Alternatives to Darwinism in the Early Twentieth Century

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Abstract Julian Huxley claimed that the period around 1900 experienced an 'eclipse of Darwinism' when natural selection was rejected in favour of alternative mechanisms of evolution. These included the Lamarckian theory of the inheritance of acquired characteristics and the belief that variation was directed by forces internal to the organism. Mendelism undermined the credibility of these earlier ideas, but they survived in some areas of biology well into the twentieth century. Mendelism itself derived in part from the theory of evolution by sudden, discrete jumps or saltations.

This chapter describes these non-Darwinian theories and notes the relationships between them. It also identifies the motivations that encouraged biologists to prefer them and describes the evidence they presented. The role of the debate over 'form' and 'function' is stressed, along with the suggestion that much of the debate was driven by disputes over the nature of variation and its role in evolution. The bulk of the chapter consists of a detailed outline of the ways in which the non-Darwinian theories survived into the early twentieth century.

Keywords Acquired characters • Lamarckism • Mutation theory • Neo-Lamarckism • Non-adaptive evolution • Orthogenesis • Saltationism

1 Introduction

The evolutionary debates of the late nineteenth century had been conducted using evidence primarily from areas such as morphology, palaeontology and field studies. Major disagreements had arisen over how the process of development had occurred. Darwin's own thinking contained components that could be developed in different ways (see Delisle 2017), but the theory of natural selection came under increasing pressure from a number of alternatives, initiating what Julian Huxley (1942: 22–26) called an 'eclipse of Darwinism' (Bowler 1983). Around 1900, the increasing level

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of experimental work in the life sciences, sometimes referred to as the ‘revolt against morphology’, intensified the crisis (Allen 1975). The new science of genetics initially added to the problems facing all of the alternatives, Darwinism included.

With hindsight we know that the dispute between the early geneticists and the Darwinians would ultimately be resolved, leading to what Huxley (1942) called the ‘modern synthesis’ (Mayr and Provine 1980). The difficulties facing alternatives such as the Lamarckian theory of the inheritance of acquired characteristics gradually intensified. But in the first decade of the twentieth century, no one could have predicted the outcome of the debate, and authoritative surveys such as that of Kellogg (1907) still argued that the Darwinian theory faced serious problems. Non-Darwinian ideas continued to play a significant role into the 1930s, especially in those areas of the life sciences least influenced by genetics. By the 1950s, the critics of Darwinism had been largely marginalized, although outside the scientific community there was increased opposition on both religious and ideological grounds. Depew (2017) shows how non-Darwinian ideas influenced the development of the modern synthesis, while this chapter focuses on those naturalists who still saw non-Darwinian mechanisms as the primary cause of evolution.

When the author of this chapter first began to study the ‘eclipse of Darwinism’ in the 1980s, the triumph of the modern Darwinian theory made it easy to dismiss the alternatives as blind alleys into which scientists had been led temporarily. It was necessary to argue that, right or wrong, those theories had played so significant a role that historians who ignored them would not produce a balanced view of how evolutionism actually developed. Hindsight was not a valid reason for dismissing non-Darwinian theories as a trivial side issue.

In recent decades, our interpretation of this episode has been transformed by the emergence of evolutionary developmental biology. This has reopened issues once marginalized by genetics and the modern Darwinian synthesis. Some enthusiasts see ‘evo-devo’ as reintroducing a role for non-selectionist factors such as Lamarckism, while even those sceptical of this view acknowledge that the older theories were not as wide of the mark as was once claimed. Esposito (2017) traces some of the developments that have prefigured the rise of evo-devo (see also Gissis and Jablonka 2011; Laublichler and Maienschein 2007).

2 Conceptual Issues

There were three major non-Darwinian positions: the Lamarckian theory of the inheritance of acquired characteristics, orthogenetic theories based on the notion of directed variation, and saltationist theories which assumed that new species appeared suddenly through discontinuous ‘leaps’. But this simple division conceals a multitude of complexities and it will be useful to identify the key conceptual issues over which the protagonists of the theories disagreed, both with the Darwinians and among themselves.

Two crucial areas can be identified. The first centres on whether evolution is directed by external factors such as adaptation to the environment, or by internal forces directing individual variation in a manner independent of external constraints. This issue interacts with a second disagreement over the nature of the variations seen as the raw material of evolution. Are those variations directed or undirected, and if they are directed is that direction controlled by factors internal or external to the organism? The debates were often perceived as a dispute over the role of form and function in the shaping of the organism's morphology (Russell 1916). If internally controlled variation directs evolution, it will determine form irrespective of the demands of functional adaptation. If adaptation is crucial, form must follow the demands of function. These disagreements were perceived differently in rival research traditions and the various national intellectual and scientific contexts (as shown for instance in Levit and Hossfeld 2017; Loison 2017).

Darwin assumed that variation is undirected in the sense that a range of slight modifications are available within the population. Something causes individuals to differ among themselves, but he did not believe that the cause predetermined the appearance of only one (or a small number) of new characters. The sheer width of variation available in a population meant that this factor could not in itself direct evolution—evolution is more or less open-ended. The only way that a direction can be imposed is by selection. Some external factor—the environment or the human breeder—allows only certain variants to breed and suppresses all the rest. Natural evolution is adaptive because only variants fitted to the environment will pass their characters on to future generations.

Lamarckism and orthogenesis both imply that variation is directed along determined channels but disagree on whether the direction is imposed by factors external or internal to the organism. Lamarckism sees new characters acquired by the organism in the course of its life as evolutionarily significant variation—significant precisely because they can be passed on to the next generation. A Darwinian or a geneticist could in principle accept that individuals can acquire new characters but would dismiss them as irrelevant because they cannot be inherited. Lamarckians took it for granted that the new characters they focused on were developed by the organism as it accommodated itself to the demands of the environment, as in the popular if misleading image of the giraffe stretching its neck. Evolution was necessarily adaptive, so Lamarckism and Darwinism supplied alternative explanations of the same phenomenon, although each had particular types of adaptation it found easier to accommodate.

This superficial agreement should not blind us to the deep conceptual gulf between the two positions. For Lamarckians, variation was conceived as an addition to the development of the organism, a new stage added in the adult phase of life. To be inherited the acquired character had to be pushed back into the process of ontogeny, so that ontogeny was, in effect, the summation of all the characters acquired by previous generations. Lamarckism was associated far more closely than Darwinism with the belief that ontogeny recapitulates phylogeny (Gould 1977). For Darwinians, the open-endedness of variation made more sense if the new characters were seen as distortions of the original ontogeny rather than additions to it, making it less likely that ancestral adult characters were recapitulated in the embryo.

More seriously for the wider debate, the Lamarckians portrayed natural selection as a purely negative process—it simply eliminated the vast majority of variations produced within the population. The survival of the organism depended on luck—if it was born with a maladaptive character, then nothing it did would prevent it being killed off in the struggle for existence. In the Lamarckian theory, organisms were active agents able to respond positively to environmental challenge, acquiring new characters that gave them a better chance in life but also shaped the future of their species.

This claim was crucial for those concerned about evolutionism's religious, moral and social implications. Some Lamarckians became vitalists, seeing the organism as an agent imbued with a power of choice that lifted it above the status of a material system. This made the theory easier to reconcile with the hope that evolution expressed a divine purpose. Others focused on the moral and social implications. Exponents of free-enterprise individualism and their opponents who favoured state-controlled education both seized on the idea that the individual can be shaped by its environment to argue that Lamarckism offered a way of improving the human race. This diversity of applications has resulted in conflicting interpretations of the theory's influence among historians.

For any theory of adaptive evolution, the concept of specialization offers a way of imagining a form of pre-direction in the results. Once a tendency to specialize for a particular way of life has been established, it will be beneficial for future generations to continue the trend as long as the environment remains suitable. Darwinists accepted this point, but some Lamarckians took it to heart and argued that their theory offered a better way of explaining the apparently directed trends seen in the fossil record. Orthogenesis too sought to explain the pre-directed nature of evolutionary trends but did so by rejecting the role of adaptation altogether. If variation was directed along predetermined channels, then a species would continue to evolve along the path marked out for it whether the results were adaptive or not. Evolution was independent of adaptive constraints and might even produce maladaptive features. The direction of variation was assumed to be controlled by the process of ontogeny. The developmental forces that produced the adult organism could somehow push further along the same path. For this reason, orthogenesis, like Lamarckism, could easily be linked to the belief in recapitulation.

For those Lamarckians who imagined that specialization would impose a trend on the acquisition of new characters, it was possible to see a link with orthogenesis. An adaptive trend leading to increased specialization might gain a kind of 'momentum' that would carry on beyond the point of maximum fit with the environment, producing overdeveloped characters that were eventually maladaptive.

By denying or limiting the role of adaptation, this approach also tended to subvert another key component of Darwinism: the image of the 'tree of life'. Because he did not believe that variation constrained the process of natural selection, Darwin could see how a species could divide when exposed to different environmental conditions. This is why biogeography played such a role in his thinking—migration explained how and why the divergences took place. Visualizing the overall pattern of evolution as an ever-branching tree was an obvious extension of this approach. As a consequence, Darwinians assumed that when a group of species shared a character, it must have been inherited from a recent common ancestor. By contrast, the orthogenetic approach encouraged naturalists to see evolution as a process in which parallel lines could advance in the same direction because they were driven by the same variation trend. They would thus independently develop the same characters, so the possession of a common character was not evidence of divergence from a common ancestor. Evolution exhibited a tree-like structure overall, but parallelism implied that each major branch consisted of a series of independent lineages developing through the same predetermined pattern of development.

Saltationism also minimized the role of adaptation by seeing forces internal to the organism as the primary agent producing new species. But instead of treating ontogeny as a positive directing agent, the saltationists focused instead on the discontinuity of variation. Saltations or sudden leaps would sometimes produce a range of forms with entirely new characters which were the true source of new species. Since the new characters were not formed by the gradual addition of small individual differences, there was no opportunity for the environment to impose any constraints on their production. Saltationism thus challenged both the Darwinians and the Lamarckians by denying two key principles, those of continuity and utility.

In principle, the supporters of orthogenesis could have accepted that their variation trends proceeded by a series of discrete steps. But most of the saltationists who became active around the turn of the century favoured a model in which a whole range of characters could suddenly appear, immediately fragmenting the species into several new subspecies. While denying the role of adaptation in the production of the new forms, this approach did at least retain the model of evolution as an ever-branching tree. Hugo De Vries even tried to work out an accommodation with Darwinism by arguing that natural selection would eventually eliminate most of the new forms.

3 Lamarckism

The term 'Lamarckism' was used in the late nineteenth century to denote what had been just a single component of the evolutionary theory advanced by J. B. Lamarck. This was the inheritance of acquired characteristics or use inheritance—the idea that if an animal modified its bodily structure by adopting new habits, the modifications would be passed on to future generations and could thus accumulate to allow the species to adapt to a changed environment. Lamarck's writings had embedded this into a theory that in many other respects was unacceptable in the post-Darwinian world (Hodge 1971). But many later naturalists adopted the idea without reading Lamarck's own writings. Alpheus Packard (1901) provided the first detailed account of Lamarck's life in English. Darwin himself had allowed a limited role for the inheritance of acquired characteristics, but by the end of the century there were many who saw this as the more significant mechanism of adaptive evolution. The term 'neo-Lamarckism' was coined by Packard in 1889 to denote this position and also came into wide use (Bowler 1983, chaps. 4 and 6).

Lamarckism was never a unified movement because its basic concept (the inheritance of acquired characteristics) could be supported by different arguments and given different implications. This creates problems for historians who tend to focus on a particular interpretation and are then reluctant to accept that others were really seen as 'Lamarckian' at the time. Some think Lamarckism is defined by commitment to vitalism and teleology. This was indeed an important Lamarckian movement, but there were also materialists and naturalistic thinkers who endorsed the inheritance of acquired characteristics.

Other historians have assumed that Lamarckism was an ideologically progressive movement linked to a rejection of 'social Darwinism' and race theory. Arthur Koestler (1971) praised the Lamarckian experiments of Paul Kammerer (discussed below), not realizing that some of his supporters held racist views. Lamarckism was linked to progressive political views by Kammerer but also by the Soviets during the repression of genetics under T. D. Lysenko. The latter episode reminds us that the theory has a darker side all too often ignored by historians. We need to recognize the breadth of support for the basic Lamarckian mechanism in wider culture and accept that many positions helped to keep interest in this non-Darwinian idea alive in science.

3.1 Lamarckism and Vitalism

In the late nineteenth century, the Lamarckian position was taken up by scientists and other thinkers who distrusted the materialistic implications of Darwinism. The author Samuel Butler campaigned against the selection theory and presented Lamarckism as a morally preferable view of evolution because it allowed animals to play an active role in shaping the future of their species. This position was defended in the twentieth century by the playwright George Bernard Shaw, who linked it to Henri Bergson's philosophy of 'creative evolution' (Shaw 1921: preface; Bergson 1911). Bergson's claim that living animals are driven by a non-material 'élan vital' or life force was an influential contribution to a revival of vitalist thinking that influenced a number of biologists and psychologists, many of whom were also tempted by the Lamarckian view of evolution. Loison and Herring (2017) note how it shaped the thinking of the later French Lamarckians. The position had a strong attraction for religious thinkers who could present it as being compatible with the belief that evolution is the unfolding of a purposeful divine plan. The Anglican churchman Charles Raven, for instance, promoted this view and was later a supporter of the teleological evolutionism of Pierre Teilhard de Chardin (Raven 1927, 1962; see Bowler 2001: 137–146, 277–286).

There was also a brief resurgence of vitalist thinking within the life sciences at the turn of the century. A number of biologists and psychologist gave credence to this approach, although as the century progressed they became increasingly out of touch with the latest developments. Nevertheless, several senior figures were able to keep up the impression that opposition to materialism was still active. The embryologist E. W. MacBride (1914: chap. 18) linked his support for Lamarckism to the recapitulation theory. Although originally opposed to the vitalism, he later wrote popular works linking Lamarckism to a rejection of materialism and the belief that evolution exhibited divine purpose (MacBride 1924, 1927; Bowler 2001: 144–145). The anatomist Frederic Wood Jones—known for his theory that humans and apes had evolved in parallel from a more primitive Primate ancestor—came out in open support of Lamarckism later in his career (Jones 1942). The psychologist William McDougal was one of the most prominent opponents of materialism and published experimental evidence for a Lamarckian effect (McDougall 1927).

There were other scientists of the older generation who opposed materialism but were more cautious over the link with Lamarckism. J. Arthur Thomson's survey of theories of heredity (1907) recognized that the evidence for the inheritance of acquired characters was suspect, but in his later career he wrote many popular works supporting an organicist (if not openly vitalist) approach and insisting that animal choice must play a role in directing evolution. He occasionally hinted that the Lamarckian effect could not be ruled out altogether (e.g. Thomson 1934, II: 993, 1010). The psychologist Conwy Lloyd Morgan's vision of 'emergent evolution' saw animals as having active mental powers. Along with James Mark Baldwin and Henry Fairfield Osborn, he had earlier proposed the mechanism of 'organic selection' (also known as the Baldwin effect) in an effort to reconcile the Darwinian and Lamarckian positions. Baldwin argued that characters acquired in response to a newly adopted habit were not necessarily inherited, but they gave the species a chance to adapt to new conditions and then directed the course taken by natural selection (Richards 1987: chaps. 8 and 10; Weber and Depew 2003).

3.2 Lamarckism and Progress

An image of Lamarckism equally popular among those who disliked the moral implications of Darwinism linked it to the ideology of social progress. Reacting against the laissez-faire policies of 'social Darwinism', many reformers sought to use state-controlled education to modify people's habits and encourage cooperation for the common good. If acquired characters can be inherited, the new habits would eventually become instincts biologically implanted in an improved human race. This vision of social progress emerged in the post-Darwinian period and continued to be popular in the new century. It was endorsed, for instance, by Paul Kammerer (1924), whose defence of Lamarckism was later praised by Arthur Koestler (1971). In Koestler's version of history, the Lamarckian project was eliminated from orthodox science because it threatened the materialistic worldview of genetics and Darwinism (for a more nuanced view, see Gliboff 2006, 2011).

Kammerer committed suicide in 1926 when his experimental support for Lamarckism was discredited. At that time he was about to move to Soviet Russia, a move that would have highlighted the link between Lamarckism and the Marxist version of the progressive ideology. The Soviets were attracted to the possibility that their social programme might have a permanently beneficial effect on the human race but were also looking for anything that might improve their wheat supply. In the 1930s, the agronomist T. D. Lysenko gained Stalin's support for a breeding programme based on Lamarckian principles. Eventually genetics and Darwinism were dismissed as manifestations of capitalist ideology and many geneticists were purged. The episode has often been seen as an illustration of what goes wrong when politicians interfere with science (e.g. Joravsky 1970). More recent studies take a less critical approach, pointing out that Lysenko's work was not completely out of touch with contemporary plant breeders' thinking and even suggesting that it anticipated modern evolutionary developmental biology (Roll-Hansen 1985, 2011; Graham 2016).

The publicity centred on Lamarckism's links with reformist ideologies has obscured the theory's wide appeal to harsher social programmes including support for unrestrained capitalism and racial inequality. In the late nineteenth century, Herbert Spencer's political philosophy argued that free enterprise, not government sponsored education, was the best way of encouraging people to acquire new characters that would allow the race to progress. His followers' willingness to emphasize the role of competition has allowed them to be described as 'social Darwinists' (Hofstadter 1959) despite the fact that Spencer invoked the Lamarckian effect to explain how individual responses to the challenge of competition were passed on to future generations. Coupled with the popular view that Lamarckism is primarily a theory favoured by idealists, this has led many historians of the social sciences to deny that Spencer can have been a Lamarckian. Nevertheless, he was seen as one of the most influential voices supporting the inheritance of acquired characteristics (Bowler 2015). Although Spencer's influence had waned in Britain by the turn of the century, in America he continued to inspire many life scientists well into the new century (Ruse 1996).

The assumed link between Lamarckism and reformist ideology has also deflected attention from the theory's use by advocates of race science and eugenics. Nineteenth-century Lamarckians such as the palaeontologist E. D. Cope argued that some races were less 'mature' than others. E. W. MacBride called for restrictions on the breeding of the Irish on the grounds that the Lamarckian effect which had adapted them to an inferior environment worked too slowly for there to be any hope of reversing the process in the modern world (Bowler 1984). Even Bernard Shaw called for a eugenics programme that would prevent those incapable of acquiring new characters from reproducing (Hale 2006).

3.3 The Experimental Defence of Lamarckism

Whatever the moral and social concerns of Lamarckism, there were still a number of biologists who sought hard evidence. As the life sciences became more dependent on laboratory work, the need to provide actual demonstrations of the inheritance of acquired characteristics became acute. In the late nineteenth century, there had been numerous efforts, but all were dogged by controversy over their adequacy. In the early decades of the new century, there was still no shortage of efforts being made, but the critics' suspicions could not be allayed. The highly respected surveys of theories of heredity by J. Arthur Thomson (1907) and of evolution theories by Vernon Kellogg (Kellogg 1907) already expressed considerable scepticism.

French biologists had never been enthusiastic about Darwinism, and here evolutionism emerged to a large extent as a by-product of the physiological tradition established by Claude Bernard. The interaction between the individual organism and its environment was seen as the source of any new characters entering the population (Loison 2010, 2011; Loison and Herring 2017). Experimental evidence for the inheritance of acquired characters was provided by C. E. Brown-Séquard and others and this work continued in the new century. Yet, French biologists became increasingly frustrated by the difficulty of rendering the evidence unambiguous. Their problems were as much conceptual as experimental. As many critics pointed out, the Lamarckian effect implied that the long-established character of the species had no power to restrict the development of the individual while demanding that any new features acquired would immediately be incorporated into the species' future inheritance. Demonstrating the acquisition of new characters was easy, but showing that they were genuinely transmitted to future generations by heredity proved impossible. As scepticism mounted, biologists such as Felix Le Dantec and Maurice Caullery began to suggest that the Lamarckian effect operated only in lower organisms and had largely disappeared by the later stages in the ascent of life.

Elsewhere there were also increasingly desperate efforts to provide experimental proof of the Lamarckian effect (Blacher 1982; Bowler 1983: 99–103; Burkhardt 1980 and for a contemporary survey Robson and Richards 1936: 30–42). Considerable excitement was aroused by the experiments on amphibians by the Austrian biologist Paul Kammerer (Gliboff 2006). In what Arthur Koestler (1971) later dubbed 'the case of the midwife toad', Kammerer's evidence was discredited in a sustained critique led by the geneticist William Bateson. Whatever Koestler's protestations of Kammerer's innocence, he was something of an outsider to the scientific community, and there were genuine concerns that his work would not stand up to scrutiny.

Kammerer's death came shortly before a planned move to the Soviet Union, where there were sustained efforts to defend Lamarckism, culminating with the work of T. D. Lysenko (Joravsky 1970; Roll-Hansen 1985, 2011; Graham 2016). Lysenko's studies of the 'vernalization' of wheat (freezing the seeds to advance the period of germination) seemed to vindicate the Lamarckian effect. His work gained the support of Stalin, with consequences noted above, but was dismissed by Western geneticists. The rush to discredit Lysenko during the Cold War did, however, conceal the fact that his approach was in line with established traditions in agronomy, and his work on graft hybrids was taken more seriously even by those who stood aside from the rest of his career (e.g. Blacher 1982).

A variety of other experimental proofs were offered. The psychologist William McDougall (1927) claimed to have shown that rats trained to run a maze could pass the knowledge on to their offspring as an inherited instinct. In America, the palaeontologist Henry Fairfield Osborn helped to set up an experimental programme designed to provide evidence for Lamarckism (Cook 1999). Charles R. Stockard claimed to find inherited defects in rats induced by the effects of alcohol. These were reported in a symposium on the inheritance of acquired characteristics held by the American Philosophical Society (Stockard 1923). Here, the emphasis seems to have switched to finding evidence of damage to the germ plasm or genes—hardly the kind of effect that had encouraged the earlier generation of Lamarckians. There had always been strong support for the inheritance of acquired characteristics among microbiologists and pathologists and many of the twentieth-century experiments focused on lower organisms.

By the 1930s, even surveys unsympathetic to Darwinism admitted that the evidence was increasingly dubious (e.g. Robson and Richards 1936). There were, perhaps, short-term effects such as the 'Dauemodifikations' of V. Jollos or the effects of 'damaged' genes noted above. But as genetics expanded its influence, the Lamarckians found it increasingly difficult to suggest plausible ways in which the effects they claimed to demonstrate could actually operate. One idea was that hormones could somehow influence the activity of the genes. More plausibly, there were efforts to suggest that work on cytoplasmic inheritance would challenge the dogmatism of chromosome-centred genetics (Sapp 1987). But as the synthesis of Darwinism and genetics gained momentum in the 1930s and 1940s, the few scientists who still expressed an interest in the Lamarckian effect switched their efforts to postulating ways in which control of the genes could be modified indirectly, as with Conrad Hal Waddington's notion of 'genetic assimilation' (Peterson 2011).

3.4 Indirect Evidence for Lamarckism

In the late nineteenth century, much of the support for Lamarckism had come from field naturalists and palaeontologists who were convinced that the theory offered the most plausible explanation of the phenomena they observed. Field naturalists such as Joel A. Allen noticed variations within species over their geographical range that seemed to correlate with climatic factors. 'Allen's law' noted the tendency for mammals to have smaller extremities (ears, tails, etc.) at the northern edge of their range. Such correlations were seen as evidence for the direct effect of the environment on the individual organisms. Another phenomenon seen as susceptible of the same explanation was the disappearance of the eyes in species inhabiting dark caves, studied for instance by Alpheus Packard (1894). It was argued that the cumulative effects of disuse offered a better explanation for the complete elimination of the organ than the mere relaxation of natural selection.

Some palaeontologists were convinced that they could see trends in the fossil record of various groups which were far too regular to be the result of so haphazard a process as natural selection. The ‘American school of neo-Lamarckism’ led by Edward Drinker Cope and Alpheus Hyatt focused on the trends towards specialization they saw in many groups (Bowler 1983: chap. 6; Pfeiffer 1965). Darwinism could, of course, explain specialization, but these palaeontologists saw an element of linearity and directness in the trends that would not be expected if variation were ‘random’. Instead, it was assumed that the power of a newly adopted habit could impose a direction on the group’s later evolution by directly controlling the acquisition of a new character. Cope and Hyatt also claimed to see evidence of parallel evolution: several lineages within the group independently advanced along the same path, predetermined by the animals’ habits. The element of parallelism would remain a key feature of twentieth-century opposition to Darwinism, converted into support for orthogenesis (see below). This approach subverted the Darwinians’ vision of divergent, open-ended evolution and saw generic characters not as the product of the species’ descent from a common ancestor, but as evidence that they had independently advanced to the same point on a predetermined scale of development. Cope (1896) provided a detailed survey of this neo-Lamarckian position.

By the turn of the century, younger palaeontologists such as Henry Fairfield Osborn were turning away from the Lamarckian explanation of parallel evolution. Along with James Mark Baldwin, Osborn was one of the proponents of the idea of ‘organic selection’ in which the animals’ chosen habit generates characters which are not inherited directly but define the channel along which natural selection will operate (Richards 1987, chaps. 8 and 10). He would later turn more to orthogenesis.

Lamarckism survived more actively among the field naturalists. The myrmecologist William Morton Wheeler preferred the Lamarckian explanation of the origin of instincts in ants to the Darwinian view (Sleigh 2004). In Germany, Bernhard Rensch was one of many students of geographical distribution and speciation who retained the Lamarckian explanation of adaptive evolution. As he and Ernst Mayr later explained (Rensch 1980; Mayr 1980a, b), the field naturalists were still suspicious of Darwinism and preferred Lamarckism despite the lack of hard evidence that acquired characteristics were really inherited. Confusion over the term ‘mutation’ (originally used to demote discontinuous evolutionary steps or saltations) fuelled their distrust of genetics and thus held up their recognition of the emerging synthesis of that science with Darwinism. Only when Theodosius Dobzhansky’s translated the new Darwinism into terms comprehensible to the field naturalists were they able to realize that there was no longer any point in retaining the Lamarckian alternative.

4 Orthogenesis

The model of evolution proposed by neo-Lamarckian palaeontologists such as Cope and Hyatt did not merely offer an alternative to natural selection as an explanation of adaptation. By focusing on habit as a driving force that could predetermine a rigid pattern of future development, they introduced the idea of evolutionary parallelism, in effect subverting the whole Darwinian vision of a constantly branching 'tree of life', at least within each group. Taking this rival model further led them to imagine that the parallel trends they envisaged might go on beyond the limit of adaptive benefit that could be gained from specialization. Structures might get overdeveloped to a point where they became positively harmful. The theory thus opened up the possibility of predetermined trends that had no relevance to the demands of the environment. The suggestion that evolution might be a non-adaptive process driven by rigid variation trends imposed by internal processes arising from ontogeny was also raised by some field naturalists. This was the foundation of what became known as the theory of orthogenesis.

The theory had emerged in the aftermath of the original Darwinian debates as perhaps the most extreme alternative to natural selection. It was extremely active within the German scientific community (Levit and Hossfeld 2017). The term 'orthogenesis' was popularized by Theodore Eimer, who worked with living species but whose trajectory of thought followed the same pattern as the American palaeontologists. He began as a Lamarckian but soon moved on to propose non-adaptive trends which he claimed to observe in the colour patterns of butterflies (Eimer 1898). Mimicry was dismissed as the result of two species independently affected by the same variation trend—it had no adaptive significance. The search for orthogenetic patterns in living species continued into the twentieth century. C. O. Whitman (1919) saw non-adaptive patterns in the colouration of pigeons, and Jepsen (1949) listed a number of similar studies (for details see Esposito 2017).

By far the most powerful line of support for orthogenesis came from palaeontology. A significant number of the specialists seeking to reconstruct phylogenies within the animal kingdom interpreted the patterns of development they saw as evidence of predetermined evolution. They included the next generation of the American school, led by Henry Fairfield Osborn, but also a number of European palaeontologists. Until this work was challenged by new fossil evidence and by a more critical evaluation of its claims, palaeontology stood as a bastion of resistance to the Darwinian viewpoint.

4.1 Mechanisms of Orthogenesis

Exactly how the orthogenetic patterns were imposed on evolution was a matter of some debate. Suggestions ranged from vaguely defined 'laws of development' to mechanistic processes imposing restrictions on the kinds of variation that could appear within a population (Bowler 1983, chap. 7; Ulett 2014). Some thought that variation might be controlled by forces intrinsic to the nature of living matter. This approach can be seen in D'Arcy Wentworth Thompson's classic *On Growth and Form* (1917). His demonstration that changing the coordinates of how a single form is represented could produce structures corresponding to a wide range of different fish species became well known. But he also insisted that this geometrical insight implied that the range of variation that had allowed the different species to evolve must be controlled by laws of growth determined by a simple system of forces (Thompson 1917: 727). Thompson wrote an introduction to the English translation of *Nomogenesis* by the Russian naturalist Leo S. Berg (1926). Berg too rejected any role for chance in evolution and saw the whole process as being directed by internally programmed laws of development. In principle, these laws were imposed by the basic chemical composition of protoplasm, but Berg also insisted that the patterns of development they imposed were purposeful and progressive, leading critics to dismiss his ideas as a relic of the old teleological approach.

Most supporters of orthogenesis insisted that their theory was not teleological—indeed, they often went out of their way to argue that the trends they saw were actually harmful and might eventually lead to extinction. C. O. Whitman (1919) quite explicitly rejected teleology and tried to render the theory more plausible by arguing that the patterns he saw represented not rigidly predetermined variation but merely restrictions on the possible range of variation. Some suggestions as to a possible mechanism still focused on the possibility that factors affecting individual ontogeny could somehow affect development in a cumulative manner. At a symposium on orthogenesis held by the American Society of Zoology, the biochemist Lawrence J. Henderson (1922) argued that a tendency to overproduce growth hormones might generate an evolutionary trend (see also MacCord and Maienschein 2017).

Henderson's approach was favoured by some palaeontologists (see below), but as the new science of Mendelian genetics began to throw light on the nature of variation, the supporters of orthogenesis needed to explain how such tendencies could be generated by mutation. Whitman's idea of restricted variation could easily be translated into terms compatible with genetics, and there were a number of efforts to demonstrate that there were limits to the kinds of new characters that were likely to be produced. Richard Goldschmidt (1933) endorsed work by V. Jollos claiming to show that mutations occurred preferentially in a particular direction. A. F. Shull (1936: 123–133) was less convinced by this work but also expressed the hope that directed mutation might turn out to be the long-sought explanation for orthogenetic trends. Most field naturalists and palaeontologists were not well versed in the new genetics and simply ignored the issue.

4.2 Orthogenesis in Palaeontology

Building on research traditions established in the late nineteenth century, a significant number of palaeontolgists in both Europe and America continued to insist that their work provided evidence of non-adaptive evolutionary trends (see also Turner 2017). In the United States, the legacy of the orthogenetic element in the thinking of the neo-Lamarckian school remained active. Among invertebrate palaeontologists, Charles E. Beecher and others continued the tradition established by Hyatt in which the recapitulation theory was used to provide a model for the evolutionary history of each group (Rainger 1981). Hyatt had argued that although unfavourable conditions might trigger non-adaptive variation, the trends that led each group to degenerate into a senile phase were also a sign that a once-progressive group exhausted its evolutionary energy. His followers continued to argue that their work revealed patterns of development driving each group towards racial senility and eventual extinction. The concept of racial old age thus remained in play and was often appealed to by pessimists commenting on modern culture (Bowler 1989).

Vertebrate palaeontologists too endorsed the model of evolution which saw degeneration as the almost inevitable fate of any phylum. But where Hyatt had emphasized the loss of complex characters, those studying vertebrate phylogeny claimed to see a process of overdevelopment by which once-useful structures eventually reached harmful proportions. Henry Fairfield Osborn was a follower of Cope and became one of the most influential American evolutionists of the early twentieth century (Rainger 1991). His work on extinct mammals led him to support the view that their evolution was governed by orthogenetic trends which he called ‘rectigradations’, leading to the overdevelopment of structures such as horns. Although now accepting that the Lamarckian effect did not work, he struggled to develop a theory in which the environment and the animals’ behaviour could somehow influence the hereditary constitution of the species (Osborn 1917). The trends thus induced were not always adaptive and could in some cases lead to overdevelopment so severe it might play a role in the order’s eventual extinction.

Osborn’s fellow palaeontologist William Berryman Scott also supported the theory of orthogenesis, although he was doubtful that the trends ever went far enough to cause extinction (Scott 1929: 532). F. B. Loomis (1905) introduced an analogy which became widely used: he wrote of once-useful trends gaining a ‘momentum’ that carried them on beyond the limit of adaptive benefit. This model was applied to explain popular examples of what were claimed to be overdeveloped structures, including the enormous horns of the so-called ‘Irish elk’ (Gould 1974). Other American palaeontologists who endorsed the view that orthogenetic trends could lead to overdevelopment and extinction included Richard Swan Lull who thought that non-adaptive trends might be triggered by unfavourable conditions and later wrote of them leading to ‘racial disease’ and extinction (Lull 1917, 1924).

Among European palaeontologists, Arthur Dendy (1911) adopted the theory that an excess production of hormones led to the overdevelopment of various structures.

W. D. Lang produced a study of the fossil Bryozoa which claimed that the group was affected by an uncontrolled tendency to produce calcium carbonate. The trend was built into the group's constitution and was only secondarily used to construct a protective shell, which is why it eventually led to overelaborate structures that were positively harmful (Lang 1921). D. M. S. Watson (1925–1926) described trends in fossil amphibians that persisted despite changes in their environment and which must therefore originate in an internal limitation on what kinds of variations could be produced. In contrast, Francis Nopsca (1930) shared Lull's view that a changed environment had led to the emergence of predetermined trends in the fossil amphibians he studied, triggering modifications in the thyroid gland affecting growth.

Although some apparently non-adaptive trends were hard for the Darwinist to explain, the supporters of the new synthesis became increasingly suspicious of the palaeontologists' evidence. Julian Huxley's concept of 'allometry' explained the huge development of horns such as those of the 'Irish elk' as a by-product of selection for increased overall size (Huxley 1932: 214–221). More seriously for the supporters of orthogenesis, the fossil evidence itself was becoming increasingly less supportive of the claim that evolution exhibited rigid trends. Showing that the evidence for parallel non-adaptive evolution was actually illusory would play a significant role in preparing the way for the emergence of the modern Darwinian synthesis. From the early decades of the century, there were palaeontologists such as W. D. Matthew who argued that as more fossils were discovered the apparently regular patterns of development seen by earlier workers fragmented into complex branching trees—just as a Darwinian would expect (Bowler 1996). The work of George Gaylord Simpson would cement the palaeontologists' rejection of the non-Darwinian stance adopted by the previous generation (but see Turner 2017).

5 Saltationism

The first decade of the twentieth century saw a dramatic resurgence of a long-standing alternative to the Darwinian theory. There had always been some naturalists who were suspicious of Darwin's insistence that small individual differences were the raw material of evolution. Even Thomas Henry Huxley thought that new characters were more likely to appear suddenly via dramatic 'leaps' or saltations that would create a new variety if not a new species instantaneously. During the 'revolt against morphology' around 1900, the search for demonstrable evidence of evolution focused renewed attention on direct observations of the processes of variation and heredity. For some naturalists, this led to renewed studies of the distinct varieties that exist within many species and generated the assumption that the most obvious explanation of their formation was by saltation.

This assumption led to a rejection of the Darwinian focus on the power of the environment to determine which variations survive and breed—the new varieties formed by saltation came into existence without any involvement by natural selection and seemed able to perpetuate themselves alongside many other forms. William Bateson's *Materials for the Study of Variation* expressed this position, and although he admitted that varieties must be 'approximately' adapted to the environment (1894: 15), it was clear that he did not think natural selection to be a powerful limiting factor. Saltationism thus reflected a similar position to orthogenesis on the role of the environment but tended to assume that a wide variety of new forms could be produced (although there were occasional suggestions that saltations might occur in a cumulative direction).

The most prominent expression of saltationism in the new century was the 'mutation theory' proposed by Hugo De Vries. He observed the appearance of apparently new and distinct varieties in a controlled environment. Although it was later shown that these were not genuinely new forms, for some time his observations were taken as evidence in favour of what he called the process of mutation. The theory became immensely popular for a short time, and it was probably the emergence of this new alternative that led Julian Huxley to refer to this period as the 'eclipse of Darwinism'. As Lamarckism declined in influence, this new rival took its place. De Vries himself sought a reconciliation with Darwinism, claiming that in the long run only better-adapted mutated forms would survive. But most of his followers—including Thomas Hunt Morgan for a time—shared Bateson's suspicion of the power of selection. It was this anti-adaptationism that led field naturalists such as Ernst Mayr to remain suspicious of the concept of mutation even after it had begun to acquire a new role as a component of Mendelian genetics.

The fact that the term 'mutation' has gained a new meaning in the modern world suggests that there was a significant link between saltationism and genetics. It was no coincidence that three major figures associated with the development of genetics began their careers as saltationists: Bateson, De Vries and Morgan. The model of evolution that pictured it as a series of events producing discrete new characters that would breed true paved the way for acceptance of the laws of heredity proposed by Gregor Mendel. As the 'rediscovery' of Mendel's laws by De Vries and others in 1900 developed into the new science of genetics, it was soon realized that new characters are indeed produced by the 'mutation' of genes—although they functioned within the existing population rather than founding a discrete new variety.

With hindsight we know that mutations would eventually be recognized as the source of the individual variations, the Darwinians postulated as the raw material of natural selection. But at the time, the anti-adaptationism of the original mutation theory carried through into the new model of heredity. Geneticists studied breeding under laboratory conditions where there was little environmental pressure and no evidence of natural selection. They thus remained suspicious of the claim that new characters had to confer adaptive benefit in order to spread in a population. Bateson in any case remained deeply hostile to the biometrical version of Darwinism developed by Karl Pearson and others, and it was only in the 1930s that this hostility was overcome. Bateson and the geneticists were certainly hostile to Lamarckism, which would undermine their concept of the gene as a fixed entity breeding true over the generations. But in the short term, at least their theory was perceived as yet another alternative to Darwinism.

5.1 The Mutation Theory

Support for saltationism surged in the first decade of the century, largely in response to the work of the Dutch botanist Hugo De Vries (Allen 1969; Bowler 1983: chap. 8). During the 1890s, De Vries had noticed apparently new varieties appearing suddenly within cultivated populations of the evening primrose, *Oenothera lamarckiana*. He interpreted these new forms as saltations produced by a sudden transformation within the species' hereditary material and dubbed them 'mutations'. He then used his observations as the basis for a complete theory of evolution, arguing that selection acting on small individual differences was powerless and that saltations were the true source of new characters. Crucially, he believed that each new form appeared in multiple individuals, allowing the instantaneous creation of a distinct new variety or even species. De Vries imagined that all species go through occasional phases in which they throw off saltations—*Oenothera* was valuable because it was currently in such a phase. His 'mutation theory' was proposed in a book (translated as De Vries 1910) and in a series of lectures delivered at the University of California (De Vries 1904).

De Vries presented himself as a reformer who would put Darwinism on a more secure footing, not replace it. He implied that most mutations were adaptively neutral and would perpetuate themselves in a natural environment but accepted that some were harmful and would soon be eliminated. In the long run, there would be some beneficial mutations, and these would replace the older forms. Natural selection still operated and would control the establishment of new species, but its raw material was mutated varieties rather than trivial individual differences. For De Vries, this was an essential point that ensured the theory did not represent a re-emergence of teleology.

The mutation theory soon became popular, being seen as a modern, experimentally verifiable form of evolutionism (Endesby 2013). However, most of its supporters did not share De Vries' willingness to compromise with Darwinism. They extended his belief that many mutations were adaptively neutral into a wholesale rejection of the claim that adaptation played a significant role in evolution. Even in the long run, they assumed, any new character produced as a mutation would be able to persist. One of the most vociferous advocates of this interpretation was Thomas Hunt Morgan (Allen 1978). Before he came to accept Mendelism, he took up the mutation theory and extended it into a wholesale critique of Darwinism. His *Evolution and Adaptation* (Morgan 1903) argued that the majority of characters defining species have no adaptive significance, including the colour schemes that the Darwinians interpreted as camouflage or the products of sexual selection. There is no 'struggle for existence' and new forms simply appear by mutation and continue to breed independent of any environmental constraint. Since there was no pressure from selection, Morgan argued that the few complex structures that do benefit the organism must be the product of a directed sequence of mutations (in effect, of an orthogenetic trend). The same argument appeared in a study of the mutation theory by R. Ruggles Gates (1915).

5.2 Saltationism and Genetics

Despite the initial enthusiasm, suspicion soon emerged that the forms observed by De Vries were not genuinely new characters and it was eventually shown that *Oenothera* is a complex hybrid species. De Vries played a major role in the rediscovery of Mendel's laws but soon lost interest. It was Bateson and Morgan who went on to help create the new science of heredity that became known as genetics. Bateson did not accept the idea that mutations create genuinely new genetic characters and interpreted the appearance of new forms as the result of destructive saltations removing genes that had originally masked the character (Bateson 1922). Morgan eventually converted to Mendelism and founded the experimental school that demonstrated how the genes could be understood as material units strung along the chromosomes (Allen 1978). The definition of 'mutation' now morphed into the meaning we accept today: far from creating entirely distinct breeding populations, mutation modifies a gene so that it codes for a new character, and the new gene feeds into the existing population. Richard Goldschmidt (1940) was one of the few geneticists who continued to support the possibility of a 'hopeful monster' establishing a new species (see also Turner 2017).

Genetics provide an explanation of the individual differences existing within each population, with mutations being seen as the ultimate source of novelties. Yet, there were at first only limited efforts to explore the possibility that this new approach could be reconciled with Darwin's belief that the range of variation within the population served as the raw material of natural selection. The appearance of discrete new characters in the laboratory did not seem an appropriate model for natural variation. Bateson retained his suspicion of the selection mechanism and continued to regard the continuous range of variation within populations as a product of short-term environmental influences. He strenuously opposed the position of Karl Pearson and the biometrical school which studied variation in wild populations and sought to demonstrate the effect of selection. Morgan too remained suspicious of natural selection, although he gradually came to admit that maladapted characters would eventually be eliminated. He still found it difficult to accept the concept of the 'struggle for existence' and to imagine selection as a creative force.

Genetics was originally perceived as a minimized saltationism, offering a similar alternative to Darwinism and the adaptationist programme. Lamarckism was undermined without strengthening Darwinism. It would take several decades for the possibility that genetics might explain the range of variation in wild populations to be recognized, let alone that natural selection might act to change gene frequencies and produce new structures beneficial to the organism. The story of how genetics was eventually synthesized with Darwinism will be told throughout the rest of this volume.

6 Conclusion

Our understanding of the rise of modern Darwinism must take into account the fact that it has not been a simple or continuous process. The theory of natural selection was controversial from the start, partly for its moral and religious implications but also because many naturalists found it unsatisfactory as a scientific explanation of evolution. The critics sought alternatives that would resolve both the scientific and the non-scientific problems. Darwinism certainly gained notable adherents in the late nineteenth century, but supporters such as August Weismann had to battle with the critics who preferred the alternatives. Far from diminishing in the early twentieth century, the alternatives proliferated, prompting Julian Huxley's later claim that the period had witnessed an 'eclipse of Darwinism'.

This chapter has surveyed the alternatives to the selection theory: the Lamarckian theory of the inheritance of acquired characteristics, orthogenesis and saltationism. It has shown how they represented a complex of positions opposed to the Darwinian view of the roles played by heredity, adaptation and continuity. The emergence of Mendelian genetics after 1900 was at first seen as a new element supporting the concept of evolution by discontinuous steps. But its supporters were hostile to the belief that acquired characters could be inherited, so as their approach to the study of heredity gained ground, the Lamarckian alternative was discredited. When genetics was synthesized with the selection theory in the 1930s, the Darwinian theory at last began to gain enough momentum to displace support for the various forms of non-adaptive evolution. Since all of the non-Darwinian theories were themselves now eclipsed, the synthetic form of Darwinism was able to gain a dominant position in the biology of the mid-twentieth century. From the perspective of its supporters, the 'Modern Synthesis' allowed Darwinism to be seen as the main line in the development of evolutionism, all the rivals being dismissed as dead ends or blind alleys.

More recent studies have increasingly suggested that the gene-centred paradigm of the twentieth-century synthesis—especially as it was consolidated in the English-speaking world—had deflected attention away from valid concerns about the role played by individual development in the shaping of organic forms. By insisting that the gene provided a complete blueprint determining the form of the organism, a whole generation of Darwinians was persuaded to ignore the possibility that the processes translating genetic information into living structures might themselves play a role. Concern for this factor was one of the main influences that had persuaded so many naturalists in the late nineteenth and early twentieth century to search for alternatives to natural selection. Whether in responding to the environment or in shaping the possible consequences of genetic mutation, developmental factors were seen as crucial. We can now appreciate that this concern was not merely a distraction from the main business of evolutionary biology, as especially shown in Depew (2017) and MacCord and Maienschein (2017). The historians who look back at these early non-Darwinian theories can, perhaps, see evidence of ideas being explored that may once again come to play a role in evolution theory. More certainly, they can see an interest being displayed in issues that became marginalized for a period in the mid-twentieth century but which have now re-emerged as areas of real interest.

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