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REVIEWS

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"In the beginning was the Word..."
John 1 : 1

Genome: Origins and Evolution of the Term

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Abstract—The appearance of a new scientific term is a significant event in the human cognitive process and the result of the realization of the separateness of an object or a phenomenon. Our article concentrates on the origins of basic genetic terms, such as *genetics, gene, genotype, genome, gene pool,* and *genomics*. We propose using the term *karyogenomics* for the special direction of genomics related to the study of the organization and evolution of eukaryotic genomes by means of modern chromosome analysis, as well as by full genome sequencing.

Keywords: genome, gene, genotype, genomics, gene pool, chromosomes, karyotype, polyploidy, karyogenomics, history of terms

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Genetic, genetics, gene, genotype, genome, gene pool, genomics; it is difficult to imagine the history of science in the 20th and, most likely, the 21st century without these terms and the underlying notions, subjects, and research styles.

The first of these words, the adjective *genetic*, presumably appeared in the English language in the 1830s and was related to the title of the Book of Genesis, which in turn comes from the Greek Γένεσις. Γένεση, which means origin, birth, or appearance. Initially, *genetic* was used in the sense of "pertaining to origins." It is noteworthy that the document recommending Charles Darwin for the Copley Medal, the oldest award of the Royal Society, pointed out his contribution to the development of genetic biology [1].

This article concerns the history of the basic terms of genetics. The appearance of a new term is a significant event in human cognition marking that an object or a phenomenon is recognized as a distinct entity (see, e.g., [2]). New phenomena cannot be described with old terms. As W. Johannsen one of the founders of genetics phrased it at the Christmas Conference of the American Naturalist Society in Ithaca (United States) in 1910, {"*Of all the Weismannian armory of notions and categories it may use nothing. It is a well-established fact that language is not only our servant when we wish to express—or even to conceal—our thoughts, but that it may also be our master, overpowering us by means of the notions attached to the current words. This is why it is desirable to create new terminology in all cases when new or revised conceptions are being developed. Old terms are merely compromised by their application in antiquated or erroneous theories and systems, from which they carry splinters of inadequate ideas, not always harmless to developing insight.*" [3].}

In his letter to Adam Sedgwick on 18 April, 1905, W. Bateson, with his exceptional feel for language, pointed out that "no single word in common use quite gives this meaning (the study of heredity and variation). Such a word is badly wanted, and if it were desirable to coin one, *genetics* might do" [4].

This idea was further developed during the 3rd Conference on Plant Breeding and Selection, which was held in London in July 1906. Bateson, the president of the conference, when addressing participants with his talk "The Progress of Genetic Research" provided compelling evidence to demonstrate that new science concerned with the phenomena of heredity and variation had appeared with the prospect of investigating the problems of evolution and systematics and dealing with applied tasks of animal and plant selection. New science still did not have a short and clear name, and such a name was proposed, i.e., *genetics*. Bateson's speech was so persuasive that W. Wilks, the editor, published the proceedings of the conference

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under the title "Report of the Third International Conference 1906 on Genetics, Hybridization (crossbreeding of genera or species), and the Crossbreeding of Varieties and General Plant Breeding" [5] (its official name was International Conference on Hybridization and Plant Breeding). The volume opened with the portrait of Gregor Mendel.

It was probably under a certain influence of this speech of Bateson's that Johannsen, who held his talk on that conference immediately afterwards, came to simplify the term *pangene* proposed by H. de Vries and to employ the word *gene* to denote Mendelian hereditary factors, as well as the term *genotype* to denote the sum of genes of a particular organism present in a gamete or a zygote [6, 7]: "*gene* is nothing but a very applicable little word, easily combined with others; hence it may be useful as an expression for unit factors, elements, or allelomorphs in gametes demonstrated by modern Mendelian researchists." [7]. Johannsen did not like the idea that genes were part of chromosomes; nevertheless, he found it possible that a genotype might be a complex organic molecule where genes can be considered an analog of radicals or side chains that branch off the backbone (genotype). However, he believed that it would be anticipatory to discuss these ideas [7]. According to F. Churchill and E. Mayr, Johannsen understood genes in all their diversity and combinations nearly typologically as the genotype of a population or a species [8, 9].

Initially, this idea was left aside, but was later reborn in the studies by A. Serebrovsky [10] and T. Dobzhansky [11], who used the new special term *gene fund* (*genetic pool*, *gene pool*) to delineate their concept [12]. Apparently, N. Koltsov was the first to employ the term *gene fund* proposed by Serebrovsky, although metaphorically, but still quite in its modern sense. The concluding line of his talk at the Annual Meeting of the Russian Eugenic Society (October 22, 1926) "Genealogy of Our Promoted Workers" was "The flow of promoted workers, talented and genial coming from the depth of the Russian population demonstrates that it possesses a valuable gene fund." [13].

In 1920, the genetic thesaurus was enriched by one more term. H. Winkler, Professor of Hamburg University and Director of the Botanical Institute, when discussing the genetic nature of the chromosomal constitution of diploid and polyploid interspecies hybrids, concluded that they were composed of qualitatively different sets of chromosomes and genes. Therefore, it would be insufficient to describe them simply as *diploids*, *triploids*, or *tetraploids*. To describe their genetic constitutions correctly, a new term was required. "I propose the expression *genom* for the haploid chromosome set, which, along with the pertinent protoplasm, specifies the material foundation of the species" [14].

According to Winkler, an organism for which the diploid or polyploid nuclei contain genomes of only one type is termed *homogenomic* (in German, *homogenomatisch*). If these genomes are of different origins and contain different sets of genes, the organism is *heterogenomic* (*heterogenomatisch*). Organisms that possess identical genomes were called *isogenomic* (*isogenomatisch*), in contrast to *anisogenomic* (*anisogenomatisch*), organism with significantly different genomes. Depending on the number of genome types present in the nucleus, organisms were classified into *monogenomic* (*monogenomatische*), *digenomic* (*digenomatische*), *trigenomic* (*trigenomatische*), and *polygenomic* (*polygenomatische*). Even diploid interspecies hybrids are *heterogenomic*, i.e., *digenomic*. According to Winkler, a triploid obtained by breeding a homogenomic tetraploid and a homogenomic diploid should be called a *digenomic* (!) *triploid*. A diploid carrying two haploid chromosome sets of the same species would be *monogenomic*, which means that its nucleus contains genomes of a single type [14].

Obviously, the meaning of these terms as originally proposed by Winkler is somewhat different from their modern interpretation; for instance, considering the *digenomic triploid* from the above example, we would now say that its nucleus contains three genomes, two of them of one type, and the third one of another type. As a taxonomist, Winkler was primarily concerned that the biological role of genomes translated into the biological diversity among taxa; first of all, he pointed out the significance of qualitative differences between genomes. In particular, in his discussion of polyploids, he asserted that a simple increase in the number of genomes of the same type, such as in polyploid *Solanum* species, does not give rise to new species that would differ significantly from the ancestral forms.

As a term, *genome* possesses several features that enabled its long and prosperous life. On one hand, it sounds good, is easily remembered, and can serve as a basis for numerous derivatives. At the same time, its semantic load is no less important. Dictionaries traditionally interpret Winkler's *genome* as a neologism obtained by combining the words *gen* and *chromosom* (see, e.g., [15]), which, however, does not seem obvious. According to Lederberg and McCray [16], as a botanist, Winkler must have been acquainted with terms such as *biome, rhizome, phyllome, thallome,* and *tracheome,* where the ending *-ome/-om* refers to the idea of totality. Similar to *thallome,* which denotes the total multinuclear a body of algae or some fungi; to biome, which is a collection of ecosystems of a given natural climatic zone; or to microbiome, an ecological community of microorganisms, *genome* could be intuitively perceived by Winkler as the collection of genes in a haploid set of chromosomes. It is also interesting to note that *genom* bears certain resemblance to the German participle *genommen*, which, means "taken" or "included" and, in fact, occurs in the very first paragraph of Winkler's book [14].

Winkler introduced the term *genom* (meaning a haploid set of chromosomes and the genes they include in a diploid nucleus; one haploid set of chromosomes in a polyploid nucleus) to describe an entity that had not previously been recognized by geneticists among the observable phenomena. It is certainly different from the Johannsen's *genotype*, which is the totality of genes of a given cell or an organism as a whole ("The genotype is the genetic constitution of a zygote" [6]). Neither is it equal to *karyotype* as understood by G. Levitskii; a diploid set of chromosome that characterizes a given organism or a group of organisms of the same species [18, 19]. Interestingly, the term *karyotype* was first proposed by L. Delaunay "to denote a systematic unit (genus) including a group of karyologically uniform species" [20]. However, according to Levitskii, the term *karyotype* came into a wide use in its modern sense [18]).

The understanding that the totality of genes present in a haploid set of chromosomes is a specific entity, "which, together with the pertinent protoplasm, specifies the material foundation of the species," soon led to the realization that the other component of this system also had its specific nature. R. von Wettstein proposed the term *plasmon* for the totality of protoplasm genes [21], which stimulated the study of genetic interactions between the genome and the plasmon [22, 23].

Giorgio Bernardi [24] pointed out that, in contrast to the conceptual notion of *genotype*, Winkler's definition of *genome* was purely operational; however, until the early 1950s, the only possible way to study, compare, or distinguish genomes was by cytological investigation, and the use of the term *genome* was therefore restricted to cytogeneticist circles.

The first research technique to be described as *genome analysis* or *genomanalyse* was proposed by H. Kihara ([25, 26], see also [27]). His method amounts to the investigation of chromosome conjugation between genomes in comparison; the polyploid in question was crossbred to all possible tester diploids. If all chromosomes of one genome exhibited pairwise conjugation to chromosomes of a tester species, it meant that the two genomes were homologous; otherwise, it meant that the genomes were different (nonhomologous, or else semi-homologous or heterologous).

According to Kihara, the genome represents a fundamental genetic and physiological system, the integrity of which is essential for normal plant development (in polyploids, it is required that all chromosomes of least one genome be present in double). Based on the system of wheat (*Triticeae*) genomes developed by Kihara and his successors, A. Löwe [29] attempted to develop a novel system of grass taxonomy. From the genetic point of view, Löwe's ideas seemed very attractive; species with identical genome combinations were classified into the same genus, and each unique genome combination corresponded to a genus. For instance, the StStYY genome combination is characteristic only for *Roegneria* species, the WWStStYY combination, for *Anthosachne*, the HHWW, for *Stenostachys*, etc. The genomic approach to taxonomy caused controversial reactions among taxonomists [30–32]; nevertheless, this idea is certainly appealing and genetically justified.

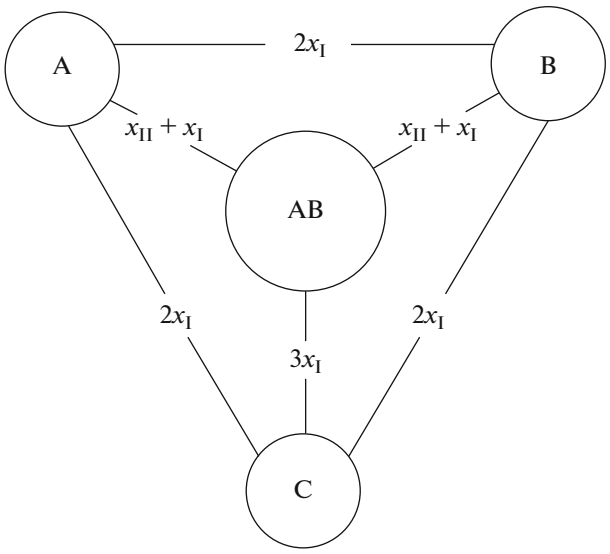

Fig. 1. Hypothetical scheme illustrating the principle of genome analysis by Kihara: test breeding of homodiploids carrying genomes A, B, and C with a heterogenomic tetraploid. Scheme shows the expected number of bivalents and univalents [28].

The new molecular biological understanding of the term genome appeared in the late 1940s with the development of cytophotometry techniques [33–35]. For the first time, it became possible to determine the sizes of haploid eukaryotic genomes. It was discovered that haploid genomes of different eukaryotic species contain different amounts of DNA; moreover, even species of the same evolutionary complexity can possess genomes of different sizes. This apparent problem was termed the *C-value paradox* [36]. At the same time, the term *genome* was coming into widespread use in developing the genetics of microorganisms, where it was not confronted with traditional notions concerning the karyotype and the chromosome set [37–39]. In the course of resolving the C-value paradox, geneticists discovered tandem and disperse repeats, as well as the mosaic organization of eukaryotic genomes; thus, it became clear that genes are but islands in the sea of nongene DNA [40, 41]. Accordingly, the understanding of the genome changed in order to include both the totality of genes and nongene DNA in the chromosomes.

In 1977, the first ever complete genome sequence was obtained, i.e., bacteriophage Φ-X174 [42]. The first bacterial genome was sequenced 1995, i.e., the genome of *Haemophilus influenzae* [43]. For a long

Number of articles containing the words *genome* or *genom* published by Springer

Years	Number of articles	Years	Number of articles
1920–1929	1	1970–1979	685
1930–1939	8	1980–1989	2304
1940–1949	4	1990–1999	12974
1950–1959	26	2000–1909	115836
1960–1969	118	2010–1919	?

time, it was believed that bacterial cells were haploid [44, 45]. However, high-resolution cytochemical analysis definitely demonstrated that both bacteria [46] and Archaea [47] are polygenomic; in particular, in rapidly growing cultures, *E. coli* cells were found to contain 11 (5 to 18) genome copies on average within one or several nucleoids. In contrast, no *E. coli* containing a single genome in their nucleoid could be detected [46]. Further studies showed that, at different developmental stages, giant cells of the bacterium *Epulopiscium* can contain from several tens of thousands to hundreds of thousands genomes amounting to 85–250 Gb DNA per cell [48]. The question of the number of genomes present in prokaryotic cells became a central issue in the study of the genetic apparatus of prokaryotes.

The first eukaryotic organism to have its genome fully sequenced was the yeast *Saccharomyces cerevisiae* [49]. At this moment, our science advanced to the next level, the level of genomics. According to witnesses, the word *genomics* was first pronounced in 1986; Thomas Roderick proposed it to Frank Ruddle and Viktor McKusick as the title for the newly conceived journal that would be focused on the investigation of genes and genomes of different species [50]. The advent of automated sequencing was a technical breakthrough that recruited numerous enthusiastic researchers to the field of genomics. The table illustrates the dynamics of growing interest in the genome as an object of research and reflection.

The appearance of genomics brought about a new understanding of the term *genome*. Currently, when eukaryotic genomes are discussed, the notion *nuclear genome* includes the DNA of a haploid set of chromosomes and all extrachromosomal genetic elements contained in the nucleus, both protein-coding and noncoding sequences. Mitochondrial and chloroplast genomes are usually considered separately, although they only seem autonomous from the nuclear genome, which is in fact closely associated with it. Gene transfer between the genomes of the nucleus, mitochondria, and chloroplasts is a recurrent phenomenon [51]. At the same time, millions of years of evolution have produced well-balanced eukaryotic organisms with the coherent allocation of functions, which implies the coordinated work of the nuclear, mitochondrial, and chloroplast genomes of the whole polygenomic complex.

Strictly speaking, apart from the mandatory nuclear, mitochondrial, and chloroplast genomes, a eukaryotic cell or an organism also contains some functioning facultative genomes of intracellular, and sometimes intranuclear bacteria. The number of different bacterial species present within cells and in the intercellular space of a higher eukaryotic organism is roughly estimated to be up to 40000. The total number of bacteria is at least equal to the total number of cells in a human body, probably amounting to at least 4×10^{13} [52, 53]. On average, each bacterial genome contains 5000 genes. Accordingly, multiplication could give as an idea about the real genetic and genomic diversity of the entity that is usually called a *eukaryotic organism*.

The characteristic feature of the current stage in the genomics of eukaryotes is that, so far, it has largely been concerned with genomes of diploid species. The human genome was one of the first genomes that were sequenced before the arrival of next-generation sequencing techniques in the international Human Genome Project (HGP, 1990–2003) and a similar study performed by the company of Craig Venter (Celera Genomics, United States). In the same years, the Human Genome Research Program was launched in the Soviet Union under the guidance of A. Baev. In 2001, the preliminary human genome sequence was published [54, 55]. Several parallels were concerned with the sequencing of genomes of other diploid species, of both model organisms, e.g., the mouse genome [56], and of small plant genomes (arabidopsis and rice [57, 58]). Nevertheless, despite the collective effort of numerous researchers, gaps still remain, even in human euchromatin sequences [59], not to mention so-called noncoding DNA that is largely composed of repetitious sequences; it has only recently become a subject of comprehensive research. With the advent of modern techniques of high-throughput sequencing (next-generation sequencing), a new era has begun in the progress of genomics and diploid genomes of numerous species, as well as of metagenomes of various microbial communities, are currently being deciphered.

However, it is known that the main pathway of plant genome evolution is interspecies hybridization and polyploidization [60–62]. It has been shown that the evolutionary history of all flowering plants includes several rounds of polyploidization [63, 64]. This involves either an increase in the copy number of the ancestral genome (autoplyploids) or, more commonly, hybridization with the duplication of the hybrid karyotype (allopolyploids). Novel hybrid or polyploid plant genomes produced experimentally or spontaneously are unstable; they undergo numerous reorganizations both in the primary sequence and on the epigenetic level [63, 65]. These new polypolids with conflicting genomes are commonly considered to

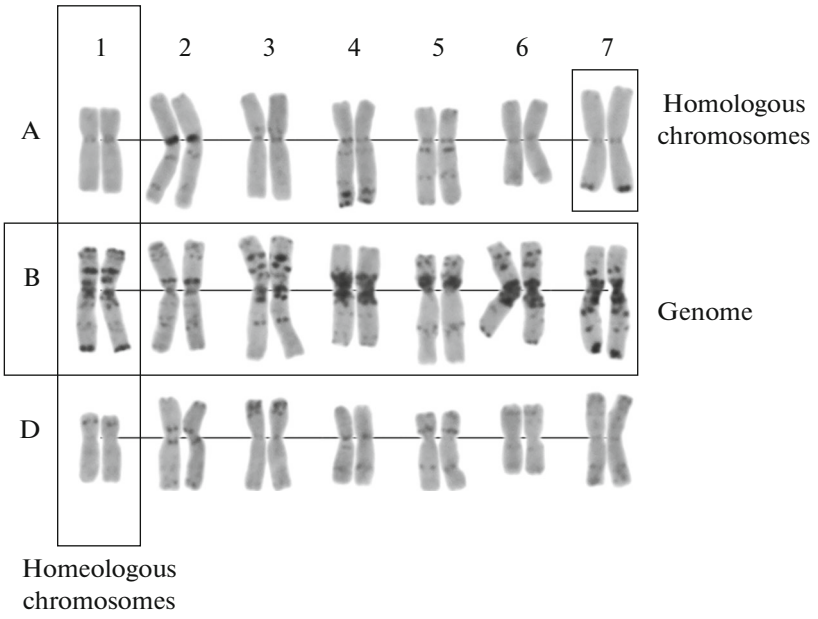

Fig. 2. Karyotype of common wheat *Triticum aestivum* L., cultivar Novosibirskaya 40.

be a special group of neopolyploids [60]; eventually, they develop into relatively stable typical auto- or allopolyploids, for which we propose to term *eupolyploids* [65]. As a result of further chromosomal rearrangements, eupolyploids transform into paleopolyploids [66]; in the metaphase of mitosis and meiosis, their karyotypes look like diploids and they also behave as diploids in the course of meiosis, but in fact their chromosome sets represent segmented polyploids. Most plants, such as, the well-known common flax, can be classified as paleopolyploids.

Obviously, it is fully appropriate to utilize the term *genome* for a haploid chromosome set when speaking about diploid and paleopolyploid species. However, when polyploid species are discussed, the conventional definition of genome as the total DNA of a *haploid* chromosome set needs to be be adjusted (see, e.g., [67]). Allopolyploid karyotypes are definitely composed of several similar but not identical genomes. For these cases, e.g., for a tetraploid cotton plant or cruciferous species, the term *subgenome* is conventionally used [68–70], unless there is a specialized genome nomenclature, such as the one for wheat described above. These species have already become the object of genomic studies. For instance, the genome of colza, a natural allopolyploid, has been sequenced [71] and the sequencing of wheat [72] and cotton plant [73] genomes is in progress. At the same, these plant cells obviously contain not a single genome but rather different types of closely related genomes if we return to the understanding of genome according to Winkler and Kihara (Fig. 2).

It should be underlined that each of these genomes represents a unique gene complex, since, after a major reorganization at the neopolypolid stage and the subsequent gradual reorganization during the further evolution of an allopolyploid, each of the ancestral genomes undergoes multiple changes. This reorganization of ancestral genomes in the course of polyploid formation is well known [62, 74]. Consider the following example: in genomes A, B, and D of the hexaploid wheat, only 10% of genes initially present in each ancestral genome are active because most paralogous genes on homeologous chromosomes have been eliminated or inactivated [75].

Another interesting example is the genome of the banana (*Musa*). The history of this genus includes several rounds of polyploidization that most likely accompanied interspecies hybridization; two of them occurred approximately 65 Ma ago and another one occurred 100 Ma ago [76]. Accordingly, each of the banana genes could be expected to be present in four copies (paralogs). However, the most part of 36542 protein-coding genes (65.4%) is present in the haploid chromosome set as just a single copy, and it is only for 10% genes that all four copies descending from ancestral genomes have been conserved [76]. Genomic reorganizations of this kind, along with repetitiveness of numerous sequences, strongly complicate the annotation and chromosome mapping of both polyploid and paleopolyploid plant genomes. Therefore, this field of research strongly relies on chromosome studies, which provide means not only to investigate the chromosomal distribution of different classes of repeat sequences or to determine the location of genes and their order on chromosomes, but also to identify genomic affiliation and synteny of chromosomes descending from related genomes.

For this specialized direction of research that investigates the organization and evolution of genomes and subgenomes in basically polyploid nuclei while employing the techniques of modern chromosome analysis and genome sequencing, we propose the name of karyogenomics. An important aspect of karyogenomics is providing the basis for direct sequencing of polyploid genomes. This approach has already proved useful in solving problems that concern the origin of certain species and their evolution, as well as the problems of comparative genomics. In particular, karyogenomic approaches have already been successfully applied in many works on the genomics of small-chromosome plants [77–81] and grasses [82–88].

Talking about the relationship between structural genomics and karyogenomics, we should underline that modern karyogenomics could come into existence only due to massive application of modern methods of molecular biology and structural genomics, such as the constantly improving techniques of fluorescent in situ hybridization and genomic in situ hybridization (see, e.g., [89–92]). These methods of molecular cytogenetics occupy an important position in the physical mapping of chromosomes and genomes. Genome fragments are usually ordered using genetic maps that provide information on the frequency of recombination between genes or genetic markers, but do not show their physical position within linkage groups. This may lead to inaccuracies in genome assembly, which is why it is necessary to directly assign genetic markers, genes, and genomic fragments to chromosomes of the corresponding species.

Karyogenomic approaches are especially important for further development of plant genomics. Specific properties of structural organization of plant genomes make it nearly impossible to perform de novo genome assembly after sequencing of high- or medium-level accuracy without employing molecular cytogenetic techniques. The most recent achievements involving the localization of unique plant genes on metaphase chromosomes [92–96] clearly demonstrate the utility of the karyogenomic approach.

The example of human genome studies shows that the development of integrated physical, genetic, and chromosomal genome maps provides revolutionary possibilities for studying the laws of their structural and functional organization and comprehending the pathways of their evolution. Thus, it gives rise to the basically new concept of genome as a integrated entity that unites all levels from nucleotide sequences of DNA molecules to the most compacted form of a haploid set of metaphase chromosomes.

This has been the helical turn in the history of origin and evolution of the term *genome*, which at first describes the morphological features of a haploid set of metaphase chromosomes, then their genetic contents and nucleotide sequences. Later it will come to include the order of genes and intergene DNA sequences, along with their functional significance and, finally, entire integrated maps of haploid chromosome sets will be obtained. In his metasemantic analysis of the word *genom*, Lederberg noticed (cited by [17]) that its second part reminds of the Sanskrit word *om*, which opens the famous six-syllabled mantra: *Om máni pádme hūm*, literally interpreted as "Oh jewel shining in the lotus"). Pronounced correctly, this syllable means completeness and divinity embracing all of the endless Universe. It is the basic sound of the world, which contains all other sounds. Just listen:

Gen-OMMM...

On the whole, this fits well with the modern understanding of genome as the ultimate source of the essential properties of what we call living organisms.

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