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Mendelism: Connecting the Dots Across Centuries

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Abstract—The year 2022 paid a bicentennial tribute to the phenomenal work of the father of Genetics, Gregor Johann Mendel for deciphering the genetic logic behind the phenotypes. His principles were distilled as the law of segregation and law of independent assortment. His work was rediscovered 34 yr later by H. De Vries, C. Correns, and E. Tschermak and popularized by W. Bateson. While C. Darwin accounted for similarities among organisms through the differences in the form of evolution, G. Mendel accounted for similarities through heredity; the ideological gaps were bridged mathematically by R. Fisher. Later with the test of time, the interaction among researchers paved Mendelian principles into different branches of genetics viz., cytogenetics, molecular genetics, population genetics, quantitative genetics, etc. At present we have landed in the era of genomics and the emerging field of phenomics which have potential to bridge the huge gap between demand and supply in different agro-industrial and allied goods. The need to connect the budding researchers in the field of genetics with Mendelism and its significance, catalyzed our concentrated effort to link Mendelism across the centuries, highlighting its importance and extrapolating the concept of heredity and variation from garden peas to different life forms. In conclusion, as our knowledge on genetics deepens, more insights on underlying mechanisms and subsequent applications will be witnessed.

Keywords: chromosome, Darwin, DNA, evolution, gene, genetics, history, Mendel, variation

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1. INTRODUCTION

We, humans, are peculiar compared to other creatures because we have a special character called "curiosity". We fascinatingly ask the question, "why" and "how" things are intricately woven to form what's happening in nature, the life narrative. In the past, certain scholars also tried to answer the question, "how the continuous evolution of myriad forms of life is occurring?" which led to the development of an important branch of science i.e., Genetics. Genetics is instrumental in providing evolutionary insights by unraveling underlying mechanisms for different traits (Andersson and Purugganan, 2022). Though the science of genetics has reached the level of genomics and transcended inter-disciplinary barriers with omics approaches, all these advances can be streamlined to Gregor Johann Mendel's idea of inheritance. July 20, 2022 commemorated the bicentennial of the birth of G.J. Mendel (1822–1884), regarded as the father of genetics, for his flag-bearing work on particulate inheritance in the 1860s. As anything which is dynamic surely has a history, we mined many reviews on the relevance of Mendel's work in modern research (Smýkal et al., 2016; Gayon, 2016; Poczai and Santiago-Blay, 2021; Sussmilch et al., 2022; Wolf et al., 2022; Van Dijk et al., 2022; Fairbanks, 2022) but those linking histories of evolution with the state-of-art are not witnessed yet. This catalyzed our concentrated effort to connect Mendelism across the centuries, highlighting its importance and relevance in extrapolating the concept of heredity and variation from garden peas to different life forms, ultimately bridging the huge gap between demand and supply in different agro-industrial and allied goods.

Prior to 1000 BC, there was a widespread acceptance of the theory of Vedas in Hinduism, the theory of creationism in Christianity, and other similar theories whose literal interpretation is that God created Earth and all modern, immutable species, for example, the trinity of the Hindu gods, viz., Brahma-Vishnu-Mahesh had their roles of cosmic creator, the preserver, and the destroyer, respectively. Later on, geological and palaeontological shreds of evidence over time led to the development of theories that form the basis of evolutionary biology. The first person who elaborated the theory of generations was Hippocrates, known as the father of medicine, who around 400 BC postulated that hereditary material has a physical form

similar to the shape of different parts of the body but in very minuscule sizes and elements from these parts, become concentrated in the semen and later develop as offspring in the womb. This is famously known as the "Bricks and mortar theory" (Gardner, 1972). Even though it seemed irrelevant to modern man, during those days (~300 BC) this led to the genesis of theories on evolution. Later around 350 BC, Aristotle came up with his theory of spontaneous generations. As the name suggests, species that co-exist at a given time have evolved independently of one another, spontaneously. He was also the first to highlight the importance of blood, in life and inheritance. Aristotle rejected the bricks-and-mortar model of inheritance. Instead, he proposed that heredity involves the transmission of information in the form of a "blueprint model" i.e., it does not have a physical form (Leroi, 2014). This remarkable insight was ignored until the middle of the 20th century. Apparently, both Hippocrates and Aristotle sketched theories that attempted to explain resemblance among relatives and account for the fact that offspring somehow show a character that is similar to their parents. The theories were further encapsulated as the "blending theory of inheritance" which says, the material basis of inheritance is analogous to a fluid. It was assumed that the hereditary material coming from the parents mixes in the progeny to produce the offspring, which appear as intermediates of the two parents.

In 1665, Robert Hooke used the term "cell" to describe plots made up of cork and other plants. This is because it reminded him of *cellula*, the small one-room apartments of the monks (Gest, 2009). Somewhat contemporarily, Anton van Leeuwenhoek (1632–1723), known as the father of microbiology, modified the microscope invented by Zacharias Janssen and Hans Janssen around the 1590s which enabled him to report single-celled organisms, "animalcules" for the first time in history. These animalcules later came to be known as microorganisms in modern terminology. Later his idea of observing microorganisms led to the establishment of the cell theory and visualization of chromosomes (Dobell, 1932).

In the 1800s, Jean-Baptiste Pierre Antoine De Monet chevalier De Lamarck gave the theory of use and disuse, also called the inheritance of acquired characters or soft inheritance (De Monet, 1914). The roots of Lamarckism have taken the shape of what we know today as Epigenetics. The concept and nomenclature of Epigenetics was given by Conrad Waddington around the 1940s, defined as the effect of both heritable and non-heritable changes that alter the gene expression, without altering the nucleotide sequence (Waddington, 1942). During 1838–1839, the "unified cell theory" by German botanist, Mathias Schleiden and German physiologist, Theodor Schwann surfaced, which narrowed down the idea of evolution to the cellular level. They concluded this theory in two tenets viz., firstly, organisms are made up of a large number of cells and secondly, cells form the basic structural, functional, and fundamental unit of life (Schwann, 1847; Maton, 1994). Rudolf Virchow, known as the father of modern pathology, added a third tenet to the series, which says, every new cell arises from previously existing cells i.e., *omnis cellula e cellula* (Virchow, 1860). The third tenet gave inkling about the replication of cells and genetic material.

Around the late 1850s, Charles Darwin and Alfred Wallace jointly came up with the idea of evolution by means of natural selection, which form the basis of modern selection theories and breeding methods (Wallace, 1855; Darwin, 1859). Fleeming Jenkin gave the theory of blending inheritance, causing the convergence of phenotypes to the population (Jenkin, 1867). The theory was vernacularly called the "blood theory of heredity". C. Darwin also postulated the theory of pangenesis, where he assumed that each organ of the body drops tiny particles called "gemmules" or "pangenes" (Darwin, 1868). Supposedly, these pangenes were microscopic particles that contained information about the characteristics of their parent cell, eventually forming an embryo. His concept was the-then modern update of the Hippocratic bricks-and-mortar theory. Nearly two decades later, pangenes were renamed as genes by Johannnsen. Hugo De Vries, while observing variations among evening primrose (*Oenothera lamarckiana*) growing in an abandoned potato field, discovered mutations. H. De Vries in 1886, tried to answer the arrival of the fittest, evoked by natural selection theory. In the next section, we shall be dealing with intracellular elements to look into the theories of life, in finer detail (De Vries, 1889).

2. RESURRECTION

G.J. Mendel's work remained in backdrop, since biologists of 1865 were less prepared to understand his insights (Dobzhansky, 1965). Between 1866 and the beginning of the 20th century, two milestones along the way of biology that had a significant bearing on the acceptance of Mendel's after work, were surpassed. Firstly, the discovery of chromosomes and their movements during cell division by Walther Flemming in 1882. These "colored bodies" were first reported in the early 1840s by Karl Wilhelm von Nageli in plants and Eduard Van Beneden in animals, although the actual word "chromosome" was coined several decades later, in 1888 by Heinrich W. Gottfried von Waldeyer-Hartz. This led to observations that are almost intuitively evident to us today as: (1) chromosomes duplicate during cell division; (2) each daughter cell receives the same number of chromosomes; (3) gametes contain half the number of chromosomes as an adult cell; (4) fertilization involves the fusion of the nuclei of sperm and egg; (5) the resulting zygote has the full chromosome complement (Paweletz, 2001).

Secondly, biometricians started using mathematics in biological research, for drawing meaningful insights from field data; this can be greatly accredited to Francis Galton for his conception of variance, standard deviation, correlation, regression, and eugenics. Eugenics influenced both the setting of objectives and methods in human genetics. He was also the first to analyze the relative importance of genetics and environment in aetiology, using twin data (Galton, 1883), and to introduce fingerprint analysis, the most valuable tool in forensic studies.

From 1892 onwards, H. De Vries started hybridizing many closely related species that differed from one another by only one or a few traits, for instance, the blue and white flowers of *Veronica longifolia* and purple and white flowers of *Aster tripolium*. He interpreted his results in the framework of intracellular pangenesis, where he used self-coined terminologies viz., pangenes, central hybrids, and old types, analogous to Mendel's terms—factors, heterozygous, and homozygous organisms, respectively (De Vries, 1889). Before publishing, H. De Vries accidentally came across the original paper of G. Mendel published in 1866, and thereby cited the Mendelian F2 genotypic ratio of 1 : 2 : 1, which was in concordance with his own work (Allen, 1969). This publication presumably triggered both Carl Correns and Erich Tschermak von Seysenegg to read G.J. Mendel's work and prioritize its importance. E. Tschermak published the first manuscript with the full knowledge of G. Mendel's paper (Tschermak, 1900). E. Tschermak, whose grandfather, the famous botanist, Eduard Fenzl taught botany to G. Mendel, conducted hybridization of plants to improve crop yield and C. Correns while experimenting hybridization in hawkweed, arrived at the typical Mendelian ratio of 3 : 1 and 9 : 3 : 3 : 1 for single traits and two traits in F2 generation, respectively (Correns, 1900, 1950), also cited G.J. Mendel in their publications. Some of C. Correns' unpublished work and most of his lab books were destroyed in the Berlin bombings of 1945, during the Second World War. Thus, these three musketeers, 16 years after his death, were rediscovered independently, cited, and attributed the priority of discovery solely to Mendel.

3. THE ROOTS

G.J. Mendel, known as the "father of genetics", was an Austrian monk. Based on the transmission of traits in hybridization experiments, he concluded that particles/factors determining the characters of an individual are inherited intact across the generations. From 1851 to 1853, he studied natural history at the University of Vienna under the guidance of Franz Unger, a well-known botanist, and cytologist at that time (Blume, 2022). G. Mendel during 1856–1868 conducted his study on 2 ha of land and analyzed 7 contrasting traits in over 28000 plants of garden pea (*Pisum sativum*) and concluded the results as follows: (a) He called agents responsible for traits as "factors" or "units", (b) Factors occur in pairs (factors now called as genes), (c) Each parent passes only one factor to offspring, (d) A trait not expressed in F_1, can reappear in F_2 and (e) Factor does not change in hybrids, it remains the same (Sutton, 1903; Boveri, 1904). He extended his hybridization experiments to at least twenty plant genera in addition to garden peas. The letters he wrote to C. Nägeli indicate that he published only a few of the results of the additional experiments (Fairbanks, 2022; Blume, 2022; Nogler, 2006; Vecerek, 1965). By conducting his research step by step, G. Mendel rose step by step to the top of his theory—predicting the principles of inheritance of genetic material, he deciphered the black box which was later distilled by C. Correns as laws of inheritance (Correns, 1900).

3.1. Law of Segregation or the Law of Purity of Gametes

Alleles of a gene segregate during gamete formation so that each gamete contains only one allele and has not been contaminated. This law was a result of monohybrid crosses and is universally accepted.

Phenotypic ratio—3 : 1;

Genotypic ratio—1 : 2 : 1.

3.2. Law of Independent Assortment

Different alleles of two genes assort independently without interacting with each other and descend to gametes in the same arrangements as in parents. This law was a result of dihybrid crosses. Linkage is an exception to this law as recombinant-type gametes can also be observed in a pool of gametes formed during gametogenesis.

Phenotypic ratio—9 : 3 : 3 : 1;

Genotypic ratio—1 : 2 : 1 : 2 : 4 : 2 :1 : 2 :1.

The essence of G.J. Mendel's postulates is that behind the phenotypic ratio of 3 : 1 lies a more fundamental genotypic ratio of 1 : 2 : 1 and that the two alleles of the same gene do not affect each other, they cannot modify each other or merge, remaining, "uncontaminated" (Blume, 2022). Thus, phenotypically expressed characters are determined by the combination of discrete particles received from the two parents, transmitted in an unbroken manner, known as the "particulate theory of inheritance", was the first theory to oppose the "blending theory of inheritance" put forward by concurring Hippocratic to Darwinian via Aristotelian ideologies. G.J. Mendel in 1865 presented his results to the Society for the Study of the Natural Sciences in Brünn as "Experiments in plant hybridization" (Mendel, 1865). Mendel himself sent copies of his work to well-known botanical researchers but could not get ample outreach (Blume, 2022). Some historians suggest that Mendel sent an offprint

to C. Darwin, but its pages were uncut perhaps due to lingual barriers. However, Focke's work citing Mendel is found in C. Darwin's archive but no copy of Mendel's work is found (Berry and Browne, 2022). Perhaps the scientific community at that time was far more influenced by C. Darwin's theory of evolution and focussed more in explaining continuously varying traits insisting that "*Natura non facit saltum*", as opposed to the never-seen-before concept of discrete inheritance as suggested by G. Mendel (Howard, 2009). G. Mendel accounted for similarities among organisms through heredity, while C. Darwin accounted for the differences in the form of evolution (Dobzhansky, 1965). G. Mendel focussed on saltations while C. Darwin was convinced by the idea of gradual changes. Moreover, at that point in time, no physical elements of the cell, like chromosomes, were known, with which G. Mendel's factors could be associated. Also, the mathematical ratios used by G. Mendel, were unfamiliar to the-then evolutionary biologists (East, 1923). Botanists during those times such as C. Darwin, worked by observation, rather than by experiment (Ayala, 2009).

Nevertheless, on political grounds, the notion of him being a monk or his idea of integrating statistics into biology was quite ahead of time for his contemporaries (Huminiecki, 2020). Moreover, G. Mendel was not well known among the scientific communities. In contrast, C. Darwin was associated with the prestigious Royal Society of London. Lastly, C. Darwin's focus on pigeon breeding at that time was hailed by pigeon fanciers in the Victorian era (Secord, 1981). Mendelian work accomplished completion of Darwinian theory, although after their deaths (Berry and Browne, 2022); when R.A. Fisher constructed mathematical bridge that an underlying discontinuous variation at many loci along with environmental effects can result in superficially continuous distribution (Fisher, 1919). Thus, his path to achieve this title was not easy, and traveled the course of the black age, until it was rediscovered by the aforementioned researchers.

4. MENDEL–FISHER CONTROVERSY

It has been said that some of the statisticians (Weldon, 1902; Fisher, 1936) during the transition phase to the 19th century argued that G. Mendel's results were not statistically significant, as the probability of getting a typical 9 : 3 : 3 :1 phenotypic ratio in dihybrid cross was 1 in every 15000 experiments! (Weiling, 1986). R. Fisher speculated that an assistant of G. Mendel must have falsified a portion of the data to agree to the approximate expectations, dismissing them as too good to be true and finally pleaded to end the debate, giving due honor to Mendel for his contribution (Franklin et al., 2008; Weeden, 2016).

5. EXCEPTIONS OF MENDEL'S LAWS

Specifically, G. Mendel's laws dictate that a locus must have two allelic variants whose effects on categorical traits must be discrete and countable, and they must show complete dominance on each other. However, these strict conditions are rarely met in real systems (Hou et al., 2016). The term "non-Mendelian inheritance" is used to describe the violation of Mendel's laws. It is also important to note that, from a broad perspective, nearly all inheritance systems display non-Mendelian inheritance (at least to some degree) (Mittelsten Scheid, 2022), hence practically following quasi-Mendelian inheritance. Discoveries like gene drives are solid examples of exceptions to quasi-Mendelian inheritance. Gene drives based on gene editing biology, CRISPR (Clustered Regularly interspaced short palindromic repeats) (Noble et al., 2017; Searle and Villena, 2022) in particular, are self-propagating mechanisms by which desired genetic variants can be spread through a population faster than traditional Mendelian inheritance (Rode et al., 2019). We have been taught in popular books that limitations to Mendel's laws are incomplete dominance, linkage, and epistasis. But some discrepancies were noted while reviewing the literature. In hybridization experiments in ornamental plants in past years, Mendel already produced evidence in forms intermediate to the parents, as an aspect of incomplete dominance (Abbott and Fairbanks, 2016). In the interspecific cross between *P. nanus* L. (with white flowers) and *P. multifloris* W. (with coloured flowers), Mendel noted partial dominance for flower colour and reduced fertility in the F1 hybrids thereby identifying interaction between characters, which is now known as epistasis today (Abbott and Fairbanks, 2016).

6. THE SEVEN MARKERS THAT MADE MENDEL LUCKY

What made Mendel successful can be traced to the type of characters he studied, i.e., qualitative traits which are controlled by one or in some cases few genes. Researchers from past centuries like Walter Frank Raphael Weldon to present century like Gregory Radick questioned Mendel's work due to the qualitative nature of traits (Weldon, 1902; Radick, 2015; 2022). Of note, 12 yr is a long time dedicated to an experiment, with no priori known and no posteriori expected, yet G. Mendel continued his series of plant hybridization experiments against all odds. This was possible because garden peas are easy to grow and cross-pollinate, have clear and distinct traits, and have a shorter generation interval of about 2 months (Ellis et al., 2011). However, pea has not been an easy model species for molecular genetics research as compared to smaller and hence more prioritized *Arabidopsis* genomes (Sussmilch et al., 2022). Interestingly, the characters, indirectly the genes studied by G. Mendel in garden peas, are located in different chromosomes

except for seed color and flower color genes which are located in 1st chromosome and flower position and stem length on the 4th chromosome but not in near sight to inherit as haplotypes (Novitski, 1978). The release of pea genome assembly helped to characterize the loci which contributed to the traits studied by G. Mendel (Kreplak et al., 2019). These include locus A for seed coat and flower color, locus LE for tall versus short, locus I for yellow versus green cotyledons, R locus for round versus wrinkled seeds, locus GP for green versus yellow pod, V/P locus for inflated versus constricted pod and FA/FAS locus for axial versus terminal flowers (Ellis et al., 2011; Reid and Ross, 2011; Smykal, 2014; Sussmilch et al., 2022).

7. GENESIS OF GENETICS

The high points in the history of Genetics after the resurfacing of G. Mendel's work had to be surveyed, as this was the time when his work began to be discussed and cited. There were only two citations of his work until the 1900s (MacRoberts, 1984; Berger, 2022) viz., Focke (1881) and Bailey (1892). The priors in population genetics were characterized as "beanbag genetics" as termed by Ernst Mayr in 1959 because the early Mendelians were using beans of various colors in bags to study Mendelian inheritance (Mayr, 1959). While it is obvious that genetics can be classified into different branches, viz., classical, cyto-, molecular, population, quantitative, etc., it is difficult to deal with their origins separately as different researchers contributed to different branches at different times and contributions span around contemporary researchers. For the sake of simplicity, they are briefly reviewed in two main sections as the classical-to-molecular group and the population-quantitative-selection theories group. The third section deals with applied genetics which mainly includes application of discoveries mentioned in sections 1 and 2 in various fields.

7.1. Molecular and Allied Genetics

Although G. Mendel's work was rediscovered by H. De Vries, C. Correns, and E. Tschermak; it was popularized by William Bateson, an English Biologist. Perhaps he would have been renowned as the first rediscoverer of Mendelian principles unless his study material were plants. William Bateson was keenly interested in embryology and investigated the development of Balanoglossus. In 1906, W. Bateson, now known as "the father of modern Genetics" now, coined the term "genetics" for the newly developing branch of science dealing with the science of heredity at the 3rd Conference on hybridization. W. Bateson is also credited with the nomenclature of terms like homozygote, heterozygote, and allelomorph (later known as Allele), "zygote", "homozygote", "heterozygote", F_1 and F_2. W. Bateson appears to be the first evolutionary biologist as he agrees that biological variation exists both continuously (Darwinism), for some characters, and discontinuously (Mendelism) for others, naming the two types as "meristic" and "substantive", respectively. Many consider him the real father of Genetics after Mendel's original discoveries, as he was the pioneer to translate G. Mendel's paper in English for a better outreach and nevertheless, also the first to show the extension of principles of Genetics to animals, for example, through his crossing experiments in domestic fowl. W. Bateson's book was translated into German in 1914 and helped to bridge the gap between Mendel's work and works on chromosomes during that time (Berger, 2022). In his honor, W. Bateson's chair was titled as the chair of Biology (Gayon, 2016). He, along with C. Correns and Reginald C. Punnett, came up with the principle of "genetic linkage", the tendency of several factors to be associated together on chromosomes in 1906 (Piegorsch, 1986). However, he failed to explain this phenomenon precisely (Bateson and Mendel, 1902). Until then, the study of Mendelian genetics was concentrated in England, popularized and dominated by W. Bateson and R. Punnett.

7.1.1. Narrating the role of chromosome. Walter Sutton and Theodor Boveri in "Chromosomal Theory of Inheritance" explained the parallel relationship between the behavior of chromosomes and the Mendelian factors transmitting across the generations during meiosis (Sutton, 1903). The race was then to convert chromosomal theory into a fact, beginning with Thomas Hunt Morgan. Starting around the year 1910, the center of scientific contributions to the field of genetics started shifting from Europe to the United States. This needs a special mention of the lab of T. Morgan at Columbia University, New York, USA, which is also known as "the fruit fly room", a small room of 23' × 16', where extensive experimentation on *Drosophila melanogaster*, the fruit fly, was carried out (Brah, 2013). In 1910, T. Morgan, who was skeptical about the chromosomal theory of inheritance, which was incidentally proposed by W. Sutton, a PhD student working in the other laboratory in the same department studied, worked on the sex-linked inheritance of white eyes in Drosophila, for which he was awarded Nobel Prize later in 1933. He insisted that genes are located linearly on the chromosomes and some genes are located and transmitted closely over and above the average, also called "linked genes". T. Morgan noticed that "linked" traits would separate occasionally, while other traits on the same chromosome were not, which may be due to recombination between the paired chromosomes to exchange information, also known as crossing over (Morgan, 1911). Today, we know that recombination occurs during the prophase of meiosis 1, and leads to different combinations of alleles in the gametes. Thus, T. Morgan ruled out the fallacies related to the chromosomal theory of Inheritance and gave wings to the concept of "gene" to fly which established the connection among diverging

Fig. 1. Past, present, and way forward vis-a-vis mendelian genetics. The pictures of scientists were assembled from the public domain for this illustration.

branches of genetics (molecular genetics, cytogenetics, biometrical genetics) at the beginning itself. Gene term was coined by Wilhelm Johannsen in 1909. Later, W. Johannsen, who criticized Mendelism as well as Darwinism, proposed yet another theory, "the genotype theory", which distinguished genotype and phenotype and evolved as pure line theory of heredity (Johannsen, 1911).

Branching out of different branches of genetics can be affiliated with interactions between researchers (Fig. 2). Since this topic is out of the scope of this review article, readers are suggested to read "A Century of Geneticists: Mutation to Medicine" book (Dronamraju, 2018). Calvin Blackman Bridges gave

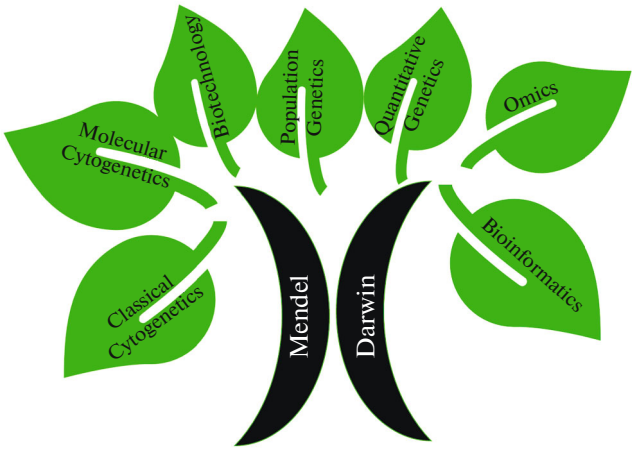

Fig. 2. Roots and branches of genetics.

the experimental proof for the chromosomal theory of inheritance through sex chromosomes (Bridges, 1914), meanwhile, Alfred H. Sturtevant, based on crossing over data, created the world's first chromosome linkage map, showing the relative location and distancing of the genes (Sturtevant, 1913). Hermann J. Muller worked on position effects, gene evolution and chromosomal aberrations (Morgan et al., 1925). He pioneered radiation genetics through his classical gene mapping experiments and received the Nobel Prize for physiology, the very first Nobel for genetic discovery. T. Morgan's model of housing all the *Drosophila* and the *Drosophila* workers in the same room was replicated by his student H. Muller at the University of Texas in a still larger room (72' × 24'), which later came to be known as the second fly room (Hales et al., 2015). The fruit fly, *D. melanogaster*, also known as vinegar fly, was the candidate of choice as they are highly prolific, have a short life cycle of 12 days, show a large number of prolific traits, and have large-sized chromosomes that are easy to study. 1952 onwards, Hughes, Hsu, and co-workers paved the way for modern cytogenetics. They described the procedure to swell cells to make preparations whereby chromosomes could be separated and accurately counted. The diploid count for human chromosomes was considered as 48 until 1956 when it was established as 46 by their procedure (Hsu, 1952; Gartler, 2010; Tijo and Levan, 1956).

7.1.2. Robustness to mutation theory. H. Muller (1890–1967) was the founder of radiation genetics and one of the early geneticists who exerted an expansive impact on development of genetics in the first half of

the twentieth century. One of H. Muller's classic works on truncated and beaded wings in *Drosophila* demonstrated the complex relationship between the gene and environmental modifiers (Altenburg and Muller, 1920). This served as the first experimental evidence for pure line theory of heredity, put forward by W. Johannsen in 1911 which differentiated genotype and phenotype and so the terms were coined. In 1926, H. Muller conducted experiments with varied doses of X-rays, using ClB stock (C-Crossover suppressor; l-recessive lethal allele; B-Partially dominant Barr eye phenotype), which he had found earlier in 1919 and successfully transmuted the gene by artificial means (Muller, 1927), which fetched him the Nobel Prize in Physiology or Medicine in 1946. H. Muller also restricted the term "mutation" to a change in the individual gene and proved more than a decade ignored English physician Archibald Garrod's concept of mutation linking to biochemical variants resulting in diseases, which was the theme in his book "Inborn errors of metabolism" in 1909. Mutation concept is often interpreted as a link between Darwinism and Mendelism (Dobzhansky, 1965). The atomic bombing of Hiroshima and Nagasaki in 1945 was the first real-world example of magnified risks by radiation that Muller had observed earlier. A. Garrod at the beginning of the 20th century, was the first to link the connection between genes and metabolism in the body. A. Garrod realized that his patients who had metabolic diseases like alkaptonuria were related and suggested genes were related to enzymes (Garrod, 1902). Regrettably, A. Garrod's idea, like G. Mendel's work went unnoticed in his lifetime. Later, two researchers, George Beadle and Edward Tatum, conducted a series of novel experiments in the 1940s that enabled A. Garrod's work to be rediscovered and appreciated. G. Beadle and E. Tatum worked with a simple organism that can be grown on minimal media (one sugar, salt and biotin) i.e., common bread mold, or *Neurospora crassa*, and showed a clear connection between genes and metabolic enzymes. This has been called the one gene-one enzyme hypothesis (Beadle and Tautum, 1941). This hypothesis later underwent certain important updates: (1) Some genes encode proteins that are not enzymes because enzymes are just one category of protein and there are many proteins in cells, which are also encoded by genes. (2) Some genes encode a subunit of a protein, not the whole protein. (3) Some genes don't encode polypeptides, instead, they code catalytic RNAs (Fedor and Williamson, 2005). Although the "one gene-one enzyme" concept is not complete, its core idea—that a gene specifies a particular protein in a one-to-one relationship - remains helpful in its own way.

7.1.3. DNA or RNA?. Frederick Griffith discovered the 'transforming principle' in *Diplococcus pneumoniae* bacteria that inspired Oswald Theodore Avery, Colin M. MacLeod, and Maclyn McCarty to prove DNA as the genetic material (Griffith, 1928). In their research with pneumococci using purified proteins and nucleic acids (DNA and RNA), they concluded, as follows: "the data obtained by chemical, enzymatic, and serological analyses together with the results of preliminary studies by electrophoresis, ultracentrifugation, and ultraviolet spectroscopy indicate that, within the limits of the methods, the active fraction contains no demonstrable protein, unbound lipid, or serologically reactive polysaccharide and consists principally, if not solely, of a highly polymerized, viscous form of deoxyribonucleic acid" (Avery et al., 1944). Subsequently, Alfred Hershey and Martha Chase demonstrated that the genetic material of bacteriophage T2 is DNA (Hershey and Chase, 1952) while in 1957, Heinz Fraenkel-Conrat and Bea Singer demonstrated in tobacco mosaic virus that the genetic information can also be stored in RNA (Fraenkel-Conrat and Singer, 1999). In the same period, the work of Mahlon Bush Hoagland confirmed that a fraction of cellular RNA was covalently bound to amino acids, hinting that RNA can also be involved in chemical reactions (Hoagland et al., 1958). Alexander Rich in 1962, assumed a primitive RNA world, where RNA served as the genetic material and catalyzed chemical reactions. Walter Gilbert in 1986 coined the term "RNA world" for the same (Gilbert, 1986). Ribosomes made up of both RNA and proteins, were believed to be remnants of this RNA world.

7.1.4. Genomes are a dynamic entity! The DNA in all living beings basically has three functions, the genotypic function viz., replication, phenotypic function (transcription and translation), and evolutionary function (mutation and recombination). The fidelity of genetic material inherited by the next generation is checked at many levels, including the ultimate level of repairs. It is interesting to note that recombination was discovered prior to DNA structure discovery. Using multiple genetic crosses, Barbara McClintock and Harriet Creighton tracked an unusual knob structure on certain maize chromosomes in 1931, establishing the role of recombination in meiosis and the inheritance of chromosomes (Creighton and McClintock, 1931). Later, B. McClintock discovered transposable elements, also known as "jumping genes", while observing the behaviour of kernel colour alleles in maize (McClintock, 1950). This discovery was revolutionary as it suggested that an organism's genome is not static, but rather a dynamic entity. This also led to the discovery that certain jumping genes are incorporated from viruses, having a role in the evolutionary time scale. This concept of transposons initially received criticism from the scientific community, however, as their role became widely appreciated, B. McClintock was awarded the Nobel Prize in 1983 in recognition of many of her contributions to the field of genetics including "jumping genes".

Recombination also plays an important role in DNA repair and replication in both prokaryotes and eukaryotes. Recombination also occurs in prokaryotic

cells, although bacteria do not undergo meiosis, they do engage in a type of sexual reproduction called conjugation, was first described by Joshua Lederberg and Edward L.e Tatum, as a phenomenon involving the exchange of markers between closely related strains of *Escherichia coli* (Lederberg and Tatum, 1946) for which J. Lederberg was awarded the Nobel in 1958. Norton Zinder and J. Lederberg described the other mode of genetic material transfer between bacteria i.e., transduction (Zinder and Lederberg, 1952).

7.1.5. Dissecting the structure of nucleic acids. Nucleic acids were first discovered in the 1860s by Friedrich Mieshner. American biochemist Phoebus Levene, discovered the order of the components of a single nucleotide as phosphate-sugar-base, then discovered the ribose and deoxyribose as carbohydrate components of RNA and DNA, respectively. Phoebus Levene's "nucleotide" model described DNA as a tetranucleotide structure, wherein the nucleotides are linked in the same order always. He was also the first to recognize two basic categories of nitrogenous bases i.e., two purines, each with two fused rings (adenine [A] and guanine [G]) and two pyrimidines each with single ring (cytosine [C], thymine [T], and uracil [U]) (Levene, 1919). Then, Erwin Chargaff, an Austrian biochemist, born in Chernivtsi (Ukraine) expanded P. Levene's work, unravelling ancillary information about the structure of DNA (Volkov and Rudenko, 2016). Influenced by Avery et al. (1944), he concluded that composition of DNA varies among the species and amount of adenine and guanine nucleotides approximates the amount of thymine and cytosine nucleotides (Chargaff, 1950) based on analysis of DNA molecules from different species through his newly developed paper chromatography technique. Many generations later, works of P. Levene and E. Chargaff, followed by X-ray crystallography work of Rosalind Franklin and Maurine Wilkins, paved the way for three-dimensional double helix structure. American biologist James Watson and English physicist Francis Crick in 1953 worked out the three-dimensional, double-helical model for the structure of B-DNA, the most common conformation in most living cells. There are also two other conformations discovered viz., A-DNA, a shorter and wider form usually in dehydrated samples, and Z-DNA which is left-handed conformation that exists in response to certain biological compounds and confers immunity to the host against some viral infections (Rich and Zhang, 2003). Later in 1962, J. Watson, F. Crick and M. Wilkins were awarded the Nobel Prize for their contributions to the elucidation of 3D-DNA structure. In 1955, Seymour Benzer published his first paper on the fine structure of the RII gene locus of phage T4, a virus of the common colon bacteria, *Escherichia coli.* By examining a large number of progeny viruses, S. Benzer was able to detect very rare genetic events. He redefined genes in molecular terms in view of function, recombination, and mutation, fundamentally called exon, recon, and muton, respectively (Benzer, 1959). The further advances in the field of molecular- and cyto- genetics and their applications are tabulated keeping in view the length of review (Table 1).

7.2. Population Genetics and Quantitative Genetics go Hand in Hand

7.2.1. Neo-Darwinism. From the beginning of the 20th century, contradictions arose between the biometricians and experimental geneticists as there was a missing link between continuous variations of Biometricians (Darwinians) and discrete inheritance of Mendelian geneticists in explaining complex character. Mendel's results were in ratios while biometricians presented results in terms of correlation and regression. The impeding gap between Darwinism and Mendelism in understanding genetics, seems to have been resolved by "Neo-Darwinism" or "Synthetic Biology". The concept was elaborated by R.A. Fisher, Sewall Wright and John Burdon Sanderson Haldane independently (Fisher, 1930a; Wright, 1931; Haldane, 1932). Neo-Darwinism was further extended by Dobzhansky (1937), Mayr (1942) and Simpson (1944). R.A. Fisher laid the foundation stone of the amalgamation of Mendelian genetics with biometry and pointed out the incompatibility of Mendelian inheritance with quantitative variation (Fisher, 1919). He proposed the concept of the "infinitesimal model", demonstrating that continuous variation amongst phenotypic traits could be the result of a large to the infinite number of discrete units (genes) and tried to unite Darwinian ideas on natural selection with Mendelian theory. R. Fisher explained that Mendelian inheritance is responsible for conserving variation, which makes natural selection a "force" of adaptive evolution (Fisher, 1930a). Darwinism and Mendelism thus proved to be complementary, indeed supplementing each other's lacunae in explaining evolution as a single concept. He also explained how the correlations could be used to partition the variation into heritable and non-heritable fractions, in turn how the heritable fraction could itself be broken down into further fractions relatable to additive gene action, to dominance, and to genic interaction with the help of ANOVA (Fisher, 1919).

F. Galton had shown continuous variation to be heritable. Udny Yule, among others, elucidated the simultaneous action of many genes whose effects were additive are responsible for the continuous variation. R. Fisher's book, The Genetical Theory of Natural Selection (Fisher, 1930b), along with S. Wright's extensive paper "Evolution in Mendelian Population" (Wright, 1931) and J.B.S. Haldane's "The Causes of Evolution" (Haldane, 1949) subsequently became foundations of population genetics. S. Wright devised a mathematical theory of evolution, showing how allele frequencies and genotypes could respond to evo-

Table 1. Milestones in the field of molecular genetics

Discovery/Invention	Role	Downstream Application	Reference
DNA related			
Karyotyping	Role in cytogenetics	Chromosomal aberrations, ploidy	Delaunay (1922)
Established normal diploid chromosome number in humans as 46	Karyotype	Chromosomal aberrations, ploidy	Tijo and Levan (1956)
DNA replication is semi-conservative.	Replication, Repair	PCR, Sequencing, gene editing	Meselson and Stahl (1958)
Operon model (Nobel Prize, 1965)	Regulating gene expression	Gene silencing	Jacob and Monod (1961)
Genetic code (Nobel Prize, 1968)	Translation	Genome editing	Crick et al. (1961)
In-situ hybridization (ISH)	Mapping DNA sequences to chromosomes	Microarray, DNA fingerprinting	Pardue and Gall (1969)
Recombinant DNA (Nobel Prize, 1980)	Genetic engineering	Gene therapy, genome editing, cloning, genetically modified organisms (GMO)	Berg et al. (1974)
Split gene concept	Intron and exon	Evolutionary role	Berget et al. (1977) and Chow (1977)
DNA sequencing techniques	Exploration of genomes	High throughput sequencing methods, genome editing, SNP chips	Sanger et al. (1977); Maxam and Gilbert (1977)
Demonstrated somatic rearrangements of genes, encoding antibodies	Antibody diversity	Blood transfusion, serology, tissue grafting, organ transplantation	Tonegawa (1983)
CRISPR discovery	Bacterial defense mechanism	Genome editing and gene drives	Ishino et al. (1987)
PCR	Amplification	Sequencing, cloning, biopharming	Mullis (1990)
Human genome project	Sequenced entire human genome	Advances in genomics	Collins and Fink (1995)
DNA microarrays	Biochip with information	Molecular biology investigations	Lockhart et al. (1996)
Ancient DNA (aDNA) analysis (Nobel prize 2020)	Genetic relationships with extinct organisms	Neanderthal genome sequenced	Pääbo et al. (2004)
Metagenomics	Environmental DNA (eDNA) analysis	Monitoring tool for exotic species	Handelsman et al. (2004)
Creation of bacterial cell with a synthetic genome	Understanding principles of cellular life	Genome assembly and genome transplantation	Gibson et al. (2010)
CRISPR-Cas9 gene editing (Nobel prize, 2020)	Genome editing technique	Basic biological research, development of biotechnological products, and treatment of diseases	Jinek et al. (2012)

Table 1. (Contd.)

Discovery/Invention	Role	Downstream Application	Reference
RNA related			
Nucleotide sequence of tRNA, in yeast alanine tRNA	Translation adapter	Gene editing	Holley et al. (1965)
Catalytic RNAs (Nobel Prize, 1989)	Enzymatic action of RNA, RNA world	Ribozyme structure discovery	Kruger et al. (1982); Guerrier-Takada et al. (1983)
Proto-oncogene (Nobel Prize, 1989)	Demonstrated proto-oncogene to oncogene relationship	Cancer genetics	Bishop (1983)
Regulatory RNA	Regulation of post transcription gene expression	RNAi, knock down	Lee et al. (1993)
RNA editing	Site-specific alteration such as, such as splicing and polyadenylation	Gene expression optimization	Brennicke et al. (1999)
RNA based therapy	Nucleoside modification	Led to Covid vaccines	Karikó et al. (2005)
Protein/Enzyme related			
Isolation of DNA Polymerase I from E. coli (Nobel Prize, 1959)	Replication	PCR, sequencing	Kornberg (1956)
RNA polymerase (Nobel Prize, 1959)	Transcription	Transcription, gene expression and checks errors	Furth et al. (1962)
Reverse transcriptase	mRNA to DNA synthesis	Reverse transcription PCR	Temin (1964)
Restriction endonuclease (Nobel Prize, 1978)	Host defense mechanism of bacteria against phages	Gene editing, markers Identification (e.g., RFLP)	Arber and Linn (1969); Smith and Welcox (1970)
Reverse transcriptase of RNA tumor viruses (Nobel Prize, 1975)	Reverse transcription	Disease therapy and ageing reversal	Panet et al. (1975)
Fluorescent protein markers	Protein-protein interactions	Bioluminescence to visualize interactions	Chalfie et al. (1994)
Infectomics	Infectious agent translation	Patient-tailored medicine, disease profiling and drug discovery	Huang et al. (2002)
Liquid biopsy	Cell-free circulating tumor DNA (ctDNA) translation	Early cancer detection, cancer staging, relapse, real- time monitoring	Pantel et al. (2010)
Drug discovery	Chemoproteomics of bioactive molecules	Drug target identification and validation	Meissner et al. (2022)

lutionary forces such as natural selection, mutation, and migration (Wright, 1932). S. Wright also probed the effects of inbreeding and random genetic drift in evolution (Wright, 1968). S. Wright made many contributions in statistics, mammalian genetics, animal breeding, population genetics, and the theory of evolution. His legacy was such that in 1988 Science Citation Index listed some 500 articles referring to Wright's works (Dronamraju, 1990). Despite having no formal academic qualifications in any field of science, J.B.S. Haldane (1892–1964) made significant contributions to the fields of physiology, genetics, biochemistry, statistics, biometry, cosmology, and philosophy (Dronamraju, 2010). He developed a theoretical version of population genetics, in the form of genetic loads and the cost of natural selection (Haldane, 1957), infectious disease and selection, estimation of human mutation rates, linkage, and human gene mapping, rates of evolution in units of "Darwin" (Haldane, 1949), and the biochemistry of gene action, to name a few. He introduced the terms "morgan" and "centimorgan" as units of map distance; he invented the idea of partial sex linkage. Recent advances in genomics led to novel methods and software for quantifying genetic diversity in addition to the conventional diversity measures (Kanaka et al., 2023). These theories further led to the development of artificial selection and breeding strategies largely in agricultural and allied sectors.

7.2.2. Neutral theory. The leading successor of this great heritage, Moto Kimura in 1953 published his first population genetics paper (which eventually turned out very influential), describing a "stepping stone" model for the structure of the population that could explain more complex immigration patterns than the "island model" of S. Wright. He introduced "infinite alleles" and "stepwise mutation" models to study genetic drift. By discovering the "quasi-linkage equilibrium" phenomenon, he showed that a population with loose linkage, produces just enough linkage disequilibrium to cancel the epistatic variance, so it can be eliminated in predictor equations, henceforth response to selection could be better modeled by additive genetic variation (Kimura, 1954). His daring, neutral theory of molecular evolution explains evolution at the molecular level. According to him most of the evolutionary changes and variation within and between species are not caused by natural selection alone but along with genetic drift of neutral mutant alleles. A neutral mutation is one that does not affect an organism's fitness (ability to survive and reproduce) (Kimura, 1983). However, the co-inheritance of neutral mutants along with beneficial mutants is known as a selective sweep, which leaves on the genome distinctive patterns of reduced genetic diversity, as relics of the selection process known as Selection signatures (Nielsen, 2005). Likewise, various Genome wide association studies (GWAS) are rolling to establish significant associations between genetic markers (say, SNPs, CNVRs) and phenotypes. Phenomics has risen to the levels of high throughput phenotyping, to increase the quality and quantity of phenotypic data. These advances in the quantitative genetics field are making genomic selection a full-fledged tool to improve agro-economic traits by bridging the gap between demand and supply of the same.

7.2.3. The way forward. G. Mendel's work highlights the importance of going interdisciplinary over being subject-centred, with a subtle mix of biology and statistical science that yielded genetics. The subject of bioinformatics is exemplary in this direction. Bioinformatics combines computer programming, big data analysis and biological data in the form of nucleotides, amino acids and corresponding annotations to these sequences.

A genetic manipulation is the deliberate modification of an animal's genome, which codes for inherited traits. These genetic interventions are needed for basic fundamental research, bioreactors, xenotransplantation, vaccine safety and toxicity tests can be done with better subject matter. Genetic gain can be accelerated by Multiple-Ovulation Embryo Transfer (MOET), Embryo sexing, In-vitro fertilization, cloning and transgenesis. Besides these, Marker Assisted Selection/Breeding (MAS/MAB) and genomic selection are being piloted in farm animals. Modern studies deal with studies focusing on Oncogenes, antibody diversity, homeotic mutations, gene regulation and r-DNA techniques. Genetic intervention in such non-ventured fields holds immense hope. Novel reverse genetics (RNA to DNA approaches) tools are being optimized for functional studies such as CRISPR/Cas9, Targeting-induced local lesions in genomes (TILLING). CRISPR will no doubt revolutionize all life forms by virtue of being able to make targeted DNA sequence modifications rather than random changes.

Consequently, genetic enhancement is expected in the form of higher disease resistance, dietary benefits like tolerance to lactose and gluten, and in improvement of other traits of interest, such as designer babies. Precision medicine configures tailored treatments based on genetic testing, thus catering to genetic idiosyncrasies. However, full-fledged usage of these techniques also has elements of technical complexities, high cost, ethical concerns and public acceptance. On the same grounds, the CRISPR technique is banned for clinical use due to ethical dilemmas and untoward mishaps. Considering the pros and cons, the extant efforts will cumulatively revamp the visions of precision nutrition envisioned by FAO and other organizations into an incredible reality.

8. CONCLUSIONS

The progress of a field is checked with the test of time and the science of genetics was reinforced with

contradictions and suggestions from different schools of thought. In the genetic sense, Mendel is the primer in the polymerization of Genetics, the subject which has grown beyond the realms of leaps and bounds. As a fitting tribute to Mendel on his 200th birthday, let us loudly support evidence-based science and resist ideology-based science, to which Mendel's findings had to succumb to for a span of not less than 34 years. As American author Robert Heinlein said, "a generation which ignores history has no past and no future". While writing this review, as we approached finalizing the content, without realizing we had created a great repository of original discoveries/inventions (in the form of bibliography) in the field of genetics, enthusiastic students of genetics can access and read topics of their choice to know the history in detail. Nevertheless, genetics has a long way to go.

COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflicts of interest. This article does not contain any studies involving animals or human participants performed by any of the authors.

AUTHOR CONTRIBUTIONS

Nidhi Sukhija and K.K. Kanaka contributed equally to this work.

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