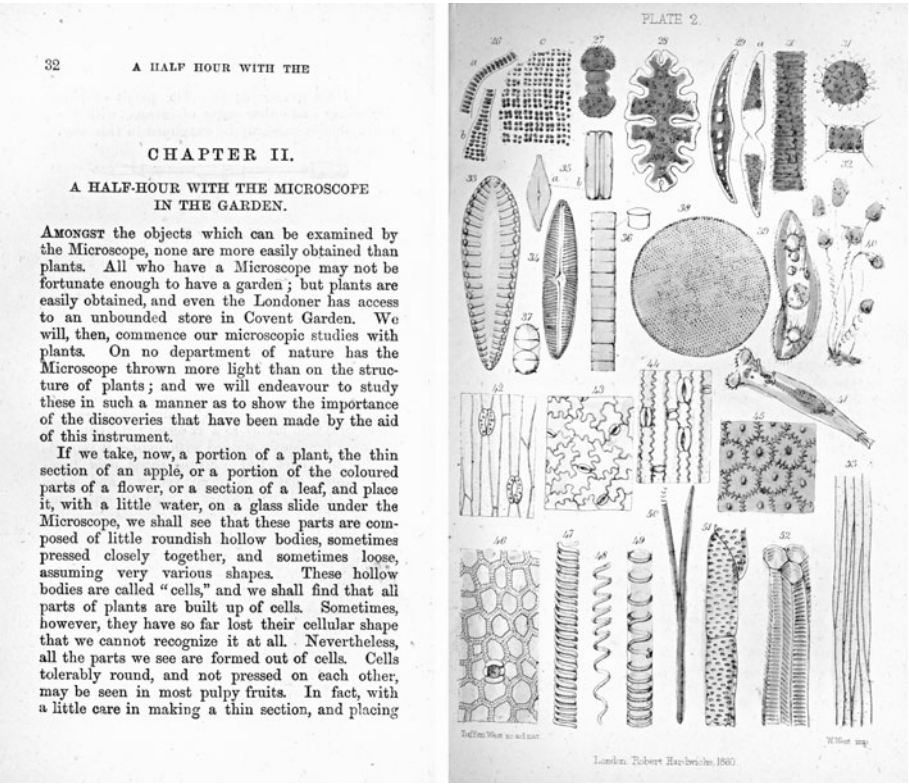
[58] The "competence-approach" is elaborated in more detail with regard to Schleiden in Charpa (1999, 2003, 2005). It also applies to cases of twentieth century research (Charpa 2001, 2008; Charpa and Deichmann 2004, 2007; Deichmann 2008).



32 A HALF HOUR WITH THE

CHAPTER II.

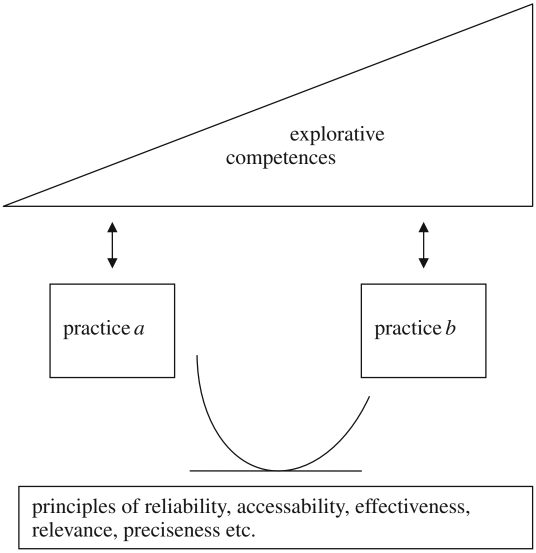
A HALF-HOUR WITH THE MICROSCOPE IN THE GARDEN.

Amongst the objects which can be examined by the Microscope, none are more easily obtained than plants. All who have a Microscope may not be fortunate enough to have a garden; but plants are easily obtained, and even the Londoner has access to an unbounded store in Covent Garden. We will, then, commence our microscopic studies with plants. On no department of nature has the Microscope thrown more light than on the structure of plants; and we will endeavour to study these in such a manner as to show the importance of the discoveries that have been made by the aid of this instrument.

If we take, now, a portion of a plant, the thin section of an apple, or a portion of the coloured parts of a flower, or a section of a leaf, and place it, with a little water, on a glass slide under the Microscope, we shall see that these parts are composed of little roundish hollow bodies, sometimes pressed closely together, and sometimes loose, assuming very various shapes. These hollow bodies are called "cells," and we shall find that all parts of plants are built up of cells. Sometimes, however, they have so far lost their cellular shape that we cannot recognize it at all. Nevertheless, all the parts we see are formed out of cells. Cells tolerably round, and not pressed on each other, may be seen in most pulpy fruits. In fact, with a little care in making a thin section, and placing

Fig. 6 (Lankester 1860, pp. 32–33)

Fig. 7



this with advanced chemical analysis, takes time and immense achievements of learning and working meticulously. This is the reason why the marriage of explorative and evolutionist approaches had not the slightest possibility of happening at the time when Darwin read Schleiden, but had to wait another century.

7 Conclusion

It has been shown that enforcing the microscopical programme was attached to a particular methodological attitude one can characterise in modern epistemological terms as reliabilist, personalist, and "collaboratist." The idea of good science is that of a practice where as many trained experts as possible explore, with confidence (through reproducibility etc.), what has not been visible before. General theorising on evolutionary processes appears as a future hope and not a current issue. In contrast, Darwin's science is that of a great explanatory programme relating to units of nature that are already—or have been—*manifest*. Irrespective of all the methodological "deficiences" that Whewell and other philosophers with "Newtonian" ideals located in Darwin's views, there were similarities between their models of science. Indeed, Darwin's approach did not present itself as theory as they had in mind, and the facts related to it were not experimentally generated. But in Darwin's conception there were components analogous to fundamental laws, to the explanation of facts by such laws and to the confirmation of lawlike assumptions based on independent classes of data. Microscopical research at that time could neither benefit from this "architecture" nor contribute to it. Meantime, the microscopists had their own agenda and their own comparatively discreet philosophical frame.

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ARTICLE

Gemmules and Elements: On Darwin's and Mendel's Concepts and Methods in Heredity

Ute Deichmann

Abstract Inheritance and variation were a major focus of Charles Darwin's studies. Small inherited variations were at the core of his theory of organic evolution by means of natural selection. He put forward a developmental theory of heredity (pangenesis) based on the assumption of the existence of material hereditary particles. However, unlike his proposition of natural selection as a new mechanism for evolutionary change, Darwin's highly speculative and contradictory hypotheses on heredity were unfruitful for further research. They attempted to explain many complex biological phenomena at the same time, disregarded the then modern developments in cell theory, and were, moreover, faithful to the widespread conceptions of blending and so-called Lamarckian inheritance. In contrast, Mendel's approaches, despite the fact that features of his ideas were later not found to be tenable, proved successful as the basis for the development of modern genetics. Mendel took the study of the transmission of traits and its causes (genetics) out of natural history; by reducing complexity to simple particulate models, he transformed it into a scientific field of research. His scientific approach and concept of discrete elements (which later gave rise to the notion of discrete genes) also contributed crucially to the explanation of the existence of stable variations as the basis for natural selection.

Keywords Variations · Discreteness · Gradualism · Statistical laws · Chance · Blending inheritance · Soft inheritance · Pangenesis · Mendel · Darwin

1 Introduction

The emergence of the science of genetics began as a result of the fruitful application of both the research methods and the concept of discrete "elements" (which later gave rise to the concept of discrete genes) developed by Mendel around 150 years ago. The gene

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concept has since changed drastically. Alterations introduced by early molecular geneticists, such as the "division" of the "classical gene" into three constituents, a unit coding for a single polypeptide, and units of mutation and of recombination, continued to adhere to the notion of discrete units. However some phenomena discovered since the 1970s with the help of new DNA technologies challenged this notion. There are those who, as a result of more recent findings, such as alternative splicing, overlapping genes, genes within genes, fused transcripts, and micro RNAs as controlling elements, hold that the concept of discrete genes is doomed to disappear. Thus we have: "Discrete genes are starting to vanish; we have a continuum of transcripts."[1] With reference to epigenetic phenomena, claims of soft, i.e. "Lamarckian", inheritance are enjoying a new revival (see e.g. Jablonka and Lamb 1995, and references therein). There are even claims that it was Darwin himself who founded genetics since he was the first to describe the most important genetic phenomena and, with his theory of pangenesis, to present a developmental theory of heredity (Liu 2008). Yet, despite these claims and recent developments in genetics, the concept, based on Mendel, of a more or less discrete gene, or, rather, various kinds of more or less discrete genes, has continued to be fruitfully employed in both basic and applied research.

Mendel's enormous impact on the development of genetics seems surprising given the fact that he never talked explicitly about heredity or put forward a genetic theory (apart from what were later called the two laws of classical genetics, segregation and independent assortment). His contemporary Darwin, in contrast, did not exert a lasting influence on genetics despite devoting considerable effort to tackling questions of heredity and variation, and establishing a novel theory of heredity. This apparent contradiction raises a number of questions: In what aspects did Darwin's and Mendel's approaches in research related to heredity differ from one another and why did they have different approaches? How is it that the genetic work of Darwin, a renowned naturalist, became marginalised and finally discarded, whereas Mendel's work, which did not receive much appreciation during his lifetime, later became the foundation of genetics? How is it that despite the recent findings, for example of overlapping genes and continuous genetic phenomena, the development of genetics started as a result of the fruitful application of Mendel's methods and his concept of discrete "elements", whereas competing concepts of blending and soft inheritance[2] (advocated also by Darwin) were insignificant? In order to answer these questions, I here analyse and compare Darwin's and Mendel's contents and methods of research related to heredity and variation and examine causes and consequences of the differences of their approaches in the context of nineteenth-century developments in biology.

2 Darwin

Darwin scholars such as Michael Ruse, M. J. S. Hodge, and Peter Bowler in most cases focus on the topic of evolutionary theory, in particular natural selection, when they discuss Darwin's arguments and methodology (Hodge 1992, and references therein). Notwithstanding the importance of natural selection for Darwin, I think that the assumption of changing conditions of life impacting on variation, heredity and evolution played a

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[1] Quoted by Roderic Guigo in Pearson (2006).

[2] Blending inheritance suggests a mixing (like mixing of liquids) of parents' traits to form the child's traits; soft inheritance is the inheritance of acquired characters, often used synonymously with "Lamarckian inheritance".

predominant role in Darwin's work, too. Here I do not discuss his evolutionary theory but instead focus on his arguments and methods related to heredity and variation. With its greater emphasis on methods and Darwin's 1868 theory of heredity (pangenesis), this section complements recent articles by Olby (2009) on Darwin's concepts of inheritance and variation in *The Origin of Species* (1859) and Howard (2009) who, analysing Darwin's basic observations and experiments, aims at understanding why Darwin, unlike Mendel, failed to solve the logic of inheritance.

2.1 Small Variations as the Basis for Natural Selection; the Problem with Their Apparent Randomness

Darwin's work on evolution as outlined in *The Origin of Species* (1859) (hereafter *Origin*) consists of three major themes, the second of which points to the major role that questions of heredity and variation played in Darwin's theory of evolution:

(a) He gave crucial support to the theory of evolution (for which he used the term descent by modification) by providing abundant empirical material from disparate geographical areas.
(b) He suggested natural selection as a new mechanism for evolutionary change. This was based on the observation of slight variations between individuals of a species, the assumption that individual differences are mostly hereditable, and political economist Malthus's theory according to which organisms reproduce geometrically, whereas resources do not, with the result of a strong competition, or a "struggle for existence".
(c) He presented the divergence of species as a major principle of evolution.

As is well known, Darwin was not the first scholar to put forward a theory of evolution; Lamarck and Darwin's grandfather Erasmus Darwin—to mention only two famous figures in this field—had thought and written about the evolutionary change of species and their possible causes before Darwin. The proposition of natural selection as a new mechanism (among others) for evolutionary change was the principal difference between Darwin's theory of evolution and the theories of his predecessors and contemporaries. As was recently pointed out by Bowler (2008),

> much late nineteenth-century evolutionism was non-Darwinian in character. Darwin convinced everyone that the basic idea of transmutation should be accepted, but natural selection was generally regarded as an inadequate theory. Most of his contemporaries preferred to believe that evolution must be directed toward a predetermined goal. The claim that selection is based on 'chance' reflects this fundamental objection. The preferred theories of the later nineteenth century were Lamarckian or orthogenetic, reflecting the adaptive and non-adaptive wings of a more general viewpoint in which the development of the embryo was seen as a model for evolution.

The extent to which Darwin's theory was "Darwinian" itself will be discussed later. Here it suffices to point again to the fact that the assumption of inherited individual differences, i.e. very small variations—Darwin strongly rejected the idea of large variations ("single variations"), which were invoked by supporters of the concept of "saltatory" (sudden and large) evolutionary changes (Ruse 1979, p. 206)—was the basis for Darwin's theory of evolution by natural selection (and also for his deep conviction in evolution as a gradual process):

> The many slight differences which appear in the offspring from the same parents, or which it may be presumed have thus arisen, from being observed in the individuals of the same species inhabiting the same confined locality, may be called individual differences. … These individual differences are of the highest importance for us, for they are often inherited … and they thus afford materials for natural selection to act on and accumulate, in the same manner as man accumulates in any given direction individual differences in his domesticated production. (Darwin 1859, p. 45)

However, this notion of individual differences based on small variations was also highly problematic for Darwin. The facts that the causes of variations were not known and that they were apparently random elements of indeterminacy, contradicting the ideal of science in nineteenth-century Britain, i.e. science modelled on physics and the Newtonian-Laplacean conception of determinism that it entailed (Schweber 1982; Ruse 1979, pp. 56–63). The final, poetic, sentence of the *Origin* points to Darwin's reverence for Newton and also to his attempt to attribute to his own evolutionary theory the same importance as Newton's law of gravity: "There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved."

Darwin developed his evolutionary theory under the influence and in close interaction with leading figures of science and philosophy, in particular geologist Charles Lyell and physicist–philosopher John Herschel, to whom Newton's notion of causality in science was crucially important (Ruse 1979; Lennox 2005, and references therein). Lyell's *Principles of Geology*, largely a methodological treatise, influenced Darwin greatly. Lyell tried to explain past geological events with the help of the same kind ("actualism") and the same degree of causes that operate in the present (Ruse 1979, pp. 40–44); he was an outspoken critic of the then widespread notion of "catastrophism" and rejected the notion of progression or direction of geological evolution. Darwin had to confront Lyell's opposition to Lamarck's and other theories of organic evolution, which were progressivist and did not fulfil the demand of actualism—there was no evidence for the generation of new species.

Lyell's attempt to find causes of a kind which already existed reflected the empiricist programme of Herschel, for whom Darwin had a special admiration (Ruse 1979, pp. 59–63). Darwin met Herschel during his *Beagle* voyage, and despite Herschel's rejection of Darwin's evolutionary theory, Darwin honoured him (without mentioning his name) in the introduction to the *Origin*: "… the origin of species—that mystery of mysteries, as it has been called by one of our greatest philosophers." Herschel's interpretation of what Newton had in mind by "true causes" (verae causae) in science placed emphasis on their real existence in nature and their abilities to account for the full range of phenomena to be explained, and to be productive of these phenomena. Herschel provided the methodological framework for Darwin, within which a solution to the problem of species generation should be sought (Lennox 2005).

Darwin, throughout his life, tried to cope with the challenges aroused by Herschel's notion of scientific causes; this was not only related to the difficulty of explaining the regular generation of new species in a deterministic way, but also, and what matters here, to the problem of the indeterminacy of chance variations (Schweber 1982) and other chance effects.[3] He did this, first, by adopting Laplace's notion of chance, according to

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[3] According to Howard (1982, p. 30), Darwin's insistence, even in the final edition of the *Origin* (1876), that speciation can occur without geographical isolation, which made his theory of evolution "truly

which probability and chance only relate to our knowledge of things and not to things in themselves: “I have hitherto sometimes spoken as if the variations so common and multiform in organic beings under domestication, and in a lesser degree in those in a state of nature had been due to chance. This, of course, is a wholly incorrect expression, but it serves to acknowledge plainly our ignorance of the cause of each particular variation” (1859, p. 131).

Darwin’s second and main way of marginalising the role of chance, and, in the end, rendering it superfluous, was the attribution to changing conditions of life, soft inheritance and the use and disuse of organs central roles in generating variations (see also Olby 2009).

2.2 Explaining Variation by Changing Conditions of Life; on Darwin’s Methods

Darwin expressed his deep conviction that the inheritance of environmental effects and use and disuse of organs played a central role in generating variability as early as in the first edition of the *Origin:* “I believe that the conditions of life, from their action on the reproductive system, are so far of the highest importance as causing variability. I do not believe that variability is an inherent and necessary contingency … Variability is governed by many unknown laws, … that of correlation of growth … the direct action of the conditions of life … use and disuse” (chap. 1, p. 43); or: “It seems pretty clear that organic beings must be exposed during several generations to the new conditions of life to cause any appreciable amount of variation; and that when the organisation has once begun to vary, it generally continues to vary for many generations” (chap. 1, p. 7). I return to this latter quotation below, comparing it to Mendel’s contrasting view.

The changed conditions acted either directly on the whole organism—with definite results so that all individuals became modified in the same way or indefinite results so that some fluctuating variability occurred—or, more frequently, indirectly through the reproductive system; i.e. part of the effect was adaptive and “Lamarckian” in character, part of it not.[4] For Darwin, the allegedly lasting effects of changed conditions of life were no contradiction to natural selection.

The following examples taken mainly from the *Origin* shed light on a methodology which Darwin used throughout, that is, vague conclusions from many single often non-quantitative observations by himself or others. Though he conducted experiments, including in plant hybridisation, there were, in the words of Olby (2009), no controlled experiments yielding convincing numerical data. Darwin’s poor experimental performance in plant physiology was strongly criticised by German botanist Julius Sachs, whose scientific standards in this field were based on experimental skill and trustworthiness (de Chadarevian 1996).

Chapter 5 of the *Origin* lists a number of adaptations to which Darwin assigned different causes. He assumed a direct result of environmental conditions on morphological features in the following cases: “E. Forbes asserts that “shells at their southern limit, and when living in shallow water are more brightly coloured than those of the same species further

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Footnote 3 continued
inadequate as a mechanism of speciation”, might be explained by the fact that the “contingent aspect of isolation … offended Darwin”.

[4] The assumption of the inheritance of acquired characters and of the use and disuse of organs has usually been related to Lamarck. However, these ideas can be found much earlier, such as in Greek antiquity. Darwin praised Lamarck for his views on evolution and the suggestion of mechanisms for it, but did not accept his law of progressive development, according to which all forms of life possess the tendency to develop upwards, and his claim of spontaneous generation.

north or from greater depths. Gould believes that birds of the same species are more brightly coloured under a clear atmosphere than when living on islands or near the coast. So with insects, Wollaston is convinced that residence near the sea affects their colour." (Darwin 1859, p. 132)

In contrast, the rudimentary status of many organs was explained by disuse, because "there can be little doubt that use in our domestic animals strengthens and enlarges certain parts, and disuse diminishes them; and that such modifications are inherited" (ibid., p. 134): "The nearly wingless condition of several birds, which now inhabit or have lately inhabited several oceanic islands, tenanted by no beast of prey, has been caused by disuse" (ibid.). Similarly, muted ears and annulated tails of domesticated animals such as dogs, cats, horses, and sheep were considered to be results of disuse (Darwin 1868, II, chap. 24). Some decades later Darwinians—unlike Darwin himself—explained phenomena of adaptation like these entirely by the effect of selection (with new phenotypes being generated by mutation and recombination).

In other cases Darwin assumed an interaction of various causes, including also natural selection, in bringing about adaptations: "… these several considerations have made me believe that the wingless condition of so many Madeira beetles is mainly due to the action of natural selection, but combined probably with disuse." With moles the order of causes was reversed: "The eyes of moles and of some burrowing rodents are rudimentary in size, and in some cases are quite covered up by skin and fur. This state of the eyes is probably due to gradual reduction from disuse, but aided perhaps by natural selection." In other cases natural selection was crucial: "Variability [of rudimentary organs] seems to result from their uselessness, and consequently from natural selection having had no power to check deviations in their structure" (Darwin 1859, chap. 5). The assignment of causes thus appears often arbitrary and speculative.

Darwin was of the opinion that there was decisive evidence for the effects of operations being occasionally inherited. The proofs consisted of unrelated cases, such as the alleged occurrence of epilepsy in animals and humans whose parents had artificially been rendered epileptic and the inheritance or semi-inheritance of circumcision. The non-inheritance of circumcision had been used as a major argument against Darwin's assumption of soft inheritance. Whereas Jewish physicians had asserted that circumcision was not inherited, Darwin approvingly cited Blumenbach (1799) according to whom in Germany many Jews were born in a condition that rendered circumcision difficult (Darwin 1868, II, 23). As in other cases, the boundaries between few exceptional cases (doubtful as they were) and regularly occurring events were blurred. Similarly, Darwin's discussion of "reversions"—a wide range of different phenomena, most of which we would today explain by mutation and recombination (see next section)—shows the lack of distinction between frequently and regularly occurring events such as the resemblance of children to grandparents (now explained by the recessivity of genes), rare and irregularly occurring events such as the blue-coloured doves, and rare but predictively occurring events such as the inheritance of polydactyly (more than the normal number of fingers or toes, now explained by dominant mutations) (Darwin 1868, II, chap. 13).

Darwin's emphasis on "Lamarckian" mechanisms as causes of variation and adaptation was particularly strong in his later publications. With few exceptions, such as what he called "reversions", changing external conditions were the main causes of variability, to the extent that if all individuals of a species were exposed to the same conditions for many generations, there would be no variability (Darwin 1868, II, chap. 22). It was the unnatural conditions, such as superabundance of food, which caused the large variability of domesticated animals and cultivated plants; Darwin assumed that after some time organisms became used to the new conditions and thus less variable. There was good evidence, Darwin thought, that the action of changed conditions might accumulate. The accumulative action of natural selection in the *Origin* was thus replaced by accumulative actions of the environment.

Darwin's emphasis on special unnatural conditions as causes of the large variability of cultivated plants is reminiscent of the views of German botanist Carl Friedrich von Gärtner, whose *Versuche und Beobachtungen über die Bastarderzeugung im Pflanzenreich* (1849) Darwin carefully studied and greatly admired (and the translation of which into English he suggested[5]). Gärtner (like Kölreuter) still clung to the static view of nature in the tradition that took the Bible quite literally, a view that in the seventeenth and eighteenth centuries was continued, especially by Protestants (Olby 1966, p. 48f). Thus Linné, when defining species and varieties in 1737, used the theological distinction between God's perfect and unchanging, and man's imperfect and changing, world, which was demonstrated, for example, by the abnormal varieties obtained by a gardener. Though Darwin rejected the idea of the fixity of species, he was strongly influenced by Gärtner's work on plant breeding and his ideas of heredity and variation.

Among the alleged environmental effects was also the (purely fictitious) direct action of the male germ cells on the mother (Darwin 1868, II, chap. 27): Darwin explained the popular belief that the fantasy of a mother might affect the embryo by referring to yet another folk opinion, according to which children of a second marriage displayed similarities with the first husband. (In the 1930s Nazi ideologue Julius Streicher would promote the idea of contamination of an "Aryan" woman through a single intercourse with a Jewish man.) Darwin came to the general conclusion that "variability is not a principle co-ordinate with life or reproduction, but results from special causes, generally from changed conditions acting during successive generations" (ibid.).

The examples show that the adoption of popular beliefs and "Lamarckian" mechanisms of inheritance, in line with the thinking of many naturalists of Darwin's time, did not prompt him to call into question the importance of natural selection. However, it was only the late nineteenth-century neo-Darwinians, in particular Romanes and Wallace, who, based on Weismann's germ plasm theory (1883), according to which it was only the hereditary material of the germ cells (germ plasm, which is separated from other cells) that was transmitted from generation to generation, liberated Darwin's evolutionary theory from its strong reliance on "Lamarckian" inheritance, and placed natural selection at the centre of Darwin's theory (see Travis, this issue).

2.3 Darwin's Genetics: Blending Inheritance; Blurring the Difference Between Sexual and Asexual Inheritance

Central to Darwin's thoughts about heredity was the idea of blending inheritance, i.e. the merging of parental differences in the offspring of bisexual reproduction; according to Robert Olby this was the most unfortunate of the assumptions underlying Darwin's mechanism of evolution (1966, p. 55). Darwin here followed an interpretation of heredity, prevalent at the time, that was based on the idea of a mixing of fluids during fertilisation, as suggested by Aristotle. In the eighteenth century it was most forcefully promoted by the German plant breeder Kölreuter, to whom the intermediacy of hybrids was a law which

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[5] C. R. Darwin to J. D. Hooker, 13 September 1864; Darwin held "that there is more useful & [I] trust worthy matter in Gärtner's work than in all others combined even including Kölreuter perhaps" (Letter 4621 of the Darwin Correspondence Project).

applied to all hybrids. According to the blending theory of heredity, the contributions from remote ancestors were gradually diluted in successive generations but occasionally had a belated expression ("reversion"; phenomena which in part were later attributed to segregation and recombination of alleles (Sturtevant 1967)).

According to Darwin, cross-breeding served to "swamp" variations within a species over a number of generations, thus being nature's mechanism to preserve the constancy and uniformity of the species for some time. That is, crossing was a means to preserve uniformity, not to generate diversity (Olby 1966, pp. 56–57; de Beer 1965, p. 89). This concept of crossing was accompanied by a tendency to reduce the difference of sexual and asexual reproduction in bringing about variation and to deny the special role of sexual reproduction and hybridisation to this end.

Darwin based his argument among other things on "sporting plants" (today somatic mutations) i.e. single buds, which "suddenly assume a new and sometimes very different character from that of the rest of the plant"; they are "extremely rare under nature but far from rare under cultivation." As with other variations, Darwin assumed that they were caused by the "treatment of parents" under unnatural conditions. Because of the similarity of buds and ovules and pollen in early stages, the existence of "sports" supported his view that variability in general could probably be "largely attributed to the ovules or pollen or to both having been affected by the treatment of the parent prior to the act of conception", and that "variation is not necessarily connected with the act of generation" (Darwin 1859, p. 10).

Some years later, Darwin finally came to the conclusion that sexual and asexual generation "are fundamentally the same. Parthenogenesis is no longer wonderful; in fact, the wonder is that it should not oftener occur. We see that the reproductive organs do not actually create the sexual elements; they merely determine or permit the aggregation of the gemmules [see next section] in a special manner." (Darwin 1868, II, p. 383) Further, "Variability is not a principle co-ordinate with life or reproduction, but results from special causes, generally from changed conditions acting during successive generation" (ibid., p. 371).

Darwin's thoughts about variation and heredity culminated in a comprehensive materialistic theory, which he called "Provisional Hypothesis of Pangenesis" (1868, II, chap. 27, hereafter Pangenesis).

2.4 Pangenesis

2.4.1 The Phenomena

With Darwin's Pangenesis (hereafter designated with a capital P), he aimed at providing a unifying explanation for a number of seemingly disparate phenomena related to various forms of heredity, causes, and laws of variation and development. Responding to criticisms concerning the speculative nature of his theory, he included a cautionary introductory remark, referring to the renowned Cambridge philosopher-scientist William Whewell, a critic of his theory of evolution:

> I am aware that my view is merely a provisional hypothesis or speculation; but until a better one be advanced, it will serve to bring together a multitude of facts which are at present left disconnected by any efficient cause. As Whewell, the historian of the inductive sciences, remarks:—"Hypotheses may often be of service to science, when they involve a certain portion of incompleteness, and even of error." Under this point of view I venture to advance the hypothesis of Pangenesis, which implies that the

> whole organization, in the sense of every separate atom or unit, reproduces itself. Hence ovules and pollen grains,—the fertilised seed or egg, as well as buds,—include and consist of a multitude of germs thrown off from each separate atom of the organism.

Probably owing to continuing criticism, including by his "bulldog", Thomas Huxley, and his cousin Francis Galton (see below), Darwin did not include Pangenesis in later editions of the *Origin*. But he remained very fond of it right until the end of his life and was convinced that it would hold true in the end.[6]

According to Olby (1966, p. 100), the hypothesis was conceived already in 1840 or 1841 probably as a result of Darwin's fascination with the ability of regeneration of Planaria at that time. Rare forms of reproduction and development along with more regularly occurring ones and their causal interpretation formed the "groups of facts which seem to demand connection". Among them were "reversion", the claimed inheritance of use and disuse of organs, the alleged (fictitious) observation that the male sexual element acts not only on the egg but occasionally also on the mother, the phenomena that a new part can be produced exactly on the place of amputation and that the same organism can be generated through processes as different as budding and genuine generation through semen.

As mentioned earlier, Darwin did not attempt to establish regularities in the occurrences of the phenomena he wanted to explain, accepting them sometimes as wonders of nature, as with "reversions"[7]: "What can be more wonderful than that characters, which have disappeared during scores, or hundreds, or even thousands of generations, should suddenly reappear perfectly developed, as in the case of pigeons and fowls, both when purely bred and especially when crossed; or as with the zebrine stripes on dun-coloured horses, and other such cases? Many monstrosities come under this same head." (1868, II, p. 367)

Most importantly, Darwin wanted the theory to explain the effects of the conditions of life and use and disuse on variation and heredity, which according to him affected not only physical but also mental and intellectual properties:

> How, again, can we explain the inherited effects of the use or disuse of particular organs? The domesticated duck flies less and walks more than the wild duck, and its limb-bones have become diminished and increased in a corresponding manner in comparison with those of the wild duck. A horse is trained to certain paces, and the colt inherits similar consensual movements. The domesticated rabbit becomes tame from close confinement; the dog, intelligent from associating with man; the retriever

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[6] This is shown clearly in his correspondence with colleagues, for example Hooker, Huxley, Lyell, and Wallace, between 1865 and 1872.

[7] Many of Darwin's crossing experiments in plants and animals were devoted to the demonstration of "reversion", for example those in fowls: "I was thus led to make the experiments, recorded in the seventh chapter, on fowls. I selected long-established pure breeds, in which there was not a trace of red, yet in several of the mongrels feathers of this colour appeared; and one magnificent bird, the offspring of a black Spanish cock and white Silk hen, was coloured almost exactly like the wild *Gallus bankiva*. All who know anything of the breeding of poultry will admit that tens of thousands of pure Spanish and of pure white Silk fowls might have been reared without the appearance of a red feather. The fact, given on the authority of Mr. Tegetmeier, of the frequent appearance, in mongrel fowls, of pencilled or transversely-barred feathers, like those common to many gallinaceous birds, is likewise apparently a case of reversion to a character formerly possessed by some ancient progenitor of the family." (1868, II, chap. 13) Other crossing experiments dealt with the possibility of generating new races; Darwin did not attempt to experimentally establish statistical laws of heredity or variation.

> is taught to fetch and carry; and these mental endowments and bodily powers are all inherited. Nothing in the whole circuit of physiology is more wonderful. (Darwin 1868, II, p. 367)

His question was not whether, or to what extent, but "how can the use or disuse of a particular limb or of the brain affect a small aggregate of reproductive cells, seated in a distant part of the body, in such a manner that the being developed from these cells inherits the characters of either one or both parents? Even an imperfect answer to this question would be satisfactory." (ibid.) And his answer was Pangenesis.

2.4.2 The Hypothesis

Pangenesis was based on the idea that all parts of the body produced units, which were able to replicate by self-division, and, after being transported to the sexual organs, were instrumental to heredity and development. Darwin's units were not clearly distinguishable from cells; most British biologists at the time kept aloof from cell theory (Howard 2009).

> I assume that cells, before their conversion into completely passive or "formed material", throw off minute granules or atoms, which circulate freely throughout the system, and when supplied with proper nutriment multiply by self-division, subsequently becoming developed into cells like those from which they were derived. These granules for the sake of distinctness may be called cell-gemmules, or, as the cellular theory is not fully established, simply gemmules. They are supposed to be transmitted from the parents to the offspring, and are generally developed in the generation which immediately succeeds, but are often transmitted in a dormant state during many generations and are then developed. Their development is supposed to depend on their union with other partially developed cells or gemmules which precede them in the regular course of growth. Why I use the term union, will be seen when we discuss the direct action of pollen on the tissues of the mother-plant. Gemmules are supposed to be thrown off by every cell or unit, not only during the adult state, but during all the stages of development. Lastly, I assume that the gemmules in their dormant state have a mutual affinity for each other, leading to their aggregation either into buds or into the sexual elements. Hence, speaking strictly, it is not the reproductive elements, nor the buds, which generate new organisms, but the cells themselves throughout the body. These assumptions constitute the provisional hypothesis which I have called Pangenesis. (Darwin 1868, II, p. 374)

Pangenesis allowed Darwin to explain all frequent and rare phenomena of inheritance:

1. The assumptions of an equal combination of gemmules, which remained unchanged themselves, between parents, on the one hand, and their superabundance, lack or dormancy, on the other, made it possible to explain blending inheritance as well as what for Darwin were exceptions from this rule, for example:
    - Dominance: "The gemmules in the fertilised germ … derived from one parent have some advantage in number, affinity, or vigour over those derived from the other parent." Darwin did not use the concept of dominance, though it had already been introduced by several British horticulturalists in the early nineteenth century, most prominently by Thomas Andrew Knight in 1823 (Zirkle 1951).

- The (incorrect) claim that graded characteristics of an offspring were brought about by different numbers of spermatozoa (containing different numbers of gemmules).[8] Darwin's uncritical acceptance, for example, of the results of Gärtner, who claimed to have found that even thirty pollen grains did not fertilise a single seed and that at least forty grains were required, finds a strong contrast in Mendel, according to whom Gärtner's hybridisation results were often not reproducible (see below). Darwin did not cite here Nathanael Pringsheim (though he cited him in other contexts), who in 1855 had shown the penetration of a single spermatozoon into an ovum of the freshwater alga Vaucheria sessilis (Orel 1996, p. 81). Physiologists based on it their work on fertilisation in higher plants, as acknowledged by Mendel: "In the opinion of renowned physiologists, for the purpose of propagation one pollen cell and one egg cell unite in Phanerogams into a single cell, which is capable by assimilation and formation of new cells to become an independent organism" (Mendel 1866, Sect. 11).
- Reversion (in the meaning stated above) was accounted for by the redevelopment of gemmules, which had been dormant.

2. The assumption that "the gemmules from the modified units will be themselves modified, and, when sufficiently multiplied, will supplant the old gemmules and be developed into new structures" (1868, II, p. 390) made it possible to explain the direct action of changed conditions and of the increased use or disuse of parts. With this hypothesis Darwin finally established the theoretical foundations for a mechanistic explanation of soft or "Lamarckian" inheritance.

Despite the apparently discrete nature of the gemmules, the fact that an unknown large number of them of all possible sizes, produced during the complete lifespan, accounted for an unknown number of phenomena, blurred any kind of discrete effects and favoured the occurrence of quantitative, i.e., infinitesimally small variations (for the importance of the latter to Darwin see Howard 2009).

Pangenesis thus supported essential conceptions and claims of Darwin: blending inheritance; the basic equality between the various forms of reproduction; inheritance of acquired characteristics; the hereditary effects of use and disuse; and small variations. The hypothesis was based in part on dubious and fictitious observations and outdated experimental findings in the fields of fertilisation and crossing. It could not serve as a basis for prediction and allowed for arbitrary interpretations. Thus despite the fact that Pangenesis shows features of a modern materialistic theory of heredity, it lacked the characteristics of a testable scientific theory.

2.5 The Notion of Hereditary Particles and its Critics

The idea of the existence of something like hereditary particles was widespread in the nineteenth century and had been independently suggested by several scholars, as stated by Darwin: "Nearly similar views have been propounded, as I find, by other authors, more especially by Mr. Herbert Spencer; but they are here modified and amplified" (1868, II,

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[8] Darwin cited several authors according to whom more than one spermatozoon was required to fertilise an egg, among them Newport, who allegedly showed that the number of spermatozoa was instrumental for the development and the rate of segmentation of Batrachians; "with respect to plants, nearly the same results were obtained by Kölreuter and Gärtner" (1868, II, 363).

p. 375). Spencer's "physiological units" (1864) "agree with my gemmules in being supposed to multiply and to be transmitted from parent to child; the sexual elements are supposed to serve merely as their vehicles; they are the efficient agents in all the forms of reproduction and in the repairs of injuries; they account for inheritance, but they are not brought to bear on reversion or atavism, and this is unintelligible to me." Among the other authors were Buffon, who proposed "organic molecules" with affinities to various organs, and, in particular, Erasmus Darwin, who in 1801 anticipated his grandson's concept of Pangenesis, suggesting that small particles were given off by parts of the bodies of both parents; and that they are circulated in the blood, ending in the sexual organs from where they could be combined during reproduction in order to form the nucleus of an offspring (*Zoonomia*, 3rd ed., cited in Ruse 1996, p. 57).

Darwin rejected the notion that germ cells were produced in the sexual organs and had different characteristics than body cells, a proposal that was first put forward by Richard Owen. Darwin's view differed "fundamentally" from Owen's: "My gemmules are supposed to be formed, quite independently of sexual concourse, by each separate cell or unit throughout the body, and to be merely aggregated within the reproductive organs" (Darwin 1868, II, p. 375).[9] Darwin related Pangenesis to his reception of modern physiologists' concepts of the "Functional Independence of the Elements or Units of the Body," such as Claude Bernard, according to whom each organ had its proper life and autonomy, and Rudolf Virchow who in his *Cellularpathologie* (1858) promoted the idea that each system consisted of an "enormous mass of minute centres of action" (Darwin 1868, vol. 2, pp. 364–5). If Darwin had considered seriously also Virchow's (and Remak's) amendment to cell theory of the early 1850s, according to which cells are only generated by other cells, he would not have proposed Pangenesis.

It is most interesting that Darwin and almost all of the critics and admirers of Pangenesis apparently did not realise, or appreciate, that a very similar materialistic hypothesis of heredity and development had been put forward in Greek antiquity by the school of Hippocrates: "From every part of the body are produced particles which mix with the bodily fluids in the vessels and are carried by them to the testicles…. The offspring resembles its parent because the particles of the semen come from every part of the body."[10] This ancient Pangenesis hypothesis was motivated by atomistic concepts and the observation that many single characters of the organism can vary quite independently of the rest and can be separately transmitted to the offspring.

Darwin was informed about Hippocrates' Pangenesis by William Ogle, who translated Aristotle's *De Partibus Animalium* into English, but only after publication of his own concept of Pangenesis; he admitted that the two hypotheses were nearly identical:

> Dear Sir,— I thank you most sincerely for your letter, which is very interesting to me. I wish I had known of these views of Hippocrates before I had published, for they seem almost identical with mine—merely a change of terms—and an application of them to classes of facts necessarily unknown to the old philosopher. The whole case is a good illustration of how rarely anything is new…. Hippocrates has

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[9] Similarly, Darwin did not make a distinction between "preformed" germs and material particles continually produced from all the body parts, as suggested e.g. by Bonnet: Bonnet's "famous but now exploded theory of emboîtement implies that perfect germs are included within germs in endless succession, preformed and ready for all succeeding generations. According to my view, the germs or gemmules of each separate part were not originally pre-formed, but are continually produced at all ages during each generation, with some handed down from preceding generations" (Darwin 1868, II, p. 375).

[10] Corpus Hippocraticum VII, pp. 471–75 (fifth century BCE), quoted in Vorzimmer (2003).

> taken the wind out of my sails, but I care very little about being forestalled. I advance the views merely as a provisional hypothesis, but with the secret expectation that sooner or later some such view will have to be admitted. … I do not expect the reviewers will be so learned as you: otherwise, no doubt, I shall be accused of wilfully stealing Pangenesis from Hippocrates,—for this is the spirit some reviewers delight to show.[11]

Striking as the similarities between Hippocrates' and Darwin's ideas were, it appears even more striking that Darwin, who believed that he had discovered laws of organic evolution as new laws of nature, seemed not to have been bothered about this obvious lack of progress in the important field of heredity, pretending to believe that rarely anything was new. Subsequently, through Mendel, Weismann, Boveri, and other biologists, the nineteenth and early twentieth centuries saw enormous progress in genetics. However, the scholarly debate about Pangenesis in the nineteenth century did not show much progress compared to that in antiquity.

Darwin was criticised because of the speculative nature of his hypothesis, its basic similarity to other concepts of material hereditary particles and the lack of experimental evidence (his cousin Francis Galton conducted blood transfusion experiments in rabbits of different colours without any observable effects on their phenotypes). The German editor of the *Origin*, Victor Carus, criticised the lack of consistency between natural selection and Pangenesis, at least judging from Darwin's reply: "I am very much obliged to you for sending me so frankly your opinion on Pangenesis, and I am sorry it is unfavourable, but I cannot quite understand your remark on Pangenesis, selection, and the struggle for life not being more methodical."[12]

In contrast, Hippocrates's pangenesis was also criticised for its logical inconsistency. The debate about pangenesis in antiquity was an early example of the controversies, throughout the centuries, between preformationists who assumed a material link between parents and offspring, to the extent that the new organisms are preformed in the germ cells, and epigeneticists, who, following Aristotle, held the view that development was a process of increasing complexity in which non-material factors were also involved (epigenesis).[13] Aristotle was the most prominent critic of preformationism and pangenesis. He not only criticised pangenesis empirically, for example because "men generate before they yet have certain characters, such as a beard or grey hair," (Aristotle, "On the Generation of Animals," Book 1, chap. 18) but also logically; he considered the hypothesis unacceptable because it led to a fundamental contradiction: According to pangenesis, the semen had to come from the smallest parts from which the organs were composed—in his time it was the elements. However, the resemblance between parents and offspring was neither on the level of the elements nor even on tissues (the "uniform parts") but on that of the organs (the "non-uniform parts") of the body.[14] Thus what, according to Aristotle, was missing in

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[11] Letter to William Ogle, Superintendent of Statistics to the Registrar-General, 6 March 1868 (in Darwin 1887, III, pp. 82–3).

[12] C. R. Darwin to Victor Carus, 21 March [1868] (in Darwin 1887, III).

[13] For the longstanding disputes between epigeneticists and preformationists, see for example Roe (1981) and Pinto-Correia (1997).

[14] "So that if really flesh and bones are composed of fire and the like elements, the semen would come rather from the elements than anything else, for how can it come from their composition? Yet without this composition there would be no resemblance. If again something creates this composition later, it would be this that would be the cause of the resemblance, not the coming of the semen from every part of the body." (Aristotle, book 1, chap. 18).

pangenesis, was an (immaterial) principle of form (we may call it a principle of organisation) without which the material particles could not form an organised body.

Because of Aristotle's emphasis on this form principle, physicist and molecular biologist Max Delbrück, tongue in cheek, credited him with the discovery of DNA. According to Delbrück, Aristotle was a clear candidate for a Nobel Prize granted posthumously, because he discovered the immaterial principle of form necessary for the development of an organism, which is, according to Delbrück, in modern language, the genetic information (Delbrück 1971).[15] To my knowledge, in the nineteenth century it was only Weismann (1892) who noticed that Darwin did not discuss at all questions of arrangement and proper locations of the gemmules. Critics did not relate to Aristotle's logical arguments against pangenesis.

Darwin's methodological preferences of quantitative traits and infinitesimally small changes in evolution, his denial of essential differences between modes of reproduction, his adherence to the notion of blending inheritance, despite many cases to the contrary, his assumption that an infinite number of gemmules, of all possible sizes, continually produced at all ages, can mix in gradual degrees with others, were strong obstacles to fruitful examination of hereditary regularities or mechanisms. Howard (2009) even considers Darwin's focus on quantitative variation ("infinitesimal small inherited modifications") as material for evolution to be the main reason for his not being able to contribute anything relevant to our understanding of the logic of inheritance.

Darwin's preferences point to an underlying basic concept or "theme" (Holton 1973 [1988]), that is gradualism. This "theme" together with a not strictly scientific methodology prevalent among natural historians at the time made him adhere to an outdated, logically questionable, vague concept of heredity which did not prove fruitful for further research in genetics.[16]

3 Mendel

In this essay I confine myself to the analysis of Mendel's most famous work, "Experiments in Plant Hybridisation", read before two meetings of the Natural History Society of Brünn in 1865, and published in the proceedings of that society in 1866 (Mendel 1866; hereafter "Experiments"). The aims of Mendel's hybridisation experiments and the scientific context of this work have been topics for scholarly debates for many decades (most notably in Fisher 1936; Olby 1966, 1997, Orel 1996; Gliboff 1999; Fairbanks and Rytting 2001, Hartl and Fairbanks 2007), and are not dealt with here in any detail.

Mendel's experiments were carried out in the framework of hybridisation studies, a focus of biological research in the nineteenth century (Olby 1966). In the first half of the century, before the publication of Darwin's *Origin*, hybridisation studies were also used to tackle problems of evolutionary theory (Orel 1996, 76). Gliboff (1999) has placed Mendel

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[15] Even though I am of the opinion, following Morange (2008), that the capacity of reproduction and transmitting information cannot be separated from the presence of complex molecular structures, I agree with Delbrück that Aristotelian logic can be rewarding for modern biologists. In my opinion the criticism raised against Delbrück's interpretation of Aristotle's form principle as a genetic programme on the grounds that development should be considered a complex phenomenon not simply a genetic affair (e.g. Vinci and Robert 2005) is lacking in cogency. For interpretations of Aristotle's understanding of the form that is contributed by the male parent, see Witt (1985).

[16] Even though Hugo de Vries in *Intracellulăre Pangenesis* used Darwin's term, the underlying concept was strictly Mendelian.

within the intellectual context of the Austrian Empire, in particular the "Austro-Ungerians", to emphasise the impact of botanist Franz Unger on plant geography and evolutionary biology in Austria. Unger aimed at creating a "scientific" approach to botany which would transcend mere collecting and classifying; he combined the quantitative statistical approach of plant geography with German idealist morphology, which aimed at uncovering the laws of developmental change, particularly in ontogeny. Mendel conducted his experiments under consideration of novel developments in cell theory and physiology, in particular fertilisation and generation.

Before discussing Mendel's approach in the field of heredity, and comparing it to Darwin's, I briefly deal with what has become the best known of Mendel's contributions to the study of genetics: his "laws".

3.1 Mendel's Laws

As stated in the introduction to "Experiments" Mendel aimed at formulating a "generally applicable law governing the formation and development of hybrids". Whereas most historians translated the German term *Entwicklung* as individual development (ontogeny), Gliboff (1999) considers that it meant evolution rather than (individual) development. I think that Mendel used the term in its general meaning—change over time—and "formation and development" included transmission of traits, the individual development from the germ cells and the development of the traits in the next generation, which might, but need not, include evolution. In the process he formulated what were later called the two Mendelian laws, the laws of segregation and of independent assortment.

In his conclusion concerning the first generation of hybrids, Mendel states, "In this generation [F_2] there reappear, together with the dominant characters, also the recessive ones with their peculiarities fully developed, and this occurs in the definitely expressed average proportion of 3:1." Mendel related this to segregation of characters. He later made it clear that he also assumed a segregation of "elements" (which would today be called alleles) during germ cell formation: "We must further assume that it is only possible for the differentiating elements to liberate themselves from the enforced union when the fertilising cells are developed." As the attribution of segregation only to the differing elements indicates, Mendel did not clearly distinguish between phenotype and genotype (Olby 1997, see also Falk and Sarkar 1991). The second "law" is best formulated in the following passage:

> There is therefore no doubt that for the whole of the characters involved in the experiments the principle applies that *the offspring of the hybrids in which several essentially different characters are combined exhibit the terms of a series of combinations, in which the developmental series for each pair of differentiating characters are united. It is demonstrated at the same time that the relation of each pair of different characters in hybrid union is independent of the other differences in the two original parental stocks*. (Emphasis in the original)

From the perspective of modern genetics the usage of the term "character", where "element" would be expected, shows that Mendel did not use the concept of a modern gene. The distinction of genotype and phenotype was introduced into genetics only in 1909 by Wilhelm Johannsen. However, even though Mendel might not have had a clear concept of this distinction, he had a clear intuition of it, and of something like a modern gene, e.g.

when he wrote, “The differentiating characters of two plants can finally, however, only depend upon differences in the composition and grouping of the elements which exist in the foundation-cells of the same in vital interaction.”

This quotation, and indeed Mendel’s paper in its entirety, also point to what I think was Mendel’s most original contribution to the science of heredity: The proposition of an explanation for discrete *and* continuous phenomena of inherited variation that included a causal mechanism involving discrete elements behind the phenomena, the behaviour of which, he showed, followed statistical laws. We do not know whether Mendel read and appreciated Plato, but we can assume that Mendel, trained in Catholic theology strongly permeated by Platonic thinking, easily arrived at explanations by relating phenomena in a Platonic-like way to something behind the visible nature of things. Relating those invisible “elements” to the real phenomena in a reliable scientific way, which made (statistical) predictions possible, rendered his approach fruitful for generations of geneticists to come.

3.2 The Structure of Mendel’s Paper

Mendel’s paper is written in a most lucid and clear style; it is exceptionally well-structured almost along the lines of a modern scientific paper. It begins with an introduction, which contains a general outline of the problem and a number of specific questions, in which he made it clear how his own approach differed from that of his predecessors (referring among others to the hybridisation experiments by Kölreuter and Gärtner):

> Those who survey the work done in this department will arrive at the conviction that among all the numerous experiments made, not one has been carried out to such an extent and in such a way as to make it possible to determine the number of different forms under which the offspring of the hybrids appear, or to arrange these forms with certainty according to their separate generations, or definitely to ascertain their statistical relations.

After stating his general aim (see previous section), he sketches out his method, “a detailed experiment” with suitable material, and delineates the broader meaning of the experiment for the question of organic evolution. The introduction is followed by a section on methods and the selection of experimental plants, and then, in a logical order by “Division and Arrangement of the Experiments”, “The Forms of the Hybrids”, “The First Generation from the Hybrids”, “The Second Generation from the Hybrids”, “The Subsequent Generations from the Hybrids”, “The Offspring of Hybrids in Which Several Differentiating Characters are Associated”, “The Reproductive Cells of the Hybrids”, and “Experiments with Hybrids of Other Species of Plants”. The concluding remarks contain a discussion and critical evaluation of the work of others and make it again clear that Mendel considered his law to be of general validity, subject to confirmation by experiment: “Whether the variable hybrids of other plant species observe an entire agreement must also be first decided experimentally. In the meantime we may assume that in material points an essential difference can scarcely occur, since the *unity* in the developmental plan of organic life is beyond question.”

3.3 Mendel’s Methods

After reviewing the literature on hybridisation, and conducting preliminary experiments with several plant species, Mendel chose *Pisum* for his experiments. He picked 22 varieties which he confirmed to be of true-breeding, by inbreeding for two years. From a large quantity of data he selected for publication those results from hybridisation experiments on seven traits, in which the varieties differed. They contain the famous 3:1 ratio of phenotypes of the hybrid offspring (explained by the 1:2:1 ratio on the level of the underlying “elements”), which formed the basis for all subsequent analyses in Mendelian genetics.

Throughout the twentieth century Mendel’s work has aroused controversies. Ronald A. Fisher’s claim that the “data from the later years of the experiment have been strongly biased in the direction of agreement of expectation” (Fisher 1936, p. 130) has led to a longstanding debate. Disregarding the fact that Mendel, as he himself stated in his paper, reported the data only from a subset of the experiments that he conducted, some accused Mendel even of fabricating data. For details, see in particular the overview in Fairbanks and Rytting (2001).

As was pointed out by Olby (1997), Mendel, unlike most of his colleagues, including Darwin, chose true breeding plant varieties the hybrids of which were highly fertile. That is, he deliberately excluded crosses between species which were mostly used by others. Most importantly, by focussing on single characters and not on organisms as a whole, he introduced the new concept of character pair as a unit of crossing experiments. The focus on a small number of clear-cut characters made his quantitative approach highly fruitful for future studies in genetics. In contrast, Darwin who sometimes also worked quantitatively—e.g. counted and weighed seed, planted them and looked for their vitality—focussed on very small differences in a large number of traits, which at the time could not be meaningful for an understanding of heredity (small, quantitative variation was later explained by multiple allelic systems of small effect) (Howard 2009).

Mendel’s strong focus on quantitative methods can be traced back on the one hand to his work in meteorology and formal training in mathematics and physics (at the University of Vienna), and on the other to the formative influence on Austrian biology of botanist Franz Unger, pioneer of quantitative biogeography and advocate of a scientific approach to botany (Gliboff 1999). Unlike Darwin, who lacked an education in the hard sciences, Mendel did not consider chance and probability as contradictions to laws. Statistically, the distribution of characters in the hybrids could be expressed in a law-like way through a binomial equation. He wrote (in the section “The Reproductive Cells of the Hybrid”): “It remains, therefore, purely a matter of chance which of the two sorts of pollen will become united with each separate egg cell. According, however, to the law of probability, it will always happen, on the average of many cases, that each pollen form **A** and **a** will unite equally often with each egg cell form **A** and **a**.”

Mendel introduced a crossing scheme, which has since become a major tool in Mendelian genetics:

Pollen cells A A a a
| |
| X |
| |
Egg cells A A a a

For the sake of clarity he put “the signs for the conjoined egg and pollen cells in the form of fractions, those for the pollen cells above and those for the egg cells below the line” and arrived at his famous formula “**A/A+A/a+a/A+a/a = A+2Aa+a**”. The term “A+2Aa+a” (instead of AA+2Aa+aa) is striking. One interpretation is that Mendel assumed that like elements (alleles) do not pair with one another and do not segregate. This was contradicted by Hartl and Orel (1992), according to whom Mendel's understanding of segregation only in the heterozygotes could be defended when the law of segregation was stated in terms of different alleles and not chromosomes, something of which Mendel was not aware (this debate has no place here).

Mendel emphasised that this scheme represented "the *average* result of the self-fertilisation of the hybrids" and that in individual flowers and plants the ratios "may suffer not inconsiderable fluctuations", because "apart from the fact that the numbers in which both sorts of egg cells occur in the seed vessels can only be regarded as equal on the average, it remains purely a matter of chance which of the two sorts of pollen may fertilise each separate egg cell." This meant that "the true ratios of the numbers can only be ascertained by an average deduced from the sum of as many single values as possible; the greater the number the more are merely chance effects eliminated."

Mendel's correspondence with Carl Naegeli, botanist at the University of Munich, sheds more light on his methodology. Considering Mendel's experiments with *Pisum* and Phaseolus as only a beginning, "far from being finished", Naegeli criticised Mendel, among other things, for his alleged lack of a theoretical basis: "You should regard the numerical expressions as being only empirical, because they cannot be proved rational."[17] In his response Mendel made it clear that his work was not only empirical but also theoretical, since his empirical approach was the basis for general statements and the formulation of quantitative laws: "A + 2Aa + a" was "the empirical simple, developmental series for two differentiating characters"; and "likewise it was shown in an empirical manner" that, if two or three differentiating characters were combined in a hybrid, the developmental series was a combination of two or three simple series. But: "If then I extend this combination of simple series to any number of differences between two parental plants, I have indeed entered the rational domain. This seems permissible, however, because I have proved by previous experiments that the development of any two differentiating characteristics proceeds independently of any other differences." He demanded that his experiments be "repeated and verified".[18]

According to Sander Gliboff, Naegeli's use of the term "rational" was probably a reference to the method of rational induction of his mentor Matthias Schleiden, a German botanist and co-founder of cell-theory, and other neo-Kantians, who argued from regularities in empirical observations to general laws and explanations with the aid of a priori assumptions (such as time, space, and causality), which included also discipline-specific, guiding maxims (see Charpa, this issue). Since Schleiden's guiding maxims for botany called for explanations in terms of cells and developmental processes at the cellular level, Mendel's intracellular elements and mechanisms of combination did not meet these criteria. "They were not rational in this specialized sense" (Gliboff 1999).

It remains an open question as to whether Naegeli disliked Mendel's approach because of its contradiction with Schleiden's a priori assumptions, or whether he used Schleiden's approach as a philosophical rationale to justify a dislike that he had for quite different reasons. As will be shown in the next section, Naegeli's predilection for concepts of gradation and continuity stood in strong contrast to Mendel's conceptual preferences.

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[17] As cited by Mendel in his 1867 reply (in Herskowitz 1962, Supplements).

[18] Ibid.

3.4 The Concept of Discreteness

One of the characteristics of Mendel's methodology was his preference for concepts of discrete entities over that of seamless gradual transitions. This is demonstrated, first, in his choice of plants for experiments. The various forms of peas which he selected for crossing differed in length and colour of the stem; size and form of the leaves; position, colour, size of the flowers; length of the flower stalk; colour, form, and size of the pods; form and size of the seeds; and colour of the seed-coats and of the albumen (endosperm). Mendel used only characters which permitted "a sharp and certain separation". Characters where the "difference is of a 'more or less' nature, which is often difficult to define, could not be utilised for the separate experiments; these could only be applied to characters which stand out clearly and definitely in the plants." (Mendel 1866, section "Division and Arrangement of the Experiments")

Second, Mendel aimed at explaining complex phenomena of inheritance with the help of simple discrete entities. He was the first to consistently use the idea of discrete invisible "elements" for the explanation of the occurrence not only of discrete characters (in *Pisum*) but also of seemingly blending characters. The latter is demonstrated in his hybridisation experiments with species of *Phaseolus*, in which he was able to confirm his results with *Pisum* only in part (Mendel 1866, section "Experiments with Hybrids of Other Species of Plants"). Whereas the development of the hybrids followed the same laws as in *Pisum*, as far as characters related to the form of the plants were concerned, this was not the case with plant colours. Here the crossing of a "white and a purple-red colouring" resulted "in a whole series of colours …, from purple to pale violet and white." In addition, the percentage of the recessive characters did not correspond to the law in *Pisum*. "However", Mendel proposed, "even these enigmatical results … might probably be explained by the law governing *Pisum* if we might assume that the colour of the flowers and seeds of *Ph. multiflorus* is a combination of two or more entirely independent colours, which individually act like any other constant character in the plant." He then explained in detail how all kinds of intermediate forms could be generated on the assumption of specific unions of discrete "elements". In Mendel's words, "from the combination of the separate developmental series a complete colour-series must result", a mode of reasoning reminiscent of later explanations of gradual (quantitative) variation by multiple alleles (genes for which at least three alternative forms, or alleles, exist). Based on this reasoning he was able to conclude that "Whoever studies the colouration which results in ornamental plants from similar fertilisation can hardly escape the conviction that here also the development follows a definite law which possibly finds its expression *in the combination of several independent colour characters*." (Emphasis in the original)

Mendel used his "elements" as abstract concepts. They were considered to be material parts of the reproductive cells (Mendel referred to the "material composition and arrangement of the elements which meet in the cell in a vivifying union"), but he was cautious enough not to speculate about details of their composition or structural basis.[19] After the "rediscovery" of his laws and the beginning of genetics as an area of research these elements were redefined as alleles, i.e. alternative forms of genes, located on chromosomes.

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[19] See Falk (2003). In contrast, Müller-Wille (2007) claims that Mendel's approach was "biological through and through" and his "elements" were structural elements of reproductive cells, a view which is not supported by this study.

Mendel's formulation of statistical laws for the transmission of traits took place at a time when atomistic and statistical concepts were increasingly accepted in chemistry and physics. Examples are the kinetic theory of heat (Bernoulli, Joule, Clausius, etc.), in which heat became linked to the motion of particles, and statistical mechanics (Maxwell, Boltzmann). The Maxwell distribution of molecular velocities (1859), in which the proportion of molecules of a particular velocity was related to a specific range, was the first statistical law in physics. Despite initial major opposition, the notions of chance and probability, and the idea that there were laws of nature which only applied to large populations, eventually became established in physics.

Geneticist and biostatistician Fisher (1930) related Mendel's theory to developments in physics: "The particulate theory of inheritance resembles the kinetic theory of gases with its perfectly elastic collisions, whereas the blending theory resembles a theory of gases with inelastic collisions, and in which some outside agency would be required to be continually at work to keep the particles astir." This statement may also be regarded as an illustration of Darwin's problems with his assumption of blending inheritance: Variations were swamped quickly, and an outside agency (according to Darwin, environmental changes) was constantly required to provide new variations as a basis for natural selection.

Mendel's training in physics and statistics helped him develop his atomistic and statistical concepts, though his study of chemistry may have contributed as well. According to geneticist Sturtevant (1967) Mendel's particulate interpretation of heredity might have been inspired not only by the atomistic interpretation of matter of Justus von Liebig but also by Liebig's idea of radicals as semi-permanent substitutable building blocks, to which Mendel was most probably exposed through Liebig's student and collaborator Redtenbacher, with whom Mendel studied chemistry.

Third, an emphasis on discreteness can be found in Mendel's handling of the notion of species. Like most naturalists, including Darwin, he was aware of the difficulties of the classification of species. He knew that some varieties of *Pisum* which he used in his experiments might not be classified under *Pisum sativum*, but under other species of *Pisum*, something that he had considered immaterial for his experiments (in which, as mentioned earlier, the central units were character pairs, not organisms as a whole or species). Though he accepted that it was "as impossible to draw a sharp line between the hybrids of species and varieties as between species and varieties themselves" (Mendel 1866, section "Selection of the Experimental Plants"), Mendel rejected the notion according to which cultivation led to a complete de-stabilising of species: "The opinion has often been expressed that the stability of the species is greatly disturbed or entirely upset by cultivation, and consequently there is an inclination to regard the development of cultivated forms as a matter of chance devoid of rules". (Mendel 1866, section "Experiments with Hybrids of Other Species of Plants")

In contrast, Mendel held that "no one will seriously maintain that in the open country the development of plants is ruled by other laws than in the garden bed". He admitted that "by cultivation the origination of new varieties is favoured and that by man's labour many varieties are acquired which, under natural conditions, would be lost." But he insisted that "nothing justifies the assumption that the tendency to formation of varieties is so extraordinarily increased that the species speedily lose all stability, and their offspring diverge into an endless series of extremely variable forms." He concluded logically that "were the change in the conditions the sole cause of variability we might expect that those cultivated plants which are grown for centuries under almost identical conditions would again attain constancy. This, as is well known, is not the case since it is precisely under such circumstances that not only the most varied but also the most variable forms are found." (ibid.)

As stated earlier, this assumption that cultivation resulted in a de-stabilisation of species was prevalent especially among Protestant botanists and plant breeders, who referred to the theological distinction between God's perfect and unchanging, and man's imperfect and changing, world. Mendel did not specify any individuals, but it can be assumed that he was referring to Gärtner whose work he had studied carefully (for the contrasting view that he referred to Darwin, see below). At the same time Mendel here also challenged Darwin who, as mentioned earlier, held a view similar to Gärtner's in regard to the variability of cultivated species. In contrast to Olby (2009, p. 46), according to whom it was actually beneficial for Darwin's theory of evolution that he did not know Mendel's critique, because in that case "his supporters would surely have drowned out his admission", I suggest that an acceptance of the critique might have helped Darwin tremendously to discard obsolete notions of variability and place more emphasis on natural selection.

With his predilection for discreteness Mendel stood in clear contrast to many contemporary biologists, who preferred continuous changes, for example Naegeli, according to whom "individuals are related to each other in the same way as successive states of the same individual. They are continuous with each other, every boundary is arbitrary, the whole movement is infinitely divisible."[20] The variance between Darwin's predilection for gradualism and Mendel's for discreteness led to decisive differences in their approaches.

3.5 Causes of Variation

Mendel not only rejected Gärtner's and other hybridists' (as well as Darwin's) claims that the high variability of cultivated plants was caused by unnatural conditions, but was also opposed altogether to the idea of "Lamarckian" inheritance. Experiments confirmed this view: He transferred plants to places characterised by very special phenotypes of the same varieties, but did not find notable changes in the transferred plants and their offspring. His idea that phenotypes resulted from combinations of various invisible elements gave rise to an explanation for the high variability of cultivated plants, as later confirmed by geneticists, i.e. heterozygosity and frequent crossings.

> It is more than probable that as regards the variability of cultivated plants there exists a factor which so far has received little attention. Various experiments force us to the conclusion that our cultivated plants, with few exceptions, are *members of various hybrid series*, whose further development in conformity with law is varied and interrupted by frequent crossings *inter se*." (Mendel, section "Experiments with Hybrids of Other Species of Plants", emphasis in the original)

Mendel was able to show that interbreeding did not annul variation but actually increased it, calculating the number of different forms (today: different genetic constitutions), which resulted from crosses in which parents differed in only seven pairs of characteristics, as a total of 2,187:

> If, for instance, the two original stocks differ in 7 characters, and 100–200 plants were raised from the seeds of their hybrids to determine the grade of relationship of the offspring, we can easily see how uncertain the decision must become since for 7 differentiating characters the combination series contains 16,384 individuals under 2,187 various forms; now one and then another relationship could assert its

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[20] Naegeli (1844), cited from Mazumdar (1995, p. 44).

> predominance, just according as chance presented this or that form to the observer in a majority of cases." (Mendel 1866, "Concluding Remarks")

According to Fisher, Mendel's paper reflected the difficulties Darwin had with his reliance on blending inheritance. As if to assist Darwin in his search for sources of variation and for a means to avoid the supposed quashing of variation by interbreeding that blending inheritance demanded, Mendel pointed out that some of the difficulties were overcome by particulate inheritance (de Beer 1965, p. 171). As before, I think that also in this case it is more likely that Mendel referred to European plant breeders, in particular Kölreuter, and not (primarily) to Darwin. Moreover, I hold that Darwin's major conceptual themes—hereditary impact of the environment, blending inheritance, and gradualism in general—would have probably prevented him from appreciating Mendel. This leads to the question: Did Mendel and Darwin know of the work of one another?

4 Mendel and Darwin

Most studies dealing with the relationship between Mendel and Darwin have focussed on the question of whether or not Mendel supported Darwin's theory of evolution, referring to a possible religious bias because of Mendel's affiliation to a monastery (see overview in Fairbanks 2002, p. 22). However, a comparison restricted only to this contention clearly overlooks a number of important issues: First, as pointed out earlier, the question of organic evolution was discussed in continental Europe well before the publication of Darwin's *Origin*. Second, Austrian Catholicism at the time was still comparatively liberal, and evolution was taught and discussed at the University of Vienna (e.g. by Unger), and presented in lectures at the Natural History Society in Brünn. There is no indication that Mendel (unlike his Protestant colleague Gärtner) was religiously biased against evolution. Third, though Mendel was interested in questions of evolution, he was mainly an experimental scientist, interested in laws related to hybridisation and character transmission in physiology, particularly fertilisation, and in cell theory and development. Viewing Darwin from the perspective of Mendel, instead of the other way round, might therefore be at least as revealing. Here I confine myself to a comparison between Mendel's and Darwin's approaches to heredity.

Mendel and Darwin never met. While Mendel visited London in July and August 1862, he does not seem to have made any attempt to contact Darwin (who in any case was not in London at the time) (Orel 1996). Since Mendel did not speak English, the language barrier might have been a reason (though Darwin spoke German). It is more likely that by then there was no point for Mendel to contact Darwin, about whom he probably first heard in September 1861 during a lecture in Brünn (ibid.). Mendel purchased his own copy of the translation of the 2nd edition of the *Origin* only in 1863. He could have read the [poor] translation of the first edition that was acquired by the Brünn Natural History Society, in late 1862 or early 1863, after he went to London. The *Origin* did not have the sort of detailed results and explanations that would have attracted Mendel's attention (Fairbanks and Rytting 2001), otherwise he might have written to Darwin after 1863. Mendel explicitly referred to Darwin briefly only four times, all in 1870, four years after publication of "Experiments" (ibid.); the references show neither strong support of nor opposition to Darwin's theories. Darwin never read Mendel's paper.

4.1 Mendel's Marginalia to Darwin's Origin

Since Mendel planned and conducted his experiments several years before he heard of Darwin or read the *Origin*, Darwin could not have played any role in this phase of Mendel's work. A number of scholars (Bateson 1913, Fisher 1936, de Beer 1964, Orel 1996, Fairbanks and Rytting 2001) assume that Mendel in the interpretation of his experiments referred several times to Darwin's *Origin* (without mentioning Darwin's name). I consider it more likely that he referred to Gärtner and other central European plant breeders, and not to Darwin, a view that is supported by the fact that Mendel's marginalia in his copy of the *Origin* are notably sparse compared to the abundant marginalia in his copy of Gärtner's 1849 book (Fairbanks and Rytting 2001).

Nevertheless, a review of Mendel's marginalia in his personal copy of the *Origin*—passages on 18 pages marked with single or double vertical lines and two very brief notes in script—and a comparison with related paragraphs in "Experiments" is most revealing concerning Mendel's and Darwin's different approaches, independently of whether or not these passages really referred to Darwin. Some of the marginalia had already been discussed by Orel (1996), before a complete version of them in English and German was published by Fairbanks and Rytting (2001; see appendix). The latter also provided a detailed and insightful analysis of Mendel's possible comments in "Experiments" to those marked paragraphs. The quotations, in which I confine myself to related questions of heredity and variation, are taken from their publication. While some paragraphs were obviously marked because Mendel agreed with Darwin, e.g. concerning the arbitrariness of the distinction between varieties and species, and the existence of heterosis phenomena, Mendel in most cases seemed to have marked passages in which he disagreed with Darwin:

- The following paragraph was marked by two vertical lines, and was the only one that gave the page number (p. 302, Mendel's German edition):

> The slight degree of variability in hybrids from the first cross or in the first generation, in contrast with their extreme variability in the succeeding generations, is a curious fact and deserves attention. For it bears on and corroborates the view which I have taken on the cause of ordinary variability; namely that it is due to the reproductive system being eminently sensitive to any change in the conditions of life … the hybrids have their reproductive system seriously affected. (Darwin 1861, p. 296)

Mendel might have found this paragraph especially interesting because he was able to establish that the uniformity of the first generation of hybrids, and a predictable variability in the second, was, as a rule, not a "curious fact" (Orel 1996, Fairbanks and Rytting 2001). In contrast to Darwin who vaguely invoked as causes the existence of different environmental effects on the reproductive systems of hybrids and their offspring, Mendel explained his rule by a clear-cut mechanism (the segregation of "elements" in germ cell formation and their combination during fertilisation).

Among the other passages dealing with conditions of life, which Mendel marked, was Darwin's statement about the variability of cultivated plants and animals: "It seems pretty clear that organic beings must be exposed during several generations to the new conditions of life to cause any appreciable amount of variation; and that when the organisation has once begun to vary, it generally continues to vary for many generations" (Darwin 1861, p. 7). Mendel's contrasting opinion ("nothing justifies the assumption that the tendency to formation of varieties is so extraordinarily increased that the species speedily lose all stability, and their offspring diverge into an endless series of extremely variable forms") has been discussed in the section above on "The Concept of Discreteness". Unlike

Fairbanks and Rytting who consider this passage possibly a direct response to Darwin, I would argue that it is plausible that it related, instead, to Gärtner.

- According to Fairbanks and Rytting (2001), Mendel underlined a paragraph in which Darwin explained the "curious adaptation between the structure of the flower [of the Leguminosae or pea family] and the manner in which bees suck the nectar" as a result of the essential role of bees for the fertilisation of these flowers (Darwin 1961, p. 102).This was because Mendel knew that peas were self-fertilising and did not require bees.
- Most markings appear in chapter 8 ("Hybridism"), for example, "It must, however, be confessed that we cannot understand, except on vague hypotheses, several facts with respect to the sterility of hybrids; for instance, the unequal fertility of hybrids produced from reciprocal crosses; or the increased sterility in those hybrids which occasionally and exceptionally resemble closely either pure parent" (Darwin 1861, p. 288). Unlike Darwin, Mendel did not observe that dominant hybrids were less fertile.
- The following paragraph may have been marked by Mendel because of his very different methodical approach:

> When two species are crossed, one has sometimes a prepotent power of impressing its likeness on the hybrid; and so I believe it to be with varieties of plants. With animals one variety certainly often has this prepotent power over another variety. Hybrid plants produced from a reciprocal cross generally resemble each other closely; and so it is with mongrels from a reciprocal cross. Both hybrids and mongrels can be reduced to either pure parent form, by repeated crosses in successive generations with either parent. (Darwin 1861, p. 297)

In contrast to Darwin, Mendel did not deal with species' crosses. He observed dominance (in the terminology of many naturalists, "prepotency") as a regularly occurring and predictable phenomenon. He was one of the first to establish and explain (through the assumption of a complete union of an egg and a pollen cell) the equality of hybrids from reciprocal crosses. He was sceptical concerning the complete transformation of species by hybridisation.

Mendel's abundant marginalia (as compared to the *Origin*) in his copies of Darwin's 1868 *Variations* (in German translation) and Gärtner's 1849 book have not yet been analysed. However, a critical attitude towards Gärtner's experimental practice, which reveals decisive features of Mendel's own approach, was expressed in Mendel's first letter to Naegeli in 1870:

> The results which Gärtner obtained in his experiments are known to me, I have repeated his work and have re-examined it carefully to find, if possible, an agreement with those laws of development which I found to be true for my experimental plant. However, try as I would, I was unable to follow his experiments completely, not in a single case! It is very regrettable that this worthy man did not publish a detailed description of his individual experiments, and that he did not diagnose his hybrid types sufficiently, especially those resulting from like fertilisations. Statements like "Some individuals showed closer resemblance to the maternal, others to the paternal type" or "the progeny has reverted to the type of the individual ancestor" are too general, too vague, to furnish a basis for sound judgment (quoted from Stern and Sherwood 1966, p. 57).

We can assume that, likewise, Mendel missed detailed descriptions of experiments or observations in Darwin's writings, however much he might have appreciated other aspects of his work.

4.2 Differences in Darwin's and Mendel's Approaches in Heredity: A Summary

Darwin and Mendel lived almost at the same time; they shared an interest in the field of heredity; and their research was conducted within the framework of the disputes on organic evolution. A comparison of their approaches thus seems legitimate, notwithstanding the fact that Darwin's work was by far more voluminous and comprehensive than Mendel's, covering a wide range of other topics. Differences in their approaches can in part be explained by differences in their education, particularly the fact that Mendel, apart from his theological studies, received a scientific education in mathematics, physics, and chemistry—he was intellectually influenced by Doppler, Redtenbacher, Unger, and Schleiden—whereas Darwin, who also studied theology, did not receive an education in the hard sciences. But Darwin was well trained in geology, natural history and philosophy and was intellectually influenced by eminent scientists and philosophers, in particular Lyell, Herschel, Hooker, and Whewell, as well as by other scholars such as Malthus and Adam Smith.

The differences between Mendel's and Darwin's approaches in heredity, most of which have been dealt with in the foregoing sections, are summarised in the following table:

Mendel	Darwin
Motives	
Solving a problem	Setting up a comprehensive unifying theory
Finding basic laws of nature	Finding basic laws of nature
Major conclusions	
Generation and development of hybrids follow general (statistical) laws	Results of hybridisation are irregular and unpredictable
Sexual reproduction and hybridisation are major sources for variability	Sexual reproduction and hybridisation result in uniformity; heredity is basically not distinguishable from growth processes
Environmental changes do not cause inherited changes	Environmental changes, and use and disuse, are the major causes for lasting variability
Chance effects play an important role in the processes of reproduction	Chance effects are only apparent, reflecting our ignorance
Basic conceptions	
Chance effects do not contradict the existence of natural laws; data have to be evaluated statistically in order to discover the underlying laws	Chance effects contradict the existence of laws and have to be got rid of
Discreteness	Gradualism
Discrete "elements" are related to discrete as well as gradual phenotypical traits	Evolution by small changes Focus on quantitative traits Claim of no essential differences between modes of reproduction Blending inheritance
Rejected idea that cultivation causes species to lose all stability and develop into an "endless series of extremely variable forms"	New conditions of life slowly cause cultivated species to vary over many generations
Tendency to abstract and reductionist reasoning	Tendency to materialistic and holistic reasoning
Research practices	
Separated problems of heredity from those of development and evolution	Tackled at the same time problems of reproduction, heredity, development and evolution

Table a continued

Mendel	Darwin
1. Chose a problem from statistical conspicuities in hybridisation experiments and conflicting opinions of other researchers	1. Made many observations and some hybridisation experiments, collected vast amounts of observations and experimental results by others
2. Looked for suitable experimental objects and planned suitable experiments, experimental details were stated exactly	2. Hybridisation experiments did not differ from those by others of his time, dealing mainly with questions of hybrid vigour, fertility, and the occasional appearance of new traits after the crossing of hybrids, interpreted as reversion; no experimental details stated
3. Proceeded from simple to more complex phenomena, evaluated his results statistically, applied them to new findings in cell theory and the physiology of fertilisation	3. Examined many complex phenomena at the same time; rarely distinguished between exceptions and regularities
4. Derived testable generalisations (laws)	4. Devised a speculative non-testable theory (Pangenesis) with the aim of unifying all the different and contradicting observations in heredity and development
Role of "folk concepts"	
	Abundant use, e.g. assumption of the inheritance of acquired characteristics; the impact of sperms on mothers
Style of presentation	
Paper is structured in a modern way, writing is concise and to the point	Way of writing is long-winded, redundant, often not consistent, even poetic
Impact	
No immediate impact; later Mendel's laws and methods became the basis for classical genetics and population genetics.	Darwin's genetic theory was immediately widely discussed, but later discarded (like other materialistic theories of heredity at the time); extremely wide and lasting impact of work on evolution

The modern concept of science was formed in the mid-nineteenth century, particularly through the work of Whewell and Herschel (Ruse 1996, pp. 126ff.). According to Ruse, science as opposed to natural philosophy has since then meant desirability of consistency, simplicity, predictability, unificatory power, and often also fertility and causal hypothesis. From this perspective Darwin's approaches are mostly those of a natural historian, whereas Mendel's are clearly those of a modern scientist.

5 Some Conclusions

This review has demonstrated that the question raised at the beginning, concerning why did Mendel's and not Darwin's approach in genetics become the dominant one on which the science of genetics was founded, cannot simply be answered from the fact that Darwin was mainly incorrect and Mendel mainly correct. Though Darwin's ideas about causes of variation and heredity proved mostly incorrect, Mendel, too, in many respects was not correct when seen from today's perspective. Genes do not act as independent factors, but interact. Most traits are not determined by single genes. Independent assortment is limited, Mendel did not observe linkage, and he did not distinguish clearly between genotype and phenotype. What makes his work successful and many of his basic ideas valuable, right until the present time, is the fact that he introduced concepts such as discrete elements, underlying discrete as well as gradual traits, and methods which proved highly successful for future work not only in genetics but also in experimental biology in general. More generally, Mendel's approach took the study of the transmission of traits out of natural history and transformed it into a scientific field of research; it reduced complex phenomena to more simple particulate models, thus rendering a quantitative analysis fruitful. In contrast, because of its vagueness, lack of logical consistency, and Darwin's attempts to explain many complex phenomena at the same time without appropriate experimental and conceptual tools, his proposition of a materialistic basis of inheritance did not contribute to research in heredity.

Darwin's greatest accomplishment, the theory of evolution by natural selection, shows the success of naturalists' methods. In my opinion, the adoption of a more scientific methodology in the fields of inheritance and variation would not, as has been suggested, have necessarily prevented Darwin from proposing his fundamental theory. But it might have made his proposition of natural selection more consistent and less diluted with prescientific notions and popular beliefs such as blending and soft inheritance, etc.

Whereas the project of organic evolution in Darwin's time was mainly a naturalists' pursuit, in which Darwin played a decisive role by introducing natural selection as a new mechanism, Mendel's approach prevailed in genetics and experimental biology in general. Mendel's analytical approaches were later supplemented by "syntheses", such as between genetics and evolution in the 1930s, which now seem to be successfully merging with developmental biology. In the words of Thomas Hunt Morgan (1934): "[Mendel's] analysis was a wonderful feat of reasoning. He verified his reasoning by the recognized experimental procedure of science."

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ARTICLE

How Evolutionary Biology Presently Pervades Cell and Molecular Biology

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Abstract The increasing place of evolutionary scenarios in functional biology is one of the major indicators of the present encounter between evolutionary biology and functional biology (such as physiology, biochemistry and molecular biology), the two branches of biology which remained separated throughout the twentieth century. Evolutionary scenarios were not absent from functional biology, but their places were limited, and they did not generate research programs. I compare two examples of these past scenarios with two present-day ones. At least three characteristics distinguish present and past efforts: An excellent description of the systems under study, a rigorous use of the evolutionary models, and the possibility to experimentally test the evolutionary scenarios. These three criteria allow us to distinguish the domains in which the encounter is likely to be fruitful, and those where the obstacles to be overcome are high and in which the proposed scenarios have to be considered with considerable circumspection.

Keywords Functional biology · Evolutionary biology · Functional synthesis · Synthetic experimental evolution · Costs and benefits · Experimental evolution

1 Introduction

In 1961, Ernst Mayr distinguished two forms of biology: Functional biology, in which researchers look for mechanisms, and answer questions as to “how?”; and evolutionary biology, in which the questions raised are “why?”, and where the answers are evolutionary scenarios (Mayr 1961). Functional biology includes physiology, but also biochemistry, molecular and cell biology. Ernst Mayr was not the first to make this distinction, but he expressed it in a very clear way. Such a separation was already visible at the time of Darwin. It was a characteristic of twentieth-century biology, but has narrowed considerably since the turn of the 21st century. The rise of evolutionary developmental biology (Evo-Devo), and the less visible developments of experimental evolution (Buckling et al. 2009)

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and functional synthesis (Dean and Thornton 2007)—see later for a description—are the signs of this encounter between the two branches of biology.

My aim, in this contribution, is twofold. The first is to explain the reasons for the most recent encounter. To achieve this, I consider two early attempts which were unfruitful, or at least did not lead to stable research programs, and analyse the causes of the failures. I then compare these early, inefficient efforts with present-day ones. I will not examine the introduction of functional biology into evolutionary biology, which corresponds to the rise of Evo-Devo, but the opposite, less visible, movement, the entrance of an evolutionary questioning into functional biology—what some authors have called "functional synthesis" (Dean and Thornton 2007). The second aim is to consider what will emerge from this encounter. I consider the harvest of results which can be expected, and also some of the difficulties that have to be overcome, and the areas where the merging will be less easy.

Introducing evolutionary questioning into functional biology can have two different meanings. The first is to describe the succession of forms that the complex functional devices existing in extant organisms successively adopt. The second is more ambitious: It consists in providing an evolutionary scenario for these transformations, that is, explaining the adaptive value that each of these transformations had in the specific environment in which the organisms were living.

2 The Early Attempts and the Difficulties They Encountered

It is possible to draw up a relatively long list of the efforts made by functional biologists to elaborate evolutionary explanations (Morange 2009). Here, however, I will focus on two examples, one from biochemistry and the other from molecular biology.

In 1981, Hans Krebs proposed an evolutionary explanation for the emergence of metabolic cycles, and in particular the cycle he had discovered 50 years earlier and to which his name has been given (Baldwin and Krebs 1981). Such an approach was not absent from comparative biochemistry, a branch of biochemistry developed by Marcel Florkin and Ernst Schoffeniels, but its place was limited.

The Krebs' cycle is one of the most central parts of metabolism, involved in the oxidation of two-carbon compounds, such as acetate. Instead of directly degrading these molecules, organisms add them to a four-carbon molecule, and progressively degrade the resulting six-carbon molecule into the initial four-carbon one, which is now ready for a new cycle of degradation.

The explanation provided by Krebs was simple: The formation of such a cycle optimises the use of resources—the direct oxidation of acetate releases less energy than indirect oxidation through the cycle. In addition, a cycle provides different possibilities of regulation and control.

Three characteristics of this explanation deserve to be emphasised. The first is the paucity of data provided to explain how the cycle was formed. Krebs mentioned only in passing that some of the reactions of the cycle already existed in a prebiotic world. The second is that the formation of the cycle is seen as a simple progress. The cost to the organism of producing such a complex ensemble of reactions requiring enzymes for the catalysis of each step is not mentioned, and was probably not perceived. Finally, the formation of the cycle is seen as a positive event, independent of the environment. It was a progress, whatever the conditions. The possibility that the formation of such a complex cycle might have been advantageous only in certain environmental conditions, for instance the presence or absence in the medium of certain molecules, was not considered.

A second example will allow us to draw the same conclusions. In 1965, Jacques Monod, Jeffries Wyman and Jean-Pierre Changeux proposed a model to explain the particular properties of a specific class of enzymes, the regulatory enzymes. The activity of these enzymes is regulated by molecules structurally distinct from the substrates and products, which bind to the enzymes at sites remote from the active site. This model was called the allosteric model (Monod et al. 1965). It proposed that the regulatory proteins (enzymes) existed in two different conformations in equilibrium, one active, and the other inactive. The preferential binding of the regulatory molecules (activators or inhibitors) to one or other of these two conformations shifted this equilibrium, resulting in a change in the enzymatic activity.

A second model was simultaneously proposed by Daniel Koshland (Koshland et al. 1966). By binding to enzymes, regulatory molecules directly induced a conformational change which moves from the regulatory site to the active site, and increased or decreased the activity of the enzyme.

In the long discussion of their article, Monod and his collaborators tried to justify the complex model that they had proposed. They described an evolutionary scenario that explained the preferential formation of regulatory enzymes obeying their model: Thanks to the symmetry of structures hypothesised in their model, the number of mutations necessary to generate a regulatory enzyme was significantly less than if one adopted the alternative model.

The resulting controversy was deep, and not clearly resolved by the experimental observations, since some enzymes seemed to obey one model and some the other model. What is notable is that no attention at all was paid to the evolutionary arguments proposed by Monod. All that was considered was the fitting of the experimental curves to those generated by the two models.

It is true that Monod had absolutely no experimental arguments to support his evolutionary scenario. It is also important to note that the cost of the formation of these complex regulatory enzymes was not considered by Monod, and that their appearance was seen as an advance in any possible environment, since it allowed an increase in regulation.

3 Why are Present Attempts so Numerous, and More Successful?

The previous examples help us to appreciate the difficulties that prevented the encounter between evolutionary biology and functional biology, and the reasons why they have been more recently overcome. The first obstacle was clearly an ignorance of the complexity of evolutionary theory, and of the transformations it underwent throughout the twentieth century in the hands of evolutionary biologists. The vision of Darwinian evolution held by most functional biologists was closer to that of Herbert Spencer—in which progress is the motor of evolution—than to the vision of Darwin himself. For Spencer, evolution was a general trend in the Universe, from matter to life, a movement of complexification and progress. For Darwin, and even more for the neo-Darwinians, evolution was a local increase in adaptation, fitness, and no more. Evolution was seen by functional biologists as absolute progress: The idea that a measure of fitness is always relative to the other organisms of the same species in a particular environment was absent. The fact that every mutation has a cost, and that it will be selected only if the benefit is greater than the cost, was also not considered. The fact that natural selection screens in the present and that, if a transformation requires more than one variation, each of these mutations has to increase fitness, was frequently forgotten in the reasoning. Only the final result was considered.

But the most significant obstacle was the absence of data to justify any scenario. Nothing was known of the structures which preceded the present ones, or of the precise nature of the modifications.

Concerning the first point, it is of course obvious that functional biologists are better informed today of the subtleties of evolutionary theory than were their predecessors. Moreover, many present-day biologists were not trained in biology, but rather in computer science, physics, and mathematics. They were not trained to consider as normal this sharp separation between functional and evolutionary questioning. The progressive disappearance of this barrier is particularly obvious in the new branches of biology, systems biology and synthetic biology, where these "new" biologists are numerous: Authors of studies rapidly shifted from a functional explanation to the elaboration of an evolutionary scenario.

A favoured path for functional biologists to follow in discovering evolutionary biology was, paradoxically, the engineering of proteins; paradoxically, because this field of functional biology was apparently one of the most impermeable to evolutionary questioning. Nothing had prepared, for this encounter, the specialists in protein structure and enzymology who decided at the beginning of the 1980s to "engineer" proteins with new characteristics and novel functions. The difficulties encountered by a "pure" rational approach; the increasing use of directed evolution to optimise the functioning of these new proteins; the discovery of the dual effects of variations, increasing the activity of a protein, but simultaneously decreasing its stability (Tokuriki et al. 2008)—evolutionary biologists' instantiation of the analysis in terms of benefits/costs—led protein engineers to link functional and evolutionary explanations more and more closely. But the major support for the encounter between functional and evolutionary biology was the precise molecular descriptions made possible by the development of genetic engineering. Sequencing of genomes and the comparison of sequences were decisive steps. A comparison could be used to guess the function of a newly discovered gene. However, the information needed to initiate evolutionary questioning was there, waiting only for the protagonists to express an interest.

I have selected two recent examples of research to contrast their sophistication with the previous examples of evolutionary questioning.

In the first case, the starting point of the study was a well-defined engineering project: To change in the bacterium *Escherichia coli* (*E. coli*) the nature of the coenzyme used by an important enzyme of the Krebs cycle, isocitrate dehydrogenase; instead of NADP, forcing the enzyme to use NAD. Coenzymes are small molecules that combine with the protein part of the enzyme and are essential for its activity. NAD (NADH) and NADP (NADPH) are electron transferring coenzymes that act as oxidising (reducing) agents in reactions of cell metabolism.

By a limited number of well-chosen amino acid replacements, the project reached its objective (Chen et al. 1995). A phylogenetic comparison showed that the ancestral enzyme used NAD (Dean and Golding 1997). This immediately led to a search for the reasons for the replacement of NAD by NADP. One hypothesis was that NADP in its reduced form is required for many biosynthetic pathways, the replacement of NAD constituted an advantage in organisms in which oxidation of isocitrate was the main source of reducing power. This hypothesis was tested by replacing in *E. coli* the present enzyme by its reconstituted ancestral (using NAD) form, and checking the fitness of bacteria in the presence of different nutrient sources, thus allowing, or preventing, the production of the reduced form of NADP by reactions other than the one catalysed by isocitrate dehydrogenase (Zhu et al. 2005). The results were in strong support of the hypothesis previously made: They showed that the fitness of the bacteria was seriously compromised when no other reactions were able to generate reduced NADP. In addition, the constant association in different bacterial species of an enzyme using NADP with another enzymatic activity essential for the use of acetate suggested that the principal selective pressure came from the use of acetate as the main nutrient (Zhu et al. 2005). The trigger for the replacement of NAD by NADP may have been an increase of acetate in the environment.

Interestingly, another enzyme structurally related to isocitrate dehydrogenase, β-isopropylmalate dehydrogenase, uses NAD. This raised the question of why it has not been replaced by NADP. A careful study combined precise in vitro kinetic studies, phylogenetic comparison and reconstruction of ancestral forms of enzymes, and the study of fitness in different environmental conditions. The conclusion was that the inhibitory effect of the reduced product NADPH prevented the replacement of NAD by NADP as a coenzyme. The use of NAD was possible because other reactions producing the reduced form of NADP existed (Miller et al. 2006).

In the second case, a similar degree of intertwining between functional and evolutionary explanations has not been achieved so far. However, this system is of interest because of the way evolutionary explanations can be added to physicochemical ones and also because the mechanisms under study might generate possibly new evolutionary scenarios.

The discussion requires a note on protein folding. This folding is a spontaneous process occurring after synthesis of the proteins on the ribosomes. The folding involves building a three-dimensional structure from the chain of amino acids as a prerequitise for function. The risks of aggregation, and thus loss of functional capability, between nascent proteins, with their hydrophobic residues exposed to the solvent, is limited by the existence of a class of proteins called chaperones. The chaperones bind nascent proteins and prevent their interaction with other unfolded proteins. Chaperones also participate in the refolding of proteins that have been accidentally unfolded.

Among chaperones, chaperonins are the most sophisticated nano-machines. They provide nascent proteins with a cavity insulated from the solvent in which they can fold. In bacteria, only 5 per cent of proteins require chaperonins to fold under normal conditions.

Many attempts have been made to discover the structural characteristics of those proteins that require the assistance of chaperonins. Some structural families of proteins, such as the α/β barrel proteins, are more represented among the substrates of chaperonins, but nothing fully informative has emerged from these studies. According to Kerner et al., some proteins of this structural family do not require the assistance of chaperonins, whereas proteins of other unrelated structural families do (Kerner et al. 2005). In the discussion of their article, the authors suggested that the present situation was just a snapshot in the long evolutionary history of the relations between chaperonins and their targets. They interpreted this evolution as the superposition of two distinct movements. Thus there is an evolutionary trend pushing proteins to fold rapidly, without assistance. Every mutation in the target protein going in this direction would be retained, because it would decrease the energetic cost of protein synthesis. But gene coding for proteins mutate, and new proteins are generated by gene duplication and mutations of one of the two copies. These mutations can introduce new functions, or provide proteins with new characteristics, such as new regulations. The benefits afforded by these new functions or new regulations can outweigh the costs represented by the possibly more difficult folding of these modified proteins. Not only are targets of chaperonins permanently evolving, with “old” targets disappearing and “new” ones taking their places, but also chaperonins might help the expansion of families of proteins whose folding would be difficult without their assistance.

A recent paper has apparently confirmed this model, and shows how the power of chaperonins might be manipulated by synthetic biologists to generate new proteins and enzymes (Tokuriki and Tawfik 2009). By increasing the level of chaperonins, the authors were able to isolate mutations generating new enzymatic capacities which otherwise would not have been obtained. The mutations responsible for these new activities have a destabilizing effect on the proteins, leading under normal conditions to their rapid unfolding and degradation. Only high concentrations of chaperonins can permanently refold these proteins, and prevent their degradation.

Interesting evolutionary scenarios are created by this capacity of chaperonins to select the viable pool of proteins at a given time. Some years ago, Susan Lindquist suggested that HSP90, another chaperone, might buffer, and therefore allow the accumulation of, genetic mutations that would be revealed in stress conditions, when the level of free HSP90 chaperone would decrease (Rutherford and Lindquist 1998).

The perspectives of Nobuhiko Tokuriki and Dan Tawfik are different. Their work suggests that, in certain conditions, the organisms might increase their levels of chaperonins and thereby increase the number of stable protein variants. These unstable (in normal conditions) variants might be stabilised by subsequent secondary mutations, permitting the mutant forms of proteins to be synthesised (again in normal conditions), with a low level of chaperonins. Such a scenario is reminiscent of, but different from, the mechanism of genetic assimilation suggested by Conrad Waddington (Waddington 1941), and also of the capacity of microorganisms to modulate their rate of mutations, by controlling the mechanisms of DNA replication and repair.

In the two above cases, the studies were enabled by an excellent molecular description of the systems; and by a careful account of the costs and benefits of mutations and of the experimental conditions in which the organisms live.

4 Great Expectations, Much Cautiousness

Many efforts are being made to introduce evolutionary explanations into fields of research that so far have been part of functional biology, such as medicine and the study of behaviour. The foregoing examples show that the wedding between evolutionary and functional explanations is possible when an excellent functional description has been made, and when we have tools—such as the reconstruction of ancestral proteins, and systems of experimental evolution—to test the proposed scenarios. By adopting these criteria, we are well placed to discriminate between lines of research where important results will be rapidly obtained, and those where the lack of suitable tools will make the testing of scenarios more difficult and, therefore, in which the proposed scenarios have to be considered very cautiously.

One of the first fields that has already contributed to this encounter between evolutionary biology and functional biology is the epidemiology of infectious diseases. The resurrection of infectious agents of the past—as in the case of the influenza virus responsible for the Spanish Flu, a precise description of the mutations responsible for the emergence of a new human pathogen, such as for the emergence of HIV, and the (at least partial) possibility of reconstructing and/or anticipating the appearance of variations by experimental evolution—will allow improved control of epidemics and pandemics.

“The failure to embrace evolution is the dark side or Achilles’ heel of molecular biology,” according to Carl Woese (Woese 2001). It is true that, apart from some exceptions such as the origin of the genetic code, little attention has been paid to the evolution of complex molecular systems, which has allowed the opponents of Darwinian theory and supporters of “Intelligent Design” to emphasise the absence of explanations for the development of these remarkable nanomachines: Haemoglobin, the protein which transports oxygen in the blood, and the flagella that propel bacteria, are the most frequently used examples of "perfect design" (Behe 2007). All conditions are now present—good phylogenetic data, permitting the reconstruction of past devices, and the possibility of testing the properties of these ancestral nanomachines in vitro and of submitting them to experimental evolution in different environmental conditions—to generate in the near future a rich harvest of results. Such a reconstruction may cast light on the evolution of the molecular machinery, but might also suggest new solutions for biotechnology and synthetic biology. As we have seen, the same is true in biochemistry, and one can expect a plethora of studies that will illuminate the early stages of life on Earth.

There are more complex fields where phenomena under study occur at different levels of organisation, such as immunology, in which the most fundamental questions, for instance the relations between innate and acquired immunity, might be answered if more attention were to be paid to the evolutionary history of these systems (Read and Allen 2000). Many observations have been made on different organisms, and they hold out the potential for generating evolutionary scenarios, some of which might be experimentally tested.

One area in which an evolutionary scenario is being actively sought is the evolution of modern humans from the last common ancestor with chimpanzees. But the difficulties are immense. There is plenty of information from the comparison of the human genome with the genomes of monkeys and apes, but this information is not filtered: It is difficult to discriminate between significant and nonsignificant variations, and the methods used to extract the significant information are not devoid of pitfalls (Hurst 2009). The experimental tests will also be difficult to realise! The synthetic experimental evolution strategy proposed by Douglas Erwin and Eric Davidson (Erwin and Davidson 2009), in which part of an evolutionary scenario is tested on a related organism easily accessible to experimentation, will be impossible in the absence of an appropriate model organism. The consequence is that scenarios risk being simplistic, focused on one or a few candidate genes, considering only the benefits of the variations and not their costs, underlining long-term possibilities offered by the mutation but ignoring its immediate negative consequences. A good example is the description of the mutation in the *MYH16* gene responsible for a loss of function in the myosin gene specifically expressed in the jaw, and therefore for a sharp reduction in the jaw muscles (Stedman et al. 2004). The long-term possible consequence, re-equilibration of the head and growth of the brain, was considered as a benefit, whereas the immediate cost—the difficulty of ingesting food to which this organism was accustomed—was not considered.

The situation is even more difficult in other areas such as evolutionary medicine and evolutionary psychology. In both cases, it is considered that modern humans were adapted to environmental conditions existing in the Pleistocene, not to the present conditions created by the actions and lifestyles of modern humans themselves.

Such scenarios and explanations face many difficulties. The first is to justify the present lack of adaptation. Were the changes too rapid? The argument seems well founded in some cases, such as the recent increase in the number of individuals suffering from allergy, which may be the result of the decrease in the number and seriousness of infectious diseases. But this is not the case for many scenarios in evolutionary psychology. The second weakness of these scenarios is that the past environment is imagined more than described on the basis of limited data. The precise mechanisms involved, and the nature of the genes mutated, are in most cases wholly ignored. Finally, experimental testing of these scenarios is obviously impossible.

The existence of such a spectrum of situations, from systems ripe for experimental study to highly speculative untestable scenarios, reflects the very different nature of the phenomena under study, and their degrees of complexity. We need to be fully conscious of these differences if we do not want serious studies to give credence to unfounded scenarios, hasty acceptance of which might raise huge and complex ethical and societal issues.

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ARTICLE

Are RNA Viruses Vestiges of an RNA World?

Susie Fisher

Abstract This paper follows the circuitous path of theories concerning the origins of viruses from the early years of the twentieth century until the present, considering RNA viruses in particular. I focus on three periods during which new understandings of the nature of viruses guided the construction and reconstruction of origin hypotheses. During the first part of the twentieth century, viruses were mostly viewed from within the framework of bacteriology and the discussion of origin centered on the "degenerative" or the "retrograde evolution theory." However, concomitantly, in the context of origin-of-life theorizing, the notion that viruses are vestiges of a prebiotic world was also being contemplated. In the 1960s the idea that viruses were genetic elements that "escaped" from cells became prevalent. These traditional hypotheses are being revisited nowadays by evolutionary virologists, who have placed them within a new conceptual framework that is supported by cutting-edge genomic and proteomic data. Two current, opposing scenarios of virus origin are presented. The philosophical dimensions of "revisiting" the original hypotheses are briefly discussed.

Keywords Protovirus · Retrograde evolution · Revisiting · RNA world · Virus origin

1 Introduction

A major topic addressed in this special issue relates to the question of whether the gap between functional biology and evolution has been successfully bridged. Powerful technologies such as computerized sequence data analysis and microarray assays allow molecular biologists today to explore, in detail, cellular mechanisms and the dynamics of cellular activities. The knowledge thus gained is providing theorists with new opportunities to re-examine traditional Darwinian themes, and to contemplate other theoretical issues in

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biology.[1] Virus research, however, is totally absent: Darwinian theory is conspicuously missing from its practice and discourse. Hence, the question of "bridging the gap" is seemingly irrelevant to this experimental field.

But why should viruses be examined from within a Darwinian framework? Are viruses alive? Virologists argue that viruses are vital members of the web of life even if we do not deem them to be truly "alive." One hundred years of virus research has led biologists to view them as occupying a grey area between the living and the nonliving; this, according to Luis P. Villarreal (2004), had a profound effect on evolutionary biologists, who for the better part of the twentieth century ignored them in the study of evolution. But though viruses were not found to be a suitable object for evolutionary studies, the question of their origin has been intensively addressed by the research community.

Stephen S. Morse (1994) pointed out that although virologists have a longstanding interest in viral evolution, viruses were rarely considered from the same evolutionary standpoint as other organisms. Even though virologists were, by the 1930s, well aware of viral genotypic variation, the evolutionary implications of this variation were barely discussed. Furthermore, other prominent Darwinian themes such as natural selection or evolutionary constraints were not put to use in virus research. Morse calls for the development of an evolutionary framework for viruses that would cover current trends in virology: Emphasis on variation; origin of virus speculations; and the study of the emergence of new viruses, an extremely important issue in the medical context, to name but a few. Indeed, the novel technologies mentioned above currently being used by virologists produce a vast amount of genomic and proteomic data concerning viral and cellular genomes and proteins. This data, according to leading evolutionary virologists, justifies the admittance of viruses into the larger family of organisms traditionally considered by evolutionary biologists. Moreover, evolutionary virologists are also approaching the community of virologists in general offering them an evolutionary framework that could serve as a platform for the construction of experiments that would test the validity of evolutionary hypotheses concerning viruses and their hosts. If this is so, then the question of a gap between virus research and evolution may soon become an issue deserving further consideration. In this paper, however, I focus on the construction of virus origin hypotheses, leaving aside the seminal question of viruses and evolution for future consideration.

According to current views, certain RNA viruses are vestiges of a prebiotic world, while others are not. What this means is that recent scenarios of RNA virus origin suggest that at least some RNA viruses appeared at a very early stage of the origin of life, preceding modern cells, whereas others emerged after these cells had evolved. Ideas regarding the origin of viruses accompanied virus research over the entire twentieth century and continue to do so today. Three hypotheses were central to the early origin discourse: A degenerative or retrograde evolution theory; viruses as vestiges of an ancient precellular or prebiotic world; and viruses as genetic elements that "escaped" from cells. Concerning RNA viruses, Howard Temin's protovirus hypothesis, relating to animal viruses, is especially noteworthy (Temin 1970). According to Morse, this hypothesis is the one most widely accepted today for RNA virus origin and may even be generalized to most and possibly all viruses (Morse 1994, p. 5).

However, a detailed description of 100 years of virus research and virus origin theorizing is not the topic of this paper. Rather, in order to examine the relationship between

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[1] Note, for example, articles appearing in *Biological Theory*, a new publication "devoted to theoretical advances in the fields of evolution and cognition with an emphasis on the conceptual integration afforded by evolutionary and developmental approaches." http://www.mitpressjournals.org/loi/biot.

empirical studies of viruses and the development of the notion of a virus on the one hand, and the conception of origin hypotheses on the other, I purposely follow a rather punctuated time-line of origin hypothesizing. I focus on three periods during which new understandings of the nature of viruses guided the construction of origin hypotheses.[2] During the first part of the twentieth century, viruses were mostly viewed from within the framework of bacteriology and the discussion of origin centered on the “degenerative” or the “retrograde evolution theory.” In the 1960s, the fruits of bacterial viruses (bacteriophage) research, tobacco mosaic virus research and the knowledge of the chemical nature of viruses’ hereditary material opened new avenues for discussing the origin of both DNA and RNA viruses; “escaped” genetic elements and “messages” became the focus of virus origin discourse. Forty years ago, Temin first presented his protovirus hypothesis to explain the origin of RNA tumor viruses (1970). The hypothesis gave the newly discovered enzyme, reverse transcriptase (RNA-directed DNA polymerase)[3] a central role, making the escaped message idea concrete: His hypothesis will also be reviewed. Finally, I present two current scenarios of origin of viruses conceived in the light of the latest advances in computerized sequence data analysis (protein and polynucleic acids). In these scenarios, traditional hypotheses, dressed anew, are being used to account for events long past.

2 Origin of Life Theories and Origin of Virus Hypotheses

The role of viruses in theories of origin-of-life has been extensively discussed by Podolsky (1996). This, however, does not fully coincide with, nor relate to, the more direct question of virus origin. To be sure, looking at the first part of the twentieth century, it is rather difficult to conceptually disentangle the two questions. As long as a clear notion of “what a virus is” was missing, viruses as hypothetical self-replicating macromolecules of an undetermined chemical nature could be imagined to exist at the dawn of life. Indeed, during the 1920s, several virus-centered origin-of-life theorists considered that “a viruslike organism was the Earth’s first organism” and that present-day viruses are their descendents (Podolsky, p. 90). This notion was adopted and further developed in the late 1920s by Jerome Alexander, Calvin Bridges and J. B. S. Haldane. Alexander and Bridges saw viruses as the contemporary representatives of the first living molecules, called by them “moleculubionets,” that arose spontaneously from “a chance event in the molecular chaos” (Podolsky, p. 91). They explained that “life began…in the molecular order of complexity with an autocalitic molecule of definite structure and less definite constituents” (quoted in Creager 2002, p. 73). Haldane, however, found life to be too dynamic to be reduced to a single particle and used the virus, for the most part, as a heuristic model of a

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[2] Histories of virology and virus research consulted in the writing of this article were Smith Hughs (1977) for general information on the history of virology, and Creager (2002) on the history of tobacco mosaic virus research. As concerns the history of bacterial virus research, Brock (1990) and Helvoort (1994a, b) were most helpful. Additional accounts of the history of virology used in this paper are listed in the text.

[3] Reverse transcriptase, also known as RNA-dependent DNA polymerase, is a DNA polymerase enzyme that transcribes single-stranded RNA into double-stranded DNA. According to the “central dogma of molecular biology,” genetic information is transferred from DNA to RNA to protein. The copying of DNA into RNA is designated transcription and the process is carried out by a transcriptase (a DNA directed RNA polymerase). However, in the case of a unique group of RNA viruses, the first step in the replication of viral RNA is actually the copying of the viral RNA into a complementary DNA. This DNA is then integrated into the cell’s DNA and transcribed, i.e., new copies of the viral RNA are made serving both as viral genomes and viral mRNA. The enzyme responsible for this process was given the name “reverse transcriptase.” RNA viruses that multiply by this “reverse” mechanism were called retroviruses.

possible mechanism for the origin of life. He suggested that life began with large molecules that were generated in a reducing atmosphere by the sun's ultraviolet radiation, where organic nutrients accumulated to form a "hot dilute soup"; and that "life may have remained in the virus stage for many millions of years before a suitable assemblage of elementary units was brought together in the first cell" (Haldane, quoted in Podolsky, pp. 93–95) Still, not fully consistent with a limited use of a virus as a heuristic tool, viruses were for him also a true phylogenetic "missing link" between life and non-life.

Beginning in the 1930s, the hypothesis that viruses were primeval organisms lost favor and the retrograde evolution theory took over, working conceptually and experimentally to disengage the two questions of origin. The retrograde evolution theory viewed viruses as evolutionary descendents of bacterial cells, thus greatly distancing the time between which viruses evolved and life began. By the late 1950s, the experimental investigation of the primal events of the origin of life was mostly led by chemists, searching for possible chemical pathways for syntheses of life's building blocks under the chemical and physical conditions that were presumed to have existed in the primordial atmosphere on Earth. Most notable was Stanley Miller's successful synthesis, in 1953, of amino-acids (Fry 2000). Origin-of-virus theorizing, in contrast, was left to the virologists that were now informed by the growing knowledge of viruses' "way of life" based upon 30 years of experimental virus research, the main actors being tobacco mosaic virus and bacterial viruses. Hence, hypotheses of origin, proposed by virologists during the 1960s and 1970s, were grounded upon what was learnt from extant cells and viruses, extrapolated back to ancient times. These hypotheses took into account the chemical constitution of viral genomes and the unique relationship that was found to exist between cells and viruses. Consequently, once viruses were defined operationally and chemically, the discussion of their origins and their role in theories of origin-of-life parted ways.[4] By the 1960s, viruses were perceived as objects with a unique history of their own, one that we can try to follow.

Today, virus origin hypothesizing is once again undergoing a conceptual turn. Owing to a large body of comparative genomic data, compiled since the mid-1990s, hypothetical molecules of the past are becoming recognizable nucleic acid sequences whose lineages can be traced. Contemporary evolutionary virologists who hold a reduced to extreme notion of a virus being nothing but functional nucleic acids[5] are bringing virus origin and origin-of-life hypotheses to converge once more. This will be demonstrated shortly.

3 The Degenerative or Retrograde Evolution Theory

Following Pasteur's and Koch's successful isolation of pathogenic bacteria in the nineteenth century, scientists were stimulated to expand the search for infectious agents. Guided by Koch's postulates and armed with microscopes, filters and a variety of media cultures, the search turned into a major enterprise involving widespread laboratory and field studies. However, it was found that in an increasing number of cases, some agents of disease seemed to evade capture or even observation. The filters used to collect bacteria from cell-free cultures failed to retain them, the microscopes failed to detect them and

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[4] This parting of ways, however, probably began even earlier when, in the late 1940s, viruses started to be used in the context of origin-of-life theories metaphorically, and archaic macromolecules were no longer expected to fulfill the role of phylogenetic ancestors of extant viruses and organisms (Podolsky 1996).

[5] For example, Eigen writes, "Perhaps the simplest form of virus is represented by a single strand of ribonucleic acid (RNA), made up of several thousand individual nucleotide subunits…" (1993, p. 42).

scientists were unable to grow them in synthetic media cultures; only their pathogenic effect pointed to their existence. Hence, a new category of infectious agent was created, defined by the inability to detect them due to the limits of the tools used for attempted isolation and characterization.[6] The infectious agents became known as "filterable viruses" and were found to be associated with diseases of many forms of life: Plant, animal, insect and bacteria.

In the 1930s, virus researchers became divided over the question of "what is a virus" and, accordingly, a number of suggestions for the problem of virus origin were presented.[7] Animal virus researchers, working from within the bacteriological paradigm, held an organismic view of viruses: Being parasitic *ultramicrobes* they depended on live cells for nutrients and growth factors (Helvoort 1994a). Paul Fildes (1882–1971), the notable British bacteriologist, suggested in 1935 that parasitism among bacteria was caused by loss of enzymes necessary for the synthesis of cellular material, thus forcing the organism to live on nutritionally complex materials that would be supplied by another host. His theory assumed that the first organism was autotrophic, next came heterotrophic bacteria, then bacteria that could not live on a synthetic media containing only an organic carbon and an energy source. A whole series of stages could be envisioned of organisms with increasingly complex nutritional requirements (Brock 1990, pp. 32–34).

In the 1930s, the virologists Robert Green and Sir Patrick Laidlaw, viewing viruses as ultramicrobes, extended Fildes theory of "parasitism of bacteria" to include filterable viruses (Green 1935; Laidlaw 1938). Like Fildes, Green assumed that the primary characteristic of retrograde evolution was a loss of function and associated substance. He suggested the possibility of a "harmonious" living together of a host and its intracellular parasite. In addition, the development of parasitism would depend upon the "conformity" of the parasite to the host, pointing to Rikettsia, which had become adapted to reside in a cell's nucleus, thus demonstrating the possibility of extreme intracellular selection and adaptation. The ability of an intracellular parasite to conform and adapt to the internal cellular environment might lead to a simplification in its structure and to a minute size. This simplification could carry a "tremendous advantage to intracellular parasitism" he claimed (1935, p. 444). But how far could this process of intracellular parasitism proceed? Green asserted that:

> Such special forms of life could develop to various degrees of simplification. It is conceivable that the retrograde process could proceed until only those molecules concerned with reproduction remained as the parasitic unit. Such a residuum could be as small as a single colloidal molecule and would correspond to the smallest of the viruses. Such a virus would be a functionally complete unit of life only when immersed in living protoplasm. (Green, p. 445)

To Green's theoretical considerations, Laidlaw (1938), in his extensive review of the then current state of knowledge of viruses and their diseases, provided additional support for the retrograde virus hypothesis. He argued that viruses "live a borrowed life" and that they were "truly the supreme summit of parasitism" (Laidlaw, pp. 49–50). The one thing that the perfect parasite possessed, he claimed, was the chemical substance which transmits

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[6] As technological advances were made during the 1930s regarding filters and microscopes, the only defining feature of viruses left was their "obligate intracellular parasitism." (Podolsky 1996, p. 86).

[7] Not all researchers viewed viruses as external agents. Prominent immunologist and Nobel laureate Jules Bordet saw viruses as internal products of the cell itself that caused the cell's own destruction (Helvoort 1994b); hence my discussion of virus origin will not refer to his concept of a bacterial virus.

the characters of the species, for it was clear that the majority of viruses bred true. Laidlaw proposed that "the absence of any clean-cut separation between the smallest free-living organisms and the larger viruses, and all the gradations we encounter within the group … also indicates how viruses probably arose." He argued that a biogenic origin of viruses is more probable than a heterogenic one (a "physico-chemical" origin theory) since "whenever, in the past, biogenesis had been on trial it ultimately emerged triumphant" (Laidlaw, p. 51).[8] The degenerative origin hypothesis that became generally known as the "Green-Laidlaw Hypothesis" was accepted by many eminent biologists, such as Wendell Stanley, André Lwoff, and Frank MacFarlane Burnet, and soon prevailed, its reign lasting until the late 1950s (Podolsky 1996).

4 Towards a "Modern Concept of a Virus"[9]

Yet, during that same period a different research programme, centred upon physical and chemical studies of viruses, was also being pursued. The introduction of this type of research into biology was inspired and financed, at large, by the Rockefeller Foundation (Kay 1993). It eventually led to the reduction of an organismic concept of a filterable virus to a macromolecular one. Biologically-oriented virus researchers, interested mainly in virus replication and not concerned directly with medical issues, adopted physicochemical procedures and technologies that were being used in protein/enzyme research to isolate viruses and to physically and chemically define them. These procedures and technologies turned the virus into a visible object that researchers could "see" rather than just follow its physiological effects upon hosts. These methods included: New procedures for virus isolation such as chemical precipitation; Biological and chemical methods for the analysis of virus composition; high-speed sedimentation machines (ultracentrifuges) for analytical and preparatory purposes; and commercial electron microscopes that provided images of the particles themselves. These tools set the path for the materialization of the virus.[10]

A leading figure in this line of research was Wendell Stanley, an experienced organic chemist who joined, in 1931, Louis Kunkel's laboratory in the Department of Animal and Plant Pathology at Princeton. This particular location provided Stanley with conceptual and material resources for the construction of an effective experimental system that led to a milestone event in biology, as the canonical story goes: The crystallization of tobacco mosaic virus (TMV). Stanley, a newcomer to the field, set out to repeat results formerly published by Carl G. Vinson and by Vinson and A. W. Petre jointly on TMV chemistry. Vinson and Petre used lead acetate and safranin to precipitate the virus and digestive enzymes to determine the virus' chemical composition (digestive enzymes, such as trypsin and pepsin, are enzymes capable of specifically breaking down proteins,). The results of their experiments were inconclusive: While some digestive enzymes had an effect on TMV activity, others had none; trypsin was shown to inactivate the virus, but pepsin had no effect on it at all. Hence, no firm conclusions regarding the chemical nature of the virus could be drawn. Stanley decided to focus on two typical digestive enzymes, pepsin and

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[8] Laidlaw does not elaborate on this particular argument; it may be that he is referring to "spontaneous generation" controversies.

[9] The convergence of two research programs, one centered upon tobacco mosaic virus and the other upon bacterial viruses, had culminated by the end of the 1950s in the conception of a virus that Helvoort (1994a) phrased as "the modern concept of virus."

[10] This Sect. 4, unless stated otherwise, is based upon Creager 2002.

trypsin, that were supplied to him by John H. Northrop's neighbouring laboratory, to investigate their effect on the virus. While Vinson and Petre showed that trypsin inactivated the virus, Stanley carefully controlled the pH of the reaction, and proved that this inactivation of the virus was not caused by the enzyme's action but was due to the interaction of trypsin with the plant leaves. As for pepsin, here he showed that at a low pH, pepsin specifically catalyzed the breakdown of the virus into constituent polypeptides. These studies were followed by a comprehensive examination of the effect of pH and some 110 chemical reagents on virus infectivity.

All these explorations were, however, but a prelude to Stanley's best remembered achievement: The crystallization of TMV. Stanley believed that the results of his investigations with pepsin and trypsin clearly indicated that the virus was protein, thus "It was obvious that the methods of protein chemistry so successfully used by Northrop and associates in their work on enzymes might prove useful with this virus" (Stanley, quoted in Creager 2002, p. 57). Instructed by Vinson and Petre's virus precipitation methods and inspired by Northorp's procedures for the isolation of proteins he began reworking and combining both their methods. Starting with 4,000 kg of infected tobacco plants that were processed into 5,000 l of extract, he finally obtained 10 grams of highly purified, biologically active, photogenic needle-shaped crystals. In 1935, he announced, in *Science*, the successful crystallization of TMV claiming that the virus was nothing but a protein molecule. His claim was soon contested by leading British biologists and crystallographers, N. W. Pirie, F. C. Bawden, J. D. Bernal and I. Fankuchen, whose analysis showed that TMV contained both protein and RNA. Following some "negotiations," Stanley consented to regard the virus as a "nucleoprotein," that is, a structure containing both protein and RNA. Further improvements in precipitation procedures greatly increased the amount of purified virus that Stanley and his coworkers could obtain, and by 1936, they had over a kilogram with which to work. The chemical and physical investigations of TMV paved the way for the introduction of new methods and machines into virus research in general. The ultracentrifuge that became a standard tool during the 1940s was first used analytically to determine a virus's molecular weight and later as a preparatory machine to produce large amounts of virus. Improvements in electron microscopical procedures provided researchers with pictures of virus particles that showed a greater complexity than could be expected from a simple protein molecule or even a nucleoprotein. Nevertheless, TMV, a representative of plant viruses, was not the only virus being investigated; knowledge of many important aspects concerning virus replication and genetic behaviour were gained through the study of bacterial viruses. Bacterial viruses were discovered in 1915, by Frederick W. Twort and independently, during World War I, by Félix d'Herelle, who named them bacteriophage (bacteria devourers, today phage) (Brock 1990).

Once again, a new set of tools for virus research was developed, yielding important information concerning viral genetics and the viral-host relationship. This research programme was led by Max Delbrück in collaboration with Salvador Luria and "members" of the "phage group," an informal community of researchers that consented to use a specific set of virulent *E. coli* phages and certain experimental methods. Delbrück, a distinguished German-born physicist became, during the 1930s, fascinated with biology believing that theoretical physics could be applied to an understanding of the gene. In 1937, with the financial support of the Rockefeller Foundation, he travelled to the United States to pursue his interests in biology. After visiting several virus research laboratories to seek out a simple experimental system suited for quantitative research, he finally met Emory Ellis, a post-doctoral student at the California Institute of Technology, who was using phage as a model for the study of cancer viruses. Ellis employed d'Herelle's original assay for the detection of an *E. coli* phage that he had isolated from sewage. In this assay a mixture of the bacteria, *E. coli* and *E. coli* phage was added to plated bacterial cells. After a while, discrete holes, "plaques" were formed on the plate. The number of plaques formed versus the dilution of the phage showed the assay to be linear. This simple tool was further refined by Delbrück and Ellis who succeeded in synchronizing bacteriophage growth, thus producing a "one-step" curve in which the burst of new viruses could be clearly seen. From this curve, the amount of infectious virus produced per infected cell could be calculated and the kinetics of the virus replication could be studied. From the linear correlation, that was found to be independent of temperature, of bacteria concentration and of agar concentration, they concluded that phage were exogenous pathogens, reproduced by the cell. This technique became the established basis for all subsequent work on bacterial genetics and biochemistry. In the early 1950s, the plaque assay was adapted by Renato Dulbecco for use with animal viruses, and some years later by Harry Rubin and Howard Temin, to detect tumor viruses (Fisher 2009). After Ellis returned to cancer research, Delbrück continued to use this bacteriological tool to study the nature of the replication process itself, firmly believing in the relevance of phage for the problem of the reproduction of the gene. In 1939, he was permitted to extend his stay in the United States, thereby becoming a war émigré. His next successful collaboration was with Salvador Luria, a physician with an inclination towards the physical study of biology, and another European émigré. Luria too thought, independently of Delbrück, that phage may provide a model system for understanding the gene. Delbrück and Luria first met in 1940, soon becoming friends and collaborators, working together on several phage investigations. During the early 1940s, Delbrück and Luria, in collaboration with Thomas F. Anderson, an electron microscopy expert, used modern electron microscopes to produce pictures of bacteriophage. The pictures that Anderson produced from samples of phage, given to him by Delbrück and Luria, revealed that phage have a far more complex and varied morphology than what was formerly believed to be correct as concerns viruses. Most surprising was the finding that, after infection, phage seemed to remain adsorbed on the outside of the bacteria. Delbrück and Luria interpreted this finding by analogy with fertilization—that only the first virus to meet the bacteria enters it and that replication occurred inside the virus. In the following years Luria, Alfred Day Hershey and other phage researchers demonstrated the functional similarity of a bacterial genetic system and that of a phage. As with bacteria, it was found that phage mutations arose spontaneously; that phage appeared to contain a (small) genome, not just a gene; that phages could be crossed; and that phage could be selected for genetically (Brock 1990). Phage thus seemed to be a far more complex entity than had been presumed during the 1930s, having unique morphological features and a genetic constitution and mode of operation quite similar to bacteria. Still, the basic characterization of viruses as infectious parasites, potentially pathogenic, remained.

This account has, so far, omitted an important part of the history of virus research that was pertinent to the formation of the "modern concept of a virus"; the understanding of the intimate relationship that exists between the genetic components of a (lysogenic) phage and its host, to which the French virologist André Lwoff contributed significantly. Beginning in the 1920s, it was suggested that there were, in fact, two kinds of phage: one a "virulent" phage, whose cells, upon infection, are lysed releasing new virus particles; the other a "temperate" phage that could bring about the lysogenic state in bacteria, lysogeny being a property of the bacterial cell itself. In a culture of lysogenic bacteria, under normal growth conditions, only a very small number of cells expressed the lysogenic property. However, when lysogeny did occur, the cell normally produced 50–200 phage particles and lyses. The lysogenic phenomena remained, for many years since its discovery in the late

1920s, a mystery and a source of controversy. Delbrück and the phage group rejected the notion, and considered the phenomena to be an artifact. Nevertheless, by the early 1950s, several characteristics of lysogeny had been established: It was found that to be the property of all cells of a lysogenic culture, bacteria in a lysogenic culture were able to adsorb the phage but were immune to its effects, and that enzymatic or physical disruption of the cells did not liberate new phage particles. It was also found that after the infection of a sensitive bacterial strain with phage, resistant bacteria could be isolated and later produce phage that was identical with the original infecting phage. Once André Lwoff had discovered that UV radiation could induce cells to release phage, phage replication was studied in a quantitative manner, similar to the way that virulent phage were studied by the phage group. Importantly, the studies of temperate phage, performed during the 1950s by André Lwoff and other researchers, showed that a close relationship existed between the genetic components of a phage and those of its bacterial host. A temperate phage could exist either as a free virus particle, or as a prophage, integrated into the cell's genome (Brock 1990; Helvoort 1994b). In 1957, André Lwoff presented an explicit formulation of a virus that managed to capture its unique features: "Viruses are infectious, potentially pathogenic, nucleoproteinic entities possessing only one type of nucleic acid, which are reproduced from their genetic material, are unable to grow and to undergo binary fission, and are devoid of a Lipmann system" (quoted in Helvoort 1994a, p. 215). By the early 1960s, virologists had accepted "the modern concept of a virus" and the discourse pertaining to its nature and its origin shifted towards a discussion of its hereditary material and genetic behavior.

A similar relationship was also found to exist between bacterial plasmids and their host cells. It was shown that both viruses and plasmids could transfer from one cell to another (by different mechanisms), could become integrated into the cell's genome, and were capable of replicating autonomously (aided by the cell's mechanisms and substrates). Thus, beginning in the 1960s, theories of virus origin referred both to viruses and plasmids, and the unique relationship of cells and these genetic elements soon affected virus origin hypothesizing.[11] Furthermore, these studies highlighted the strict metabolic and genetic dependence of viruses on their hosts and an evolutionary "cells first" model for virus origin became predominant.

5 Viruses and Cells: Ancient and Modern Companions

Ultimately, after three decades of physically and chemically oriented virus research, the unique genetic features of viruses and their intimate relation with cells' genomes became established, setting in motion a new wave of virus origin hypothesizing. In the 1960s, virologists proposed that viruses had emerged by an opportunistic process of integration and re-localization of genetic elements coming from within cells. In 1966, renowned virologist Christopher Andrewes suggested the "Galatea Hypothesis." According to this, since bacteria produce various substances that benefit their existence, they may also produce, for their own end, a nucleoprotein such that, "if this nucleoprotein should gain access to another organism and be capable of replication, it would, if not under strict control by

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[11] During the 1960s, Howard Temin claimed that the relationship between Rous sarcoma virus (RSV), an avian RNA cancer virus and its host cell, greatly resembled that of temperate phage/lysogenic bacteria, thus extending this special relationship between viruses and their host cells to include animal cancer viruses as well (Fisher 2009; Temin 1964).

the genome of its new host, be automatically subject to the laws of natural selection and the debutante virus Galatea would be 'out.'" Natural selection would have played the part of Aphrodite (who gave life to Pygmalion's ivory statue). According to Andrewes, the emergence of viruses occurred in ancient times and probably began with plasmids which later became independent of cellular conjugation. He wondered whether nucleoproteins were "viruses in process of emerging … or defective viruses being submerged into the cells?" (Andrewes 1966, p. 2).

Significantly, shortly after this, Luria and J. E. Darnell devoted the last chapter of their *General Virology* textbook to a discussion of the nature and the origin of viruses (1967, pp. 439–454). They firmly rejected the retrograde evolution theory in its original nutritional form, arguing that no transitional stages between viruses and obligatory parasitic protozoa or bacteria were found. Rickettsiae and Chlamydozoaceae that were taken, in the past, to be candidates for intermediate life forms between bacteria and viruses were found, in fact, to be small parasitic bacteria. The strongest argument against the regressive origin of viruses from cellular parasites was, according to these authors, the noncellular organization of viruses: viral capsids were made of protein subunits and did not resemble cellular membranes. These objections and additional ones led them to conclude that "The break between the various intracellular parasites and the viruses is very wide" (Luria and Darnell 1967, p. 443).

Luria and Darnell instead offered a theory that was informed by current scientific knowledge and inspired by the results of investigations of bacteria and their viruses. Viruses and cells were presumed to have had a long and lasting genetic relationship: "A long-persisting virus is practically indistinguishable from a cell component. It might be considered a virus, or a plasmid, or a gene, depending on the type of effect by which it happens to be detected" (Luria and Darnell, p. 452). Thus, they regarded the problem of virus origin to be concerned both with the relation of viruses to cellular components and with the origin of cellular components. In their account, viruses arose in what we may call "Darwin's warm pond" where primitive cells already existed. Cells could either be monophyletic in origin, that is, the cell's genome was the product of the differentiation of an original self-reproducing single element, or cells could be polyphyletic, their genome being the result of several primitive self-replicating molecules coming together. According to this model, the essence of the evolution of a cell's genome was the merging of two or more, self-replicating genetic elements to make a functioning genetic system. In a rather similar way, the emergence of viruses in ancient times consisted first of the merging of genetic elements into a cell's genome and then an occasional transfer of parts of the genome that possessed the ability to self-replicate from one cell to another. If the merging of genetic lines occurred early in the evolution of the cell, the case of genetic elements becoming transmissible from cell to cell would represent a reacquisition of the original independence of the genetic elements and a repetition of the original merging process. In support of this possibility they presented the "viroid" hypothesis[12] that postulated on how in early evolution, free, self reproducing elements that had preserved their primordial characteristics, and their ability to regain infectivity by mutation, had entered into cells. These elements could later give rise to new viruses.

In general, Luria and Darnell wondered "whether viruses may have evolved from entire cells, or individual cellular components, or precellular or acellular forms of genetic materials." To this, they opined that these different theories varied only in their interpretation of "the relative duration of the companionship between cell components." They

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[12] Luria and Darnell 1967, p. 453, referring to "Altenburg 1946" (Altenburg 1946).

asserted that the common denominator of all these theories was the merging of genetic lines, stating that: “Viruses could derive from any one (or several) of the genetically specific components of cells, either by regressive evolution or transfer from cell to cell” (Luria and Darnell, pp. 440, 454).

In the scenario described above, while a DNA world is implied, RNA viruses could no longer be ignored. Luria and Darnell acknowledged the need to consider RNA and DNA virus origins’ separately: “In this search, we must keep in mind that there is no *a priori* reason to assume that all viruses have originated in the same way. In fact, the existence of RNA and DNA viruses is sufficient proof that at least two major avenues of evolution must have been followed” (Luria and Darnell, p. 440). On the face of it, the model that they suggested for the emergence of DNA viruses from cells could not be applied directly to those RNA viruses that were not known to interact with a cell’s genome in the way that genetic elements consisting of DNA did. Moreover, a basic condition of a genetic element to become a virus was that it was capable of replicating autonomously. In the period under discussion, mechanisms for RNA replication were still being investigated and it could not be said with certainty that an RNA virus was even capable of being directly copied.[13] Quite understandably, Luria and Darnell felt that RNA viruses “present formidable problems” (Luria and Darnell, p. 450).

Two possibilities for RNA virus origins were discussed by them: (1) RNA viruses may be a unique group of genetic elements forming a separate line of evolution, something they found quite unappealing, since RNA viruses were known to perform well as mRNAs utilizing the cell’s mechanisms and substrates; and (2) A virus was an “escaped message”—RNA viruses could have been derived from “DNA viruses whose messenger RNA has become capable of direct replication, so that transcription from DNA is unnecessary” (Luria and Darnell, p. 450). However, if this model of evolution was possible, then why restrict origins of RNA viruses to viral mRNA only? Just as the origin of DNA viruses from cellular DNA could be seriously considered, a possible origin of RNA viruses from cellular RNA messengers should also be entertained.[14] In this case, the required steps for a “message” to become a virus would be the acquisition of a replicative mechanism and the ability to form a virion. Luria and Darnell found the origin of RNA viruses to be rather puzzling; however, a more promising version of the “escaped message” hypothesis was soon to be presented.

6 The Protovirus Hypothesis

In 2006, Robin Weiss, a renowned retrovirologist wrote: “If Charles Darwin reappeared today, he might be surprised to learn that humans are descended from viruses as well as from apes. Some 8% of human genome represents retroviral genomes” (Weiss 2006, p. 1). Weiss was here referring to endoviruses, DNA sequences of retrovirus RNA, a unique group of viruses that replicates by reverse transcription and that have been found in all taxa examined so far (see footnote 3).

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[13] During the early 1960s, some leading scientists, Sol Spiegelman in particular, actually thought that DNA might be a necessary intermediate in the process of RNA replication (Fisher 2009).

[14] This is precisely where new genomic data assists virologists today to determine sequence relationships between a host cell’s genome and its virus and construct evidence-based virus origin hypotheses. See Sect. 8 in this paper.

The possibility of reverse transcription had been advocated by Temin since the early 1960s (Fisher 2009; Marcum 2002), but was accepted by the scientific community only after the discovery of an RNA-directed DNA polymerase (reverse transcriptase, RT), in virions of RNA tumor viruses by Temin and Mizutani, and independently by David Baltimore, in 1970 (Baltimore 1970; Temin and Mizutani 1970). Furthermore, researchers in the 1970s confirmed earlier suspicions that host cells that were *not* infected by tumor viruses did contain viral transcripts, that is, endoviruses. The discovery of the enzyme and the indication that endoviruses do exist led Temin, in 1970, to propose his "protovirus hypothesis" to explain the origin of RNA tumor viruses from cellular moveable genetic elements (1970). He soon extended this hypothesis to account for cellular differentiation and evolution as well. The hypothesis stated that "RNA tumor viruses evolved from elements in normal cells that could give rise, through transcription and reverse transcription, to a DNA copy that was incorporated into the cell genome" (Temin 1983, p. 7). This evolution happened "a long time ago and in the germ line" (Temin 1983, p. 10). The hypothesis predicted that the unique mode of information transfer from RNA to DNA was not restricted to viruses but would also be found in healthy cells. Reasoning that normal development of multicellular organisms may demand, in different types of cells, some rearrangement of the genetic message, he suggested that this could be achieved by mobile sets of genes travelling not only between various regions of the cell's chromosomes but occasionally even from one cell to another. To become transferable from one cell to another, these mobile RNA elements would require mechanisms for packing and for transferring, a gene for reverse transcriptase and a mechanism for the integration of reversed transcribed DNA into a cell's genome. In effect, what was being described was an "internal" RNA virus. If this genetic element became independent of the organism it belonged to, it indeed could represent the creation of a new virus. The protovirus hypothesis was, no doubt, inspired by Temin's work with Rous sarcoma virus, an efficient RNA tumor virus that he presumed to be an artifact of laboratory procedures.[15]

In his 1975 Nobel lecture, Temin offered, in addition to this model of retrovirus origin, a model for the origin of enveloped RNA viruses,[16] and another one for the origin of small DNA viruses. Both models were based upon his ongoing investigations of spleen necrosis virus (SNV), a retrovirus (1975). Regarding small DNA viruses, Temin suggested that these could have originated from retroviruses by reverse transcription. It was found that in some cases, immediately after infection, a large number of unintegrated DNA copies, reverse transcribed from the virus's genome, are present in the cells. These could represent precursors of animal small DNA viruses; continued replication of unintegrated viral DNA and encapsidation in viral proteins would be required to produce a viable virus.

As to enveloped RNA viruses, Temin admitted that the protovirus hypothesis did not help in understanding their origin. Still, he thought that the presence of RNA polymerase activity (RNA-directed RNA synthesis) in some retroviruses, such as SNV, might present a

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[15] RSV was the RNA tumor virus that Temin used, during the 1960s, in his in vitro investigation of viral induced cell transformation. The virus was first discovered in 1911 by the renowned virologist Peyton Rous, who attempted to isolate a filterable agent that apparently caused chicken sarcomas. In his Nobel lecture, Temin suggested that the virus was formed by a rare event of recombination of an avian leukosis virus (non-cancerous) and pre-existing cellular cancer genes while Rous was attempting to produce and isolate the infectious agent (Temin 1975; Cairns 1978). This way, by recombining with a functional virus, the newly formed virus would not have to acquire all the missing mechanisms to become independent (Temin 1975, p. 19).

[16] All viruses are covered with a protein coat but some viruses—enveloped viruses—are also covered with a lipid membrane, picked up from the host cell when it is released. The lipid membrane is called an envelope.

clue to the origin of other RNA viruses. These viruses could have originated from retroviruses. RNA viruses (not retroviruses) use a replicase (RNA-directed RNA polymerase) for the replication of their RNA genome; apparently, this activity is also found in retroviruses, but only a small incomplete RNA copy of the viral genome is formed. Temin surmised that if a genetic change were to occur, this might allow for a complete molecule to be synthesized, and with additional changes many copies of the complete RNA molecule could be made. In that way, enveloped RNA viruses emerge from retrovirus infected cells without the synthesis of a DNA intermediate. This proposition was, in effect, an "escaped RNA genome" hypothesis for the emergence of enveloped RNA viruses. In the following sections, when I discuss contemporary scenarios of RNA virus emergence, we shall meet again "escaped" RNA elements and the reverse transcriptase enzyme.

7 Modern and Ancient RNA Worlds

In 1967, Luria and Darnell described RNA in the following manner:

> … RNA, a coded polymer that in the evolution of cells has been relegated to a subordinate position, serving as a delegate bearer rather than a primary repository of genetic messages. If DNA is the sun, cellular RNA resembles the planets, shining with reflected light; but in RNA viruses we discover that some planets may glow with a radiance of their own. (1967, p. 439)

Today it is possible to assert quite safely that molecular genetics has gone through a "Copernican Revolution." Recent discoveries of catalytic and other functional (non-coding) RNAs attest to the important roles of RNA in information transfer and expression in present-day cells.[17] The study of cellular RNAs is reshaping our knowledge of biochemical processes and it may also bring about the realization of biomedical possibilities. Furthermore, "RNA World" theorists believe that modern RNA roles may be "molecular fossils" that can provide insights into primordial ones (Gesteland et al. 2006). The phrase "RNA World" was coined by Walter Gilbert, referring to a world that may have existed in the early stages of the evolution of life, before DNA appeared (Gilbert 1986). This imaginary, prebiotic world is assumed to be populated with free RNA molecules competing with each other for nutrients. The RNA World theory includes three basic assumptions: (1) that in the early stage of evolution of life, RNA molecules served as the genetic repository of ancient life forms; (2) that RNA replication was based upon a Watson–Crick base pairing mechanism; and (3) that it was not assisted by genetically encoded proteins i.e. enzymes (Joyce and Orgel 2006, p. 23). Later, a transition from an RNA world to a DNA-RNA- protein world is presumed to have occurred. There is strong evidence indicating that an RNA world did exist on the early Earth, though scientists are not sure that life on Earth actually began with RNA; it may have been preceded by some other replicating, evolving molecule (Fry 2000). The RNA world theory is widely accepted by origin-of-life theorists (Ricardo and Szostak 2009).

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[17] Such as one of the ribosomal RNAs being responsible for linking the amino acids to form a new polypeptide, and not the protein component of the ribosome, as was once thought (Gesteland et al. 2006). In general, in addition to the three traditional informational roles of RNA messenger, RNA transfer and ribosomal RNA, it is now recognized that RNA takes part in down regulating gene expression; various types of RNAs have been discovered in different biological systems acting in this capacity, such as siRNA, microRNAs and RNAi (Watson et al. 2004).

The idea that RNA is the primitive self-replicating molecule had been proposed earlier, during the 1960s, by a number of notable molecular biologists (Rich 1962; Woese 1967, pp. 179–195; Crick 1968; Orgel 1968). This radical suggestion was based on theoretical considerations pertaining to the chemical, physical and informational nature of RNA. Rich was apparently the first to suggest, in 1962, that the primordial molecule may have been an "RNA-like" molecule rather than DNA, as was commonly thought.[18] He postulated that this molecule carried genetic information (as RNA containing viruses do), that it had the capacity to self-replicate and that it could direct amino acids into a specific sequence to make proteins. Later in the decade, this concept was further advanced by Crick, Orgel and Woese; though Crick recalls that the idea was "largely forgotten" (Crick 2006, p. xi) until the discovery of catalytic RNA molecules in the 1980s, by Thomas R. Cech and independently by Sidney Altman (Kruger et al. 1982; Guerrier-Takada et al. 1983). It soon became clear that RNA can indeed perform two jobs: Carry genetic information and act as an enzyme. So, the two necessary conditions for the continued evolution of primitive life forms could apparently be fulfilled by this one molecule. This understanding made the RNA world-view of origin of life far more convincing.

8 Modern Scenarios of Virus Origin

Let us now return to the traditional hypotheses of virus origin and examine their current status among evolutionary virologists. As described above, the hypotheses offered since the 1960s were conceived in a biological world ruled by DNA, in which viruses were understood to be obligate genetic parasites completely dependent on their hosts for their development. In this context, it seemed reasonable to assume that cells preceded viruses, thus giving credence to the escape hypothesis. As we have seen, the degenerative theory was essentially dismissed and the idea that RNA viruses descended from primeval RNA molecules was difficult to defend experimentally. Today, these hypotheses are still being used to construe virus origin scenarios but are set within a significantly different theoretical and technological framework.

Most twenty first-century virus origin theorists hold a reductionist viewpoint of viruses focusing on genes and genomes, and offer origin hypotheses that are grounded in the RNA world theory. The speculative conceptualization of the 1960s is replaced by evidence-based theorizing.[19] Two major findings inform origin hypothesizing nowadays: The first is that several genes, called by Eugene Koonin (2006) "hallmark genes," that are central to virus replication and structure, are shared by many groups of RNA and DNA viruses but are missing from cellular genomes; the second is that ample genomic data points to the existence of extensive genetic exchange between diverse viruses. Koonin and Patrick Forterre, two leading evolutionary virologists, whose origin hypotheses I present below, believe that these findings and additional ones attest to the antiquity of viruses.

Koonin and Forterre share a number of basic assumptions and agree on much of the available data but they differ appreciably in their general model of origin, in their choice of

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[18] Interestingly, while Rich speculated on the origin of this molecule, he still proposed a degenerative evolution theory: "It is possible that the RNA containing viruses may be regarded as present-day examples which may have *degenerated* evolutionarily from such a primitive life" (1962, p. 124).

[19] In both articles (Koonin et al. 2006; Forterre 2006) extensive experimental data is provided. For example, Forterre notes that the results of analyzing more than 250 cellular genomes from the three domains of life: Archaea, Bacteria and Eukarya show that most of the viral proteins detected in viral genomes have no cellular homologues.

the object that is supposedly the archaic RNA virus and in the evolutionary age in which the origin event should have happened. Important, in relation to this article, is their differing opinion regarding the virus origin hypothesis that best agrees with today's cutting-edge experimental evidence.

These virologists assume that RNA viruses first emerged in the prebiotic RNA world: Koonin et al. (2006) speaks of an "ancient virus world" and Forterre (2006) of a "virosphere" that preceded our familiar biosphere. A genetic continuum from the primeval days of the RNA world to present-day cells and viruses is postulated, such that, expressly, viral genes continuously retain their identity throughout the entire history of life. Koonin and Forterre posit that virus evolution and cell evolution are inextricably linked, yet their scenarios of virus origin are founded upon different models of evolution of cells. However, their differing opinions regarding evolution of cells concerns us here only to a limited extent since we are mainly interested in the very first appearance of viruses upon Earth rather than their continued evolution. Both scientists place this event even before the formation of the Last Universal Common Ancestor (LUCA).[20] For that reason, their account does not refer to any specific ancestor of modern cells. Since the origin schemas offered by them are rather intricate, we focus on three central aspects only: The primeval entity that is presumed to be the archaic virus; the evolutionary stage in which it supposedly first appeared; and their choice of virus origin hypothesis.

Koonin proposes that viruses originated twice during the evolution of life. First, in the precellular RNA world, RNA viruses and some DNA viruses arose; these continued to evolve up to the point when bacterial and archeael cells emerged and their viruses arrived (see Fig. 1). Eukaryotic viruses came after the appearance of eukaryotic cells (that some evolutionists consider to be the result of a fusion between a bacterial cell and an archaeal cell; see Fig. 2).[21] Notwithstanding these multiple stages of virus evolution, a genetic continuum is presumed such that present day viruses are the descendents of the primordial ones.

Koonin is concerned with the deepest roots of viruses represented by hallmark genes. His scenario of virus origin presupposes a model of the emergence of cells and genomes within networks of inorganic compartments. He explicitly embraces the "viruses as vestiges of an ancient precellular world" hypothesis, that is, "the principal lineages of viruses and related agents emerged from the primordial pool of primitive genetic elements, the ancestors of both cellular and viral genes." (Koonin et al. 2006: in "Results"). In this primordial genetic pool extensive "mixing and matching" of genetic elements was possible, hence the similarity found today between viral genomes belonging to diverse groups of viruses. As can be seen in Fig. 1, the first viruses to emerge were RNA selfish agents, that is, RNA molecules with some catalytic capability, predicated on today's ribozymes. In the second stage of life evolution, that is in the RNA–protein world, RNA viruses that contain an RNA genome and a protein coat appeared. Origin-of-life theories postulate that this was followed by a transition from an RNA to a DNA world. In this RNA/DNA/protein age, Koonin surmises, genetic elements that replicate via a DNA intermediate were spawned and several lineages of DNA viruses emerged.

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[20] The idea of Last Universal Common Ancestor (LUCA) presumes a single cell from which all life has evolved.

[21] Koonin et al. (2006). This is an open access article, which allows unrestricted use, distribution and reproduction in any medium, provided the original work is properly cited. Page numbers of the online version are not for citation purposes. Therefore, I note section titles when possible.

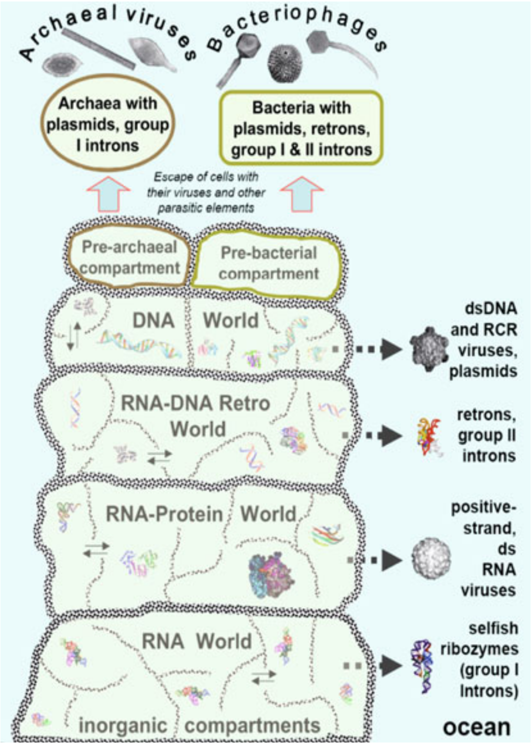

Fig. 1 Evolution of the virus world: Origin of the main lineages from the primordial gene pool (This figure is taken from Koonin et al. 2006.)

In sum, Koonin's idea of archaic virus origin is strictly an "RNA virus first" model. As to the two other virus origin hypotheses, he states that "the existence of hallmark virus genes seems to effectively falsify both the cell degeneration and the escaped genes concepts of viral origin." The "virus first" model being more plausible than the other two (the "degenerative" or the "escape"), since an ad-hoc non-parsimonious scenario "such as a concerted loss of hallmark genes from all known cellular life forms or their derivation from an extinct major lineage of cell evolution,"[22] would have to be assumed in order to explain their absence from present day cells. Regarding eukaryotic viruses, their emergence is described along the lines suggested by Temin's hypotheses i.e. that later viruses could indeed have escaped from modern cells.

Forterre's RNA virus origin scenario is also set in the primordial RNA, but in the RNA–protein stage (2006). Unlike Koonin's virus-like entities, the former's ancestral RNA viruses are protein-coated genetic elements and not merely ribozymes-like RNA molecules. Forterre argues that protein-synthesizing ribozymes could not have evolved in a "primitive soup" occupying mineral compartments: "…it appears unlikely that a world of free molecules could have evolved to such an extent to produce a ribozyme capable to synthesize proteins (the ancestor of present-day ribosomes)" (Forterre, p. 8). For this evolution to occur, membrane-bound primitive cells with simple metabolic capabilities for the synthesis of RNA and lipid precursors and a simple mechanism for energy supply had to exist. Forterre claims that it is difficult to imagine the emergence of such mechanisms of metabolism without Darwinian selection, and this requires competition between

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[22] Koonin et al. (2006), in section "Conflicting concepts."

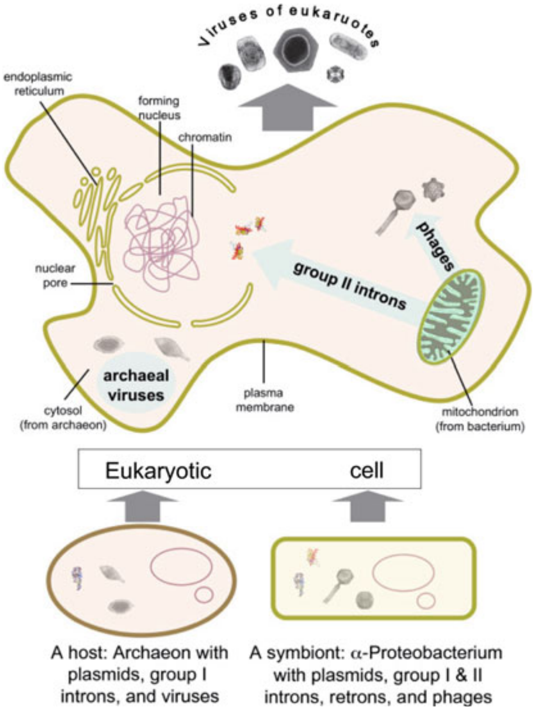

Fig. 2 The second melting pot of virus evolution: origin of eukaryotic viruses (This figure is taken from Koonin et al. (2006), who observe: “The emergence of the eukaryotic cell is construed as the second melting pot of virus evolution from which the major groups of eukaryotic viruses originated as a result of extensive recombination of genes from various bacteriophages, archaeal viruses, plasmids, and the evolving eukaryotic genomes.”)

well-defined individual entities, at least proto-cells. He states: “Since modern viruses contain proteins, they should have originated after the emergence of the ancestral ribosome, i.e. well after the apparition of primitive RNA-cells (in the second age of the RNA world)” (Forterre, p. 8). This theoretical consideration is further supported by the existence of homologous proteins functioning at the membrane level that are encoded by all sequenced genomes from all domains of life. This strongly suggests that these proteins (and hence a membrane) were already present in the Last Universal Cellular Ancestor (LUCA). Evidently he rejects a *virus first* theory, leaving him to consider the other two traditional hypotheses: “either the first RNA viruses originated from RNA cells by regressive evolution (a new version of the reduction theory), or from RNA fragments that escaped from cells (a new version of the escape theory)” (Forterre, p. 8).

Forterre’s escape hypothesis appears to contain an element of surprise, because his “escaped elements” are RNA molecules escaping from RNA cells. But is this really surprising? Not if we recall that evolutionary virologists now set their origin hypotheses in a prebiotic RNA world. Forterre argues that a pre-LUCA scenario of virus origin is easier to defend since no specific relationship between proteins encoded by viruses and those encoded by their hosts is to be expected, as indeed is the case. Additionally, since the molecular mechanisms operating in these ancient RNA cells were probably simpler and less integrated than those found in DNA cells, it may have been “easier” for “escaped” elements to become autonomous. But a “reduction” hypothesis is also quite plausible, according to Forterre. In a world of RNA cells it may have been quite simple for an RNA cell to become an RNA virus, again because these cells were much simpler than modern ones. Just as some bacterial cells could have become parasitic so could a small RNA cell become parasitic, living as an endosymbiont within a larger RNA cell, losing its translation apparatus while retaining its replicative autonomy and gaining the ability to infect other cells.

To conclude, virus origin hypotheses of the past were informed but also constrained by the then current knowledge available from genetic and biochemical studies of viruses and cells. Scientists, in mid-twentieth century, presumed that what they learnt about the way *modern* cells and viruses behave can be applied to prebiotic scenarios, though this back extrapolation was, as we have seen, problematic. Today, virologists believe that the results of computerized analysis of protein and polynucleotide sequences of cells and their viruses calls for the rethinking of the origin hypotheses. However, the mass of genomic data currently available to researchers is open to wide interpretation warranting the construction of distinct evolutionary scenarios. Indeed, the two scenarios presented above are instructed by the virologists' primary metaphysical decision pertaining to the choice of the archaic RNA virus-entity which effectively delimits the time of the event and largely determines the plausibility of the origin hypotheses.

9 Afterthought: "Revisiting" Virus Origin Hypotheses

What do we understand by "revisiting"? Very often in the history of science, we encounter a move to re-examine a certain episode in the light of new information and/or from a novel perspective.[23] In this sense, one can say that "revisiting" is used metaphorically, announcing an attempt to reconstruct past events over again. But, in the broadest sense, what can we say about contemporary scientists "revisiting" older hypotheses? Is this merely a rhetorical device or does it serve another purpose? We have seen that in twenty first-century accounts, the essential relationship between viruses and cells is preserved; nevertheless, the specific content of the hypotheses differs significantly. For example, cells can now be either mineral compartments or membranous, organic vesicles containing an RNA genome. Both of these notions of a cell are a far cry from the customary conception. So, in what sense can past and current hypotheses of virus origin be compared?

If we take the notions of "retrograde evolution," "escape" and "primordial self-replicating molecules" to designate general schemas expressing an evolutionary relationship between a virus and a host cell, then once specific scientific details are supplied, these frames gain their particular meanings, and a comparison becomes possible. Forterre's choice of an "escape" hypothesis brings to mind the 1960s and 1970s "escape" theories which proposed that viruses were genetic elements, first a part of a cellular DNA genome, later becoming autonomous. But, as we have seen, Forterre is speaking of "escaped" genetic elements and host cells that now consist of RNA. Hence, the general idea of "escape" can still be employed though the implications of his primordial RNA origin hypothesis for future research differ considerably from those of four decades ago. Koonin's virus origin hypothesis may present us with a different case, but perhaps only in rough measure. His "virus first" model is reminiscent of Haldane's early hypothesis: Both speak of a spontaneously formed prebiotic, self-replicating macromolecule that later becomes part of a more complex life form. Since, in Haldane's case, the molecule is not defined chemically, it may be relatively easy, in the context of the RNA world, to accept an additional characterization of it, now presumably consisting of RNA. Thus, I argue,

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[23] A basic search in JSTOR brought up the following: "Results 1–25 of 5517 for <<revisit>>". JSTOR search conducted 10 October 2009.

revisiting the traditional hypotheses is certainly feasible, and this brings us to the question of what purpose does "revisiting" serve here?

Clearly evolutionary virologists are attempting to implement a new epistemology and methodology within an existing field-virus research. The use of high throughput genomics for constructing origin hypotheses may need some convincing of the active virologists. Hence, by relating to older, familiar hypotheses, a conceptual continuity can be constructed, and "revisiting" may indeed be seen as a rhetorical device. However, evolutionary virologists may be also trying to strengthen their position within origin-of-life theorizing. The genomic information obtained by virologists could, in fact, be directly fed into the origin-of-life theories, without the mediation of another field, virology. Thus, in order to reserve the viruses a unique place within origin-of-life theories, the conceptual autonomy and historicity of origin of virus hypothesizing is emphasized.[24] Apparently evolutionary virologists are working to persuade origin-of-life theorists, once again, to bestow viruses a role in the origin and evolution of life.

Not only are origin-of-life theorists being approached by virologists, the same applies to evolutionary biologists. Although viruses are not "alive" in any ordinary sense, many virologists believe that the new through-put genomic and proteomic information warrants the attention of evolutionary biologists, who are called upon to incorporate viruses into their theoretical framework (Villarreal 2004; Morse 1994). Morse, in *Towards an Evolutionary Biology of Viruses* lamented the separate paths that evolutionary biologists and virologists had taken. His book was an appeal for scientists in both fields to join forces. A special chapter was Mayr's own reworking of his seminal paper "Driving Forces in Evolution." This revised version offered a somewhat novel theoretical framework for viral evolution which Morse hoped would be further developed so that viruses could be accommodated within the "evolutionary synthesis" (Morse 1994). Indeed, today, some theories of evolution of cells do accord viruses and their enzymes a significant role in the process of cell evolution and also in major transitions in the evolution of life (Forterre 2006; Goldenfeld and Woese 2007).[25] Hence revisiting virus origin hypotheses could convince biologists that viruses have always been vital members of the web of life, and that as such are worthy of being studied by evolutionary biologists just as other members of life's community are studied. As a result, perhaps in the near future further examination of the relationship between virology and evolutionary theory will become an imperative.

Nigel Goldenfeld and Carl Woese (2007) in "Biology's Next Revolution" argue that the mass of computerized data related to microbes and viruses now available to evolutionary biologists calls for a revolution in biological thought:

> The new window on the Universe opened up by satellite-based astronomy has in the last decade overthrown our most cherished notions of Cosmology, especially related to the size, dynamics and composition of the Universe. Similarly, the convergence of new theoretical ideas in evolution together with the coming avalanche of environmental genomic data, especially from marine microbes and viruses, will fundamentally alter our understanding of the global biosphere, and is likely to cause a revision of such basic and widely-held notions as species, organism and evolution."

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[24] For example, in Fry's extensive study of theories of origin of life (2000), the idea that viruses may have taken part in origin-of-life processes is barely mentioned, and the term "virus" does not even appear in the index.

[25] Goldenfeld and Woese write: "Equally exciting is the growing realization that the virosphere plays an absolutely fundamental role in the biosphere on both immediate and long term evolutionary senses" (Goldenfeld and Woese 2007).

The conceptualization of a virus and speculations on its origin is an excellent example for demonstrating the intricate relationship of scientific technique, methodology and theory-making in the twentieth century. Nevertheless, this is clearly a case in which even a significant growth of scientific knowledge and advances in research practice and technology may not necessarily bring us any closer to understanding events that occurred almost 4 billion years ago. Here, biologists may be in good company with physicists attempting to solve the mystery of the birth of our entire universe, not just our living one.

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ARTICLE

Raphael Meldola and the Nineteenth-Century Neo-Darwinians

Anthony S. Travis

Abstract Raphael Meldola (1849–1915), an industrial chemist and keen naturalist, under the influence of Darwin, brought new German studies on evolution by natural selection that appeared in the 1870s to the attention of the British scientific community. Meldola's special interest was in mimicry among butterflies; through this he became a prominent neo-Darwinian. His wide-ranging achievements in science led to appointments as president of important professional scientific societies, and of a local club of like-minded amateurs, particularly field naturalists. This is an account of Meldola's early scientific connections and studies related to entomology and natural selection, his contributions to the study of mimicry, and his promotion in the mid-1890s of a more theory driven approach among entomologists.

Keywords Entomology · Hypothesis · Mimicry · Natural selection · Darwin · Meldola · Müller · Poulton

1 Introduction

Charles Darwin's *The Origin of Species* (1859) dealt with adaptation, or evolutionary change, of organisms through natural selection. According to Darwin, the selection process favoured the fittest individuals in a population. In many cases survival was seen to be as much a function of morphological features, such as colour, form and patterns, as it was of physiological and behavioural features. Observations on the morphology of butterflies and moths in their natural environments led to some of the strongest early evidence for natural selection. Thus adult butterflies resorted to camouflage, adopting the colour of background foliage, to imitation of objects in their environments (crypsis), or to mimicry by copying the colour or patterns of a creature, the model, that was unpalatable to birds. In the latter form of mimicry, it was believed, the colour acted as a warning signal, that is, it was

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aposematic; mimicry explained how butterflies, moths and other insects evaded predators, and in particular, what made certain butterflies so repulsive to birds.

It was in the 1860s and 1870s that independent observations on mimicry in butterflies were first used to demonstrate how natural selection works in real time. Though there were many critics, including those who did not believe arguments based on the unpalatability of butterflies, it was the elegance and simplicity of the concepts that eventually led to the widespread acceptance of what became known as Batesian and Müllerian mimicry. Moreover, it appeared that toxic protective substances taken up by insects, particularly larvae, from plants were of great significance, though there was no suitable way of undertaking isolation and chemical identification of these substances.

Fortunately, the poverty of side issues worked in favour of the early explanation of natural selection based on mimicry. Nevertheless the critics were in part correct, even if they did not have access to facts that would have enabled them to argue more persuasively. There were, for example, situations in which mimicry seemed to break down altogether. Some believed that insect morphology was a function of the total environment, and not of the interaction between creatures. Interest in morphology and warning coloration declined after new theories of evolution appeared from around 1900. The defenders of "hard" inheritance, the neo-Darwinians—favouring the almost exclusive role of natural selection—who placed so much emphasis on mimicry, struggled in the face of the new explanatory challenges of evolution.

In the second half of the twentieth century, with the emergence of various branches of ecology, there was a revival of interest in mimicry, particularly through the work of the English entomologist Miriam Rothschild and colleagues. Rothschild suggested that perhaps the acute discrimination of the eye of the avian predator was responsible for mimicry, or at least dictated the morphology of both the model and its seeming mimic, and also that the relationship between an insect and toxic plant substances that it sequestered was mutually beneficial. She also drew attention to the fact that there was a delay of a century "between the brilliant and intuitive generalizations put forward by Bates (1862), Müller (1878, 1879a) and Wallace (1889) and the laboratory experiments which proved that certain aposematic insects—the models—sequester and store toxins derived from their food-plants" (Rothschild 1972a, p. 70). Moreover, since early in the twenty-first century the field has attracted both ecologists and practitioners in evolutionary genetics.

The main theme of this paper concerns how a particularly striking aspect of morphological variation, a foundation of evolutionary change based on natural selection, came to be promoted and applied in the nineteenth century. It will also draw out the important distinction between Darwinism and neo-Darwinism. Key protagonists are from the worlds of natural history, entomology and biology, with an emphasis on an English chemist with a passion for field naturalism and entomology. This was Raphael Meldola (1849–1915), who in the late 1870s, under the influence of Darwin, brought to the attention of the British scientific community the novel studies on natural selection by the German systematists August Weismann and Fritz Müller. Thus it was Meldola who communicated Müller's 1878 findings and 1879 paper (the latter translated by Jenner Weir and Henry Bates) to the Entomological Society of London. No less significant is the fact that it was Meldola who in 1883 stimulated Edward Bagnall Poulton's interest in mimicry and natural selection. Both contributed to the story of nineteenth-century neo- or ultra-Darwinism, that emerged during the 1880s and came under attack at the turn of the century.

Raphael Meldola made a number of remarkably prescient observations, particularly in 1882, when he discussed the relationship between avian predators and the warning coloration of butterflies that so impressed Rothschild 90 years later; he expanded on how coloration protected a highly conspicuous, slow moving butterfly from being devoured by a bird of prey. Meldola also engaged in the debate over mimicry and sexual selection, though for him the principle purpose of colour and pattern was for defense rather than attraction.

The next section reviews the way in which Meldola's early inspiration derived from some of the great Victorian naturalist-adventurers. This provides a brief introduction to the select network of naturalists, amateur and semi-professional, and their clubs, societies and publications, during the 1860s and early 1870s. The account then moves onto the convergence of interests of adventurers, field naturalists, and entomologists through natural selection based mainly on Lepidoptera; Meldola's connection with the two prominent Germans; his own contributions to mimicry; the decline of late nineteenth-century neo-Darwinism; and, drawing on Meldola's interest in mimicry, and his career as a professional chemist, reflections on the "the scientific use of imagination."

2 Raphael Meldola

For five years, 1869–1874, the young entomologist and chemist Raphael Meldola kept an entomological diary "which held the records of first years of collecting at Leyton [Essex, northeast of London] and elsewhere." Meldola was particularly fascinated with the magnificent variety of patterns, colours and shapes of Lepidoptera (the order of insects, the butterflies and moths, having four membranous wings, covered with scales). He quickly picked up the Linnaean naming of species, and, probably by the end of 1870, had read *The Origin of Species*. These years were, he later recorded, "five happy years of my life!" (Poulton 1916, pp. 83–84) During that time he made contact with numerous amateur and professional field naturalists, and embarked on the serious study of mimicry, an interest that he would maintain throughout his life. The "old entomological diary" is now long lost, as are most of Meldola's notebooks. Fortunately Meldola's surviving correspondence and his many publications enable a reconstruction of his engagement with mimicry while still a youth, and how it brought him to the forefront of the debates concerning natural selection.

Raphael Meldola was born in London in 1849, and named after his grandfather, a leader (Hakham) of London's Jewish Sephardic community. From late childhood until 1886, when he married, Meldola lived in John Street, Bedford Row (just off Theobolds Road), London.[1] He attended three Jewish private schools, the first a primary school at Bristol, then at Kew (Gloucester House, from age seven until about fourteen; the modern location is Richmond), and finally at Maida Vale, London (Northwick College). At Kew and after he was known for his interest in nature and science and his complete lack of interest in sports (Marchant 1916, pp. 12–13, 14–15).

The year 1859 was notable for two major events, one in science, the other in technology, that would come to influence Meldola's entire scientific career. One was the publication by John Murray in November of Charles Darwin's *On the Origin of Species by Means of Natural Selection, or The Preservation of Favoured Races in the Struggle for Life*. The

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[1] Hannah Gay, personal communication to author, 22 August 2008. I thank Hannah Gay for kindly sharing her research on Meldola's early years. For the Meldola papers see McEwan (2003/2004). The bulk of Meldola's papers were left to the Essex Field Club, and in the 1990s, after the closure of the Passmore Edwards Museum, were stored in a warehouse in east London. Through the efforts of Hannah Gay, they were moved to Imperial College Archives for more suitable preservation. For correspondence between Meldola and Darwin, see http://www.lib.cam.ac.uk/Departments/Darwin/; and "The Darwin Correspondence Online Database," http://darwin.lib.cam.ac.uk. Some 75 letters between Darwin and Meldola are listed in Burkhardt (1994).

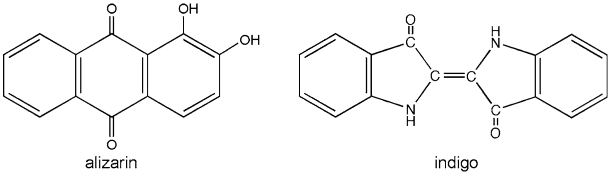

Fig. 1 Kekulé's benzene ring theory (1865) was the single most important development in nineteenth-century organic chemistry. It enabled the structural elucidation of the industrially important dyes and natural products alizarin, by Adolf Baeyer and Heinrich Caro (1874), and indigo, by Baeyer (1883). Raphael Meldola's own engagement with the dye industry began in 1871 and, after a break, ended in 1885. During this time the German dye industry achieved supremacy, much to the concern of Meldola, as described in decidedly social Darwinist terms in his May 1886 presentation to the Society of Arts in London

second event followed from the popularity of a novel purple textile dye made from coal-tar aniline. It had been discovered in 1856 by the teenaged William Henry Perkin, and was the colour of fashion on the streets of London from early in 1859. The English called it mauve. Late in 1859 the commercial route to an aniline red was established by two chemists working independently, also in London. This set off a major research effort that resulted in the emergence of the first-science based industry, the synthetic or aniline dyestuff industry (Travis 1993). It stimulated major developments in theories that were used to understand processes, determine chemical structures, and successfully predict outcomes of reactions. In the late 1860s, Meldola would become aware of the industry's massive growth in Europe while a student, from 1866, in the chemistry department at London's Royal School of Mines, successor to the Royal College of Chemistry, directed by Edward Frankland.

Most critical to the endeavour of academic and industrial chemistry was the application of Kekulé's 1865 benzene ring theory in around 1870, a triumph of chemical philosophy, to the elucidation of the partial structure of alizarin, an important red dye that was also the first natural product of some complexity to be replicated on the laboratory bench. The benzene ring was a model of how the six carbon atoms and six hydrogen atoms in this simplest of aromatic molecules were arranged. With attached groupings of atoms known as side chains, or functional groups, the benzene ring provided the imagery for predicting reaction pathways (and outcomes) based on appropriate chemical modifications that drove the field of aromatic chemistry. Like Darwin's mechanism of natural selection that explained biological evolution, the benzene ring, which afforded a generalized, predictive mechanism, was an example of the use of hypothesis and imagery that came to dominate developments in science during the second half of the nineteenth century (Rocke 2010). As a unifying theory, whose predictive and heuristic applications were immediately applicable, in both science and industry, it was in many ways far more readily accepted than Darwin's theory.

Moreover, the benzene ring conception was singularly relevant as a guide for both academic and industrial chemistry from the time that Meldola joined the synthetic dye industry in 1871 and left it in 1885 to become professor of chemistry at London's Finsbury Technical College.[2] During those years the modern structures (showing the location of each atom in the molecule) of the dyes alizarin and indigo were established (in 1874 and 1883, respectively; Fig. 1) (Reinhardt and Travis 2000).

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[2] During 1868–1871, Meldola was an assistant of John Stenhouse at the Royal Mint, and began to act as chemical adviser to W. & E. H. Stead, seed crushers and oil refiners of Liverpool.

It was through Meldola's parallel interests in two branches of scientific endeavour, chemistry and entomology, particularly his wide knowledge of chemistry, that he would in the 1890s promote the role of the "speculative" or "philosophic faculty" guided by field observations on living organisms, rather than by collecting alone, in the discovery of new mechanisms and theories in the biological sciences. This was the driving force of science, and for Meldola it began with entomology.

In the mid-1860s, as a curious teenager, Raphael Meldola embarked on entomological excursions in Epping Forest, northeast of London, including Leyton, in the county of Essex. Around 1868–1869, this brought him life-long friendships and introduced him to the serious study of the small creatures of nature, particularly Lepidoptera, and soon after, natural selection. Meldola's first exchanges with Charles Darwin date from early 1871, around the time that Darwin began to correspond with the German-born field naturalist Fritz Müller on mimicry.

A particularly close friend of Meldola from shortly after the death of Darwin in 1882 was evolutionary biologist Edward Bagnall Poulton (1856–1943), from 1893 on Hope Professor of Invertebrate Zoology at Oxford. Poulton, originally trained in geology, met Meldola in 1883, and published his first entomological paper on the colours and protective attitudes of caterpillars in 1884. In 1886, Meldola introduced Poulton to Alfred Russel Wallace. In 1890, Poulton published *The Colours of Animals: Their Meaning and Use, Especially Considered in the Case of Insects* (Poulton 1890). This thorough study based on entomological observations was in part aided by Poulton's access to the Hope Entomological Collection at Oxford (that Poulton would use from around 1900 to argue for natural selection). In the preface, Poulton thanked the man who had contributed most to his embarking on the study of insect coloration and mimicry: "I owe to Professor Meldola more than I can possibly express: his writings first induced me to enter upon this line of investigation, and I have had the benefit of his great experience and wise advice during the whole of the time that I have been at work" (Poulton 1890, p. xi).[3]

3 Early Influences on Meldola

Meldola's "first natural history friend" was John Keast Lord, one of the several Victorian Englishmen that independently, and adopting the spirit of enquiry regardless of means, made journeys to the Americas and elsewhere, as naturalists, hunters, and explorers. Motivated by adventure, and sustained by funding from sales of specimens to collectors and museums (that also sometimes left good profits), they, and many of those obsessed with gathering insects and butterflies, were at first hardly recognized as scientists (Clark 2009). While Lord was a minor player, at least compared with Henry Walter Bates and Alfred Russel Wallace, his story is far less well known, which calls for a short account, and a better understanding of the influences on Meldola's early interest in entomology.

Lord, born around 1817, and trained in medicine and veterinary science, was in the early 1850s in British North America, engaged by the Hudson's Bay Company as an independent trapper, and moved to the eastern side of the Rockies (in what was later Alberta). During the Crimean War (1854–1856), he served as horse veterinarian with Turkish forces.

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[3] There survives an undated note in the Wallace papers at the British Library which shows that Poulton had intended to dedicate his 1896 book to Meldola, "whose earlier writings under the inspiring influence of Charles Darwin & Alfred Russel Wallace were the foundation of a friendship and a life-work."

Subsequently he became naturalist and transport manager to the British North America Boundary Commission (1858–1862) in the newly created British Columbia (Buckland 1872; Baker 2002).

After his return to England in 1863, Lord became a close friend of Francis (Frank) Trevelyan Buckland, a populariser of natural history. Buckland introduced Lord to John Crockford, editor of the *Field*, which led to a writing post with that journal until 1865. From 1866, Lord was involved with Buckland's new journal *Land and Water*. It was probably in 1867 that Lord first met Meldola, at the Royal School of Mines, then in Jermyn Street, London, and inculcated a love of the scientific study of nature in the young student of chemistry.

The escapades and achievements of Lord captured Meldola's imagination, and turned Lord into an influential role model. Tellingly, perhaps, Lord's letters began with the familiar "My Dear Raphael." Indeed there is also the possibility that Lord, if not a father figure for Meldola, was at least a willing protégé, since Meldola's own father was unable to contribute greatly to his son's upbringing due to the collapse of his printing business (Gay 2010).[4]

Lord was in Egypt during 1868–1869, and subsequently appointed manager of the Brighton Aquarium, then under construction. The aquarium, even at this stage, served as a research station providing opportunities for extensive observations on the life histories of aquatic organisms, the details of which were shared with Meldola (1870–1872). Lord, however, was suffering from poor health; "Dear old Lord" died on 9 December 1872. It was after Meldola's own death in 1915 that Poulton came across his personal copy of Lord's 1867 book, *At Home in the Wilderness*, in which Meldola had penned the following: "This book was written by my first natural history friend—my ideal of manliness—my first subject of hero-worship as a youth. His death in 1872 was the first real grief I ever experienced. I was with him at Brighton almost to the end—Raphael Meldola" (Poulton 1916, p. 83).

Epping Forest was Meldola's early hunting ground for the simple reason that he often spent time at the house of an aunt who lived nearby, at Leyton, perhaps to get away from the heavily polluted and unhealthy atmosphere of central London (he often suffered from bouts of poor health), or as a result of his father's illness. He participated throughout his life in the Victorian obsession with insect hunting, in his case collecting butterflies and moths, and mounting them for display in special cabinets. However, unlike most other collectors, whose interests lay solely in the cabinet and wall displays, he also had an interest in observing butterflies flutter from one plant to another, in broad daylight, as if careless of the presence of predators, and went out at night with a lamp to observe the nocturnal activities of the forest's moth population (Travis 2009).

4 Natural History Clubs

It was in Epping Forest that Meldola spent time with his "*first* entomological friend," William John Argent of Wanstead, Essex, through whom he came to know the enthusiastic

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[4] I thank Hannah Gay for information gleaned from correspondence between Poulton and Meldola held with the papers of Sir Edward Bagnall Poulton, Bodleian Library, University of Oxford.

naturalist William Cole and his brothers, of Buckhurst Hill, Essex (Poulton 1916, p. 84). Cole later reminisced that: “Argent and Meldola had become acquainted at one of the naturalists’ reunions or ‘evenings’ held by the late Edward Newman, editor of the *Zoologist*, and custodian of the Entomological Club’s collection of insects [at Deptford]. We were all enthusiastic collectors, and this fact at once created and cemented a bond of union in our little coterie. I and my brothers soon became most friendly with Meldola, being attracted by his kindly attitude and buoyant spirits and his love for our favourite amusement…. Our assemblies [from around 1870] at the Entomological Society [of London] and in his little study at his father’s house in John Street …were much valued by us all” (Cole 1916, pp. 119–120).

Later, Meldola’s wide ranging achievements in science, particularly chemistry and entomology, and his energies and organizational skills, led to appointments as president of scientific societies. The first was his presidency of that quintessentially English institution, the local club of amateur field naturalists, from 1880–1883, in this case the Essex Field Club, co-founded by Meldola, Argent and the Cole brothers early in 1880. At Meldola’s instigation Darwin and Alfred R. Wallace were appointed honorary members. Safeguards for wildlife sites were uppermost in the minds of members of the club. Epping Forest was frequently on the agenda at meetings, with the emphasis on preservation of its wildlife and retention of the natural features. The natural history club, with its links to personages of various distinctions, increasingly fostered a strong sense of civic pride and involvement among its generally public-spirited members, including both amateur and professional scientists. The club defined a specific community and its local scientific endeavours, and offered a useful low level of professional affiliation (Allen 1994 [1976]; Finnegan 2009; Salmon et al. 2001).

It is not without interest to observe that it was before a natural history club comprised of like-minded enthusiasts that in 1865 Gregor Johann Mendel lectured on, and then published in the club’s journal, experimental details of a discovery that later contributed to the basic laws of genetics. Unfortunately for Mendel the club was in Moravia (central Czechoslovakia); the first English rendition of his findings appeared some years later in the journal of a leading British horticultural society (though Mendel visited London in the 1860s he made no contact with Darwin; see Deichmann this issue).

Raphael Meldola was also involved in the Entomological Society of London from around 1870. The successive presidents at that time were two men who would soon share with Meldola their own interests in mimetics and natural selection: Henry Walter Bates (president, 1868–1869), followed by Alfred R. Wallace (1870–1871).

5 Bates, Wallace and Trimen

Bates (1862) and Wallace (1865) were the first to publish on mimicry in butterflies. Bates, while in the Amazon Valley, observed that many species of butterfly mimic other species, even if unrelated. The main feature of Batesian mimicry was the fact that edible butterflies mimicked unedible butterflies and thereby developed a defence mechanism against avian predators. Mimicry, as a form of adaptation, was used by Bates as early evidence in support of natural selection. In 1866, Wallace suggested to Darwin that some creatures were brightly coloured not for reasons of sexual attraction, since they did not participate in sexual activity, but to ward off predators. Bates and Wallace were followed by Roland Trimen (1840–1916), based in Cape Town (Trimen 1869). During 1862–1866, Trimen catalogued the South African butterflies; he made occasional trips to England, including in

1868 when he addressed the Linnean Society. A correspondent of Meldola, he also had to struggle in the cause of naturalism (Cohen 2002).[5]

Bates, Wallace and Trimen, whether romantics, adventurers or opportunists, or all three, as was Lord, were opening up a new scientific endeavour in natural history in which novel ideas were based on observations of living organisms in the field. Meldola was embarking on a hot topic, and a serious avocation. Edward Newman, Quaker, entomologist, botanist, and founding member of both the Entomological Club (1826) and the Entomological Society of London (1833), may also have influenced Meldola through his own interest in moths and butterflies. In 1869, Newman published the *Illustrated Natural History of British Moths* and in 1871 the *Illustrated Natural History of British Butterflies*. Newman, incidentally, was not an enthusiast for evolutionary theories.

Undoubtedly it was Lord who, recognizing Meldola's "strong bent towards natural history," encouraged his first publications, short notes of his observations in Epping Forest, that appeared in the *Entomologist* (Meldola 1868–1869a). While mimicry was not tackled before 1871, right from the start Meldola was observing moths and butterflies. In his note on "Noctuas on Stinging Nettles," Meldola explained how the leaves of stinging nettles attracted moths. "I have searched the nettles in our neighbourhood with a lantern on every mild evening … I believe I have been fortunate to discover the attraction … the sticky substance known as 'honey-dew'" that had fallen on the leaves (Meldola 1868–1869b). Lord, and, probably also Buckland, encouraged Meldola to submit a series of notes to *Land and Water* during 1870–1871.[6]

6 Darwin, Mimicry, *Nature*

By the beginning of 1871, perhaps through an introduction from Buckland, Meldola had made contact with Charles Darwin, who was to offer valuable advice on how to study natural selection. On 28 January 1871, Darwin thanked Meldola for information on a case of hexadactyl, that is, individuals born with six digits on hands and feet. However, Darwin remarked, "I do not think, except under very special circumstances, it would be worth your while further to investigate it" (Poulton 1896, p. 200). The influence of Darwin was quick to become apparent. In "Are Monkeys Quadrumanous?," published in *Land and Water* on 4 February 1871, Meldola took issue, "[A]s a Darwinian" with a correspondent, a certain "J. H." a supporter of Lamarck, who suggested that "natural selection is a myth." It was the first occasion on which Meldola declared his allegiance to Darwinism. Meldola opined: "Natural selection acts only and solely for the good of the being" (Meldola 1871a, p. 91).

In March 1871, Meldola first published on "Mimicry in the Insect World," again in *Land and Water* (Meldola 1871b). Two further contributions to this journal with the same title appeared in May 1871. In the first, published on May 6, he observed "The subject of mimicry is divisible into two distinct portions: (1) resemblance to some inanimate object or part of vegetable, and (2) resemblance to another species. The former of these divisions … is better known as 'protective resemblance.' The second phase is designated as true 'mimicry.'… Many orders in the animal kingdom present us with cases of mimicry, but it

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[5] While Carl Linnaeus divided the order Lepidoptera into three genera, *Papilio*, butterflies, *Sphinx*, hawkmoths, and *Phalaena*, all other moths, Trimen preferred another classification, based on just two groups, *Rhopalocera*, butterflies, and *Heterocera*, moths. See also Salmon et al. (2001), which includes a useful summary of the role of field clubs and entomological societies.

[6] For Buckland, see Burgess (1967).

is the Lepidoptera that exhibit it in the most striking manner, and with this order we will therefore first occupy ourselves…. The tribes mimicked are always very abundant, brightly coloured, and of conspicuous habits, so that they are evidently 'favoured races.' Indeed, in the case of the South American family, *Heliconidae*, the cause of their rejectment has been traced to a disagreeable odour diffused through the tissues of the body. The mimicking species, on the other hand, are comparatively rare, and always occur in company with their models, which they frequently imitate, even in flight." This was an interesting early suggestion of mimicry, and protection, related to olfactory senses rather than coloration.

Meldola gave various other examples of mimicry based on the work of Bates, Wallace, and naturalist Jenner Weir, who in 1869 had advised Wallace that birds kept in an aviary did not eat a certain common and highly visible white moth, as well as drawing attention to the observations of Trimen. From their studies, Meldola opined, the "wonderful facts which have just been adduced are perfectly intelligible on Darwin's theory of the 'survival of the fittest.' … it is quite possible to conceive the manner in which these resemblances could have been brought about by the accumulative action of 'natural selection' always tending to preserve those varieties which resembled in any way the 'favoured races.'" In other words, edible insects were protected from predators by resembling (as Bates had shown) through mimicry others that were inedible or unattractive to predators.

Meldola, in his second contribution on May 27, responded to the criticisms of "A Constant Reader" who suggested that mimicry was "a voluntary imitation on the part of the insects." While not altogether rejecting the role of chance, Meldola rejected "mere accidents, or 'freaks of nature' … others will see in them cases of *'design'* by the Author of the universe for the protection of species. Neither of these views do I hold, for I think the theory of 'natural selection' quite competent to satisfactorily explain all the facts collected in this article" (Meldola 1871c, pp. 321–322).

On June 7, Meldola wrote to Darwin on the origin and advantages of sexual differentiation in terms of division of labour. Two days later a main topic was the origin of the giraffe's neck (Poulton 1896, p. 200). Darwin was then in his early 60s and, as a result of improved health, passing through an extremely productive period. Drawing on ideas that had occupied his mind for many years, he had published not long before *The Variation of Animals and Plants under Domestication* (1868). It was notable for inclusion of pangenesis (heredity attributes from "germs" or gemmules derived from cells in every part of the organism). Darwin also included a discussion of variations in individuals, and multiple variations in specific populations. He focussed on the fact that closely related species could be persuaded to interbreed in captivity (unlike in the wild). From this artificial selection he drew support for natural selection. Darwin even adopted inheritance of acquired character[istic]s, or Lamarckism, as a feature of heredity. Moreover, his theory of pangenesis was not unlike a similar theory of Herbert Spencer, who accepted strong contributions from a Lamarckian mechanism in evolution (Taylor 2007; see also Deichmann this issue). Among those who opposed pangenesis was Francis Galton, a cousin of Darwin. Early in 1871, Charles Darwin published *The Descent of Man and Selection in Relation to Sex*, and in 1872 *Expression of Emotions*.

In 1871, Meldola began to publish in the then struggling new journal *Nature*, again no doubt with the encouragement of Lord (MacLeod 1969a, b). The topic was sexual selection. Meldola supported "the suggestion that butterflies whose females are handsomer than the males are those in which the former sex takes the active part in courtship…. Though I am not convinced of the action of sexual selection in producing the colours of insects, it cannot be denied that these facts are strikingly corroborative of Mr Darwin's views" (Meldola 1871d, p. 508). Coloration of Lepidoptera could thus perform one of two functions, sexual selection, as Darwin originally preferred, or, as Meldola preferred, mimicry. This paper in *Nature* was cited by Darwin in the 1874 edition of *The Descent of Man* (Darwin 1874, p. 319). In 1872, Meldola in the *Entomologist's Monthly Magazine* extended the discussion to colour and edibility, based on Wallace's suggestion that related dullness of colour with edibility, and brightness of colour with inedibility, though there was no discussion as to whether or not there were inherent or contingent connections (Meldola 1872, p. 68).

Following his first stint in the synthetic dye industry, during 1871–1873, at Williams, Thomas & Dower, of Brentford, West London, Meldola joined the successor to the Royal School of Mines, the newly opened Normal School of Science, at South Kensington, as an instructor in inorganic chemistry. J. Norman Lockyer, editor of *Nature*, was in charge of the school's solar physics laboratory. In January 1874, Meldola joined Lockyer as assistant and became involved in spectrum analysis (spectroscopy) (Lockyer and Lockyer 1928, p. 73).[7] Meldola, who had already published widely, was soon appointed a sub-editor of *Nature*. The editorial and writing experiences at a time of growth and stability in London-based scientific periodicals, both lay and specialist, and secretarial and presidential posts at learned societies, would prove to be of tremendous help to Meldola when the opportunity arose to disseminate novel scientific ideas, particularly those pertaining to natural selection. Thus at the inaugural meeting of the Essex Field Club in February 1880, Meldola emphasized the importance of publication.[8] At the same time he called upon members to draw inspiration from the great seventeenth-century naturalist and resident of Essex, John Ray, who undertook pioneering work in taxonomy: "who knows but that in the County of Essex there may be another John Ray or some future Darwin waiting only for encouragement and the spirit of emulation to develop faculties which will subsequently establish him in a high position in the world of science. The discovery of such an individual would surely be of far greater importance to science than the discovery of a species new to the British fauna or flora" (Meldola 1880, p. 5).

In 1875, Lockyer invited Meldola to become involved in the Royal Society's 1875 expedition to the Nicobar Islands, east of India, directed by Arthur Schuster. Meldola was well qualified, since not only was he now an expert in spectroscopy but he also had a strong interest in photography. He was placed in charge of a small team whose purpose was to record the total solar eclipse. While the expedition was not a success, due to inclement weather, Meldola managed to record, at least in part, the UV spectrum. Anthropological and entomological investigations carried out during the trip brought about connections with Herbert Spencer, then engaged in a study on descriptive sociology, and in 1877/1878, Henry Bates, whose then recently revived involvement in entomology led to an interest in Meldola's collection of specimens from the Nicobar and Andaman Islands.[9]

In 1876, Meldola was lecturer in science at the Ratcliffe School of the Cooper's Company, in Stepney, East London. In the following year he returned to the dye industry,

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[7] Lockyer received a letter of reference on Meldola, a "capital man for original chemical work," from Edward Frankland, on 23 January 1874. Sir Joseph Norman Lockyer correspondence, Special Collections, University of Exeter Library, MS 110.

[8] Meldola published in *Nature* papers originally presented before the Essex Field Club, in addition to many review articles and letters. His prior experience with various journals was brought to bear on the club's own publication policy, particularly with regard to what from 1886 was known as the *Essex Naturalist*.

[9] Bates was president, for a second time, of the Entomological Society of London in 1878. Charles Owen Waterhouse of the British Museum also expressed interest in Meldola's collection. Waterhouse to Meldola, 29 September 1875, Imperial College Archives (hereafter ICA). Meldola, however, refused to accede to his request for donation of specimens.

this time at the Atlas Works of Brooke, Simpson & Spiller, of Hackney Wick, where he made several discoveries, including the important dye Meldola's blue and a photographic developer. Meldola left the industry when in 1885 an opportunity for an academic post at Finsbury Technical College became available (Travis 2007).

6.1 [A] *Power of Adaptability*

Meldola's investigations as a naturalist continued to focus mainly on mimicry, and in particular on how a butterfly took on the physical characteristics, including colour, of a more hardy (at least unpalatable) species in order to ensure its survival. This was an impressive example of Batesian mimicry—applicable to Darwin's ideas on natural selection—and of developments in a field-based science that would contribute to later concepts in the study of evolution, notably morphological plasticity.

In 1873, in a paper entitled, "On a Certain Class of Cases of Variable Protective Colouring in Insects," Meldola drew attention to "a *power of adaptability* on the part of each individual" (Meldola 1873). He suggested how mimetic power and protective resemblance were based on adaptability through variation, that is, natural selection, though, as Meldola was careful to admit, the mechanism of the process was unknown. Among the examples was the colour of larvae that corresponded to the colour of the plant that it fed on. Meldola would cite this paper several times in presidential addresses and publications over the next quarter century, including support of Poulton's results on lepidopterous larvae, pupae and cocoons ("to a large extent an expansion and experimental confirmation of views to which I gave expression in a paper published in 1873").[10] It was one of Meldola's most significant early contributions to mimicry and natural selection, including protective resemblance, in which "the disguised species simulates some object in the environment." Moreover the study was probably inspired by his late friend, Lord. Thus the colours of insects changed according to the colour of "soil, fish (on bank), as confirmed by Lord at Brighton Aquarium with regards to Pleuronectidae. As for natural selection and colour, colours change according to background, surface, etc." Meldola specified five classes of protective resemblance, of which the fifth class was "Variable protective colouring."

> Here natural selection works, as before, in producing and maintaining a power to change colour, it being immaterial to this agency at what period of the insect's life the change of colour is produced, whether it occurs in individuals born in the district, or in individuals that have roamed into the district in the perfect state and undergone subsequent change (Meldola 1873, p. 161).

After Lord's death in 1872, it was the close contact with Darwin that provided Meldola with an important network of like-minded biologists and field naturalists. Through Darwin and the Entomological Society, Meldola befriended Alfred Wallace in the 1870s. Mimicry and concealment was a common topic. Lord and Wallace were probably responsible for Meldola's great interest in fluctuating variability. Another friend from the 1870s was entomologist Arthur G. Butler, who introduced Meldola to William Lucas Distant, who in turn suggested that Butler further encourage Meldola's interest in entomology.

The correspondence between Meldola and Darwin came to a close shortly before Darwin's death in 1882. Meldola's influence in disseminating widely in the

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[10] See, for example, correspondence under the heading "Lamarckism *versus* Darwinism," *Nature*, *23*, August 1888, 388–389.

English-speaking world the studies of two Germans, experimental biologist August Weismann (1834–1918) and naturalist and zoologist Fritz (Johannes Friedrich) Müller (1821–1897), through his contact with Darwin, were of such significance, and his devotion to Darwin so great, that in 1896 Poulton devoted one chapter of his *Charles Darwin and the Theory of Natural Selection* to the correspondence between Darwin and Meldola. The exchanges, according to Poulton, demonstrated the "unfailing courtesy to a younger worker … who was thereby stimulated and encouraged" (Poulton 1896, p. 199). From the end of the 1880s, Poulton, in company with Meldola and Wallace and others, through what was soon referred to as neo-Darwinism, minimized the possibilities for inheritance of acquired characters in evolutionary processes. These selectionists were influenced by and in alliance with Weismann whose theory of the germ plasm and rejection of soft inheritance laid the main foundation of the most extreme or rigid form of Darwinism (Weismann 1893) (The term neo-Darwinism was introduced in the 1890s and is usually credited to George Romanes; "Neo-Lamarckism" had been introduced in 1885). As for what was also called Weissmanism, in 1908 the physicist Oliver Lodge called it the "biological dogma."

7 Fritz Müller and August Weismann

Müller and Weismann were among the main German investigators of natural selection of that time. Fritz Müller who developed ideas about the selectionist origin of mimicry together with Bates, was called by Darwin the "prince of observers," and had advanced the cause of Darwinism with *Für Darwin*, published in 1864. In this study, Müller used the example of crustacea, for which he was best known, to demonstrate similarities with related species at different stages of embryonic development. Müller and his family had emigrated to Brazil in 1848. There, he later took a great interest in mimicry among butterflies, and sent Darwin extensive reports bearing on natural selection. The findings, as well as some letters, were passed onto Meldola from 1871. One letter received by Meldola in 1872 contained the suggestion that mimicry was responsible for sexual selection, the females of the mimicking species having been biased in their choice by the patterns of other species (the models) in their locality. In other words, Müller also introduced sexual selection by speculating that females of a mimicking species were affected in their choices by coloration and patterns of other species. Meldola's dissemination of Müller's findings and ideas in the English-speaking world was a considerable achievement, despite the poor initial reception. Though they never met, "A warm friendship sprang up in this way between Meldola and the great German naturalist, many of whose observations were published in this country [as a result of Meldola's efforts]."

Meldola was secretary of the Entomological Society from 1876 to 1880 (and later vice president and president). He was particularly taken with a letter that Darwin received in 1876 from Müller and passed on for communication to the society. So impressed was Meldola with Müller's observations that he included extensive extracts in a paper on "Entomological Notes Bearing on Evolution" (Meldola 1878). He advised readers: "In 1871, when working at the subjects of 'mimicry' and 'protective resemblance,' Mr Darwin was so good as to send me for perusal a letter which he had received from Fritz Muller, then in St Catharina, Brazil. As this letter contains many entomological observations of interest, I have thought it advisable to take steps to secure their being placed upon record in a permanent form; and, with the permission of Mr Darwin, I have selected extracts which I beg to make known in the present paper, together with other observations from various sources which tend to throw light on subjects connected with descent theory."

The topics of Meldola's (1878) paper covered descriptions and evaluations of sound, colour, mimicry, attitude, shape, all treated with some bearing on, and in support of, natural selection. They including the following observations:

"Sounds Made by Butterflies." This had been noted in 1845 by Darwin of the South American butterfly *Ageronia feronia*, and was later observed by Müller, who, on the basis of observations made by his children, agreed with Darwin that sounds were made during the "courtship of sexes." Meldola, here drawing on his more local observations, added "that our common *Vanessa Io* is stated to make a faint hissing sound;"

"Display of Colour by Lepidoptera." This included both sexual selection and warning coloration. As an example of the former, Darwin had "recorded the case of a species of *Castnia* which possesses ornamental hind wings and displays them, while other species with plain hind wings do not display them." In contrast, Fritz Müller had discussed the "interesting case" of "our *Hesperidae*." Meldola opined, as he had done in 1871, "Without further observation it cannot be assumed in this case that the colour is displayed as a sexual attraction, since it is well known that colour is displayed for other purposes, e.g. *protection*, when the colour is a signal of distastefulness (as with brightly coloured larvae and those species which serve as models for mimicry), or for giving resemblance to some coloured objects such as flowers;"

"Insects Distinguishing Colours." Here reference was made to the observations on bees and wasps by the banker, politician, entomologist, and supporter of Meldola's various enterprises, Sir John Lubbock: "This facility is of paramount importance to the theory of sexual selection." Thus Müller pointed out that "Butterflies not only discover flowers by colour, but certain species even give an unmistakable preference to certain colours" (Meldola 1878, p. 156)[11];

"Mimicry," or true warning coloration, was a topic of special, and perhaps the greatest, interest. While the rule hitherto, at least according to Bates (1862), was that "a mimicked species is commoner than the species which mimics it," Müller recorded exceptions, of which Meldola opined, "it is quite conceivable that in certain districts external conditions may so change that a species dominant in other regions may become rare or altogether extinct, while the species which mimics it may remain unaffected… I am disposed to believe that such instances show us the process of mimetic resemblance in actual progress" (Meldola 1878, pp. 156–157). Moreover, under these conditions, the mimic would appear less like its own relatives and more like the model. Meldola also referred to the work of Trimen and Butler on this and related topics, and specific examples of mimicry.

"Correlation of Habit with Protective Resemblance." This included cases of crypsis. "Mr Bates has already recorded the resemblance of a caterpillar (supposed to be a species of *Notodontidae*) to a venomous snake… and Dr [August] Weismann has likewise shown [Studien zur Descendenz-Theorie] that the ear-like markings of *Choerocampa*-larvae actually frightened away birds." Müller had observed "the caterpillar of a *Papilio* which strikingly resembled the head of a venomous snake." From "Mr Bates's description it will be seen that the mimicry extended even to *attitude*. All observers have noticed how in some instances a mimicking insect *copies the flight* of its model; and such cases of correspondence between habit and resemblance are of great theoretical value to the evolutionist." Wallace had shown "in the case of the well-known 'leaf butterflies' (*Kallima*), how the insects settle on the bushes in an attitude which perfects their resemblance to dead

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[11] Lubbock was president of the Entomological Society of London in 1866–1867 and 1879–1880. During 1882–1883, he assisted Meldola with a petition in support of the Jews of Russia, who were suffering from pogroms, and with the objections to a Bill for construction of a railway through Epping Forest (Travis 2009).

leaves." Müller observed a caterpillar that resembled fresh bird excrement when at rest on leaves. Meldola pointed out that: "Even among our own insects hundreds of such cases might be noted. Thus the weevils, which resemble pellets of earth, tuck in their legs and feign death when alarmed, and the stick-like geometer larvae erect themselves stiffly from the twigs on which they rest. *Cucullia chamomillae* and *Galeria cerella* both resemble broken splinters of wood when at rest; and I have seen these moths at the extreme ends of pointed pailings, where they had erected themselves at an angle to the wood, making the resemblance to a broken-off splinter remarkably deceptive." Meldola reported his own observations on moths, including those that resembled a broken stick, a withered leaf, or bird excrement when at rest on leaves (Meldola 1878, p. 158).

Thus through protective resemblance and mimicry, Meldola brought together the work of leading British and German scholars and his own studies. He concluded by stating that he was inclined to believe that natural selection has "taken advantage of and improved upon the original habit that had been acquired for a distinct purpose."

Darwin's correspondence with Meldola concerned all aspects of mimicry, as well as seasonal dimorphism, in which the same species is found to exist in one of two forms, with quite different characteristics, depending on the time of year. This had brought Meldola's attention to August Weismann's *Studien zur Descendenz-Theorie* (1875), based on a series of papers published from 1868. It was Weismann, professor of zoology at Freiburg, and considered by evolutionary biologist and historian Ernst Mayr to be the most significant nineteenth-century evolutionist after Darwin, who first suggested seasonal dimorphism. Darwin, greatly impressed by the German original of Weismann's book, in 1877 wrote about it to Meldola, offering to lend him the book (and suggesting that Meldola purchase his own copy). Later, Darwin was prompted to write that it should be "a public benefit to bring out a translation." This led to another close contact between Meldola and a German disciple of natural selection. Moreover, Meldola was so enthusiastic that he not only considered translating Weismann's book into English, but began to learn German so that he could undertake the task.[12] The translation was completed about one year later. Darwin, Meldola and Weismann all contributed prefaces. Darwin's prefatory note was very short, just two pages.[13] Meldola, however, wanted a more substantial contribution, and asked Darwin to include, within the text, references to *The Origin of Species* in order to demonstrate "how far he had already traced out the path which Weismann went over." Darwin politely declined, writing in November 1878: "An author is never a fit judge of his own work, and I should dislike extremely pointing out when and how Weismann's conclusions and work, agreed with my own."[14]

Macmillan, the publisher of Meldola's translation, complained that the list of subscribers was disappointing. Despite the perceived significance of the translation, Meldola had to raise funds to support publication. Macmillan suggested that sales might be increased if Darwin's preface was longer. This was not to be; Darwin's last letter to Meldola, penned on 3 February 1882 (Darwin died in April), just expressed satisfaction with Meldola's preface. Darwin was unhappy that pre-sales were extremely poor both for the sake of science in Britain and the financial loss. He offered to assist with publishing costs. "I am sorry in many ways, including the honour of England as a scientific country, that your translation has as yet sold badly. If the publisher, though I shall be sorry for him,

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[12] Meldola, writing from the Atlas Works, Hackney Wick, to Darwin, 20 October 1878, letter 11192, Darwin correspondence project; Poulton (1896, pp. 208–209).

[13] Darwin to Meldola, 31 October 1878, ICA; Poulton (1896, pp. 208–209).

[14] Darwin to Meldola, 26 November 1878 (in Darwin 1903, vol. 1, p. 381); and Poulton (1896, p. 210).

yet it is in the way of business; but if you yourself lose by it, I earnestly beg you to allow me to subscribe a trifle, viz., ten guineas, towards the expense of this work, which you have undertaken on public grounds."[15] Meldola declined the offer and instead requested Darwin's sponsorship in gaining election as Fellow of the Royal Society.[16] The application was submitted to the Royal Society on 23 February 1882, but was rejected. In 1916, it was noted that: "The biological work … formed the ground on which Meldola was proposed by Charles Darwin for the Fellowship of the Royal Society. He was elected in 1886, after too long an interval, as many thought at the time and all will acknowledge now. His claims would probably have been recognized earlier if they had been strong in only a single scientific subject instead of being strong in many" (Poulton 1916, pp. 101–102). The Weismann translation appeared later in the year (Weismann 1882).[17]

8 Müllerian Mimicry

In May 1879, Fritz Müller published in the German natural history journal *Kosmos* a paper on mimicry, involving the Danainae *Ituna* and *Thyridia*, whose significance, according to Poulton, was not appreciated in England, except by Darwin and Meldola. "Meldola did far more than bring out the translation: he defended the hypothesis in controversy and brought new and important classes of facts to support it" (Poulton 1916, p. 99).

Müller expanded on the studies of Bates, Wallace and Trimen into warning coloration, namely the similarity between species of butterfly that were distasteful to birds and those that were not. The latter had taken on, through mimicry, a characteristic of butterflies that were distasteful, and were thus endowed with a defensive mechanism. This was the basis of Batesian mimicry, in which predation determined selection. Müller's paper, developed from studies made in 1878, dealt with two or more unpalatable species. He used *Ituna* and *Thyridia* to show mathematically that the greater the number of individuals that appeared to be alike the greater was the chance of survival. A young avian predator after encountering one distasteful butterfly would in future avoid all those with similar markings and colours (Müller 1879a).

In summary, Batesian mimicry involved deception through imitation by adaptation of external features of a poisonous species by a species that was harmless to predators when eaten. Müllerian mimicry, in contrast, took into account the presence of different species, of similar though less close resemblance, but that were all toxic or unpalatable. The collective of unpalatable species that came to resemble one another, through aposematism, effectively confused bird predators during the learning process, and ensured a greater chance of survival.

Once more, Meldola received an important paper from Darwin. According to Poulton, Müller's article, on resemblance between species belonging to protected, unpalatable,

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[15] Darwin to Meldola, 2 February 1882 (in Darwin 1903, vol. 1, p. 397).

[16] Meldola to Darwin, 3 February 1882, log no. 2701, item 13655, Darwin Correspondence Online.

[17] One section was devoted to studies of the changes of the Mexican axolotl, according to habitat. This remarkable amphibian was brought to France in the 1860s as a curiosity and soon became a topic of zoological research, and of evolutionary studies by Weismann, who was assisted by Marie von Chauvin. Meldola probably first met Weismann at the 1887 meeting of the British Association for the Advancement of Science held in Manchester. On that occasion, Weismann participated in a debate over natural selection led by E. Ray Lankester. Meldola's attendance at the meeting is confirmed by a note held at Imperial College Archives dated 5 September 1887 sent from the reception room of the association, requesting that he find a new chair for a session.

groups, “was of the highest importance in relation to the theory of mimicry, as Meldola at once perceived” (Poulton 1896, p. 212). Darwin remarked: “F. Muller’s view of the mutual protection was quite new to me.” Though the translation of the Weismann book was still not yet complete, Meldola advised Darwin that he wished to translate Müller’s paper into English, and asked for assistance in arranging permission. On 6 June 1879, Darwin suggested that Meldola contact one of the editors of *Kosmos*. The paper, translated mainly by Jenner Weir and Henry Bates, appeared in *Proceedings of the Entomological Society of London* (Müller 1879b).

In 1882, shortly after Darwin’s death, Meldola published a paper on “Mimicry Between Butterflies of Protected Genera” in which he answered the various objections to Müllerian mimicry. Meldola described his first acquaintance with this aspect of Müller’s work: “In 1879 the late Charles Darwin called my attention to a paper by Fritz Muller, in ‘Kosmos,’ in which this naturalist attempted to explain the outstanding cases of mimicry, viz. those cases in which both the genera concerned are protected by distastefulness, by an extended application of the principle of natural selection, thus bringing the whole of these interesting phenomena under the action of Darwinian factors. I was at the time so much struck by the ingenuity of the reasoning employed, that I published a translation of the paper in the ‘Proceedings of the Entomological Society of London.’ The same author has recently published a second paper on this subject, an account of which has already been given in ‘Nature’ [xxvi, p. 86] by Mr Wallace, who not only states Fritz Muller’s case with his usual force and clearness, but gives the additional weight of his own authority to the proposed extension of the meaning of the term ‘mimicry’” (Meldola 1882). The translation of Müller’s 1879 paper was, however, not warmly received; William Distant was among the critics. Only in 1896 did the Oxford entomologist Frederick A. Dixey, a friend of Meldola, publish an account that gave credence to Müller’s theory, which must have given much satisfaction to Poulton just as he was completing his own book on Darwinism (Poulton 1896).

Meldola opined in his 1882 paper “that the extension of the theory of mimicry proposed by Fritz Muller marks a great advance in our views on this subject, which is so interesting as having been the first to which the Darwinian Theory of Evolution was applied with such success by Mr Bates. Not only are we now in possession of a consistent theory which enables us to dispense with mysterious and ‘unknown local causes,’ but other groups of facts hitherto incomprehensible are capable of explanation” (Meldola 1882, p. 425). This defence mechanism became known as Müllerian mimicry, particularly in relation to the reciprocal co-adaptations of unpalatable species, and the importance of this form of mimicry for less common species.[18] Müller’s theory has subsequently been extended to other forms of mimicry (Sherratt 2008; Thompson 1994, pp. 29–32).

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[18] A particularly interesting correspondence on mimicry and inedibility of butterflies, with no direct reference to Müller, was later entered into by Frederick A. Dixey and Wallace. Dixey drew attention to South American butterflies in which mimicry “cannot be accounted for on Batesian principles. Such are the cases of interchange where each has acted on the other as both mimic and the model. Such again are the instances where two ‘mimics’ have approached each other more closely than either of them has approached the common ‘model’. These cases are explicable if we assume inedibility as a property not confined to one member of the group, but shared by some of the ‘mimics’; they are not explicable on any other supposition hitherto advanced. We are then justified in making this assumption, especially as evidence exists that both groups… include distasteful members.” Dixey to Wallace, 16 November 1907, British Library, Addit. MSS 46437: folios 248–252.

9 Darwinism Under Attack

In July 1886, Meldola married Ella Frederica Davis, daughter of the physician and surgeon, Maurice Davis. The newlyweds moved a short distance northeast to Brunswick Square, London, in a home provided by Meldola's father-in-law. Wallace, as a close friend (though this is rarely emphasized in historical studies, see e.g. Raby 2001; Fichman 2004), was a frequent visitor to and guest of the Meldola household, and played chess with Meldola's mother, who had a considerable store of knowledge about moths, since she, and Meldola's wife, participated in excursions and holidays that were devoted to observations of nature and collecting specimens.

It was also in 1886 that strong differences of opinion emerged over evolutionary theory on the question of speciation, in which Meldola argued forcefully against George J. Romanes, who favoured physiological selection (Meldola 1886a; Lesch 1975, pp. 490–491). It was, in addition, recognized that Darwin's pangenesis theory of inheritance of 1868 was far too vague and speculative (see Deichmann, this issue). The ongoing interest in inheritance led to what Meldola in 1888 had referred to as "'pure' Lamarckism," notably in 1894, when the English biologist William Bateson (Bateson 1894; Cock and Forsdyke 2008) dealt with the discontinuity of variation (that is, intermediates between parent forms are not produced on crossing) in his *Materials for the Study of Variation, Treated with Special Regard to Discontinuity in* The Origin of Species. At this time, Meldola had just been appointed president of the Entomological Society of London. He had been proposed in 1892 by Poulton and entomologist Colonel C. Swinhoe, but was opposed by the committee, some of whom, particularly David Sharp of Cambridge, considered that entomologists were being supplanted by the lepidopterists. Perhaps with good reason, since Meldola, Poulton, and those of a neo-Darwinist persuasion, almost certainly planned to use the society as the main platform for promoting natural selection based on Lepidoptera and other insects. There were certainly some unseemly and extraordinary goings on behind the scenes in the matter of the presidency.[19]

Sharp was soon proved correct. Despite advances in the understanding of the selectionist theories of mimicry, including Frederick Dixey's 1896 theory—strongly supported by Meldola—Poulton found at a meeting of the Entomological Society in 1897 that very few of those present were prepared to accept such ideas. Some had serious doubts about the arguments based on butterflies and unpalatability, while others called into question the role of birds as tools with which to observe selectivity. Partly this was a reflection of the

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[19] Henry John Elwes to Meldola, 24 December 1892, and David Sharp to Meldola, 11 January 1893, Meldola papers, ICA. While Poulton and Swinhoe favoured Meldola, the ten other members of the committee were against Meldola's appointment. Francis Galton, who supported Meldola, remarked: "What a row there seems to be at the Entomological. Of course I shall vote for you." Galton to Meldola, 7 January 1893, Meldola papers, ICA. In the event Elwes was appointed president for 1893–1894, and Meldola for 1894–1895. There was also the issue of the takeover of the society by professional scientists, who threatened to undermine the efforts of the main membership, amateur entomologists, as reflected in a letter from W. E. Distant to Meldola: "I quite agree with you about entomologists and evolution, but you must remember that the larger percentage of our society have no scientific training whatever & […] have undergone little scientific reading. Their admittance as you remember is owing to 'their being much attached to the subject of insects,' which might be put more correctly as 'much attached to the pinning of insects.' Consequently these friends 'think [about] when they might be more profitably engaged in sugaring a fence, or [think that] to ask them to 'enquire' when they might be papering a drawer, is perhaps inconsiderate on our part. Is it because the objects studied are small that the ideas follow the same ratio?… An observant entomologist loses nothing by doing classifying work, in fact he thereby often see[s] a question and obtains evolutionary material." Distant to Meldola, 10 April 1891, Meldola papers, ICA. Meldola's successor as president was Trimen.

tensions that continued to exist between the majority of members, the amateur entomologists, mainly collectors of dead specimens, and professional scientists and specialists, including Meldola, who were intent on garnering support for natural selection.

Meldola and Poulton were on the defensive now that Bateson posed a serious threat to what had been revered since the late 1880s as a matter of faith among Meldola, Poulton, Wallace and Weismann, the "hard" adherence to natural selection, that is, neo-Darwinism. Bateson opposed the pan-selectionism of Wallace, and especially of Weismann, whose experiments were used to argue for the non-inheritance of acquired characters. Bateson's emphasis on discontinuous variation was given support in 1900 by Dutch biologist Hugo de Vries who advocated a discontinuous or mutationist concept of evolution, that allowed for disruptions and random, sudden changes. Mutation and not natural selection became a driving force. Bateson had edited an English translation (from the journal of the Royal Horticultural Society) of Mendel's work and published it as *Mendel's Principles of Heredity: A Defence* (Bateson 1902). Followers of neo-Lamarckian, or adaptive evolution, and Mendelian, or hybridization, theories, though they had nothing in common, rejected neo-Darwinian evolution.

Meldola developed a strong antipathy towards those who were inimical to neo-Darwinism, particularly after the new Mendelian-de Vries concepts had gained a stronghold among biologists. For them it was a revelation, if not an apocalypse. For the followers of Darwin it was a crisis. In February 1900, Bateson was appointed secretary of the Royal Society's evolution committee, replacing Walter F. R. Weldon, who resigned, along with Meldola, Francis Galton, Karl Pearson, and Sir William Thiselton-Dyer. A few years later, Meldola could barely hide his great disappointment at not being invited to speak at the Cambridge conference that marked the centenary of Darwin's birth, nor to contribute to the memorial volume (Seward 1909). A devoted neo-Darwinian, he advised readers of *Nature* in his almost five-page review of *Darwin and Modern Science* that the "essay of de Vries is referred to as lacking in lucidity…. [and Ernst] Haeckel's contribution still rings with the battle cries of the victor over his defeated German anthropological opponents." Meldola was content to report that "Weismann's, Poulton's, and D. H. Scott's contributions will be found delightful reading by those who (like the present writer) still believe that the Darwinian theory is a theory of adaptation." Poulton's contribution was mainly historical, but also a spirited defence of mimicry as the most significant evidence for natural selection, in which Meldola had played an important role.

Meldola, too discreet to make a fuss in print about why he was not asked to contribute, merely pointed out that those "who look to the work as an authoritative expression of evolutionary opinion must perforce be struck by the omission of certain names which we should have liked to see on the list of contributors. The names of Alfred Russel Wallace and Francis Galton are conspicuous by their absence" (Meldola 1909, p. 482). In private, when writing to his close friend Wallace, Meldola was less discreet: "It is astonishing to see the great hold upon the Cambridge school obtained by de Vries and Bateson. Even Francis Darwin is more or less under their dominion! I dare say you noticed that his Presidential Address to the Brit. Assoc. in Dublin last year was distinctly Lamarckian. But I for one feel sure that in a few years we shall see 'Mutationism' defunct and 'Mendelism' assigned to its proper place. Among the speeches delivered in the Senate House [E.] Ray Lankester's was the only one which really reaffirmed the true Darwin-Wallace position—which he did (like E. R. L.!) somewhat aggressively in view of the fact that de Vries himself was present. I cannot make out why I was not asked to contribute to the Memorial volume. I suppose I am too

'Darwinian' for that school!"[20] For others, including Jacques Loeb in the United States and William Bateson, the issues were hardly worth considering. For Loeb, natural selection was self-evident, as Francis Darwin reminded Meldola.[21] As for Wallace, he was at least considered as a contributor to the special volume.

One reason why Meldola was not invited to contribute to the memorial volume, apart from the denial of Lamarckism, for which Weissman's long contribution sufficed, was the emergence of genetics, and the need to provide sufficient space for all branches of new and revised views on evolution and inheritance. The latter would be at the forefront of the emergence of twentieth-century life sciences. Thus, Bateson had advised readers of his *Mendel's Principles of Heredity* that "The concept of evolution as proceeding through the gradual transformation of masses of individuals by the accumulation of impalpable changes is one that the study of genetics shows immediately to be false" (Bateson 1902, p. 289). This explains why Meldola was mostly left out of the newer debates on evolution, though not out of organic chemistry (Travis 2007). The sheer volume of correspondence between Meldola and scientists, politicians, and religious leaders, is the true testimony to his neo-Darwinian beliefs.

10 Weismann and Neo-Darwinism

Meldola's commitment to Darwinism in the early 1880s—shortly before he turned to the creed of ''hard'' Darwinism—is perhaps best demonstrated in his presidential address to the Essex Field Club at the annual meeting held in January 1883. Under the heading "Darwin and Modern Evolution" it was a tribute to his late friend and honorary member. It is a valuable contemporary record of Meldola's own commitment to natural selection. He explained that "Because of widespread ignorance… I think I cannot do better than occupy your time by recapitulating the main points in the theory of the origin of species" (Meldola 1884, p. 68).

Meldola began by discussing the multiplication of animals, starting with the elephant "reckoned the slowest breeder of all known animals" (Meldola 1884, p. 69), then moved on to birds, rabbits, etc. "Granting this fact, that all organisms tend to increase at a geometric rate, it is clear that every species must have in itself the potentiality of unlimited extension, and must constantly be endeavouring to extend itself at the expense of others; every species must be waiting to fill any vacancy in the polity of nature; there must be a perpetual competition going on—a continual 'struggle for existence,' which keeps in check the undue increase of any particular species. Thus the animals and plants of any region are in a state of nicely balanced equilibrium, the result of long ages of adjustment to their surroundings both organic and inorganic" (Meldola 1884, p. 74).

In his 1883 lecture, Meldola turned to the work of experimental biologist August Weismann. It was to Weismann, who worked on natural populations, that Meldola stated, "we owe the first full recognition of the important part played by the organism itself in the process of evolution, but it must be borne in mind that the part thus played is… a purely passive one" (Meldola 1884, p. 86). Meldola, in support, referred to his own studies a decade earlier (Meldola 1873): "I cited a certain class of cases in illustration of the fact that

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[20] Meldola to Wallace, 28 June 1909, British Library, Addit. MSS 46437: folio 46. See also Seward (1909), Browne (2005), Cantor (2006, p. 23), and Richmond (2006). Lankester was a son of Edwin Lankester (see Charpa this issue).

[21] Francis Darwin to Meldola, 17 June 1909, ICA.

natural selection acts upon such variations as arise, with entire regard to the *causes* of these variations…. It is not variability but constancy which demands an explanation" (Meldola 1884, p. 87). While natural selection was the most important influence, Meldola emphasized the fact that Darwin did not discount Lamarckian influences (Meldola 1884, p. 88).

If Meldola, early in 1883, was prepared to acknowledge that Darwin, in common with most scientists engaged in evolutionary studies, accepted inheritance of acquired characteristics, he would himself soon come increasingly under the influence of a new "dogma," one-first espoused later in the same year.

The principal proponent was Weismann, who had until then also accepted Lamarckian notions. However, in his inaugural address, "On Heredity" ("Uber die Vererbung"), as the new pro-rector of the University of Freiburg, on 21 June 1883, Weismann publicly distanced himself from Lamarckian elements when he stated that acquired characters cannot be transmitted (Weismann 1883; Churchill 1968). Weismann favoured "hard" inheritance and thus minimised the inclusion of any mechanism other than natural selection in evolutionary change. In 1888, the proof sheets of Weismann's forthcoming book, *Essays upon Heredity* (1889), greatly impressed Wallace (who received the proofs from the main editor, Poulton[22]), and contributed towards arguments for natural selection in his *Darwinism* (Weismann 1889[23]; Wallace 1889). Weismann frankly admitted that until around 1880 he had accepted the Lamarckian elements adopted by Darwin (Weismann 1889, p. 422). In 1892, Weismann's fully developed mechanism based on his germ-plasm concept appeared in print as *Das Keimplasma: Eine Theorie der Vererbung* (in 1893 in English, as *The Germ-Plasm: A Theory of Heredity*) (Weismann 1892). This mechanism was based on separation of germ line cells from soma cells.

Most of the followers of "hard" Darwinism or inheritance were in fact not biologists, like Weismann, but field naturalists, as were the strict selectionists Wallace and Meldola. In support of Meldola's own proto-neo-Darwinian view, that appears to have developed during the mid- to late 1880s (perhaps under the influence of Wallace, who placed more emphasis on natural selection than even Darwin), he published over the course of several years notable papers and thoughtful reviews, particularly in *Nature* (Meldola 1891a, b, 1909). To fellow physiologist and entomologist Frederick Dixey, he wrote when discussing seasonal dimorphism: "Of *course* there is no vestige of Lamarckism in my notion."[24] At the turn of the century, however, what was generally referred to as neo-Darwinism was under attack from many quarters, and not just the religious establishment (Bowler 1992).

There were two reasons. First, the Lamarckian model based on inheritance of acquired traits was making a comeback, relativising the importance of natural selection. Second, the emergence of Mendelian genetics challenged a view that was central to Darwinism and neo-Darwinism, i.e., very small individual differences were sufficient for natural selection to generate major evolutionary changes. This led to a critical backlash against, and sometimes excited furious responses to, hard Darwinism. The neo-Darwinians, numbers diminished, stood their ground, supported, particularly, with emphasis on mimicry in butterflies. It was Meldola's adherence to the rigid brand of neo-Darwinism, as already suggested, that no doubt prevented him from leaving his mark on twentieth-century biological science.

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[22] Wallace to Poulton, 4 and 8 November 1888, papers of Sir Edward Bagnall Poulton, Bodleian Library, University of Oxford.

[23] "On Heredity" appears on pp. 69–105.

[24] Meldola to Dixey, 1897, Dixey Family Papers, Bodleian Library, University of Oxford. Dixey received considerable support from Meldola. For Dixey, see Poulton (1935).

11 Society, "Survival of the Fittest," and Spencer

Meldola's adoption of Darwinism, and experience of and observations on the dye industry, were put to good use in the debate over industrial competition between Britain and Germany. In May 1886, Meldola, as the new professor of chemistry at Finsbury Technical College, gave before the Society of Arts in London a lecture on the decline of Britain's coal-tar dye industry and the emergence of the German dye industry. Much of the lecture, for which he received the society's silver medal (1886b), was couched in social Darwinist terms. Shortly after giving the lecture, Meldola, who now commanded much respect in the scientific community, was elected a Fellow of the Royal Society.

Two years earlier, in 1884, Spencer had applied the "survival of the fittest" concept to his political philosophy in *The Man Versus the State*. As referred to competition and industry, according to Meldola, this brand of Darwinism was explicit: Only those firms that offered the best goods and services would survive and dominate the market. Those that were unable to adapt to new conditions would be "killed." The history of the dye industry, according to Meldola,

> reveals that fundamental law of the "survival of the fittest." Old products have been displaced by newer ones as fresh discoveries were made, or processes improved.… The moral conveyed to the manufacturer is sufficiently obvious. If we are to recover our former supremacy in this country, we must begin by dispelling conservative ideas—we must realise the fact that no existing process is final, and that no product at present sent into the market is destined to survive for an unlimited period (Meldola 1886b, p. 97).

In a single lecture, a severe warning to the British, he used social Darwinism with greater clarity than even Herbert Spencer.[25]

This is an example of how Meldola's energy and talents were directed in other directions, including planning of and funding for scientific education and research. In this instance, however, he was an enthusiast for the wider application of Darwinism, and concepts similar to natural selection beyond biology, through the influence of biologist-turned-social philosopher Herbert Spencer. Despite differences of opinion, Meldola held Spencer in particularly high regard. It was Spencer, whose ideas preceded those of Darwin, who extended his own theory to psychology and sociology, and is credited with the development of social Darwinism. Compared with Wallace, an enthusiast for socialism, championing the vulnerable and nationalisation of land, Spencer represented the extreme opposite end of the political spectrum, with economic ideas that have long placed him on the right. In other respects, however, his philosophy incorporated many features that were in accord with the outlook of Meldola. As early as 1852, Spencer dealt with utility and aesthetics, emphasizing how the former led to the latter, by reference to past human activities. Thus, in "Use and Beauty" he considered how a Victorian excursionist found London's Hampstead Heath a place of "relaxation and enjoyment… afternoon strolls and for gathering flowers," while primitive man would have seen it as "merely a haunt of wild animals, and a ground on which roots might be dug." The same applied to ruined castles, Stonehenge and Greek sculptures, all formerly of great utilitarian value, but now appreciated for their attractive settings and links to the past. This must have appealed greatly to

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[25] Following Spencer's death in 1903, Meldola lobbied for a plaque or other memorial to be erected in Westminster Abbey, though it was ultimately rejected by the Dean of Westminster, mainly due to Spencer's avowed agnosticism. See Gay (1998).

Meldola when he turned to the conservation of Epping Forest, and the preservation of ancient earthworks.

12 The “Philosophic Faculty”

As well as dealing with the “cooperation” between past and present, Spencer had a special interest in cooperation between altruism and self-interest in human activity. For example, in 1898, he wrote to Meldola: “I recently came across a passage in the work of [French zoologist] Prof. Yves Delage on Heredity to the effect that there was a great advantage in the cooperation of the speculator and the expert, and I am reminded of a remark made somewhere by you to the effect that the two were rarely united in the same person. I was struck by the coincidence of thought. Can you tell me where your remark was made? I think it was in a lecture or address reported in *Nature* some two, three, or 4 years ago. I should like to refer to it.”[26]

Spencer was probably referring to Meldola’s 1895 presidential address to the Entomological Society, on “The Speculative Method in Entomology,” that emphasized the “scientific use of imagination,” and was published in both the society’s *Transactions* (Meldola 1896, pp. lii–xlviii), and, as Spencer correctly remembered, in *Nature*. While it may not have answered Spencer’s needs, this paper did offer considerable insight into Meldola’s own approach to the validity of speculation within a scientific context, most particularly the development of theories guided by careful observation and wide-ranging knowledge of natural history. It provided an opportunity to explore the relationships between the physical sciences, such as chemistry, physics, and even various areas of biology, and sciences that had strong historical and descriptive aspects, including entomology, palaeontology, geology, and archaeology.

Meldola argued that “The philosophic faculty is quite as powerful an agent in the advancement of science as the gift of acquiring new knowledge by observation and experiment” (Meldola 1896, p. lxiv). His address, directed towards enhancing the status of research in entomology, undoubtedly was inspired by the success of laboratory-based chemistry. If advancement was to be achieved there was a need to test, with the greatest possible rigour, speculative theories based on entomological and biological investigations. The same applied to geological investigations and records of the sort that had aided Darwin in developing his theory of natural selection. These were field-based activities relying on keen observation, and were seemingly fixed within the domain of empirical knowledge, museum and private collections, and historical understanding. The question was: Could explanations in these domains incorporate the sort of laws that were critical to the successes of chemistry and physics? Though they required different approaches to research at the conceptual level, Meldola speculated, they might well be amenable to similar modes of reasoning drawing on the hypothetic-deductive model, as indeed Darwin had demonstrated when deriving general laws of natural selection from a mass of facts about organisms and their environments, the complexity of which was enormous. The same applied to chemistry, where observation invariably came before theory, as Meldola well knew from his own engagement with synthetic dyes and aromatic organic chemistry. Meldola alluded to the philosophy of comparative scientific methods, based on correlation of observation, experiment and theory, that was typical of the physical sciences, but much needed in entomology. To be scientific required an understanding of the philosophy of science, and

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[26] Spencer to Meldola, 9 February 1898, Meldola papers, ICA.

the genius of a Darwin. Observation, experience, and intuition of the naturalist scientist were no less valuable than the results of experiments. Both were sources of valuable philosophical reasoning, and of theory-driven hypothesis testing. Even poor theory was better than no theory, for it was the stimulus for improved theory.

> The Association of Chemistry and Biology in researches such as those to which I have drawn attention, has suggested a comparison between the methods of research in vogue in the two great departments of science of which these two subjects are respectively typical. All science necessarily begins with observation or experiment, i.e., with ascertained facts, and it is perhaps unnecessary to assert that no mere collection of facts can constitute a science. We begin to be scientific when we compare and coordinate our facts with a view to arriving at generalisations on which to base hypotheses or to make guesses at the principles underlying the facts. Having formed the hypothesis we then proceed to test its accuracy by seeing how far it enables us to explain or to discover new facts, and if it fails to do this to our satisfaction we conclude that our guess has been a bad one and requires modification or replacing by a better one, i.e., by one more in harmony with the facts (Meldola 1896, p. lii).

> Now I venture to think that entomology in this country has been retarded in its development for want of a little more of this "philosophic science"; by an unwillingness on the part of our most active workers to give rein to the imagination—by an overcautiousness which is damping to the speculative faculty (Meldola 1896, p. liii).

Meldola now emphasized the scientific study of insects by reminding his audience that entomology was suffering from a "plethora of facts." He did not see how it was possible to "advance unless a more generous use is made of hypothesis as a scientific guide." Gathering field notes and other worthy information was just not enough.

In the physical sciences, observation stimulated hypothesis, which in turn was tested by further observations and experiments. Drawing on the example set by Michael Faraday, Meldola observed that "We have… long ceased to collect random facts; observations and experiments are suggested by hypothesis."

> And now let us consider how far these methods, recognized as valid in the physical sciences, are applicable to the biological sciences, of which entomology constitutes a branch…. I have felt it a duty to urge a claim for the speculative method, not as displacing the older method of collecting and recording facts altogether, but as a stimulus to more systematic investigation, rendered imperative by the general advance of biological science (Meldola 1896, pp. liv–lv).

To argue his case further, Meldola reverted, deliberately and sensibly, to the one area that he knew most intimately, mimicry in Lepidoptera, and the way in which speculation, or theory, and field observation worked together in facilitating improved scientific knowledge. This area of study had been developed successfully within the framework of natural selection by Bates, Wallace, and Müller. It was an outstanding example of the application of a scientific method to a field that relied on description and explanation.

> I may be permitted to draw some illustrations from the Lepidoptera, the only order to which I can lay claim to some slight special knowledge… my sole aim in this address is to clear the atmosphere for the more healthy use of the speculative faculty by our younger and rising workers…. I begin with the phenomena of mimicry and protective resemblance among butterflies and moths… this was the first application of

> the theory of natural selection of Darwin and Wallace to explain a new set of phenomena. It was a speculation evolved by Bates, not when collecting in the Amazon Valley, as is generally supposed, but while looking over his specimens when he had reached London, and was pondering, at his own fireside, over the meaning of the remarkable superficial resemblances among the butterflies of different groups which he had brought home (Meldola 1896, p. lvi).

Allowing for the fact that there were those in the audience who were cynical of explanations of mimicry based on natural selection, and in deference to critics, Meldola moderated his argument when introducing Müller:

> The theory of Bates left unexplained the resemblance between species belonging to protected groups to which he had himself called attention in his original paper; an extension was required and was made by our Hon. Fellow, Fritz Muller in 1879, and as a result, whether this extension be considered valid or not—a point which I am not now raising—the systematist is now more fully alive to the superposition of external similarity upon structural resemblance due to true blood-relationship (Meldola 1896, p. lvii).

Thus, Meldola opined in support of his systematist colleagues, "From the observation that the species which are mimicked are generally gaudily coloured and take no special means to hide themselves, it is but a step to the well-known theory of warning colours propounded by Wallace in [1866 and] 1867" (Meldola 1896, p. lviii). This theory was derived from Darwin's interest in sexual selection, and had encouraged experiments by Jenner Weir and A. G. Butler, observations by Thomas Belt in Nicaragua, research by Weismann into the colour of caterpillars, and "later systematic studies" by Poulton.

These were the very issues that stimulated further observations and speculations. Here Meldola could draw again on his own expertise by discussing the nature of variation in colour of organisms as a mode of "individual adaptability" resulting from natural selection, and raising a critical question in insect physiology, the nature and function of chemicals absorbed from plants. This went back, according to Meldola, to his 1873 paper, which carried with it "the implication that natural selection could work on physiological processes if they were of use, just as well as upon external morphological character… a fundamental problem in insect physiology, the solution of which we are anxiously awaiting" (Meldola 1896, pp. lviii–lix).

The emphasis was that in any approach to such questions, the field naturalist had a major advantage over the "cabinet entomologist," namely, the ability to observe the living organism at work in different environments.[27] Use of the "philosophic" or "speculative

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[27] As further examples of Meldola's eloquence, critiques of many entomologists, and enthusiasm for analyzing and evaluating scientific data, it is worth drawing attention to some other statements made in his paper:

> In view of the splendid opportunities afforded by insects for treatment as living organisms capable of revealing natural laws by skilled experimental research, is it not pardonable if we sometimes give way to the unphilosophic thought that the possession of chitinous exo-skeletons by these creatures, whereby they lend themselves so admirably for preservation as cabinet specimens, is an arrangement expressly designed for the retardation of entomological science? (Meldola 1896, p. lix).

> The philosophic faculty is quite as powerful an agent in the advancement of science as the gift of acquiring new knowledge by observation and experiment. It is not often that the faculties are combined in one individual…

faculty" gave the naturalist a greater facility for engaging in speculation, or a philosophy of science, as the following passage made abundantly clear.

> … it must be confessed that the greater part of our systematic work has emanated from cabinet entomologists, who know nothing of the species they describe as living organisms by direct observation, and to me it appears doubtful whether this kind of work does confer any special faculty of speculating with advantage on the species question. It seems rather that the "field-naturalist" in the old sense of the term has the advantage (Meldola 1896, p. lxvii).

Meldola closed with a reminder of the endeavours of Darwin and Wallace, the great field naturalists, whose observations had engendered their own remarkable speculations.[28] They had both described and explained behaviour and evolution in the natural world through a distinct biological mechanism, or theory, that is, natural selection, based on information gathered by observation in the field.

The significance of the address was that not only was it critical of the cynicism shown by many amateur collectors towards natural selection, but it was also a powerful response to those experimental scientists who were becoming increasingly sceptical of this mechanism. Meldola's 1896 presidential address before the Entomological Society on "The Utility of Specific Characters and Physiological Correlation" (Meldola 1897, pp. lxiv–xcii), with extensive discussion of plant-sequestered products as foods or poisons, according to Poulton, carried much the same message. Poulton opined: "hypothesis remains, and ever must remain, as the guide and inspirer of observation and the discovery of fact" (Poulton 1896, p. 15). Poulton emphasized that in studies of evolution the field naturalist had a distinct advantage over the laboratory scientist. Meldola, he opined, "argues that systematic work of those who know nothing of the living states of the species they are describing does not specially fit them for theorising" (Poulton 1896, pp. 37–38).

A few years earlier, in the 6 October 1892 issue of *Nature*, Poulton had shown considerable hostility toward F. E. Beddard, whose *Animal Colouration* (1892) strongly criticized mimicry-based theories that supported natural selection. Beddard, along with Charles Coe (1895) and the American palaeontologist and neo-Lamarckian Edward Drinker Cope (1896), favoured external causes for mimicry, such as food and environmental factors. After 1910, Poulton opposed Reginald Crundall Punnett who provided a Mendelian explanation of butterfly mimicry. Punnett, in his *Mimicry in Butterflies* (1915), argued that natural selection was unsatisfactory in explaining mimetic resemblance. Just as Meldola believed that Mendelism would soon be assigned to its proper place, so did John Gerould in the United States believe that mimicry would soon be assigned to its proper place.[29] Poulton long outlived Meldola and the other nineteenth-century neo-Darwinians, and witnessed the merging of evolution with genetics. In 1942, one year before Poulton's

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Footnote 27 continued

> The irresponsible manipulation of biological hypotheses by pure speculators does no real or permanent damage to the cause of science, and may indirectly do good by directing public attention to the work which is being carried on… It is possible to be quite as unscientific in the accumulation of facts as it is to become metaphysical by over-speculation (Meldola 1896, pp. lxiv–lxv).

> I do raise the question here as to the kind of biological work which is to be recognized as a fitting preparation for the exercise of the speculative faculty (Meldola 1896, p. lxvi).

[28] For examples of more recent discussion see Hempel (1956), and Dodick et al. (2009).

[29] See http://faculty.kirkwood.edu/ryost/poulton.htm (accessed 6 April 2009).

death, Julian Sorell Huxley, a fervent believer in natural selection, who as a new graduate had attended the 1909 Darwin celebrations in Cambridge, published *Evolution: The Modern Synthesis*, containing the first-stirrings of the twentieth-century neo-Darwinian theory that emerged as a dominant force in the 1950s. Huxley's brilliance was of the kind that Meldola had yearned for in the mid-1890s. He had brought together the otherwise disparate mechanistic studies and data of others into a truly coherent whole (Walters and Van Helden 1993).

13 Conclusion

Raphael Meldola's scientific life was remarkably broad in scope. Under the tutelage of explorers, entomologists, naturalists, chemists, and editors, he acquired the practices of science, including a keen sense of observation, systematic record keeping and the ability to explain ideas simply. He left no grand new theory, but his engagement with entomology and natural selection led him to become one of the most outstanding spokesmen for Darwinism in the nineteenth century. This was enabled by his own studies on butterflies and moths, the strong feel induced for these and other organisms, and the networks of enthusiasts and adventurers, and their professional and amateur associations. His high standing in chemistry, an experimental science that flourished with the emergence of viable theories, encouraged its application as a model for the further improvement of entomology and biological science. Thus, as in the case of the benzene ring theory, had simplicity and lack of complexity not intervened, it would have been much more difficult for new theories to find acceptance. His expertise in two fields enabled him to draw effective analogies from both biology, when discussing the decline of Britain's dye industry, and chemistry, when suggesting a more scientific approach to the study of entomology and certain areas of the biological sciences.

Meldola's unflinching devotion to the cause of neo-Darwinism, however, led him to be increasingly sidelined after alternative and competing theories appeared around the turn of the century. This hastened his perceived loss of relevance among the community of life scientists by the time of the Darwin centenary events in 1909. By then he and his like-minded colleagues had become members of a scientific endangered species. The outcome was that Meldola's contributions, mainly promoting and expanding on the work of German researchers, particularly Müller's studies on mutual protection and Weismann's hard inheritance, have been largely forgotten. In some respects this was because he was well ahead of his time. Thus, in 1972, Miriam Rothschild, when writing on the "role of birds in determining the life-style of warningly coloured insects," recognized that in 1882, Meldola "suggested that it was the keen avian eye which selected the basic types of warning coloration characteristic of Danaid, Acraeid and Heliconid butterflies" (Rothschild 1972b).[30] Moreover, in the 1930s, it was Meldola's close friend Poulton who, she continued, "agreed emphatically … on this point, and was convinced the theory explained the parallel evolution of the aposematic life-style of these unrelated groups." Rothschild, along with Trimen in 1887, and Poulton in 1914, "stressed the benefit accruing to the early stages of insects which have succeeded in establishing themselves on plants avoided by large herbivores." With the newer laboratory technologies, she and others performed the critical experiments on the storage in insects of plant poisons, such as pyrrolizidine alkaloids and cardiac glycosides (Parsons 1965; Reichstein et al. 1968). These were shown to be the

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[30] See also Brower et al. (1968).

main line of defence against learning predators. Instant recognition of warning colouring of butterflies and other insects that had sequestered toxic plant chemicals was what kept the avian attacker at bay. Meldola's speculation in the 1880s proved to be correct. These issues of predation, mimicry, distasteful prey, defence in animals, toxins in plants, and phenotype plasticity continue to attract scholarly interest among ecologists, and, from the mid-twentieth century on, those engaged in evolutionary genetics.[31]

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[31] See for example, Barnett et al. (2007).

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ARTICLE

Beyond Darwinism's Eclipse: Functional Evolution, Biochemical Recapitulation and Spencerian Emergence in the 1920s and 1930s

Rony Armon

Abstract During the 1920s and 1930s, many biologists questioned the viability of Darwin's theory as a mechanism of evolutionary change. In the early 1940s, and only after a number of alternatives were suggested, Darwinists succeeded to establish natural selection and gene mutation as the main evolutionary mechanisms. While that move, today known as the neo-Darwinian synthesis, is taken as signalling a triumph of evolutionary theory, certain critical problems in evolution—in particular the evolution of animal function—could not be addressed with this approach. Here I demonstrate this through reconstruction of the evolutionary theory of Joseph Needham (1900–1995), who pioneered the biochemical study of evolution and development. In order to address such problems, Needham employed Herbert Spencer's principles of emergence and Ernst Haeckel's theory of recapitulation. While Needham did not reject Darwinian theory, Spencerian and Haeckelian frameworks happened to better fit his findings and their evolutionary relevance. He believed selectionist and genetic approaches to be important but far from sufficient for explaining how evolutionary transformations occur.

Keywords Comparative biochemistry · Physiological evolution · Recapitulation · Needham · Haeckel · Spencer · Lucas

1 Introduction

It was the neo-Darwinian synthesis of the early 1940s that laid the basis for evolutionary theory and research during the following decades. The view that evolution results from natural selection among organisms, which acquire beneficial characters through random mutations to their genetic constituencies, became paradigmatic. But while the synthesis represents a scientific triumph, its establishment took shape within the context of high levels of scepticism, serious challenges and even doubts. Using a phrase coined by Julian

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Huxley, historian Peter Bowler referred to early twentieth-century evolutionary thought as "the eclipse of Darwinism," while other historians have noted an abundance of "Darwinian Heresies." Their studies demonstrate that the mechanism of natural selection was far from unanimously agreed upon by Darwin's contemporaries and successors, and that the polemics and debates continued well into the 1920s. For example, experimental biologist Jacques Loeb accepted natural selection as a principle governing evolution but claimed that it did not supply a mechanistic explanation for the formation of novel species. Many biologists claimed that findings in natural populations and in fossil records pointed to evolution of non-adaptive traits or what seemed as directional changes through geological times. Neo-Lamarckian claims for the inheritance of acquired characters, the conception of evolution as an intrinsically driven teleological process (orthogenesis), and the saltationist view-point of evolution as proceeding through radical changes, stood as powerful alternatives to the gradualist and selectionist Darwinian approach (Bowler 1988, 1992; Lustig et al. 2004; Deichmann 2009).[1] Jonathan Harwood and Jan Sapp demonstrate that doubts over the importance of gene mutation drove certain geneticists to accept both Darwinian selection and neo-Lamarckian environmental interactions as guiding the formation of species and of novel characters (Harwood 1993; Sapp 1987). Vassiliki B. Smocovitis interprets the success of the evolutionary synthesis not as a scientific victory in a conventional sense, but rather as resulting from efforts to establish biology as a unified and autonomous science (Smocovitis 1992). The picture that emerges is that natural selection was never part of mainstream evolutionary theory before the late 1930s.

And yet, the establishment of the neo-Darwinian synthesis from the 1940s masked the objections and grave scientific concerns over its ability to fully explain evolutionary change. The synthesis' architects anchored alternative models as product of prejudice and mistakes. Introducing his seminal book *Evolution: The Modern Synthesis*, Julian Huxley wrote that Darwinism emerged as a phoenix from the pyre kindled by the too sceptical biologists (Huxley 1942, p. 28). In a review written some four decades later, Ernst Mayr claimed that consensus was delayed primarily due to misunderstandings (Mayr 1980, p. 2). Although neo-Lamarckism was in part adopted also by Darwin, Mayr saw it as not much more than "a stumbling block in the path of a neo-Darwinian approach" (Mayr 1980, p. 15).[2] Jean Gayon claims that even during the 1920s scientists demonstrated experimentally the verities of Mendelism and the mutation theory, and that as a result "the crisis of Darwinism had largely been resolved" (Gayon 1998, p. 320).

While historians discuss in depth biological concerns with Darwinism, their accounts focus on—and thus emphasize mainly—ideological, professional or religious interests of the promoters of alternatives. Jonathan Harwood and Jan Sapp demonstrate an important role for the professional context under which geneticists worked in shaping the view of Darwinians and dissenters. Whereas Harwood emphasises institutional factors and resulting styles of scientific thought, Sapp points at struggles for authority and for position. Bowler depicts strong religious and philosophical motives as motivating conceptualizations of neo-Lamarckian and orthogenetic mechanisms. Scholars examining the reception of Darwinism in different countries place social, cultural, and political factors as leading to dominant conceptions of evolution in each particular place (Glick 1988; Todes 1989). Historians survey the scientific issues at stake, but the historiographical emphasis lies on cultural and professional issues. While current historiography explores Darwinism's

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[1] For late nineteenth-century challenges see Bowler (1988), Gayon (1998, part 2), Travis (2010).

[2] See Deichmann (2010).

scientific obstacles it leaves the synthesis' portrait as explanatory victory almost intact (Largent 2009).

This paper, which is based on analysis of the evolutionary conceptions of Joseph Needham, demonstrates that non-Darwinian approaches were crucial for studying mechanisms of evolutionary change. While cultural and professional issues were at stake Darwinism was ignored also due to its basic inability to explain how novel functions evolved. Needham's case is important because he pioneered the biochemical study of evolution and development and while he did not reject Darwin's theory his explanations relied on the approaches of Herbert Spencer and Ernst Haeckel instead. From Spencer, Needham took the conception of a tendency of biological systems to increase in complexity and to produce novelties in that process. From Haeckel Needham took the view of a close relationship between evolution and development and that evolutionary and developmental mechanisms are bound closely together. Contrary to Huxley and Mayr's positioning of the synthesis as a scientific triumph against prejudicial views, Needham's research demonstrates the conceptual importance of non-Darwinian approaches for addressing a central evolutionary question.

Significantly, other historical studies place Spencer's and Haeckel's ideas as historically influential, by demonstrating Spencerian lines of thought in evolutionary theory, and the endurance of Haeckel's theory of recapitulation (Gould 1977; Churchill 1980; Ben-Gal 1980; Rasmussen 1991; Ruse 2004; Renwick 2009). This study offers further exploration of Haeckelian and Spencerian influences as well as demonstrating that their ideas were answers to a serious deficiency in the neo-Darwinian approach. Neo-Darwinians could explain the selection of fit organisms, but were unable to place formation of fitness-attributing functions on a concrete physiological basis. Spencer's principles of emergence and Haeckel's emphasis on a relationship between evolutionary and developmental stages played an important role in filling that crucial gap. Currently the neo-Darwinian synthesis retains its paradigmatic status; and yet it is criticized for ignoring developmental mechanisms and for its limited ability to explain how evolutionary innovations are generated.

2 The Evolution of Animal Function

Joseph Needham (1900–1995) is known for his pioneering work on the history of science in China, which he commenced in the early 1940s and continued to promote until his death. His encyclopedic series, *Science and Civilization in China*, remains as the single main reference in the field and continues to promote scholarship on history of science in non-western traditions.[3] However, his work on China was the result of the second and major phase of his life after he ended a rich career as a biochemist.

During the years 1922–1942, Needham conducted research at the Cambridge Biochemical Institute under the directorship of Frederick G. Hopkins. Widely known as "the father of British biochemistry," Hopkins looked at biochemistry as an independent biological discipline and encouraged his students to extend biochemical research to novel biological fields. Needham was inspired both by Hopkins' vision and by the development of experimental zoology during his time, and targeted his research at developmental and evolutionary mechanisms. His research became geared primarily towards embryonic development; and yet a strong interest in evolution remained throughout his career

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[3] On Needham's career in Sinology see Winchester (2008). On his impact on other scholars see Habib and Dhruv (1999, p. 546).

(Needham 1931b, 1938, 1941 [1943]). He reviewed his embryological findings for their evolutionary implications and conducted studies in comparative biochemistry aimed at explaining significant transitions in evolution.[4] However, his efforts bore fruit only in a very limited way. Though Needham conducted diverse research programs and published widely, the experimental resources he needed were hardly available at Cambridge, and in the 1940s his research finally came to a halt (Armon 2009). Notwistanding this, during the 1920s and the 1930s, his efforts to address biochemically evolutionary and developmental mechanisms won wide recognition. In the early 1930s he earned the prominent position of a Reader in Biochemistry and became a leading figure in *The Society of Experimental Biology*.

Needham's evolutionary research built on the ideas of the Cambridge neurophysiologist Keith Lucas. In 1909 Lucas published a call for the study of the evolution of animal function. "No serious student of biological thought," he wrote, "can have failed to observe how small a part the hypothesis of evolution has played in the development of animal physiology" (Lucas 1909, p. 472). Tracing the course of evolution relied on morphological rather than physiological clues, and the study of evolution had not hitherto been called upon for a better understanding of animal function. "There is no break in the history of physiology to mark the pre-Darwinian from the post-Darwinian period," Lucas claimed, and "if the hypothesis of evolution were tomorrow to be proved untenable, physiologists would scarcely be concerned."[5]

Significantly, Lucas published his ideas just after Cambridge University hosted a magnificent celebration of Darwin's contribution in 1909; the centenary of Darwin's birth and the fiftieth anniversary of *The Origin of Species* (1859). Scientists and dignitaries from many countries and from leading British institutions took part in what became known as the most glorious among scientific commemorations. But whereas the event celebrated Darwin's ingeniousness, it was an occasion for strong doubts as well. At the time Darwinian theory was challenged by claims that recent findings concerning adaptation and speciation could hardly be explained by a gradual selectionist process. Certain delegates examined potential future directions for research in the light of recent findings in genetics and cytology while others debated whether Darwin's theory explained currently known biological facts (Richmond 2006). In that context Lucas pointed at an important concern that was barely touched upon by the conference attendants.[6]

Lucas called for addressing the evolution of animal function on a fundamental level and suggested comparative and developmental approaches for that purpose. While morphologists compared organisms' form and organs' shape, he claimed that physiologists need to isolate and compare functional cells. However, charting the function's evolution hinged on the availability of "a number of animals which formed a continuous series of successive steps in a process of evolution" (Lucas 1910, p. 328). Acknowledging the unlikelihood of such a series existing, Lucas suggested looking into embryogenesis for hints. He noted that

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[4] Whereas Needham invested primarily in the study of embryology, Ernest Baldwin, who joined Needham as research student in 1930, came to lead research in comparative biochemistry (Needham et al. 1932; Needham 1950; Baldwin 1937; Kerkut 1970).

[5] On the importance and centrality of morphological research in the establishment of Darwin's research see Richards (1992).

[6] Lucas' presence in the celebrations is undocumented though it is probable that he was in the audience during the proceedings. Preparations for the celebration involved leading Cambridge physiologists as well as of Sir Horace Darwin (Charles' ninth child), who owned the Cambridge Scientific Instrument Company in which Lucas served as director. Lucas' publishing on evolutionary theory and its deficiencies soon after the celebrations attest to their influence (Anonymous 1909, pp. 7–8; Richmond 2006, p. 455).

from the early nineteenth century leading morphologists had observed similarities between ontogenetic and phylogenetic stages. Towards the end of the century Ernst Haeckel promoted the claim that stages of embryonic development of an animal recapitulate the phylogenetic stages that its species went through. The theory of recapitulation, which in 1872 gained the title of The Biogenetic Law, guided many comparative studies in embryology. Haeckel's theory, according to which phylogeny determines ontogeny, was rejected but similarities of developmental and evolutionary sequences attracted the interests of leading biologists (Ridley 1986; Hall 2000; Richards 2004). For Lucas it sufficed to take note of the fact that development of the organism resembled, at least to a certain extent, stages in the evolution of its species. Therefore studying embryonic development of animal functions could supply important hints for their evolution in ancestors and compensate at least partially for the lack of living transition stages (Lucas 1910, pp. 329–331).

Lucas' evolutionary research program did not materialize; in 1916, tragically, he lost his life in a flight accident. However, his words deeply influenced Needham who arrived at the Cambridge Medical School two years later. The courses in physiology and biochemistry touched mainly on function in vertebrates, because both disciplines were by then primarily fields of medical research. Nevertheless his mentors promoted the widening of investigations to other organisms as well (Erlingsson 2007). Joseph Barcroft, leader in vertebrate respiratory physiology, and his co-worker Thomas Parsons, studied invertebrates' respiratory pigments as well (Barcroft and Barcroft 1924; Parsons and Parsons 1923). Hopkins, considered the founder of biochemistry as an independent biological discipline, encouraged his students to study metabolism in a diversity of living systems (Kamminga and Weatherall 1996). Needham read Lucas' papers and was in close contact and very much inspired by promoters of the comparative approach.[7] "[Though] the ultimate physico-chemical analysis of any particular function must be carried on with whatever species and tissue best suits the methods employed," he wrote in an undergraduate essay, "…vertebrate physiology alone gives a one sided outlook." Physiologists needed to examine organisms "the whole way from Amoeba to man."[8] But whereas his mentors aimed comparative research at enhancing the study of functional mechanisms, he aimed directly at evolutionary questions. Following Lucas, he wrote that "the greatest ignorance exists as to the evolution of the various functions of the body" (Needham 1923, p. 97). Respiration in an amoeba differed considerably from respiration in the mammal and it should be the comparative physiologist's purpose to decipher how the difference developed. To Lucas' decade old call and rhetorical question, "may there not be an independent science of the development of function, whose value will lie in its direct contribution to the understanding of evolution?," Needham replied in the affirmative and followed where Lucas had left off.

Whereas Lucas looked into cells, Needham believed that biochemistry—which examined physico-chemical compositions of tissues and cells—could approach physiological evolution on a more fundamental level. "[I]mportant as the distribution and form of organisms may be, it cannot be so much so as the actual examination of the physico-chemical attributes of living matter itself," he wrote (Needham 1925a, p. 224). Studies demonstrating relationships between respiratory and photosynthetic pigments, and that functional pigments formed as by-products of metabolism, confirmed for Needham that

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[7] Needham (1929, p. 633); Needham, Notes on papers by Keith Lucas, Joseph Needham's Papers, Cambridge University Library (hereafter: JNP-CUL), file E.76; Needham to his mother, 20 and 28 November 1920, JNP-CUL-A.75.

[8] Needham, "Outstanding Problems in Physiology" (Typescript), 1922, JNP-CUL-A.724, p. 6.

slight molecular modifications could underlie significant functional shifts.[9] He saw these studies as exemplifying the task of the biochemist in the study of evolutionary mechanisms. Decades before molecular evolution made its first steps as a field of research Needham promoted the search for molecular clues for significant transitions in evolution.[10]

Needham's first essays, written as part of his student examinations, touched on the biochemical basis of physiological evolution. Whereas his mentors and fellow students looked primarily into the functions of vertebrates, Needham began to speculate on these functions' evolutionary origins. In a first undergraduate essay, as required, he discussed whether blood should be considered an animal tissue.[11] His paper, based to a large extent on evolutionary considerations, was sent for publication under the title "The Evolution of the Functions of the Blood" (Needham 1923). He speculated that the animal respiratory pigment was originally a metabolic by-product that upon combination with a certain protein moiety acquired an oxygen-binding capacity. The complex, known as haemoglobin, turned functional upon its incorporation into certain types of circulating cells. That event began their transformation into functioning red blood cells, which in turn revolutionized the organism's energy-producing arsenal. In a second undergraduate essay Needham was asked to discuss the phenomena of muscle tonus and to compare it with muscle contraction. His paper presented a speculative survey of the evolution of muscle tonus in relation to changes in the biochemical components of the tissue.[12]

Interest in evolution guided some of Needham's experimental programs as well. In the mid-1920s he compared changes in oxidation states between species of protozoa and between eggs of diverse invertebrates (Needham and Needham 1927). In 1932, joined by Ernest Baldwin, Needham conducted research on comparative muscle metabolism that built on ideas he had expressed in his muscle tone essay (Needham et al. 1932). Two years later Needham and Baldwin conducted a study of nitrogen metabolism in snails, in which they searched for characters that distinguished molluscan from vertebrate mechanisms (Baldwin and Needham 1934). Needham surveyed molluscs from different species and correlated patterns of migration and habitat with transformation in the organism's metabolic machinery (Needham 1935). Three years later he reviewed his study "as an instance of the way in which comparative biochemistry may contribute to the problems of evolution" (Needham 1938, p. 240). Interest in the evolution of animal function was instilled in Needham from the time he had first read Lucas' papers and it was a central concern throughout his career.

3 From Phylogeny to Ontogeny, and Back

From the mid-1920s, Needham's main focus became the biochemistry of the developing embryo. However, he retained a strong interest in evolutionary mechanisms. In fact, his developmental research was also aimed at evolutionary questions. He recognized that the comparative biochemist, just like the comparative physiologist, was limited in approaching

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[9] Needham, "Notes on lecture on pigments, biochemistry undergraduate notebook", JNP-CUL-E.16; Needham, "Notes on Hemoglobin and Chlorophyll", JNP-CUL-E.190; Needham, "Note on Melanin and similar pigments", 1922, JNP-CUL-E.37.

[10] Progress in molecular evolution and comparative biochemistry took place mainly with the improvement of molecular techniques in the 1950s and 1960s. See Dietrich (1998).

[11] Needham, "The Blood as a Tissue," JNP-CUL-E.86.

[12] Needham, "Muscular Tone," 1922, JNP-CUL-F.4-F.5.

concrete stages in the evolution of a trait. Lucas' advice to investigate the ontogeny of function as a guide to its evolution formed an important motivation for Needham's investments in embryology.

In his first embryological programme Needham demonstrated a succession of physiological functions in development. While he aimed primarily at the physiology of the developing chick he noted evolutionary implications as well. The study demonstrated that the embryo makes a differential use of energy sources in the course of his development. Whereas it was the accepted view that fat is the only important nutrient, Needham found dominant use of carbohydrates and a subsequent employment of proteins as energy sources. He suggested that the embryo first uses carbohydrate, then protein, and only then the fat (Fig. 1). Another important finding concerned with the metabolic process that was involved in excretion. Needham found that in using proteins as energy source the chick's by-products were first urea, than ammonia, and then its primary excretory product—uric acid (Fig. 2). The results he obtained suggested a succession of both energetic and excretory metabolic products (Needham 1926a, c). By comparing his findings in the chick with the results of studies on other species, he demonstrated that whereas chicks combust minimal amounts of protein and excrete primarily uric acid, fish and amphibians make significant energetic use of proteins and excrete primarily urea (Gray 1926; Needham 1927, 1930).

Needham suggested that nutrition and excretion patterns reflected the organism's conditions of living. Animals living in aquatic environments "need exercise no economy in the combustion of protein" because they excreted the products of the process to the environment (Needham 1927, p. 158). However, the chick had a very limited space in which to excrete and so its ability to exist depended on reduction in protein use. The chick's employment of uric acid reflected a similar situation. Ammonia and urea are soluble and therefore would tend to diffuse in the egg and could have toxic effects on the chick. However, insoluble uric acid could be packed into a well defined store in the chick's

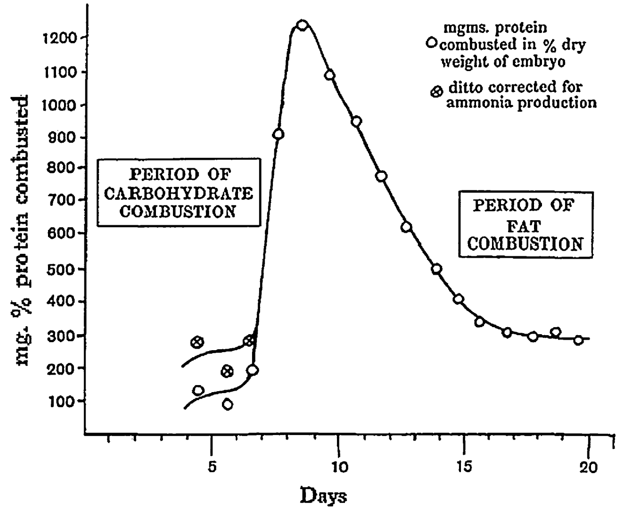

Fig. 1 Graph by Needham depicting a peak in protein combustion (i.e., use as energy source) situated between periods defined by the data of previous investigators as reflecting sugar and fat use (Needham 1926c, p. 150. Reproduced with permission of the Company of Biologists.)

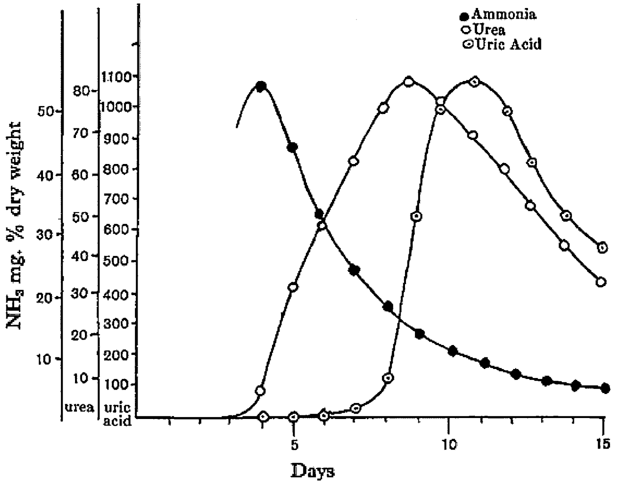

Fig. 2 Graph by Needham depicting changes in the levels of protein combustion products during development. Though absolute levels differed considerably, Needham claimed that a clear pattern of succession could be observed (Needham 1926c, p. 149. Reproduced with permission of the Company of Biologists.)

allantoic fluids. "The form of excretion of nitrogen adopted by an animal depends principally on the conditions under which its embryo has to live," he wrote, "…shut up as it is in its closed box the chick embryo would evidently find uric acid by far the most convenient excretory product" (Needham 1929, p. 636). The chick's metabolic use of protein and uric acid enabled egg-laying species "to pack their embryos into solid and liquid tight boxes," thus allowing for the emergence of terrestrial life. Avian evolution, he claimed, depended on the emergence of metabolic mechanisms that minimized protein use as energy source during embryogenesis, and that maximized the use of uric acid as its product (Fig. 3).

Needham observed in evolutionary processes a gradual increase in the organisms' independence from the environment, and embryonic repetition of phylogenetic stages. He showed, based on integration of biochemical data, that as an animal appears higher on the taxonomic scale its egg demonstrates an "increasing isolation from dependence of the outside world" (Needham 1931a, p. 1617). Lower vertebrates were laid only with organic substances and needed to absorb ions, water, and oxygen from the outside. Bony fishes and amphibians which are higher vertebrates supplied their eggs with ions but still demanded a water supply from the environment. Reptiles provided embryos with water as well and birds even with some level of oxygen (Fig. 4). The avian embryo's development depended on gas exchange but other than that the egg was practically a closed box (Needham 1931a, pp. 1613–1624).[13] That highly advanced stage and its freedom from environmental dependency was achieved by means of protection against water loss, and, as Needham claimed to have discovered, by pre-modifications of the organism's metabolic apparatus.

Embryonic repetition of evolutionary stages was the second general phenomena that Needham described. The metabolic excretory succession he observed reminded him of a similar sequence in phylogeny, as yeasts and insect larvae excrete ammonia, amphibians

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[13] Needham coined the term "Cleidoic Egg" to describe the eggs of avian species. Cleidoic is the Greek for "to enclose."

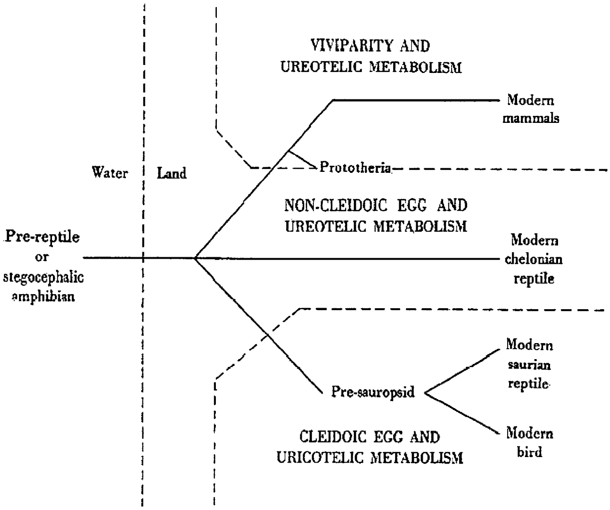

Fig. 3 Graph by Needham depicting a correlation between urea- and uric acid-based protein metabolism (uerotelic and uricotelic metabolism, respectively) of the embryo, and the habitat of the conditions of living of the species (from Needham 1938, p. 238. Reproduced by courtesy of John Wiley and Sons.)

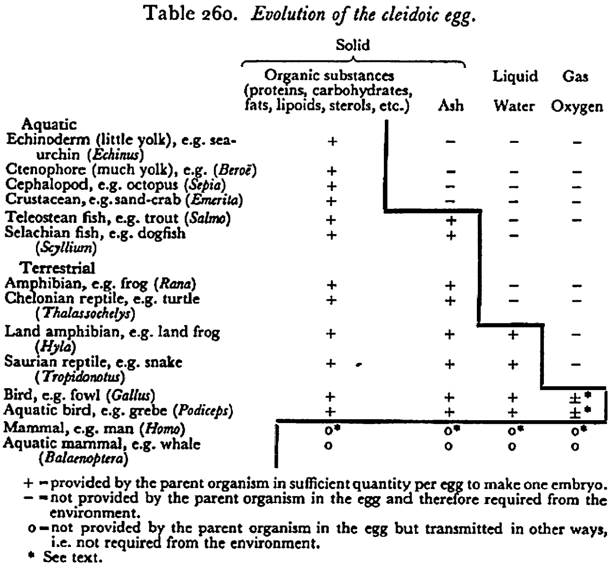

Table 260. *Evolution of the cleidoic egg.*

	Solid		Liquid	Gas
	Organic substances (proteins, carbohydrates, fats, lipoids, sterols, etc.)	Ash	Water	Oxygen
Aquatic				
Echinoderm (little yolk), e.g. sea-urchin (*Echinus*)	+	–	–	–
Ctenophore (much yolk), e.g. (*Beroë*)	+	–	–	–
Cephalopod, e.g. octopus (*Sepia*)	+	–	–	–
Crustacean, e.g. sand-crab (*Emerita*)	+	–	–	–
Teleostean fish, e.g. trout (*Salmo*)	+	+	–	–
Selachian fish, e.g. dogfish (*Scyllium*)	+	+	–	
Terrestrial				
Amphibian, e.g. frog (*Rana*)	+	+	–	–
Chelonian reptile, e.g. turtle (*Thalassochelys*)	+	+	–	–
Land amphibian, e.g. land frog (*Hyla*)	+	+	+	–
Saurian reptile, e.g. snake (*Tropidonotus*)	+	+	+	–
Bird, e.g. fowl (*Gallus*)	+	+	+	±*
Aquatic bird, e.g. grebe (*Podiceps*)	+	+	+	±*
Mammal, e.g. man (*Homo*)	o*	o*	o*	o*
Aquatic mammal, e.g. whale (*Balaenoptera*)	o	o	o	o

+ = provided by the parent organism in sufficient quantity per egg to make one embryo.
– = not provided by the parent organism in the egg and therefore required from the environment.
o = not provided by the parent organism in the egg but transmitted in other ways, i.e. not required from the environment.
* See text.

Fig. 4 Table by Needham depicting the concomitant increase in nutrient supply to the embryo and in its independence from the environment (from Needham 1931a, p. 1617. Reproduced by courtesy of the Cambridge University Press.)

excrete urea, and adult birds and reptiles excrete uric acid. He suggested that the passage of the developing embryo through the use of the three end-products could reflect a recapitulation of its pre-terrestrial or aquatic ancestry (Needham 1926c). Needham viewed the rise in the organisms' independence and repetition of phylogenetic stages in ontogeny as important components in the process of animal evolution. His research was primarily in embryology but he placed his findings as pointing to evolutionary transitions as well.

4 A Spencerian Approach

The first principle that Needham found—an inherent tendency for increasing organismic complexity towards greater independence from the environment—drew strongly on principles enunciated by Herbert Spencer. Spencer was Darwin's contemporary and among the main promoters of evolutionary thought in the second half of the nineteenth century.[14] Whereas Darwin examined biological evolution, Spencer suggested a theory that described evolution in physical and sociological systems as well. In his *System of Synthetic Philosophy*, published sequentially during the second half of the nineteenth century, Spencer claimed that all systems were formed in evolutionary processes guided by similar principles. According to his conceptions, evolution began with a relatively indefinite, incoherent, and homogeneous aggregate that gradually evolved into coherent, heterogeneous and organized structures: Complex organic constituents formed from simple organic substances; cells evolved into multicultural organisms; and primitive tribes differentiated into highly specialized nation-like communities.

An evolutionary process, Spencer claimed, is that of transition from homogeneity to heterogeneity through both integration and differentiation: Simple components are integrated, and form simple aggregates, that concomitantly, due to interactions of their parts, go through internal differentiation and specialization (Thomson 1906, pp. 209–215). Spencer wrote extensively on embryonic development and biological evolution. In accordance with his principles, he described embryonic development as the transformation of a homogenous egg into a highly organized embryo. The embryo grows in bulk and thus goes through the process of integration; in parallel—due to interactions in and between its parts—it differentiates into an organized formation of tissues and organs. Gradually, as its parts specialize, the organism frees itself from dependence on its nurturing environment and becomes master of its fate. Similar processes take place in organic evolution and guide the gradual process of species formation from amoeba to man. Spencer was essentially Lamarckian and believed that modifications acquired during the life of individual animals are transmitted to the progeny (Spencer 1866; Thomson 1906, pp. 93–115; Ben-Gal 1980, pp. 42–80). As evolution proceeded, it produced organisms with ever higher levels of complexity and independence.

Needham recognized Spencer as the main relevant authority in evolutionary matters and drew on his system of thought in examining mechanisms of change. He credited Spencer with influencing a move from vitalist and teleological understandings of biological processes to their being placed on physico-chemical and mechanical principles (Needham 1925a, p. 247, 1925c, p. 37). Studies of physiological evolution, he claimed, were anchored in Spencer's definition of life as "the continuous adjustment and adaptation of the organism to the environment" effected by ceaseless activity among its components. Spencer anchored the process in physical and energetic processes taking place between the components of the evolving system. Needham believed that biochemists could address these processes in concrete physico-chemical and molecular terms.[15] Throughout his career

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[14] On the diversity of approaches to evolution in this period see Bowler (1988). On Spencer's influence see Ruse (2004).

[15] Needham, "The Blood as a Tissue" (undergraduate essay), JNP-CUL-E.86, p. 4.

he posited Spencer's principles of an evolutionary rise in the levels of organization and a tendency for increased independence from the environment as guides for studies in comparative physiology and biochemistry (Needham 1937 [1943], pp. 247–248).

Spencer's reliance on the inheritance of acquired characters did not disturb Needham. Like other scientists in Britain, chiefly Imperial College's Professor of Zoology Ernest W. MacBride, Needham took the Lamarckian option seriously (Burkhardt 1980). When Needham learned that certain degenerative states induced in cultured cells seemed to be transmitted to future generations, he wondered whether that proved inheritance of acquired characters.[16] In discussing the blood's evolution he suggested that "the long-accustomed presence of the red blood-cells must have influenced the germ-plasm which was to produce the immediate offspring in such a way that in its development cells were set apart for the work" (Needham 1923, p. 106). Needham's understanding of hereditary mechanisms fitted well with the Lamarckian conceptions on which Spencer's system relied.

Needham's interest in the Spencerian approach increased following an informal collaboration with physiologist-turned-psychologist Henry A. Murray. Murray is known today for studies on personality and his contributions to the development of American psychology. However during the 1920s he conducted research in physiology at the Rockefeller Institute for Medical Research in New York (Robinson 1992; Triplet 1992). Murray employed the chick in testing the correlation of functional differentiation with the changing biochemical constitution of the organism (Murray 1926b, 1927). His study, which he titled "Physiological Ontogeny," sat well with Needham's programme insofar as it examined developmental changes in physiological functions. In 1924, Murray visited Cambridge to complete his dissertation research and they both shared data and ideas (Armon 2009). Murray found Spencer's principles highly suitable for explaining his experimental results. He demonstrated that while rapid growth in mass and differentiation of organs took place in early development, chemical concentration and differentiation took place primarily in later stages. He explained the distinction between the gross- and the micro-integration processes as reflecting Spencer's principles of integration and differentiation, and chemical differentiation as reflecting a rise in complexity of the developing embryo (Murray 1926a, pp. 428–431).

Needham and Murray shared Spencerian views, they differed in that while Murray took the rise in complexity for granted, almost as a law of nature, whereas Needham wished to explain that phenomena by changing physico-chemical conditions in developing and evolving animals. Building on Spencer's principles and Murray's findings, Needham viewed embryonic development as the transformation of the homogenous egg to a heterogeneous organism; and evolution as the formation of organisms with greater independence from the environment. The biochemist entering into the study of embryology, he wrote, was struck by "the vivid contrast between the homogenous unorganized character of the raw materials and the heterogeneous organized character of the embryo" (Needham 1931a, p. 1653). He aimed at offering "a reasonable causal explanation of the origin of all the measurable properties of adult living beings from the measurable properties of their eggs," and explaining "how from moment to moment the level of actual organization in the embryo can rise" (Needham 1931a, p. 558). Spencerian principles directed Needham's view of evolution as well. He defined evolution of function as "the actual series of steps by which function grew from its simplest to its most complex form" (Needham 1923, p. 97), and laid emphasis on evolvement of chemical and metabolic processes which enabled animals greater independence from their environment. He directed his programmes of

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[16] Needham, note titled "Visit to Research Hospital, Babraham Road," 13 February 1921, JNP-CUL-E.88.

research towards exposing such novelties and at least indirectly into placing the Spencerian evolutionary framework within concrete biochemical and molecular terms.

5 Biochemistry and the Biogenetic Law

Needham also formulated evolutionary mechanisms based on Haeckel's claims for close parallelism of ontogeny and phylogeny. Like most biologists, Needham rejected the biogenetic law, but viewed the repetition of phylogeny by ontogeny to be an illuminating phenomenon. He demonstrated evidence for recapitulatory phenomena in his and others' studies of embryonic and comparative biochemistry, and declared that while Haeckel's explanation was untenable, "on the fundamental thesis that embryonic development is a historical document there is no disagreement" (Needham 1931b, p. 653). He suggested a biochemical explanation of recapitulation and with it a novel understanding of the mechanism of evolutionary change. Needham did not accept Haeckel's view point, but it guided his conception of development and evolution, and inspired him to look in the former the causes for the latter.

By the 1920s, Haeckel's, view that embryos recapitulate the history of their species by carrying the stamp of the phylogenetic past was to a large extent rejected. However, zoologists tried to find the meaning and the causal basis for similarities between ontogenetic and phylogenetic stages. In the late nineteenth century, British zoologist Arthur Milnes-Marshall claimed (1890 [1894]) that animals retain (and so "recapitulate") rudiments of their ancestors, because these rudiments serve as the basis for the development of functional organs. For example, higher vertebrates retain the notochord of lower animal orders, because this organ supports the development of their cartilaginous skeleton. In the early 1920s, marine biologist Walter Garstang offered another perspective. His studies of marine invertebrates' larvae demonstrated that important adaptive modifications take place in larval rather than adult stages. Haeckel, he claimed, wrongly interpreted the repetition as a recapitulatory phenomenon. Instead of placing phylogeny as imprinting ontogeny, biologists should look at embryonic development as shaping and constraining future evolutionary changes (Garstang 1922). Garstang's explanation challenged Haeckel's claims but opened rather than sealed the problem of recapitulation. Needham and certain leading zoologists sought to establish the phenomena's causal basis on physiological, genetical, and biochemical grounds.

Leading among Needham's contemporaries were Julian Huxley and Gavin de Beer. Huxley, who was among the leaders of experimental biology in Britain, related the recapitulation that *morphologists* described, to processes that *physiologists* were already able to measure. He studied differential growth rates in and between the organs of growing insects and suggested that what seemed as recapitulation of morphological patterns actually reflected differential growth rates among the growing organism's parts. If the rate of a certain process was slowed down sufficiently, the appearance of the character that this process underlies could be pushed back from an adult to an embryonic stage (Huxley 1932). Gavin de Beer, who began his research as Huxley's student, built on Huxley's claims and explained ontogenetic-phylogenetic similarities as reflecting evolutionary changes in the timing of developmental events. The concept of heterochrony that de Beer coined in 1930 formed the basis for much of the later work on the relation between ontogeny and phylogeny. Huxley and de Beer speculated that the activity of specific rate-determining genes underlay rates and timing changes, which governed what seemed as morphological recapitulatory phenomena (Brigandt 2006; Horder 2006).

Needham was familiar with Huxley's work and it was Huxley who called his attention to Garstang's paper.[17] But while Huxley and de Beer aimed at genetics, Needham looked for biochemical mechanisms. "The theory of recapitulation," Needham wrote, "…has been of great service as a stimulant to morphological research, though untenable in its extremer forms. But in biochemistry, its applications have so far been few" (Needham 1926c, p. 152). Based on his and others' studies, he demonstrated biochemical and physiological evidence for repetitions of phylogeny in ontogeny. As a student, Needham had written to Marcus Pembrey, professor of physiology at Guy's Hospital in London, who lectured on embryonic physiology, to ask for his views on Lucas' ideas. In reply to Needham's letter, Pembrey wrote that he "always held the position that the theory of evolution is the best guide in physiology" and that he had tried to apply it in research.[18] He shared with Needham his finding that in early development the chick responded like a cold-blooded animal, whereas at hatching it showed regulation of its temperature, just like warm-blooded animals (Pembrey 1894). Initially Needham appreciated the study chiefly as a contribution to embryonic physiology (Needham 1925b, p. 42). Yet as he became interested in recapitulation he interpreted Pembrey's results in a similar manner. The chick's transition from the cold-blooded to the warm-blooded state, he wrote, suggested a recapitulation of its phylogenetic past (Needham 1926c, p. 153).

With his own, with Pembrey's, and with additional examples that Needham found of similarities in ontogenetic and phylogenetic sequences, he became convinced that biochemistry could explain recapitulatory phenomena. In a paper titled "The biochemical aspect of the recapitulation theory," sent in 1929 to *The Biological Reviews*, he surveyed morphologists' deliberations with Haeckel's theory and offered a physico-chemical explanation for the repetitions observed. Needham modified Milnes-Marshall's theory and claimed that ancient structures may supply not only scaffolds, but also specific biochemical stimuli. He built on findings by Hans Spemann and his colleagues concerning the role of tissue induction in embryogenesis. They found that certain tissues could induce the differentiation of their neighboring ones, and conceived of development as a succession of such inducing interactions. Integrating these findings and Garstang's formulation, Needham suggested that the observed repetitions reflected conserved biochemical stimulatory processes which the retained structures mediated.[19]

Integrating Haeckelian with Spencerian frameworks, Needham placed recapitulation "as fundamentally the result of the necessary passage from simplicity to complexity, from low to high levels of organization" (Needham 1930, p. 156). It was hard to imagine, he figured, "that the mechanism which produces urea is essential as containing the formative stimulus for the mechanism which produces uric acid" (Needham 1930, p. 151). Rather, "just as in the phylogenetic order, urea excretion succeeded ammonia excretion, being one step more complicated, and in the same way uric acid succeeded urea; so the avian embryo, moving forward through its ontogeny in stages of ever increasing complexity and heterogeneity, excretes in the same order, ammonia, urea, and uric acid." The succession of biochemical functions resulted in a general tendency of passage—in evolution of a species and in development of individual animals—from simplicity to complexity. With modifications thus produced, animals acquired the potential for adaptation to novel environments. Needham's conception of mechanisms of evolutionary changes drew heavily on

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[17] Huxley to Needham, 1 February 1929, JNP-CUL-M.34.

[18] Pembrey to Needham, 1 February 1921, JNP-CUL-M.114.

[19] In the following decade, Needham made significant efforts to isolate such inducing molecular agents.

Spencerian and Haeckelian principles, but in a form that adapted these principles to the biochemical knowledge of his time.

6 Darwinism and Genetics

Needham's conceptions of the mechanism of evolutionary change had little in common with Darwinian principles. He was in close contact with leading biologists who already during the 1920s and the 1930s claimed that evolutionary processes need to be described in terms of mutation and selection. His colleagues Huxley and de Beer made efforts to defend Darwinian theory and place genes as central evolutionary units (Horder 2006). Ronald A. Fisher and J. B. S. Haldane, prime architects of population and evolutionary genetics, advised Needham on different aspects of his research.[20] But while Needham learned to appreciate the emerging neo-Darwinian approach he questioned the utility of selection and mutation for explaining evolutionary processes. "[Darwin] did not account for the early stages of a favourable variation; a lung so little developed as to confer no power of breathing air would be of no advantage," he wrote. "Indeed," he continued, "neither Darwinian variation nor Mendelian mutation seems as yet quite to account for those fundamental differences on which the genera and species depend." The theory of the gene is able to demonstrate "why one animal has a green liver and another a pink liver," but far less "why one animal has a liver and another a hepatopancreas" (Needham 1931b, pp. 651–652).

While Darwinians emphasized selection and adaptation, Needham's conceptions were based on emergence and innovation. Darwinians viewed natural selection as the main force in shaping the organism's characters and adaptation as enhanced fitness and reproductive success. Needham did not allude to natural selection at all; he considered the generative mechanism of evolution as a tendency for increasing complexity and organization, and looked at generation of novel characters as leading the process. "If haem [the animal respiratory pigment] was the molecule that made the mammals possible" he wrote, "uric acid was the substance that made the terrestrial oviparous animals possible" (Needham 1931a, p. 1657). He did not identify natural selection with a creative force but anchored evolutionary transformations in emergent innovations at the organism's physico-chemical and metabolic apparatus. Needham retained similar views even when the selection-mutation approach was vigorously promoted. A rise in physiological complexity and in independence of the environment were fundamental components of the law of evolution, he still strongly maintained (Needham 1941 [1943], p. 211).

Neo-Darwinians saw genes and their mutations as prime agents of evolutionary change. Needham was aware of progress in genetics, yet he conceived gene function as integrated in—rather than as the main motor of—developmental and evolutionary mechanisms. He suggested that a gene mediated the formation of a morphological character by triggering a chain of biochemical reactions that led to the formation of that particular trait. Thus, "a good deal of morphogenesis may be associated with a 'delegation of function,' the gene activating secondary key-factors, just as statesmen delegate many of their duties to

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[20] Fisher advised Needham in matters of statistics. Haldane was the reader in biochemistry who Needham came to succeed. At Needham's request, Haldane read and commented on the section on genetics and development in *Chemical Embryology* (Provine 1971, Chapter 5; Needham 1931a, pp. 608–612). Fisher to Needham, 18 January 1927, JNP-CUL-M.17; Needham to Haldane, 25 May 1930; draft corrected by Haldane, undated, JNP-CUL-F.100).

subsidiary but competent officials" (Needham 1931a, pp. 556–557). However, he claimed, there is no need to attribute all responsibility for the adult form and functions to its genetic equipment. Genes play their role in combination with other physico-chemical constituents of the egg's raw materials, and it is the composition of the egg as a whole that carries the stamp of the embryo's evolutionary past and developmental plan (Needham 1931a, pp. 554–558).

Neo-Darwinians posited gene mutations as prime generators of evolutionary innovation. The establishment of the theory of the gene in the early 1900s by T. H. Morgan and his associates marked a turning point in the understanding of evolution, though it took three decades for that view to become paradigmatic. Placing genes in the role of agents of transmission of properties across generations suggested an important evolutionary role as well. However Needham, like many other biologists in the 1920s and the 1930s, could not take such a view for granted. Geneticists demonstrated deleterious mutations and mutations effecting trivial characters, rather than mutations that could be strongly connected with fully formed animal traits. Resistance was especially strong among embryologists, since genetics could hardly offer a research approach towards the study of differentiation. The fact that all embryonic cells contain identical genetic material, but differentiate to different roles, undermined any claim for the role of genes as important determinants. Embryologists in the 1920s and the 1930s were suspicious of genetic-based explanations of development and remained distant from genetic theory and methodology (Burian 2005; Gilbert 1988). Evidence for inheritance through cytoplasmic mechanisms convinced many biologists of the possibility of a non-Mendelian, environmentally sensitive mode of heredity and trait formation (Sapp 1987; Harwood 1993; Burian 2005; Amundson 2005, pp. 175–189). Needham incorporated gene action as part of his interactive and developmental picture of evolution. Yet his reluctance to grant genes and mutation central places as generators of evolutionary innovation stood well with his colleagues' doubts.

Unlike approaches of embryologists, Needham viewed positively attempts to study genes in development and anticipated the collaboration between biochemists and geneticists in the study of embryonic development (Needham 1931a, pp. 37, 608–612). Whereas embryologists did not go for genetics, certain geneticists went for embryology, aiming to break the boundaries between the two disciplines (Davis et al. 2009). Attempts, primarily by Richard Goldschmidt and Leslie C. Dunn, inspired Needham in conceptualizing and integrating a role for genes in development and evolution. Goldschmidt, who studied sex differentiation in moths claimed that genes performed developmental effects through determining the rates of important physiological processes. Needham learned about Goldschmidt's work from Huxley, who promoted Goldschmidt's ideas in Britain and built on them as a basis for his experimental research (Richmond 2007). Dunn, a future leader of American developmental genetics, led during the 1920s research in poultry. He investigated the genetical basis of developing chicks' skeletal diseases, and made landmark findings on embryonic interactions between genetic, nutritional and physiological factors.[21] Needham corresponded with and was visited by Dunn, and both strongly appreciated each others' work (Marie 2004). Needham learned that genes play a role in development but one that is strongly anchored in the nutritional and physiological conditions of the organism (Needham 1931a, pp. 250, 608, 1363, 1430). While accepting a role for genes in evolution and development, he anchored gene action in an emergent

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[21] In 1928, Dunn took the chair of zoology at Columbia University. The studies he conducted in the 1930s and 1940s and their follow up by his student Salome Gluecksohn-Walesch led to him being considered as the founder of American developmental genetics (Dobzhansky 1978; Gluecksohn-Walesch 1989).

developmental-evolutionary framework, rather than in the selectionist-Mendelian framework that later became dominant.

7 Mechanisms of Evolutionary Change

In the foregoing I have shown how Needham's biochemical studies of evolution and development built on Spencer's and Haeckel's approaches. Several historians have demonstrated that other scientists of Needham's period were influenced by both evolutionists. But there is a significant difference. My study emphasizes that non-Darwinian approaches were needed for addressing crucial problems of evolutionary theory, which is the mechanism of evolutionary innovation. Those problems a neo-Darwinian framework could hardly approach. The mechanism of gene mutations that became accepted as the main generator of innovations from the 1940s was not adopted or realized beforehand. The decades that followed the synthesis saw its paradigmatic entrenchment, but also recognition of the importance of emergent, developmental, and epigenetic mechanisms for explaining evolutionary change.

Spencer's contributions to evolutionary biology may have been sidelined but they were certainly not overlooked. In 1906 the Scottish naturalist Sir John A. Thomson praised Spencer's 1866 *The Principles of Biology* as a classic, with much of its content as having become common biological property—either absorbed or its conclusions independently arrived at by others. "Consciously or unconsciously," Thomson wrote, "we are now, as it were, standing on Spencer's shoulders" (Thomson 1906, p. 93). Though Spencer is recognized primarily for his influence on sociological and political thought, recent scholarship finds strong Spencerian lines of thought in biology as well. Shraga Ben-Gal finds Spencerian influences in Ludwig Van Bertallanfy's formulations of his organicist "General Systems Theory" (Ben-Gal 1980). Michael Ruse finds Spencerian lines of thought in the shifting balance theory of Sewall Wright. Wright's conception of adaptive landscape with fitness peaks, suggests Ruse, was guided by Spencer's dynamic evolutionary framework (Ruse 2004). Christopher Renwick has demonstrated the Spencerian foundation of Patrick Geddes' late nineteenth-century studies in symbiosis. His theory emphasized a strong association and a reciprocal accommodation between the symbionts, reflecting interactive evolutionary mechanisms that Spencer formulated (Renwick 2009).

Historians also emphasize the endurance of Haeckel's conceptions, anchoring that endurance primarily in the observed similarities of evolutionary and ontogenetic developments. Nick Hopwood claims that despite charges that Haeckel's comparative illustrations of vertebrate embryos were distorted so as to support his claims, they continued to be reproduced in textbooks and to encourage further research (Hopwood 2006, 2007). However, opinions differ over the extent to which the theory of recapitulation blocked or encouraged novel understandings of evolutionary mechanisms. According to Viktor Hamburger, experimental embryologists broke away from Haeckel's emphasis on evolutionary causes to embryogenesis in their search for proximate mechanist causes. In that sense, the biogenetic law—or rather reaction to the law—placed a gap between evolutionary biology and the study of development (Hamburger 1980, p. 99). Frederick Churchill describes the theory as a scientific generalization that was "difficult and time-consuming to filter out from the great sump of common wisdom," and posits the work of Needham and his colleagues as a campaign in order "to dispatch the biogenetic law in both its descriptive and casual meanings" (Churchill

1980, p. 115). In a recent reappraisal Churchill claims that biologists did recognize conserved developmental patterns but explained them as adaptations to embryonic living conditions rather than as a recapitulation of a species' history (Churchill 2007). Bowler documents studies by descriptive embryologists and evolutionary morphologists as supplying convincing evidence that indeed dispatched Haeckel's claim (Bowler 1996).

And yet, not all appreciations are negative. Stephan J. Gould and Nicolas Rasmussen present an appreciative interpretation of the status of Haeckel's generalization. Gould credits Haeckel's theory with emphasizing a strong link between evolutionary and developmental mechanisms. Gould and Rasmussen claim that the theory fell into decline due to the rise of experimental embryology and genetics, with concomitant preferences for different explanatory approaches. Recapitulationism was not and could not be disproved; rather it became unfashionable and was replaced by mechanist accounts that better suited novel research practices (Gould 1977; Rasmussen 1991). Examining Haeckel's original formulations, Richard J. Richards, Michael Richardson, and Gerhard Keuck demonstrate that Haeckel's views of species descent, similarities of ontogeny and phylogeny, hereditary adaptations, and the role of selection in adaptation, incorporated and were very close to Darwin's formulations at the period (Richardson and Keuck 2002). Richardson and Keuck even claim that Haeckel's emphasis on the conserved sequence of developmental changes contributed to a phylogenetic approach to embryonic development. Tim Horder concludes that while the law had a problematic status it nevertheless remained an actively discussed perspective. Biologists could reject Haeckel's explanation but hardly his insistence that ontogeny and phylogeny are closely bound (Horder 2008). Needham's response to the biogenetic law demonstrates that he was very much inspired by efforts to explain it mechanistically. By synthesizing Haeckel's recapitulation with Spencer's emergence principle he offered a novel way to think about evolution.

This study of Needham's work adds to those quoted and cited above in demonstrating the influences of Spencerian and Haeckelian approaches on twentieth-century research in evolution. However, the main contribution of this paper is in revealing an important scientific rationale as to why non-Darwinian approaches were called for in the first place. Needham turned to Haeckel and Spencer since selectionist explanations could not address the fundamental problem with which he was occupied. He did not accept Spencerian emergence or Haeckelian recapitulation as mechanisms, but he could rely on these conceptions in studying evolution's physiological basis. Natural selection's creative capabilities were questioned not only during Needham's time, but also following the establishment of the modern synthesis (Kutschera 2009). In a 1959 paper, Haldane wrote that selection can encourage variations which, if inheritable, will cause evolution to take place. Yet he alluded to recent findings to demonstrate that selection primarily discourages "most variations from the structures and functions normal in the species" (Haldane 1959, p. 711). Robert Reid, who examined the history of evolutionary thought from the perspective of physiology, wrote that "natural selection, as differential reproduction, appears as the products of these events and not the initiating cause" (Reid 1985, p. 8). Surveying methods for detecting natural selection in natural populations and for quantifying its influence, John Endler concludes that "natural selection does not explain the origin of new variants, only the process of changes in their frequency." The main potentials and constraints on innovations result primarily from the developmental and genetic system of the organism (Endler 1986, p. 245). Indeed, recent studies also position embryonic processes as major generators of evolutionary novelties (Müller 2007; Arthur

2004, Gilbert et al. 1996; Laubichler 2009). Eric Davidson uses his studies of the function of genetic regulatory elements in development to demonstrate that gradual mutations cannot account for radical changes in body forms observed in evolution (Davidson 2006). Needham's reliance on Spencerian and Haeckelian principles reflected his wish to investigate the mechanism by which evolutionary novelties emerged. Similar concerns continue to form a guide for evolutionary thought.

Needham departed from active research when natural selection became accepted as a primary evolutionary mechanism. The establishment of the one-gene—one enzyme theory, the DNA structure and its role in protein synthesis, and the operon model of gene regulation, strengthened neo-Darwinian claims, and laid the basis for genetic conceptions of evolution and development. But while most biologists granted the neo-Darwinian theory a paradigmatic, if not dogmatic, status, certain leading researchers suggested other evolutionary models. Conrad H. Waddington, Needham's collaborator and a founder of developmental genetics, placed evolutionary processes on developmental grounds and promoted a semi-Lamarckian mechanism for the production of adaptive changes. Waddington's concepts of "canalization" and "genetic assimilation" still guide certain lines of research in developmental genetics (Siegal and Bergman 2002). Eva Jablonka and Marion Lamb demonstrate that Waddington was not alone, and point to wide recognition of epigenetic inheritance mechanisms by which acquired characters are transmitted (Jablonka and Lamb 2005). Susan Oyama, Paul E. Griffiths, and Russell D. Gray emphasize that evolution proceeds through developmental processes that incorporate—but are not solely guided by—gene function (Oyama et al. 2003). Current studies demonstrate the need to go beyond gene-based selectionist interpretations and to examine the role of environmental clues, tissue structures, cell–cell interactions, and additional physico-chemical factors as guides for evolutionary and developmental changes (Müller and Newman 2003). Massimo Pigliucci claims that findings concerning the role of emergent systemic properties and embryogenesis in evolution call for "extended evolutionary synthesis," embracing Darwinism and Mendelism, but as part of rather than as the main evolutionary mechanisms (Pigliucci 2009). Needham, who pioneered the biochemical approach to evolution and development, would not be surprised. Though neo-Darwinism reigns, many biologists find that it is not sufficient for the explanation of evolutionary processes, far from it.

The history of biology describes an eclipse that blocked progression from Darwin's theory in the mid-nineteenth century to its unification with genetics and the establishment of the neo-Darwinian synthesis less than a century later. Needham's research suggests that Darwinism was not eclipsed, but was surpassed by other approaches that proved efficient for the study of evolutionary mechanisms. In a recent re-visit of the eclipse of Darwinism, Bowler writes that "we need more attention focused on non-Darwinian theories such as neo-Lamarckism and orthogenesis, and more generally on the whole 'developmental' model of evolution best seen in the recapitulation theory" (Bowler 2009, p. 3). Science educators Eugenie C. Scott and Glenn Branch claim that evolutionary theory should not be equated with Darwinism, and that conceptions of evolutionary mechanisms should not be equated with selection and mutation alone. In the 150 years since the first publication of Darwin's *Origin* evolutionary theory was reshaped by numerous conceptual and theoretical approaches (Scott and Branch 2009). The survey of Needham's evolutionary theory demonstrates the endurance of Spencerian and Haeckelian approaches and further emphasizes the need to study the history of evolutionary theory in all its strands.

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