

Charles Darwin's Theory of Pangenesis ^[1]

By: Zou, Yawen Keywords: [pangenesis](#) ^[2] [gemmule](#) ^[3] [The Variation of Animals and Plants under Domestication](#) ^[4]

In 1868 in England, [Charles Darwin](#) ^[5] proposed his [pangenesis](#) ^[6] theory to describe the units of inheritance between parents and offspring and the processes by which those units control development in offspring. Darwin coined the concept of gemmules, which he said referred to hypothesized minute particles of inheritance thrown off by all cells of the body. The theory suggested that an organism's environment could modify the gemmules in any parts of the body, and that these modified gemmules would congregate in the reproductive organs of parents to be passed on to their offspring. Darwin's theory of [pangenesis](#) ^[6] gradually lost popularity in the 1890s when biologists increasingly abandoned the theory of inheritance of acquired characteristics (IAC), on which the [pangenesis](#) ^[6] theory partially relied. Around the turn of the twentieth century, biologists replaced the theory of [pangenesis](#) ^[6] with germ plasm theory and then with chromosomal theories of inheritance, and they replaced the concept of gemmules with that of [genes](#) ^[7].

Pangenesis theory originated from the claim that characteristics acquired during an organism's life were heritable. A theory of inheritance of acquired characteristics (IAC) had persisted for almost two thousand years, since Greek antiquity. For example, [Hippocrates](#) ^[8], who lived during the fifth to fourth centuries BCE in Hellas, which later became Greece, used this theory to explain why some people had longer than normal heads. [Hippocrates](#) ^[8] said that some parents by custom bandaged their children in such a way that the children developed long heads as they grew. He said that nature would reinforce this custom after many generations, so that even if parents stopped using bandages, the heads of their offspring would be still grow long. Many scientists and philosophers in the eighteenth and nineteenth century favored some form of IAC theory, including Jean-Baptiste Lamarck in Paris, France, Charles Lyell in London, England, and, to some extent, [Charles Darwin](#) ^[5]. Lamarck's contribution to the theory of IAC garnered for it the label Larmarckian. Lamarck stated that all the characters acquired during an individual's life transmitted to their offspring. Darwin at times adopted forms of an IAC theory, and he attempted to further describe the unit of inheritance that passed between parents and offspring.

During the nineteenth century, many scientists sought to explain how traits passed from one generation to another, although most hypotheses lacked experimental support. For example, Herbert Spencer in London, England, propounded the theory of physiological units in his 1864 book *Principles of Biology*. Spencer postulated that cells contained physiological units, an intermediate structure between what he called chemical units, such as proteins, and morphological units, such as cells. Spencer implied that those physiological units in parents transmitted to their offspring, so that parents and offspring looked similar to each other. Spencer continued to explain that use or disuse of structures could alter physiological units. Darwin had noted the concept, and later admitted that Spencer's theory coincided with his own.

In 1868, Darwin proposed the [pangenesis](#) ^[6] theory in the concluding chapter of his book *The Variation of Animals and Plants under Domestication*. In Darwin's account, the theory of [pangenesis](#) ^[6] complemented his theory of natural selection, described in his 1859 *On the Origin of Species by Means of Natural Selection*. The theory of [natural selection](#) ^[9] said that species adapted to their environments through selection on those organisms to fit in those environments. Critics highlighted the theory's lack of mechanisms for inheritance and development. In his 1859 book, Darwin had not explained how environments caused different organisms in the same population to vary in their traits, or how offspring inherited those variations from their parents.

Darwin proposed [pangenesis](#) ^[6] theory to complement his 1859 theory of [evolution](#) ^[10] via [natural selection](#) ^[9]. Darwin coined the term [pangenesis](#) ^[6], with "pan-" meaning whole, and "genesis" indicating origin. With the term [pangenesis](#) ^[6], Darwin suggested that all parts of the parents could contribute to the [evolution](#) ^[10] and development of the offspring.

Darwin postulated the existence of a hereditary material inside cells. Nonetheless, Darwin had not experimented on cells to demonstrate his theory, so he called it a provisional hypothesis. Darwin argued that, in what he called higher animals or plants, every cell in their bodies emitted small particles, which were units of heredity, that he called gemmules. The gemmules could either circulate and disperse in the body system, or they could aggregate in the sexual cells located in reproductive organs. As hereditary units, the gemmules transmitted from parents to offspring, where they developed into cells that resembled the parents' cells. It was not sexual cells alone that generated a new organism, but rather all cells in the body as a whole. Darwin argued that environments could cause variations to gemmules of body cells or to those in sexual cells, so a collection of gemmules could reflect changes that had occurred to all parts of an organism's body.

Darwin used the concept of gemmules to explain some phenomena regarding heredity, variation, and development. These phenomena included regeneration of body parts, reversion, and sexual and asexual reproduction. For example, Darwin offered an explanation for reversion, the phenomenon that a trait of remote ancestors would reappear in organisms whose more immediate ancestors lacked the trait. He claimed that gemmules could either go into the state of dormancy or be active. Darwin said that, in the phenomenon of reversion, a gemmule transmitted from the remote ancestors to immediate parents and then to

the offspring, but the gemmule was dormant in direct parents, and it was only active in remote ancestors and in the offspring.

Darwin also used gemmules to explain sexual reproduction and asexual reproduction. Sexual reproduction involves two parents of different sexes, while asexual reproduction concerns reproduction from only one parent, often involving budding. Darwin claimed that, in asexual reproduction, gemmules from every cell type in a parent aggregated in a bud, which would develop into a new individual. In sexual reproduction, gemmules from both parents blended in the sexual organs to be passed to the offspring.

Darwin never had any experimental results to support the existence of gemmules. Darwin based his [pangenesis](#)^[6] theory, as well as the theory of [natural selection](#)^[9], on his observation of [turtles](#)^[11], finches, and other species in different environments, and on fossils he had gathered from his voyage on the *Beagle*, a ship of the British Navy, in the 1830s. Darwin's [pangenesis](#)^[6] theory lacked details at cell and molecular levels.

Many criticized Darwin's theory of [pangenesis](#)^[6]. To test the theory, Darwin's cousin [Francis Galton](#)^[12] in London, England, conducted a series of blood transfusion experiments. Galton transfused blood between different colored rabbits. Galton hypothesized that the blood contained gemmules that would shape the color of the offspring. By transfusing the blood from a white [rabbit](#)^[13] to a black [rabbit](#)^[13], the black [rabbit](#)^[13] would have different colored descendants than normal black rabbits, which did not get transfused blood. But the result of the experiment contrasted Darwin's prediction, black rabbits with the blood from white rabbits produced offspring that were black, and Galton claimed that gemmules did not exist. Darwin responded by implying that gemmules might exist in other bodily fluid, and he did not explicitly say they were in blood.

Scientists such as [Hugo de Vries](#)^[14] in the Netherlands and [August Weismann](#)^[15] in Germany formulated theories of heredity shortly after Darwin. De Vries propounded the intracellular [pangenesis](#)^[6] theory in 1889, a modified theory of [pangenesis](#)^[6]. According to De Vries, gemmules cannot transfer from body cells to sexual cells. De Vries argued that gemmules could only move between the [nucleus](#)^[16] and the cytoplasm inside a single cell, so his theory was called intracellular [pangenesis](#)^[6] theory. To distinguish between his theory and Darwin's, De Vries used the term pangene to replace the term gemmules for the unit of hereditary materials. By 1909, Wilhelm Johannsen in Denmark shortened the term pangene to the term gene.

In a passage of his 1893 book *The Germ Plasm: a theory of heredity*, Weismann stated that small units of materials in the cells of organisms pass from parents to their offspring. Nonetheless, Weismann argued that only the hereditary material in the sexual cells, or [germ cells](#)^[17], could transmit to offspring. Weismann called his theory germ-plasm theory. Principles of the germ-plasm theory gradually replaced Darwin's [pangenesis](#)^[6] theory, but biologists adopted little of Weismann's terminology.

Darwin's theory of [pangenesis](#)^[6] proved obsolete after the rediscovery of Gregor Mendel's laws of heredity in 1900. In the 1860s in Brno, Austrian Empire, which later became the Czech Republic, Mendel had studied how heritable factors in sexually reproducing plants behaved across generations, and he had inferred laws to describe those behaviors. Mendel did not study the actual units of inheritance, but only the phenotypes or traits hypothesized to develop in organisms that had those factors. With his laws, Mendel could predict phenotypes among the offspring from data about the phenotypes of parents. Mendel's laws, unstudied for decades, were rediscovered in 1900, and Walter Sutton in the US and [Theodor Boveri](#)^[18] in Europe soon paired those laws to the mechanistic descriptions of how chromosomes behaved in replicating cells, creating a chromosomal theory of inheritance.

Following [William Bateson](#)^[19] in England and Wilhelm Johannsen in Denmark, most biologists eventually rejected theories of the inheritance of acquired characteristics and Darwin's [pangenesis](#)^[6] theory, and they used the term gene to refer to those things that Mendel had called factors. Furthermore, they followed Weismann and held that only [genes](#)^[7] from sex cells, and not [genes](#)^[7] from body cells, transmitted from parents to offspring. Additionally, many adopted the chromosomal theory of inheritance, which held that the mechanisms of replicating cells and chromosomes physically explained the behaviors, postulated by Mendel, of [genes](#)^[7], which biologists postulated to be in the chromosomes of cells. Scientists in the early and middle decades of the twentieth century worked to fit the chromosomal and genetic theories of inheritance with Darwin's theory of the [evolution](#)^[10] of species by [natural selection](#)^[9].

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