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Review article

Darwin’s contributions to genetics

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Abstract. Darwin’s contributions to evolutionary biology are well known, but his contributions to genetics are much less known. His main contribution was the collection of a tremendous amount of genetic data, and an attempt to provide a theoretical framework for its interpretation. Darwin clearly described almost all genetic phenomena of fundamental importance, such as prepotency (Mendelian inheritance), bud variation (mutation), heterosis, reversion (atavism), graft hybridization (Michurinian inheritance), sex-limited inheritance, the direct action of the male element on the female (xenia and telegony), the effect of use and disuse, the inheritance of acquired characters (Lamarckian inheritance), and many other observations pertaining to variation, heredity and development. To explain all these observations, Darwin formulated a developmental theory of heredity – Pangenesis – which not only greatly influenced many subsequent theories, but also is supported by recent evidence.

Keywords: Darwin, genetics, Pangenesis, variation and heredity, breeding.

Introduction

In 1906, the late William Bateson coined the word *genetics* in his inaugural address to the Third Conference on Hybridization and Plant-Breeding: “I suggest for the consideration of this Congress the term *Genetics*, which sufficiently indicates that our labours are devoted to the elucidation of the phenomena of heredity and variation: in other words, to the physiology of Descent, with implied bearing on the theoretical problems of the evolutionist and the systematist, and application to the practical problems of breeders, whether of animals or plants” (Bateson 1906).

More than 100 years after the introduction of the science of genetics, Darwin’s contributions to genetics are still not well known. As early as in 1859, Darwin predicted the emergence of the science of genetics. In the last chapter of *The Origin*, we read: “A grand and almost untrodden field of inquiry will be opened, on the causes and laws of variation, on correlation, on the effects of use and disuse, on the direct action of external conditions, and so forth.” Darwin’s interest in genetics was a consequence of his studies of evolution. He fully realized that his theory of natural selection must be based on a sound understanding of the mechanism of inheritance. One of the striking things about Darwin was that he had a detailed firsthand knowledge of both animals and plants, and painstakingly collated every bit of information about heredity that he found in the literature (Sturtevant 1965). Darwin saw and clearly described almost all genetic phenomena of fundamental importance and formulated a developmental theory of heredity – Pangenesis. Thus in Bateson’s opinion, Darwin was a pioneer of genetics, because “Darwin made a more significant contribution. Not for a few generations, but through all ages he should be remembered as the first who showed clearly that the problems of heredity and variation are soluble by observation, and laid down the course by which we must proceed to their solution. Evolution is a process of variation and heredity. The older writers, though they had some vague idea that it must be so, did not study variation and heredity. Darwin

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did, and so begat not a theory, but a science" (Bateson 1910).

Darwin's collection of a tremendous amount of genetic data

Prepotency (Mendelian inheritance)

Many people thought that Darwin did not read Mendel's paper, thus he did not know Mendelian inheritance. This is not the case. Segregation in the Mendelian sense was well known to Darwin. In the chapter "Hybridism" in *The Origin,* Darwin clearly states: "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" (Darwin 1872). In Chapter 27 of *The Variation*, Darwin wrote: "When two forms are crossed, one is not rarely found to be prepotent in the transmission of its characters over the other; … for instance, there is a latent tendency in all pigeons to become blue, and, when a blue pigeon is crossed with one of any other colour, the blue tint is generally prepotent". In the section "Prepotency in the transmission of character" in *The Variation*, Darwin presented an instance of segregation in the second hybrid generation from a cross between peloric and normal-flowered snapdragons: The first hybrid generation completely resembled the normal plant, and of the second hybrid generation of 127 seedlings, 88 proved normal, 37 perfectly peloric, and 2 imperfectly so. This is a good example of a Mendelian experiment in which there is a single factor difference between the parental plants, with dominance in the first hybrid generation, and a second generation segregation ratio being 2.4:1, approaching 3:1. Of course, in Darwin's work it was just one of many examples, not the crucial mechanism, as it was in Mendel's research.

Darwin also mentioned Yarrell's law, which was named for William Yarrell, a British naturalist and animal breeder. Yarrell maintained that a parent of an older breed will have more influence on the character of the offspring than a parent of a young breed (Darwin 1987). Yarrell's law was of great interest to Charles Darwin, as he was trying to understand why certain breeds seemed to have a greater ability to *impress* their characters on the offspring. Interestingly, Yarrell's law was later confirmed by Ivan Michurin, who found that old varieties of fruit plants have a stronger capacity for transmitting their characters than young varieties. "The older the plant chosen as a progenitor, the greater is the force with which it transmits its genes to the offspring, and conversely, if the plant is young, in its first year of bearing, and particularly if it is a hybrid of recent origin, its hereditary power reaches a minimum" (Michurin 1949). Yarrell's law was also confirmed by other researchers (Beardmore et al. 1975; Lizana and Prado 1994). It should be noted that the so-called Yarrell's law might be a tendency rather than a law, though Darwin believed that "Yarrell's law must be partly true" (Darwin 1987).

Graft hybridization (Michurinian inheritance)

Graft hybridization is a type of asexual hybridization, in which heritable changes may be induced by grafting. In 1868, Darwin coined the terms *graft hybrid* and *graft hybridization*. In Chapter 11 of *The Variation*, Darwin recorded various cases, in which shoots that developed from grafted trees have exhibited the characters of both stock and scion, either blended together uniformly or disposed in a mosaic of the parental types. He mentioned that such shoots are sometimes capable of bearing progenies, which segregate in respect of their morphological characters and he proposed that they are actually true hybrids. Based on Darwin's research, Michurin elaborated a simple and efficient method for producing graft hybrids – the mentor-grafting method. Later, graft hybridization as a chapter was included in the textbook of Michurinian genetics. Over the past decades, several independent groups of scientists have confirmed the existence of graft hybrids (Frankel 1956; Ohta 1991; Taller et al. 1999; Stegemann and Bock 2009). Recently, grafting experiments proved that endogenous mRNA enters and moves the phloem long-distance translocation system (Lucas et al. 2001). The establishment that novel mRNA species may move between cells and around the plant, and the ability of retroviruses or retrotransposons to reverse transcribe mRNA into cDNA capable of being integrated into the genome, indicate that some mechanisms exist for the horizontal gene transfer from stock to scion and *vice versa* by grafting (Liu 2006).

Bud variation (mutation)

In his analysis of the causes of biological variation, Darwin encountered several cases in which the characters of the parents were incapable of fusion and did not show the blending inheritance. He called them *sports*, *spontaneous variations* or *transmutations*. He stated that some few characters are incapable of fusion but are unimportant, of semi-monstrous nature, and have been known to appear suddenly. One of the most striking cases in animals is that of the *japanned* or *black-shouldered* peacocks, which have occasionally appeared "suddenly in flocks of the common kind", but "propagate their kind quite truly", and tend "at all times and in many places to reappear". Concerning useful and ornamental trees, he wrote: "All the recorded varieties, as far as I can find out, have been suddenly produced by one single act of variation", and as to roses, he remarked on their marked tendency to *sport* and to produce varieties "not only by grafting and budding, but often by seed". In *The Variation,* Darwin (1868) dealt with numerous cases among domesticated animals and plants, many of which – he freely acknowledged – were the starting points of new and constant races. From his descriptions it is evident that such characters were conditioned by single mutant genes and we now call them mutations.

Several times Darwin expressed the opinion that the establishment of mutations would in some ways be an advantage to the evolution theory. It is worth mentioning that de Vries, the author of *The Mutation Theory*, claimed that his work is "in full accord with the principles laid down by Darwin", and boldly asserts that Darwin recognized both *mutation* and individual variation, or *fluctuation* (cited in Cox 1909).

Reversion (atavism)

Reversion or atavism is the reappearance of a lost character typical of remote ancestors and not seen in the parents or recent ancestors of the organisms displaying the atavistic character. In Chapter 13 of *The Variation*, Darwin described the problem of reversion or atavism. He believed that the principle of reversion is one of the most wonderful attributes of inheritance. "Reversion is not a rare event, depending on some unusual or favourable combination of circumstances, but occurs so regularly with crossed animals and plants, and so regularly with uncrossed breeds, that it is evidently an essential part of the principle of inheritance". Hall (1995) cited numerous facts pertaining to reversion or atavism, which can be revealed in 3 ways: (1) through features that appear spontaneously in natural populations; (2) through artificial breeding and selection; or (3) by experimental induction. Here we would take 2 examples. Belyaev et al. (1981) reported a fused gene in the mouse, with about 6% of mutants producing wild-type young, and after a few generations, 1% reverting to the mutant type. Those authors offered an explanation that relies on the notion that inactive (*dormant*) genes may be activated and reverted toward an inactive state. This explanation was similar to Darwin's. More recently, Lolle et al. (2005) have shown that *Arabidopsis* plants homozygous for recessive mutant alleles of the organ fusion gene (HTH) can inherit allele-specific DNA sequence information that was not present in the chromosomal genome of their parents but was present in previous generations. They proposed a model in which a type of stable RNA can be replicated and transmitted over multiple generations. This provides further evidence for reversion or atavism (Liu, 2005). We should recognize that this phenomenon with the RNA of *Arabidopsis* must be rather rare, though it is a fact.

Inheritance of acquired characters

In 1809, Lamarck published his most famous book, *Philosophie Zoologique*, in which the first scientific explanation of the process of evolution was presented. Darwin accepted to some degree the views of Lamarck. For example, Darwin was a firm believer in the inheritance of acquired characters, an important notion proposed by Lamarck in that book. Darwin claimed that "selection does nothing without variability, and this depends in some manner on the act of the surrounding circumstances on the organism". Throughout his career, Darwin consistently linked the cause of variation with changes in the environment.

There were cases where mutilations appeared to be inherited and they were given on such good authority that Darwin found it "difficult not to believe them." One of these was: "a cow lost a horn from an accident with consequent suppuration, and she produced three calves which were hornless on the same side of the head". To demonstrate the fallacy of the idea of inheritance of acquired characters, Weismann performed an influential experiment: he cut off the tails of male and female mice, and showed that, in breeding experiments extending over many generations, such tail chopping at birth never produced tailless offspring. Critics of this experiment have pointed out that such experiments did not test the inheritance of acquired characters. First, a short tail caused by chopping is a modification that was not produced by the mice. In contrast, Lamarck and Darwin believed that only modifications produced by a response of the mice to the environment would be inherited (Steele et al. 1998). Second, Darwin stated clearly that "a part or organ may be removed during several successive generations, and if the operation be not followed by disease, the lost part reappears in the offspring". Darwin's explanation of inherited mutilations, which as he notes, occur "especially or perhaps exclusively" when the injury has been followed by disease – is that all the representative *gemmules*, which would develop or repair or reproduce the injured part are attracted to the diseased surface during the reparative process and are there destroyed by the morbid action. Third, there is good evidence for inheritance of mutilations in bacteria, ciliates and animals (Davenport 1933; Landman 1991; Tchang et al. 1964).

It should be noted that the conversion of spring and winter wheat, a typical example for the inheritance of acquired characters, was regarded as Lysenko's discovery in the textbook of Michurinian genetics. Actually, Darwin (1968) mentioned Monnier's experiments in which winter wheat was sown in the spring and spring wheat in the autumn to produce spring or winter wheat, respectively. Recently, there is increasing evidence for the inheritance of acquired characters (Landman 1991; Steele et al. 1998; Liu 2007), which can be explained by different mechanisms based on epigenetic inheritance, environmentally induced DNA rearrangement, and horizontal gene transfer.

Direct action of the male element on the female (xenia and telegony)

Xenia is described as the direct or immediate pollen effect on the size, shape, colour, developmental timing and chemical composition of seeds and fruits (Denney 1992). In *The Variation*, Darwin (1868) devoted 6 pages to "the direct or immediate action of the male element on the mother form" (now referred to as xenia), and described it as being "of the highest theoretical importance." de Vries and Correns, the 2 chief actors in the founding of genetics, also held strong belief in xenia (Dunn 1973). Over the past century, there has been increasing evidence for the xenia phenomenon, which has applications not only in genetics and physiological research but also in plant breeding and crop production. For example, there is good evidence for xenia in maize (Bulant and Gallais 1998), cotton (Pahlavani and Abolhasani 2006), bean (Duc et al. 2001) and many fruit trees (Denney 1992; Wallace and Lee 1999). Recently, mRNAs have been reported not only in mammalian spermatozoa, but also in the male gametes of plants. For example, Engel et al. (2003) showed that the sperm cells of *Zea mays* have a complex complement of mRNAs. This has led to a proposition that, during fertilization, pollen grains release mRNAs, which diffuse out into the tissues of the mother plant and there the translocated mRNAs cause changes in size, shape, colour, developmental timing, and chemical composition of seeds and fruits, varying according to the particular male parent (Liu 2008b).

The subject of telegony is an exceptional, alleged phenomenon that enjoyed a remarkable career in the 19th century. Its principle is that females are impregnated by the first males to which they are bred, so that some of their subsequent offspring, regardless of their actual father, will show influence of the first male. In Chapter 11 of *The Variation*, Darwin collected many alleged examples of "the direct action of the male element on the female form". The most notorious instance of this alleged fact is that of Lord Morton's Arabian chestnut mare, which had her first foal to a quagga – a zebra-like, South American member of the horse family (now extinct). The first offspring was intermediate in form and colour. Subsequently she produced two colts by a black Arabian horse. They were both partially dun-coloured, and striped on the legs more plainly than the real hybrid had been. Darwin concluded that "there can be no doubt that the quagga affected the character of the offspring subsequently begot by the black Arabian horse". He considered it to be of special importance for understanding the mechanisms of heredity and development. In recent years, direct and indirect evidence has accumulated for telegony (Gorcynski et al. 1983; Hui 1989; Mei 2000; Mole 2006). The penetration of spermatozoa into the somatic tissues of the female genital tract and the incorporation of the DNA and RNA released by spermatozoa into maternal somatic cells, the presence of fetal DNA in maternal blood as well as sperm RNA-mediated non-Mendelian inheritance of epigenetic changes are considered to provide a basis for telegony (Austin et al. 1959).

Effects of crossing and inbreeding

In *The Origin*, Darwin had summarized his views on effects of crossing and inbreeding by stating that he had "collected so large a body of facts, and made so many experiments, showing, in accordance with the almost universal belief of breeders, that with animals and plants a cross between different varieties, or between individuals of the same variety but of another strain, gives vigour and fertility to the offspring; and on the other hand that close interbreeding diminishes vigour and fertility". In *The Variation*, Darwin repeatedly discussed the evil effects of inbreeding and the beneficial effects of crosses between unrelated individuals or different races. As plants and animals behaved essentially alike in this respect, he was convinced that it is a great law of nature that long-continued close inbreeding is injurious, whereas crossing is beneficial. Darwin believed that the main cause of these phenomena was the variation in the conditions of life to which all individuals are exposed, and that these exterior influences by means of modified gemmules caused a differentiation of the sexual elements. This conclusion was further supported by the results of his comprehensive experiments. Although most geneticists are not satisfied with Darwin's explanation, they do agree that hybrid vigour and degeneration resulting from inbreeding are of paramount importance not only for the life of the wild organisms but also for the production of good domestic animals and high-yielding cultivated plants (Muntzing 1959).

Sex-limited inheritance

Although most characters appeared to be inherited with equal facility from either the father or the mother, Darwin knew of a few instances in which the sex of the parent is important. Some traits are transmitted from father to son but never to daughters, or from mother to daughter but never to sons. In colour blindness, males are much more commonly affected than females, yet the defect can be transmitted by normal females. It seemed probable to Darwin that fathers can never transmit colour blindness to their sons. Daughters of colour-blind fathers, though normal themselves, transmit colour blindness to their sons. Therefore, the father, grandson, and great-great-grandson will exhibit a peculiarity – the grandmother, daughters, and great-granddaughter having transmitted it in a latent state (cited in Moore 1963).

Unification of variation, heredity and development

While today inheritance and development are generally considered to be 2 distinct processes, for Darwin they were tied together in a dynamic process of change over time (Bartley 1992). He believed that heredity was a developmental, not a transmissional process; variation occurred when the environment caused a change in the developmental process of change (Winther 2000). Thus Darwin's Pangenesis is regarded as a developmental theory of heredity. It had to do with what we now call genetics, but – like our contemporary molecular genetics – its primary concern was with developmental, rather than with transmissional genetics (Ghiselin 1975).

Darwin's theory of heredity

Darwin's Pangenesis: a developmental theory of heredity

In his theory of Pangenesis, Darwin assumed that cells are not only able to grow by means of cell division but are also capable of *throwing off* gemmules – minute particles or molecules – that are self-replicating, movable, variable, and capable of dormancy. He assumed that all cells of the body throw off gemmules at various developmental stages, and these gemmules are able to circulate throughout the body and enter the buds and the sex cells. The cases in which the characteristics of one parent dominate were believed to be a consequence of that parent's gemmules having some advantage in number, affinity, or vigour over those derived from the other parent. Thus Pangenesis explains the *Mendelian inheritance*. If the cells of one part of the body underwent change as a result of environmental change, they consequently throw off modified gemmules, which are transmitted to the offspring. Thus Pangenesis accounted for the inheritance of acquired characters – the *Lamarckian inheritance.* Gemmules released in the stock would be transferred into the scion and incorporated into the sex cells and meristematic cells in the scion, resulting in heritable changes of the scion and their progenies. Thus Pangenesis explains graft hybridization, the main content in Michurinian genetics. In addition, Pangenesis can also explain reversion, regeneration, xenia, telegony and many other facts pertaining to variation, heredity and development (Liu 2008a).

It is a historical fact that many subsequent theories of inheritance, particularly those of Galton, Brooks, Weismann and de Vries, were influenced by Darwin's Pangenesis, as Mayr (1991) pointed out. Weismann (1904) recognized that "Darwin was the first to think out a theory of heredity which was worthy of the name of theory, for it was not merely an idea hastily suggested, but an attempt, though only in outline, at elaborating a definite hypothesis". De Vries was one of the 3 re-discoverers of Mendelian inheritance. The starting point of his thinking on heredity was Darwin's Pangenesis. In his book *The Mutation Theory*, de Vries wrote: "For myself Pangenesis has always been the starting point of my inquiries; at first only in a theoretical way, but afterwards also for the experimental investigations described in this book. Especially is it this hypothesis which has led me to search for mutations in the field". He stated clearly that he considered Darwin as one of his most important predecessors. From Darwin he had adopted the idea of independent hereditary particles (gemmules), which he gave a new name and called them *pangens* in honour of Darwin (de Vries 1910).

Although Darwin's theory never gained wide acceptance, it had been greatly appreciated by several famous plant and animal breeders. For example, Luther Burbank, the greatest plant breeder, in his book *The Harvest of the Years*, said that his lifelong adherence to the theory of Darwin was not due to blind faith in Darwin's authority. Owing to his insufficient experience, he at first even doubted some of Darwin's theories. In the course of time, however, he had more and more occasions to test Darwin's theory in the orchard and field, and the older he grew, the more convinced he became that Darwin was the real teacher (Burbank 1927). According to Hammond (1958), Darwin's works have had a profound influence on animal breeding.

Recent evidence in favour of Pangenesis

The main reason why Pangenesis has been met with scepticism was Galton's failure to test Pangenesis by blood transfusion (Galton 1871). He concluded that Darwin's Pangenesis was purely and simply incorrect. However, Sopikov (1954) showed that repeated transfusion of blood of Australorp roosters (black feathers) to White Leghorn hens, and subsequent mating of these hens with roosters of the same breed (White Leghorn) had yielded progeny of a modified inheritance. During the 1950s and 1970s, Sopikov's observations were confirmed by many Soviet researchers. The confirmed experiments were also conducted in France, Switzerland and other countries. Among 50 reports on blood transfusion reviewed by Liu (2008a), 45 obtained positive results and only 5 obtained negative results. There is thus a considerable body of experimental evidence for animal vegetative hybridization by blood transfusion, which cannot be disregarded simply because Galton had obtained negative results. The facts of heritable changes induced by blood transfusion led Stroun and Anker (2005) to suggest the hypothesis that nucleic acids are released by living cells and circulate throughout the organism. Over the past several decades, detection of circulating DNA/RNA in the plasma and serum of healthy and diseased individuals has resulted in substantial interest and hundreds of publications in the medical literature. The discovery of circulating DNA in blood and the ability of foreign DNA to be integrated into the host genome and expressed in the progeny, indicates that a mechanism exists for horizontal gene transfer from one animal to another by blood transfusion.

Darwin's gemmules: the embryonic form of our modern genes

An important part of Darwin's theory of Pangenesis are the gemmules, the basic role of which is the control of heredity, variation and development. Was there any evidence? Darwin reasoned this way: if cells can divide and produce other cells, perhaps they can produce other bodies with the assumed characteristics of gemmules by a similar process. Darwin's Pangenesis was based on gemmules, but he had no real evidence for their existence (Moore 1963). No one had detected any gemmule; yet Darwin was convinced that they must exist, because, if they did exist, the diverse and often puzzling phenomena of inheritance could be combined into a single explanatory scheme (Endersby 2003).

The word *gene* is well known in our modern biology. Less well known is that Darwin's gemmule is the embryonic form of our modern gene. The word *gene*, which was coined in 1909 by Johannsen, was derived from de Vries's term *pangen* (*pangene*), itself a substitute of *gemmules* – genetic elements in Darwin's Pangenesis. Now we know that Morgan's genes have fixed positions on the chromosome and McClintock's *jumping genes* can move within and between chromosomes. But Darwin's gemmules can circulate throughout the whole organism. A striking similarity between Darwin's gemmules and circulating DNA/RNA can be found by comparing their nature and function (see Table 1). Thus it has been suggested that Darwin's so-called gemmules could include RNAs, circulating DNA, mobile elements, prions or as yet unknown molecules (Steele et al. 1998; Liu 2005).

Table 1. A comparison of gemmules, circulating DNA/RNA, and prions

Characteristics	Gemmules	Circulating DNA/RNA	Prions
Size	molecules	molecules	molecules
Function	formative matter	genes	genetic elements
Mobility	movable	movable	movable
Replicability	self-division	self-replication	self-propagation
Quantity	numerous	a large number	N/A

Conclusions

As Bunting (1974) pointed out, "Darwin was a great man in every respect and it will be many, many years – if ever – before we see his like again. He opened up an entirely new field for scientific investigation – a field later to be exploited by such leading biologists as Mendel, Morgan and others, and it is doubtful whether we could have acquired our present knowledge of heredity had not it been for Darwin's painstaking work of a lifetime". We greatly appreciate Bunting's views. Darwin's main contribution to genetics was the collection of a tremendous amount of genetic data, and an attempt to provide a theoretical framework for its interpretation (Moore 1963). Generally speaking, if a hypothesis could explain numerous and diverse kinds of facts, it was much more likely to be true than if supported by facts of just one kind (Endersby 2003). There is a considerable body of experimental evidence for heritable changes induced by blood transfusion, the inheritance of acquired characters, graft hybridization, xenia, telegony, and reversion, which Pangenesis supposedly explains. Furthermore, evidence for gemmule's chemical existence is also provided. Darwin's Pangenesis, at first sight, seems rather startling; but the more one considers it, the more one feels convinced that it points to the fundamental problems of genetics.

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