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ARTICLE

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

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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

[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

[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

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

[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

[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,

[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

[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

[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

[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 *Intracelluläre 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.

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.

[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

[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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