

be the quality of life that does not contravene them. The social sciences of ethics, education, economics, politics and government will become what they never have been—genuine sciences; fashioned by a just conception of man, they will cooperate to fashion the state; and the state, which may ultimately embrace the world, will rescue itself from ignorant politicians and commit its destiny to the guidance of *honest men who know*.

And when guided by honest men who know—when guided, that is, by the coming science of human engineering, which will be intelligence applied to human affairs—when thus guided in the light of the true conception of man as the binder of time—then and only then our human civilization—the living issue of time-binding toil, mainly that of the dead—will advance, not haltingly as hitherto, but, as said, in accord with the natural law thereof, in a warless world, swiftly and endlessly.

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MEDELIAN OR NON-MEDELIAN?

IN 1907, several years after the Mendelian discoveries had begun to attract general interest, a writer endeavored to limit "Mendelian heredity" to the occurrence of 3 to 1 phenotypic ratios. All other ratios were held to represent other systems of inheritance. This extreme view was not held by any one actually engaged at that time in genetical investigations, and the paper referred to was entirely ignored by geneticists because its author was so obviously ignorant of the real implications of the Mendelian discoveries.

Recently, two of our foremost geneticists¹ have gone to the opposite extreme in stating what should be included in Mendelian heredity, declaring that "Mendelian heredity has proved to be the heredity of sexual reproduction; the heredity of sexual reproduction is Mendelian." Certainly few geneticists would at the present time include so much under

¹ East, E. M., and Jones, D. F., "Inbreeding and Outbreeding." 285 pp. Philadelphia: J. B. Lippincott Co., 1919. See p. 50.

the term "Mendelian heredity," though one,² at least, there is, who sympathizes with this dictum.

Between these extreme views as to the meaning to be attached to the expression "Mendelian heredity" different geneticists have taken different positions and even one and the same writer has given the term different meanings at different times. These differences of usage have led to misunderstandings and to some controversy.

Davis³ has placed the mere occurrence of segregation in the *Oenothera* equivalent to Mendelian inheritance, thus accepting the validity of a criticism made by East⁴ based on the same conception as that quoted above from East and Jones, that all heredity in sexual reproduction is Mendelian. As I understand it, however, the occurrence or non-occurrence of segregation in the *Oenothera* has never been an important issue; the real question has been whether the segregation which does quite obviously occur is of the Mendelian type, *i.e.*, whether the hereditary factors are distributed during gametogenesis and fertilization according to the formulation actually developed by Mendel in interpreting the results of his experiments.

Other writers⁵ have grouped the phenomena of segregation under the terms "Mendelism" and "neo-Mendelism," but include under the latter name several phenomena which are now generally recognized among geneticists as differing in no essential way from the actual cases studied by Mendel. Still others speak of "orthodox" Mendelism, implying that there is also a "heterodox" Mendelism, or they use the expressions "strictly Mendelian,"

² Wright, S., "Systems of mating. I. The biometric relations between parent and offspring." *Genetics*, 6: 111-123. 1921. See p. 111.

³ Davis, B. M., "Hybrids of *Oenothera biennis* and *Oenothera franciscana* in the first and second generations," *Genetics*, 1: 197-251. 1916.

⁴ East, E. M., "The Mendelian notation as a description of physiological facts," *Amer. Nat.*, 46: 633-655. 1912.

⁵ Coulter, J. M., and Coulter, Merle C., "Plant Genetics." ix + 214 pp. Chicago: Univ. of Chicago Press. 1918. See pp. 40-96.

"typical Mendelian," etc. All such qualifying expressions give evidence of the recognition of the fact that usage varies regarding the significance of the words "Mendelism" and "Mendelian."

Since there are these differences of usage among geneticists, it would seem to be necessary for any one who describes a genetical situation as Mendelian or non-Mendelian, to state just what meaning is to be attached to the expression he uses. In my own usage of the expression "Mendelian heredity" it has always referred to cases such as Mendel actually observed, in which there is (statistically) independent segregation of unit factors during gametogenesis and chance recombinations at fertilization. I had this conception in mind in declaring^a that the genetical phenomena in the *Oenothera*s are, with rare exceptions, non-Mendelian.

As Mendel never observed a case of linkage and no provision is made for such a phenomenon in the theory by which he interpreted his results, such cases are, on this basis, to be considered non-Mendelian,—especially as they definitely contradict the fundamental Mendelian postulate of *independent* segregation. This may perhaps with some justice be termed the strict-constructionist view. On the other hand, since it is now obvious that strictly Mendelian phenomena and linkage phenomena are products of the same mechanism and indeed that linked genes are in many cases quite indistinguishable from wholly independent ones, there is some justification for those who give a broader construction to the term Mendelian, making it essentially synonymous with chromosomal heredity as distinguished from cytoplasmic heredity.

In view of these discrepancies in usage by different authors, has not the time come to abandon the use of "Mendelian" and "non-Mendelian" as definite categories, and to adopt other terms which will have greater precision of meaning? It seems to me that the accumulation of facts from genetical

^a Shull, G. H., "A peculiar negative correlation in *Oenothera* hybrids," *Jour. Genetics*, 4: 83-102. 1914.

investigations has reached such magnitude as to justify an attempt in this direction.

In offering a terminology for several of the fundamental categories of genetical phenomena my object is chiefly to emphasize by this means the fact that the categories themselves do exist and that they have been (and are) recognized by geneticists.

Very few (if any) geneticists will now fail to agree that the relation of hereditary factors to linkage groups, or to paired paternal and maternal material bodies, the chromosomes, must provide the basis for such a classification. Since we have long been familiar users of two words, homozygous and heterozygous, derived from the Greek root *ζυγ-* (*ζεύννμι*, to join, *ζεύξίς*, a yoking; *ζυγόν*, a yoke), it seems appropriate to use the same Greek root as the basis of the more complete terminology here suggested.

To distinguish between phenomena which are dependent upon the distribution of the chromosomes, and those phenomena which are to be referred to extra-chromosomal bodies or substances, we may use the nouns, *zeuxis* and *exozeuxis*, and corresponding adjectives *zygous* and *exozygous*. These alternatives correspond closely with chromosomal and cytoplasmic inheritance; but "exozeuxis" has an advantage over "cytoplasmic heredity," since some exozygous phenomena may conceivably be associated with nucleoplasmic structures or substances instead of the cytoplasm.

Under *zeuxis* or chromosomal heredity three fundamental relationships of hereditary factors are to be noted, depending on whether only one chromosome pair or linkage group is involved, or more than one, and whether the chromosomes concerned are behaving in typical or atypical fashion. These three categories may be named, respectively, *monozeuxis* (one pair involved), *pleiozeuxis* (two or more pairs involved), and *anomozeuxis* (involving chromosomal irregularities), and the corresponding adjectives will be *monozygous*, *pleiozygous* and *anomozygous*.

The last of these categories, *anomozeuxis*, is a composite made up of several phenomena

of diverse nature, which have been occasionally lumped together under the expression "chromosome-exceptional," including non-disjunction (primary and secondary), triploidy, tetraploidy, etc., chromosome elimination, fragmentation, chromosomal fusions, rearrangements of whole chromosomes, or of genes in the chromosomes, etc.

Accepting the four categories represented by the terms monozeuxis, pleiozeuxis, anomozeuxis and exozeuxis, what is their relation to Mendelism? This question can be profitably discussed only if prefaced by a statement that Mendelism is here taken to include only the phenomena to which Mendel's interpretation applies, namely to the separation of each pair of alternative factors into equal numbers of germ cells in both sexes, and a purely chance assortment of the several alternatives among the several gametes, so that the permutational groupings of unit factors shall be potentially represented by equal numbers of germ cells.

Such behavior of the genes during gametogenesis provides for the production of the typical Mendelian ratios if there is neither selective fertilization nor selective elimination.

With this understanding of the phenomena to which the words "Mendelism" and "Mendelian" are appropriately applied, it will be obvious (1) that all zygous monohybrids are Mendelian. In other words, monozeuxis is Mendelian if only one pair of factors is concerned and the chromosome pair involved is behaving typically. (2) Monozygous dihybrids are likewise Mendelian whenever crossing over equals or exceeds 50 per cent. (3) All pleiozygous dihybrids or polyhybrids are Mendelian so long as no two factors in the series are monozygous with a frequency of crossing over lower than 50 per cent. (4) Anomoeuxis may under certain circumstances exhibit Mendelian phenomena. Thus in the case of non-disjunction, if the odd (unpaired) chromosome does not interfere with the normal disjunction of any other pair of chromosomes the genetical behavior with respect to qualities determined by the un-

paired chromosome gives the results expected of a typical Mendelian monoheterozygote.

Non-Mendelian phenomena will be found (1) in monozygous dihybrids whenever crossing over is less than 50 per cent.; (2) in most cases of anomoeuxis, and (3) in all cases of exozeuxis.

In the *Oenotheras* where the question of Mendelian or non-Mendelian heredity has been most sharply and persistently raised, the situation seems now in fair way to be cleared up:

1. Exozeuxis is probably concerned in the inheritance of a variegation of the foliage which is occasionally found.

2. The *brevistylis* factor which has seemed thus far to be inherited independently of other known factors, probably represents, in relation to these other factors, a case of pleiozeuxis.

3. The occurrence of frequent irregularities in chromosome behavior (anomoeuxis) is illustrated (a) by the oft-repeated occurrence of the 15-chromosome forms, *albida*, *lata*, *semilata*, *scintillans*, *bipartita*, etc.; (b) the triploid or "*semi-gigas*" individuals sometimes called "heroes" because of their robust, *gigas*-like appearance; (c) the tetraploid *gigas*; and (d) by cases of probable fragmentation of chromosomes in forms with an extra diminutive chromosome.⁷

4. I now have on record data which demonstrate beyond question that the factors for the following characters are monozygous, being located in a single chromosome pair (chromosome I) and at a maximum distance of considerably less than 50 units: (a) *rubricalyx* bud pigmentation; (b) intense reddening of the stems; (c) *nanella* stature; (d) pink-coned buds; (e) *sulfurea* flower-color; and (f) and (g) two zygote lethals ("balanced"). As this group of characters makes up so large a block of those which have attracted the attention of geneticists, and as there are preliminary indications that still other factors are linked with the factors for

⁷ Lutz, Anne M., "*Oenothera* mutants with diminutive chromosomes," *Amer. Jour. Bot.*, 3: 502-526. 1916.

the above-mentioned characters,—notably, (*h*) a pollen lethal, and (*i*) a factor for revolute leaves^s—it can be safely stated that inheritance in the *Oenotheras* is comprised almost wholly in the two categories, anomoeuxis and monoeuxis, while pleiozeuxis seems at the present time to be exemplified clearly only by the relation between the factor for *brevistylis* and the other known factors, with the possibility that even *brevistylis* may one day be connected up with the same linkage group as the others, through the discovery of an immediately placed gene.

On the whole it is now clear that while the genetical phenomena in the *Oenotheras*, with exception of the case of variegated foliage, can be referred definitely to the chromosomes (zeuxis), the occurrence of independent segregation which is necessary for the production of typical Mendelian behavior is so rare as to be almost negligible.

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SCIENTIFIC EVENTS

MEMORIAL TO JAMES ORTON

THE governments of Bolivia and Peru have erected a monument to James Orton, the American explorer, whose grave is on Esteves island in Lake Titicaca. The funds for the memorial were given by the alumnae of Vassar College, where at the time of his death Dr. Orton was professor of natural history. The execution of the memorial was entrusted to John Ettl, the New York sculptor. It will be placed on the crest of the island which rises several hundred feet above the lake. The memorial is nine feet in height, circular in pattern with a square plinth, and in its ensemble suggests a tomb. The circular character was inspired by the tall shaft-like structures of the Incas. The dedicatory exercises will be held on September 25, the forty-fourth anniversary of Orton's death. The

^s Since this was written the factor for revolute leaves has been fully demonstrated to lie in chromosome I at or very near the same level as the factor for *rubricalyx* buds and that for red stems.

Peruvian Government will be officially represented, and a large attendance is expected from Arequipa, Peru and La Paz, Bolivia.

Miss Anna P. Orton, the daughter of the explorer, Mrs. Alice P. Sanford and Miss Ellen W. Farrar, Vassar alumnae, will represent the college. They take to the ceremony a stand of flags, including the Peruvian, Bolivian and American, presented by the United States Government.

James Orton was born at Seneca Falls, New York, April 21, 1830. He graduated from Williams College in 1855 and at Andover Theological Seminary in 1858. In 1866, he was appointed instructor in natural sciences in Rochester University. In 1867 a scientific expedition to the equatorial Andes and the River Amazon was organized under the auspices of the Smithsonian Institution, and Professor Orton was selected as its leader. The expedition sailed from New York on July 1, 1867, and after crossing the Isthmus of Panama, the route was from Guayaquil to Quito, over the Western Cordillera; thence over the Eastern Cordillera and through the forest on foot to the Napo; down the Rio Napo by canoe to Pebas, on to Marañon; and thence by steamer to Para, Brazil. As a result of this expedition many hitherto unknown specimens of natural history were collected and from portions of the collections in the museums of the Smithsonian Institution, the Philadelphia Academy of Natural Science, the Boston Society of Natural History, the Peabody Academy of Science, and Vassar College, while the bulk of the collection was purchased by Ingham University, Leroy, New York.

Upon his return to the United States in 1869, Professor Orton was offered the chair of natural history at Vassar College with which institution he remained until his death in 1877. In 1873 he made a second journey across South America from Para up the Amazon to Lima and Lake Titicaca, making valuable ethnological collections of Inca relics. In 1876 he organized a third expedition, with the object of exploring the great Beni River, a branch of the Madeira. This