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VERITAS TEMPORIS FILIA EST (TRUTH IS THE DAUGHTER OF TIME)

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Abstract

In 1865, Gregor Mendel presented the lectures "Experiments in Plant Hybridization" concerning his results from cross-breeding experiments with different types of garden pea, performed in his monastery garden in Brno. Mendel studied easily observed pairs of opposite traits, such as purple or white flower, and discovered dominant and recessive traits. He concluded that parents pass separate and distinct factors (today called genes) on to their offspring that are responsible for inherited traits. However, the scientific community did not understand that; indeed it was the beginning of what becomes genetics. The lectures published in 1866, Mendel sent to more than 30 biologists across Europe, but almost no one commented them. In the next 35 years, these papers were only three times cited. The genetics became more important at the beginning of the 20th century, when three different research groups (Hugo de Vries, Carl Erich Correns and Erich von Tschermak with their co-workers) independently re-discovered Mendel's Laws of inheritance. However, as soon as the work was rediscovered, it created controversy. The closeness of Mendel's experimental observations to those predicted by his theories has led to numerous articles and ongoing debate about whether the data could have been obtained in the published form without some falsification. There have been many plausible arguments made for and against this view by a range of eminent geneticists and statisticians. Some have gone so far, as to suggest that the theories ensued from Mendel's two laws were not even correctly formulated in his original paper. The strongest supporters of Mendel's theory became biologist William Bateson and zoologist and geneticist Thomas Hunt Morgan. Morgan argued that genes are located on chromosomes and that the cells chromosomes hold the actual hereditary material, thus created what is now known as classical genetics. For his discovery concerning the role play by the

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chromosome in heredity, Morgan received the Nobel Prize in 1933. As the architect of genetic experimental and statistical analysis, Mendel remains the acknowledged father of genetics.

Key words: Gregor Mendel, genetics, inheritance, falsification

Introduction

Since the beginning of human history, people have been wondered how are the traits inherited from one generation to the next. The fact that living organisms inherit traits from their parents has been used since prehistoric times to improve crop plants and animals through selective breeding. Although children often look more like one parent, most of the offspring seem to be a blend of the characteristics of both parents. Centuries of domestic plants and animals breeding had shown that useful traits - yield of wheat, speed in dogs, protein content in grain - can be improved by controlled mating. However, there was no scientific way to predict the outcome of a cross between two particular parents.

A number of hypotheses were suggested to explain heredity. During the 19th century, prior to the discovery of genetics, many biologists support the idea of blending inheritance (Jenkin, 1867, by Bulmer, 2004). By this theory, inherited traits were determined randomly, from a range bound by the homologous traits found in the parents. For example, the height of a person, with one short and another tall parent, was always to be of some intermediate value between both parents' heights. The shortcoming of this idea was how the person of intermediate height, in turn, became one of the limiting bounds (either upper or lower) for future offspring, and so on down the entire lineage. Thus, in each family, the potential for variation would tend to narrow with each generation, and it would lead to uniform population for every trait. If the idea of blending inheritance was correct, in this example, all individuals of a species would eventually converge upon a single value for height, variation will disappear and every next generation should be more uniform than the previous one. By now, all individuals should be as indistinguishable as clones. Blending inheritance failed to explain how traits that seemingly disappeared for several generations, often reasserted themselves down the line, unaltered. Blue eyes and blond hair, for example, often could disappear from a family's lineage for several generations, and after that two brown-haired, brown-eyed parents give birth to a blond, blue-eyed child. If blending inheritance is the fact, this could not be possible.

In 1868, Charles Darwin proposed his pangenesis theory (*pan*- whole, *genesis*-origin) to describe the units of inheritance between parents and offspring and the processes by which those units control development in offspring (Zou, 2014). Indeed, pangenesis theory originated from the claim that characteristics acquired during an organism's life were heritable. A theory of inheritance for acquired characteristics had been persistent for almost two thousand years, since Greek antiquity. Many scientists and philosophers in the eighteenth and nineteenth century favored some form of inheritance of acquired characteristics theory, including Jean-Baptiste Lamarck in Paris, France. Lamarck stated that all the characters acquired during an individual's life transmitted to their offspring.

Darwin proposed the concept of gemmules, referring to hypothesized small particles of inheritance inside cells. Namely, every cell in the organism of higher animals or plants emitted small particles, considered as the units of heredity, Darvin called gemmules. The gemmules could either circulate or disperse in the body system, or they could aggregate in the sexual cells, located in reproductive organs. As hereditary units, the gemmules were transmitted from parents to offspring and 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. The theory suggested that an organism's environment could modify the gemmules in any part of the body, and that these modified gemmules would congregate in the reproductive organs of parents to be passed to their offspring. In sexual reproduction, gemmules from both parents blended in the sexual organs are to be passed to the offspring. For the term pangenesis, Darwin suggested that all parts of the parents could contribute to the evolution and development of the offspring. Darwin's theory of pangenesis gradually lost popularity in the 1890s, when biologists increasingly rejected the theory of inheritance of acquired characteristics, on which the pangenesis theory partially relied.

Around the turn of the twentieth century, biologists replaced the theory of pangenesis with germplasm theory and then with chromosomal theories of inheritance, and they replaced the concept of gemmules with that of genes. Still in 1893 Weismann stated that small units of materials in the cells of organisms pass from parents to their offspring (Winther, 2001). Nonetheless, Weismann argued that only the hereditary material in the sexual cells, or germ cells, could transmit to offspring. Weismann called his theory germplasm theory. Principles of the germplasm theory gradually replaced Darwin's pangenesis theory.

The particulate hypothesis states that parents pass on to their offspring distinct factors that retain their offspring while the blending hypothesis states that parents′ hereditary material blends in their offspring.

In the 1860s, 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 be developed in organisms that had those factors. With his laws, Mendel could predict phenotypes among the offspring from parental phenotypic data. Mendel's laws, unstudied for decades, were rediscovered in 1900. Walter Sutton in the US and Theodor Boveri in Europe soon paired those laws to the mechanistic descriptions of how chromosomes behave in replicating cells, thus creating a chromosomal theory of inheritance (Satzinger, 2008). Mendel's hypothesis states that parents pass on to their offspring separate and distinct factors (today called genes) that are responsible for inherited traits.

Following the work of Bateson from 1900 in England and Johannsen from 1909 in Denmark, most of biologists eventually rejected theories of the inheritance of acquired characteristics and Darwin's pangenesis theory, and they used the term "gene" referring to that Mendel had called factors (http://www.esp.org/foundations/genetics/classical/wb-1.pdf; http://dx.doi.org/10.5962/bhl.title.1060. (pristup 25.01.2016). Until the middle of the twentieth century, scientists worked to fit the chromosomal and genetic theories of inheritance with Darwin's theory of the evolution of species by natural selection.

Education and early career of Johann Mendel

Johann Mendel was born 1822 in a farmers family in Hynčice, about 120 km north of Brno. From his mother Johann Gregor inherited some of his character traits, for he seems to have been good-natured, quiet, and modest. Probably his talent came also from the mother's side of the family. During his childhood, Johann helped his father farm their land, working as a gardener and studding beekeeping. On the farm Johann developed his love for the science.

Johan began to attend the village school and his teachers noticed that he was an exceptionally intelligent boy. Johann′s teachers recommended him to an upper elementary school in Leipnik. This was a school where exceptional students were sent to be prepared for the gymnasium. Later, when Johann was 11 years old, he attended Gymnasium in Opava, in 1834. In 1938, Johann's father was seriously injured while working and that situation places a lot of stress on Johann, because his parents were no longer able to pay for his schooling, leaving him to support himself entirely. Due to that, Johann become quite sick and stayed in bed for four months. He graduated in 1840.

Johann wanted to continue his education at a university, and prerequisite for that was two year of philosophical study. From 1840 to 1843, he studied religion, philosophy, ethic, pedagogy, mathematics and physics at the Faculty of Philosophy, University of Olomouc, taking another year off because of illness. When Mendel entered the Faculty of Philosophy, the head of Natural History and Agriculture Department was Johann Karl Nestler, who conducted extensive research of hereditary traits of plants and animals, especially sheep. Johann was excelled in physics and mathematics.

Indeed, Friedrich Franz, his professor of physics who was a priest, urged Johann to become a monk. For Mendel, that was the only way for obtaining education, since monasteries were known to be centers of learning. In late 1843, Johann Mendel at the age of twenty one joined the Augustinian monastery of St. Thomas and began his training as a priest; born Johann Mendel took the name Gregor. Gregor Mendel was ordained into the priesthood in August 1947. As a priest, Mendel found his parish duty to visit the sick in hospital. It quickly became clear that he was not fit for these duties, because whenever he visited the patients he became very upset. Mendel wanted to teach. Head of the monastery, Abbot Napp, found him a substitute-teaching position at Znojno, where he proved to be very successful in teaching mathematics and literature at the high school. Mendel began teaching in 1849, even he did not yet have an official document from a university approving him to do so. In 1850, he failed the oral part, the last of three parts, of his exams to become a certified high school teacher.

In 1851, Mendel was sent to the University of Vienna to study under the sponsorship of Abbot Napp, so that he could get more formal education. As at Olomouc, Mendel devoted his time at Vienna to physics and mathematics. He also studied the anatomy and plant physiology and the use of the microscope. In the summer of 1853, Mendel returned to the monastery in Brno, and in the following year he was again given a teaching position, primarily of physics, this time at the Brno high school, where he remained until elected abbot 14 years later.

After Mendel was elevated as abbot in 1868, his scientific work mostly ended, because he became occupied with his increased administrative responsibilities. The increased responsibilities prevented him from conducting any further scientific experiments. Mendel died on January 6th 1884, at the age of 61, in Brno, from chronic nephritis. After his death, the succeeding abbot burned all papers in Mendel's collection, to mark an end to the disputes over taxation.

Mendel's Genetics

In 1854, in the garden of monastery, Gregor Mendel established the experimental program in hybridization. Between 1856 and 1863, he planted and tested about 5,000 pea plants. The aim of this program was to trace the transmission of hereditary characters in successive generations of hybrid progeny. Mendel found that garden pea (*Pisum sativum*) has many distinct varieties and he selected it to conduct his studies. Pea is suitable due to ease of growing and control of pollination. In order to understand the transmission of characters, Mendel observed seven traits that are easily recognized and apparently occur only in one of two forms: purple or white flower color, axil or terminal flower position, tall or short plant, round or wrinkled seed shape, yellow or green seed color, inflated or constricted pod shape and yellow or green pod color. This observation that these traits do not present in offspring plants with intermediate forms was crucial, because the leading theory in biology at the time was that inherited traits blend from generation to generation.

He crossed varieties that differed in one trait- for instance, purple flower varieties with white flowers varieties. The F_1 generation displayed the character of one variety but not that of the other. In Mendel's terms, one character was dominant and the other recessive. He grown numerous plants from this hybrid and obtained the F_2 generation, in which the recessive character reappeared, and the proportion of offspring containing the dominant to offspring containing the recessive was very close to 3:1 ratio. Study of the F_3 generations of the dominant group showed that one-third of them were pure line and two-thirds were of hybrid constitution. Hence, the 3:1 ratio could be rewritten as 1:2:1, meaning that 50% of the F_2 generation was pure line and 50% were still hybrid.

This was Mendel's major discovery, and it was unlikely to have been made by his predecessors, since they did not grow statistically significant populations, nor did they follow the individual characters separately to establish their statistical relations.

Mendel′s knowledge in physics and mathematics, especially combinatorial mathematics served him to represent obtained results. If dominant form of a trait is denoted by A and the recessive by a, then the 1:2:1 ratio recalls the terms in the expansion of the binomial equation: $(A+a)^2=A^2+2Aa+a^2$.

From these experiments, Mendel induced two generalizations which later became known as Mendel's Principles of Heredity or Mendelian inheritance. He described these principles in a two-part paper "Experiments on Plant Hybridization" that he read to the Natural History Society of Brno, on February 8th and March 8th 1865, and which was published in 1866. Mendel's Laws of heredity are usually stated as:

1) The Law of segregation: Each inherited trait is defined by a gene pair. Parental genes are randomly separated to the sex cells so that sex cells contain only one gene of the pair. Although Mendel did not know the physical basis of heredity, he observed that organisms inherit traits *via* discrete units of inheritance, which are now called genes. Offspring therefore inherit one genetic allele from each parent when sex cells unite in fertilization.

2) The Law of Independent Assortment: Mendel realized that he could test his expectation that the seven traits are transmitted independently of one another. Crosses involve first two and then three of his seven traits yielded categories of offspring in proportions

following the terms produced from combining two binomial equations, indicating that their transmission was mutually independent. So, genes for different traits are sorted separately from one another, so that the inheritance of one trait is not dependent on the inheritance of another.

3) The Law of dominance: Therefore, a cross between a homozygous dominant and a homozygous recessive will always express the dominant phenotype, while still having a heterozygous genotype. Recessive alleles will always be masked by dominant alleles. In a cross between two organisms pure for any pair of contrasting characters, the character that appears in the F_1 generation is called dominant and the one which is not expressed is called recessive.

Mendelism - important and controversial theory

It is obvious that Mendel did not make effort to publicize his work. Today it is not known how many reprints of his paper he distributed. He had ordered 40 reprints, and only eight of which are known. Except for the journal where Mendel published his paper, in 19th century only a few sources are known in which Mendel′s plant hybridization work is mentioned. Few of these provide a clear picture of his achievement.

Indeed, Mendel's results were largely ignored. Although Mendel's laws were not completely unknown to biologists of that time, they were not seen as generally applicable. A major barrier to understand their significance was in the apparent blending of inherited traits in the overall appearance of the progeny, now known to be due to multigene interactions, while Mendel studied the organ-specific binary characters. In 1900, however, his work was “re-discovered” by three European scientists, Hugo de Vries, Carl Correns, and Erich von Tschermak, but they partially still ignored Mendel’s findings.

Bateson (by Cock and Forsdyke, 2008) was the strongest promoter of Mendel’s theory. Until 1902, he translated Mendel’s works into English and was a strong supporter of the Mendelian laws of inheritance. Bateson was credited for creating the terms “genetics,” “allele”, “zygote,” “heterozygote” and “homozygote”. Bateson first used the term “genetics” publicly at the Third International Conference on Plant Hybridization in London, in 1906, and Johannsen first used the word “gene” in 1909 to describe the units of hereditary information (Edwards 2013). Many other biologists were against Mendel’s model of heredity because it implied that heredity was discontinuous, opposite to the apparently continuous variation observable for many traits. Later, however, Fisher in article published 1936 showed that if multiple Mendelian factors were involved in the expression of an individual trait, they could produce the diverse results observed (https://drmc.library.adelaide.edu.au/dspace/bitstream/2440/15123/1/144.pdf (pristup 10.01.2016.)). After the rediscovery of Mendel’s work, scientists tried to determine which molecules in the cell were responsible for inheritance. In 1911, Thomas Hunt Morgan argued that genes are on chromosomes and the chromosomes of cells were thought to hold the actual hereditary material, and created what is now known as classical genetics. This finally strengthen Mendel’s place in history of genetics.

Discussion

The fundamental laws of inheritance are now known as Mendel’s laws, and the science on which they are based is called Mendelian genetics. However, because

Mendel's importance was unrecognized during his lifetime, little original information about his scientific work was preserved. Most unfortunately, his scientific records were apparently burned around the time of his death (Orel, 1996). Classical study of seven genes by Gregor Mendel was basis for modern genetics development, although relatively recently little was known about their function. Progress in molecular genetics in last few decades dramatically changed this situation and identity of Mendel′s genes in pea has been discovered. The gene Mendel studied that determinates seed shape trait is ***r*** on chromosome VII, the gene that determinates cotyledon color is ***i*** on chromosome I, the gene that determinates seed coat color is ***a*** on chromosome I, the gene that determinates pod shape is either ***v*** on chromosome IV or ***p*** on chromosome VI, the gene that determinates pod color is ***gp*** on chromosome 5, the gene that determinates flower position is ***fa*** on chromosome IV and the gene that determinates stem length is ***le*** on chromosome IV (Fairbanks and Rytting, 2001).

Although Mendel's paper is considered as classic in the history of biology, it generated much controversy throughout the century that elapsed since the rediscovery of Mendelian laws in 1900. Some authors glorify Mendel as a brilliant scientist whose work was ahead of his time, others criticize his methods, and a few claim he was a deception (Monaghan and Corcos, 1993; Weldon, 1902 by Edwards 2013; Hartl and Fairbanks, 2007). The closeness of Mendel's experimental observations to those predicted by his theories has led to numerous articles and ongoing debate about whether the data could have been obtained in the published form without some falsification (Weldon, 1902, by Edwards 2013). There is substantial disagreement about his objectives, the accuracy of his presentation, the statistical validity of his data, and the relationship of his work to evolutionary theories of his time. Fairbanks and Rytting (2001) apostrophize five of the most contentiously debated issues by looking at the historical record through the view of current science: (1) Are Mendel's data too good to be true? (2) Is Mendel's description of his experiments fictitious? (3) Did Mendel articulate the laws of inheritance attributed to him? (4) Did Mendel detect but not mention linkage? (5) Did Mendel support or oppose Darwin? Some scientists disagree about Mendel's integrity in his presentation, his formulation of the fundamental laws of inheritance, experimental design, motives for conducting his experiments, and his conclusions. However, given the lack of suitable terminology at that time, this seems a very stiff judgment. Fisher saw, in 1936, certainly the significance of Mendel's contribution to the field even though he was the one who raised several concerns about the data. Some of these concerns still exist, and the controversy has not been resolved, despite recent implications to the contrary (Franklin, 2008; Stigler, 2008).

Fairbanks and Rytting (2001) concluded that Mendel did not contrived his data, his description of his experiments is literal, he formulated the laws of inheritance attributed to him insofar as was possible given the information he had, he did not detect linkage, and he neither strongly supported nor opposed Darwin.

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ISTINA JE KĆI VREMENA

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Sažetak

Rezultate ukrštanja različitih tipova vrtnog graška, koje je dobio u manastirskoj bašti u Brnu, Mendel je izneo 1865. godine u predavanju "Eksperimenti u hibridizaciji biljaka". Proučavajući osobine graška koje imaju lako prepozantljive dve alternative, kao što je npr. ljubičasta ili bela boja cveta, Mendel je otkrio dominantne i recesivne osobine. Zaključio je da roditelji prenose na svoje potomke posebne i različite faktore (koje danas nazivamo geni), koji su odgovorni za nasleđivanje osobina. Tadašnja naučna zajednica nije razumela da je to u stvari bio početak razvoja genetike. Predavanja su publikovana 1866. i Mendel ih je poslao na adresu više od 30 biologa širom Evrope, ali ih skoro niko nije komentarisao. U narednih 35 godina ovi radovi citirani su samo tri puta. Genetika je postala značajnija početkom 20. veka kada su istraživači iz tri različite istraživačke grupe (Hugo de Vries, Carl Erich Correns i Erich von Tschermak sa saradnicima), nezavisno jedan od drugih, ponovo otkrili Menedelove zakone. Međutim, odmah nakon ponovnog otkrića Mendelovih zakona došlo je do kontraverznih stavova. Mala odstupanja između eksperimentalnih i teorijskih frekvencija pokrenule su intenzivne debate o mogućnosti dobijanja takvih podataka, dok su neki izražavali sumnju da su podaci falsifikovani. Stavovi eminentnih statističara i genetičara u vezi Mendelove teorije kretali su se od njenog podržavanja do odbacivanja. Pojedinci su iznosili sumnju da teorije nisu pravilno postavljene ni u originalnom radu. Biolog Wiliam Bateson i zoolog i genetičar Thomas Hunt Morgan bili su najveće pristalice Mendelove teorije. Morgan je tvrdio da se geni nalaze na hromozomima, odnosno da hromozomi sadrže nasledni material, što je u suštini značilo promovisanje klasične genetike, za što je Morgan dobio Nobelovu nagradu. Kao osnivač genetičkih eksperimenata i statističke analize Mendel se smatra ocem genetike.

Ključne reči: Gregor Mendel, genetika, nasleđivanje, polemika

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