The dissemination of the chromosome theory of Mendelian heredity by Morgan and his collaborators around 1915: a case study on the distortion of science by scientists

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Abstract: In the transposition of scientific concepts, teachers usually provide their students with a knowledge that does not correspond to the complex science that is produced by scientists. This difference between the results of research and the science that is taught also may be found when scientists disseminate their own ideas. In such a process they may oversimplify the scientific results and present a "clean" and attractive account that will help them to gain adepts, at the cost of hiding the intricacy of the scientific process. This paper presents a historical case study of the dissemination by Thomas Morgan, Alfred Sturtevant, Herman Muller and Calvin Bridges of their ideas concerning the Mendelian chromosome theory in the *The Mechanism of Mendelian Heredity* (1915). It analyses the process of simplification in this case, discussing some educational parallels, pointing out the resulting distortion of the scientific image and suggesting means of circumventing those problems.
Key-words: history of genetics; chromosome theory; Morgan, Thomas Hunt; transposition

A difusão da teoria cromossômica da herança mendeliana por Morgan e seus colaboradores em torno de 1915: um estudo de caso de distorção da ciência por cientistas

Resumo: Na transposição de conceitos científicos, os professores costumam apresentar a seus estudantes um conhecimento que não corresponde à ciência complexa produzida pelos cientistas. Esta diferença entre os resultados da pesquisa e a ciência que é ensinada pode também ser encontrada quando os cientistas divulgam suas próprias idéias. Nesse processo, eles podem simplificar exageradamente os resultados científicos e apresentar uma versão "limpa" e atraente que os ajudará a obter adeptos,

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pagando o custo de ocultar as dificuldades do processo científico. Este trabalho apresenta um estudo de caso histórico da disseminação por Thomas Morgan, Alfred Sturtevant, Herman Muller e Calvin Bridges de suas idéias sobre a teoria cromossômica mendeliana no livro *The Mechanism of Mendelian Heredity* (1915). O artigo analisa o processo de simplificação ocorrido neste caso, discutindo alguns paralelos educacionais, apontando a distorção resultante da imagem de ciência e sugerindo meios de contornar tais problemas.
Palavras-chave: história da genética; teoria cromossômica; Morgan, Thomas Hunt; transposição

1 INTRODUCTION

In the transposition of scientific subjects teachers usually provide their students with knowledge that does not correspond to the complexity of the science that is produced by scientists. Facts and theories are oversimplified, the limitations and problems found by scientists are hidden, the existence of alternatives or competing ideas is not mentioned, etc.[1] This difference between the results of research and the science that is taught may also be found when scientists disseminate their own ideas. In such a process they may oversimplify the scientific results and present a "clean" and attractive account that will help them to gain adepts, at the cost of hiding the intricacy of the scientific process and distorting the actual status of the ideas they uphold[2].

This paper presents a historical case study of the dissemination by Thomas Morgan (1866 – 1945), Alfred Sturtevant (1891 – 1970), Herman Muller (1890 – 1967) and Calvin Bridges (1889 – 1838) of their ideas concerning the Mendelian chromosome theory, in the book *The Mechanism of Mendelian Heredity* (1915).

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[1] The process of *didactic transposition* as described by Yves Chevallard (1985) is related to the necessary changes that are received by the body of knowledge and its use, enabling it to be learned at school. The *didactic transposition* involves a distinction between (1) the original knowledge; (2) the knowledge that should be taught (that is part of the *curriculum*); (3) the knowledge that is taught by teachers in the classroom; and (4) the knowledge that is actually learned by students. This approach also contains a basic theoretical model for the researcher (Chevallard, 1985; Bosch, Chevallard & Gascon, 2005, p. 4).

[2] A similar result occurs when the science educator presents a history of science that romanticises scientists, inflates the drama of their discoveries, and oversimplifies the process of science (*pseudo-history*). Both processes contribute to the creation of false ideas about *how science works* (Allchin, 2004, p. 179; Allchin, 2003).

The book had a strong influence and is usually regarded as a landmark of "Mendelism" and the chromosome theory (Sturtevant, 1965, p. 49; Allen, 1972, p. vi). Several scholars, including not only some of Morgan's coeval scientists such as Robert H. Lock (Muller, 1943, p. 154; Martins, 1997, p. 8:29) but also some historians of science such as Ernst Mayr (Mayr 1982, p. 771), agree that the Mendelian chromosome theory was made consistent by the genetic data presented in *The Mechanism*, in 1915. According to Stephen Brush, "Morgan's theory began to reach a wider audience of biologists through books and reviews articles published soon after the 4-man work of 1915" (Brush, 2002, p. 510). However, in a critical review of the *Mechanism* published in *Nature*, William Bateson criticised several points of the theory. Mayr found it difficult to understand why some of Morgan's colleagues could not accept chromosome theory at that time:

> It is therefore somewhat puzzling why Bateson, Johannsen, and others continued in their opposition, and why, instead of ignoring them, Morgan's two closest associates, Sturtevant and Bridges, felt the need to substantiate the validity of chromosome theory by ever new experiments. (Mayr, 1982, p. 771)

It seems that Mayr did not perceive any problem in the work published by Morgan and his collaborators. However, the book was not a flawless presentation of current knowledge since several crucial problems still existed at that time and were concealed by the authors.

This paper aims to discuss whether *The Mechanism* did really present a solid ground for Mendelian chromosome theory or not. Besides that, it will discuss to what extent Morgan and his close associates used convincing strategies (rhetoric and pictorial representation) when the situation was not clear and there was a lack of evidence. It analyses several shortcomings of *The Mechanism* and discusses the relevance of the fabrication of science in teaching.

2 "THE MECHANISM OF MENDELIAN HEREDITY"

It is well known that Morgan was a strong opponent of both the chromosome hypothesis and the Mendelian theory, until 1910-11,

when he became converted to both of them[3]. From this time onwards he and his group (Alfred Henry Sturtevant, Herman Joseph Muller and Calvin Blackman Bridges) intensely dedicated themselves to the study of mutations and heredity patterns in *Drosophila*. They discovered several sex-linked characters, and other linked factors that were not related to sex. They explained the association between factors as due to their location in the same chromosome. Very soon they found some cases in which the association was not complete – a phenomenon which had been previously described by William Bateson and Reginald C. Punnett in *Primula*[4].

The partial (incomplete) linkage of factors in *Drosophila* was interpreted by Morgan, Sturtevant, Muller and Bridges as a result of the exchange of parts between homologous chromosomes. This interpretation was based on the cytological study made by Franz Alphons Janssens using the salamander *Batracoseps attenuatus* (Janssens, 1909). Morgan, Sturtevant, Muller and Bridges tried to explain the numerical results of the recombination process by analysing the mechanism through which homologous chromosomes exchanged parts (*crossing-over*), and they attempted to determine the distance between the factors found in the same chromosome through the frequency of crossing-over. They built the so-called "chromosome-maps", assuming that the factors were linearly arranged along the chromosomes. This idea, regarded as a vital step in the establishment of chromosome

[3] This issue will not be discussed in this paper. There are several works that deal direct or indirectly with Morgan's change of mind concerning both Mendelian and chromosome theories. Some of these works admit that this turn happened around 1910-11 (Allen 1974; Allen 1983; Allen 1985; Moore 1983; Gilbert 1978; Blanc 1985; Vicedo 1990). Other authors claim that Morgan was converted in 1910-11, but not completely (Roll-Hansen 1978). There are still other works that claim that Morgan was gradually converted between 1910 and 1915 (Carlson, 1974).

[4] Bateson, Punnett and Edith Saunders around 1906, when making crossing experiments with sweet-peas, realised that some characters were inherited together, in disagreement with Mendel's principle of independent segregation (Bateson, Saunders & Punnett 1906). At the outset they only *described* the phenomenon, without trying to explain it, and they called it *coupling*. In 1911 they tried to explain it through a special cell division process (reduplication hypothesis). This hypothesis was independent of the chromosome hypothesis. The same phenomenon was later called *linkage* by Morgan and his associates (Martins, 1997, p. 5:1).

theory, was not, however, accepted by the whole scientific community at that time.

The discovery of non-disjunction of the sexual chromosomes in *Drosophila* by Bridges (Bridges, 1913a; Bridges, 1913b) allowed the establishment of a new parallel between cytological phenomena and experimental crossings. Soon after that, Morgan and his collaborators felt the need of presenting their views in a systematic way, in book form.

Despite the title of their book, *The Mechanism of Mendelian Heredity*, the authors' purpose was not simply to present the Mendelian theory of heredity and afterwards discussing the chromosome hypothesis. The book began by the introduction of chromosome hypothesis, followed by the introduction and discussion of Mendel's theory based on experimental crossings in *Drosophila*, and this strategy transmuted the specific phenomena studied by Morgan's group into the central basis of Genetics. Mendel's work, and the Mendelian research that had been developed by William Bateson and other authors in the early 20th century, are either dismissed or presented as secondary evidence. At some points the authors not only attacked several aspects of Bateson's work – the presence-absence hypothesis and the reduplication hypothesis – but also severely criticised the terminology employed by the early Mendelians.

The book did not present (nor intended to present) new results. Its purpose was to acquaint biologists in general (those who were not experts in heredity) with the new genetics (Morgan *et al.*, 1915, Preface, pp. vii-viii). The book was dedicated to Edmund Beecher Wilson, who was a cytologist[5].

Since Sturtevant's pioneer work (Sturtevant, 1913), linkage data about several factors of *Drosophila* had been accumulated and factors had been classified under four groups. Each group was interpreted as belonging to one of four chromosomes. From this set of data the

[5] Although they worked in the same department at the University of Columbia and despite being friends, Wilson and Morgan strongly disagreed concerning the Mendelian theory and the chromosome hypothesis until 1910-1911, when Morgan changed his mind. From that time onwards the mutual criticisms disappeared. The dedication at the front page of *The Mechanism*, "To Edmund Beecher Wilson", was a token of this conciliation.

authors constructed the chromosome maps of *Drosophila*, showing the relative position of 36 factors, as presented on the frontispiece of the book.

In the preface the authors tried to convince the readers that the chromosome theory was not the sole contribution of the book and that even if it would be rejected in the future, the results presented by them in the book would still be valid:

> [...] We have, of course, put our own interpretation on the facts, and while this may not be agreed to on all sides, yet we believe that in what is essential we have not departed from the point of view that is held by many of our co-workers at the present time. Exception may perhaps be taken to the emphasis we have laid on the chromosomes as the material basis of inheritance. Whether we are right here, the future – probably a very near future – will decide. But it should not pass unnoticed that even if the chromosome theory be denied, there is no result within the following pages that may not be treated independently of chromosomes; for, we have made no assumption concerning heredity that cannot also be made abstractly without the chromosomes as bearers of the postulated hereditary factors. Why then, we are often asked, do you drag in the chromosomes? Our answer is that since the chromosomes furnish exactly the kind of mechanism that Mendelian laws call for; and since there is an ever-increasing body of information that points clearly to the chromosomes as the bearers of the Mendelian factors, it would be folly to close one's eyes to so patent a relation. (Morgan *et al.*, 1915, pp. viii-ix)

However, as Garland Allen pointed out, although the authors *in principle* admitted that the Mendelian laws could be accepted independently of the chromosome theory, this was not the view they actually adopted in their work, but only a mere strategy (Allen, 1981, pp. 524-525).

At the beginning of chapter 1, where the authors described Mendelian segregation, they commented:

> Mendel did not know of any mechanism by which such a process could take place. In fact, in 1865 very little was known about the ripening of the germ cells. But **in 1900,** when Mendel's long-forgotten discovery was brought to light once more, **a mechanism had been discovered that fulfils exactly the Mendelian requirements of pairing and separation**. (Morgan *et al.*, 1915, p. 1; our emphasis)

In this quotation the authors tried to convey the impression that since 1900 the chromosome hypothesis furnished an adequate explanation for the Mendelian theory. However, that was not a historical fact because at that time (1900-1903) little was known about cell division or concerning the nature and behaviour of the chromosomes. This early situation led several scholars, including Morgan himself, to reject the chromosome hypothesis (Rostand, 1933, pp. 75-76; Martins, 1997, p. 3:1; Martins, 1998, pp. 104-106). Besides that, there were several cytological and embryological studies that were inconclusive, concerning the explanation of heredity as related to the chromosomes or cell nucleus. Moreover, although some hereditary phenomena could be explained by Mendel's principles, others were in conflict with them or even had no relationship with them (Martins, 1997, p. 3:1). Therefore, the impression that Morgan and his group tried to convey was false.

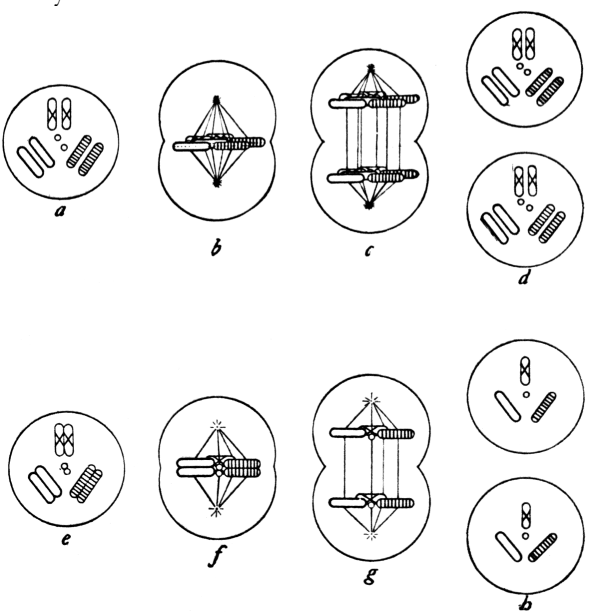

Fig. 1. The representation of chromosomes in the diagrams published by Morgan and collaborators (Morgan *et al.*, 1915, p. 3) conveyed the wrong idea that they could be observed in all stages of the cell division and that they always had the same form.

The authors continued by discussing the gametogenesis process in a didactic fashion, using theoretical diagrams that showed the presumed behaviour of chromosomes. The chromosomes that are shown in their diagram (Morgan *et al.*, 1915, p. 3) presented the same form in all stages of cell division (Fig. 1). In addition, the text expressed no doubts regarding both the individuality and constancy of chromosomes during cell division (Morgan, *et al.*, 1915, pp. 2-5). The readers who were not familiar with the cytological studies around 1900 could be led to believe that everything was clear and that the diagrams presented exactly what was really seen in cytological observation[6]. However, those diagrams were not in agreement with the cytological studies of that time, because the cytological data were not sufficiently clear. The chromosomes could be seen only during cell division. The number of chromosomes that could be seen during what is now called 'mitosis' seemed to be twice the number of chromosomes found during some steps of what we call today 'meiosis'. During mitosis it seemed that each chromosome was longitudinally split into halves, but the process was not well known. Besides that, it was not clear at that period whether chromosomes always maintained their identity or not, since it seemed to several cytologists that between cellular divisions they all combined to build a continuous thread (*spireme*) or a network (Martins, 1999, p. 262).

Besides trying to convey the impression that since 1900 the chromosome hypothesis furnished the adequate explanation for the Mendelian theory, the authors presented their own version of the recent history of genetics. They stated that: "Sutton was the first to present the idea [chromosome hypothesis] **in the form in which we recognize it today**" (Morgan *et al.*, 1915, p. 4, our emphasis). That was not a true historic version (see for instance Martins, 1999). Sutton's

[6] In didactic books, pictorical representation is a highly important factor that may lead to a non-critical acceptance of theories. Not only in elementary but also at higher levels, many students believe that the drawings of atomic and molecular orbitals are real (presumably photographed with an electronic microscope) and not an artistic representation of a theory. A similar effect occurs in the case of the drawings shown in Genetics textbooks.

chromosome hypothesis as put forward in 1902-3 was widely different from the chromosome theory that was defended in 1915. In the first place, there was no coherent chromosome hypothesis in 1902-3. In those early years there was no cytological basis for Mendel's laws, because the cytological studies used pure types, while the heredity experiments used cross breeds, and cytological phenomena could be different in those cases. Secondly, the cytological processes were still obscure. There were serious doubts about the synapsis process, which was a central point of the whole hypothesis. In addition to this, the individuality and constancy of the chromosomes were still doubtful. Boveri's research brought only indirect evidence concerning this issue. Such a difficulty was only solved in 1909. Without assuming the individuality and constancy of chromosomes it was difficult to explain the constancy of Mendel's factors and the purity of gametes. On the other hand, those who believed in the individuality and constancy of chromosomes had difficulty in explaining the independent segregation of factors admitted by Mendel. In short, there was no coherent chromosome hypothesis establishing a parallel between the behavior of Mendelian factors and cytological behavior of chromosomes in 1902-3 (Martins, 1999, p. 270).

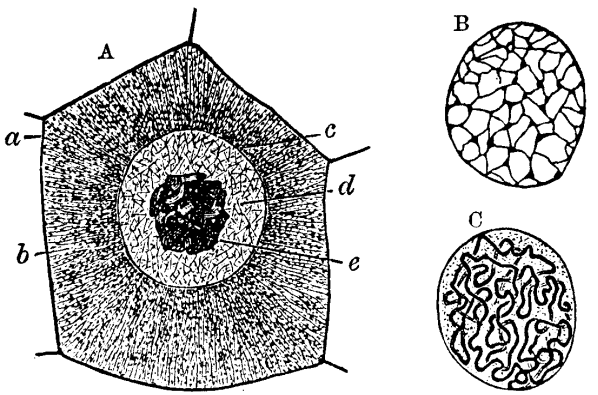

Fig. 2. Many cytological representations of the chromosomes published in the early 20th century assumed that between the cellular divisions they all combined to build a continuous thread or a network (Thomson, 1902, vol. 3, p. 49).

3 PROBLEMS FOUND IN *THE MECHANISM*

3.1 The relationship between linkage groups and chromosomes

According to Morgan and his associates, from its very beginning the chromosome hypothesis was able to predict that "all the factors carried by the *same* chromosome should tend to remain together" (Morgan *et al.*, 1915, p. 4). This was not true. There were lots of possibilities. Sutton, for instance, admitted that factors *must remain together* because he regarded chromosomes as indivisible units (Sutton, 1902, p. 126; Sutton, 1903, pp. 232, 237, 240). De Vries, on the other hand supposed that some factors could be exchanged in fertilization and probably at the beginning of the formation of the sexual cells, because he regarded chromosomes as temporary associations of elements. In this way, in sexual reproduction, characters varying in different degrees and directions could unite in every possible kinds of combination (De Vries, 1910, vol. 2, p. 647). There were several possibilities and no definite prediction. However, by their slight historical reinterpretation, Morgan and his group led the reader to believe that the main point to substantiate chromosome theory was to confirm the prediction that there were factors that tended to be transmitted together.

The authors talked about groups of sex-linked factors as well as other groups of non-sex-linked factors emphasising that there were four kinds of chromosomes and four linkage groups. However, they did not mention that there were in fact *five* kinds of chromosomes (the fifth kind was the Y chromosome found in the male *Drosophila*) and they did not associate any factor to this chromosome, although it was bigger than the X chromosome, as seen in Figure 3 (Morgan *et al.*, 1915, pp. 5-8). It is relevant to point out here that, five years before, Morgan regarded the Y chromosome as a problem: the sex chromosome hypothesis could not explain it because although in some insects the Y chromosome could be related to the production of a male, there were other insects in which the Y chromosome was not present (there was no chromosome dimorphism) although they could also be male or female (Morgan, 1910a, pp. 490-491).

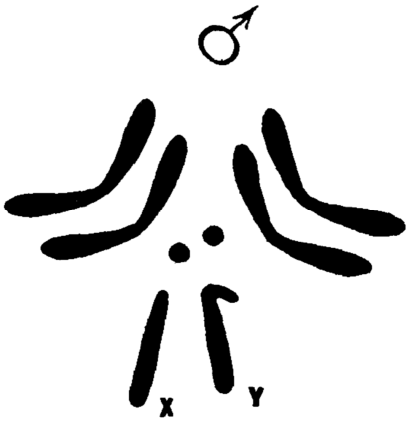

Fig. 3. A diagram showing the chromosomes of the male Drosophila (Morgan *et al.*, 1915, p. 7).

At another point of the book the authors briefly stated: "The curious fact also comes to light that no mutations have been discovered in the Y chromosome, nor does it contain any factors dominant to any known mutant or normal factors in its mate, the X chromosome" (Morgan *et al.*, 1915, p. 54). In the book this was not presented as a problem, but it is possible to infer that they regarded it as an important difficulty, since Muller published an article mentioning the fact that they had not discovered any factor yet that could be associated to the Y chromosome, suggesting several explanations for this fact (Muller, 1914, pp. 18-19).

Group:	Frontispiece:	Table, p. 6:
I	19 factors	47 factors
II	9 factors	27 factors
III	6 factors	22 factors
IV	2 factors	2 factors

Table 1. Relation between linkage groups and chromosomes, according to Morgan and collaborators.

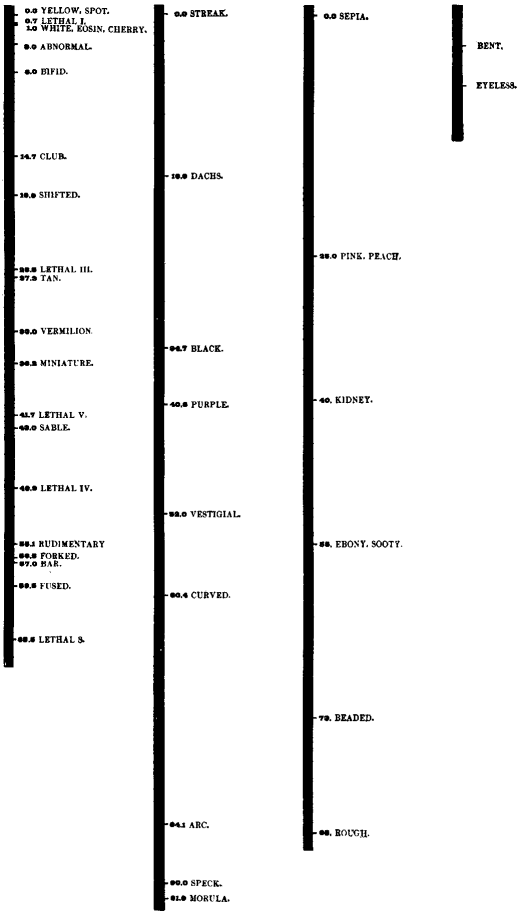

Fig. 4. The frontispiece of *The Mechanism of Mendelian Heredity*, showing chromosome maps (Morgan *et al.*, 1915, frontispiece).

They also stated that the biggest chromosomes contained more factors: "Moreover, the size relations of the groups of chromosomes correspond" (Morgan *et al.*, 1915, p. 8). The figure on the frontispiece of the book, showing four chromosome maps, also conveyed the same idea (Figure 4). However, this was not the case. The only chromosome that could be identified at that time as being associated with certain factors was the X chromosome. Although it was not the big-

gest one, the X chromosome was associated with a much larger number of factors (linkage group I). The number of factors associated to each linkage group is shown in Table 1.

Despite this fact the authors stated:

> There is one great group of characters that are sex-linked. There are two other groups of characters slightly **greater in number** (Morgan *et al.*, 1915, p. 5; our emphasis).

So the text *suggested* that the number of factors of each group was in direct proportion to the size of its respective chromosome. Group IV would be associated with the smaller pair of chromosomes. However, there were more known factors associated with the X chromosome, the *third* in size (in cytological terms) than with the other chromosomes (see Figure 3). On the other hand, there was *no evidence* that could associate any non-sexual (autosome) chromosome to any linkage group. Even if it were admitted that each group corresponded to a definite kind of chromosome, it could be possible that group IV corresponded to a big chromosome and that the smallest chromosome corresponded to the linkage groups II or III. We must remember that there was no known factor associated with the biggest chromosome (Y). In this way, it would be possible that group IV (which had only two known factors) could correspond to a big chromosome.

To sum up: it seems that Morgan and his colleagues tried to convince the reader from the very beginning that the chromosome hypothesis was able to predict that some factors carried by the same chromosome tended to remain together, because this would reinforce what they intended to substantiate afterwards: there were several linkage groups associated with some particular chromosomes in *Drosophila*. When talking about linkage groups they made wrong generalisations such as "bigger chromosomes bear a greater number of associate factors than the smaller ones", perhaps because this could convince the reader of the truth of the hypothesis. They avoided talking about the Y chromosome (probably deliberately) because, although it was bigger than the others, there was no factor associated with that chromosome, and this represented a problem for their theory. Trying to convey the impression that the situation was clear and simple, and hiding problems from the reader, were persuasion strategies used by Morgan and his associates.

3.2 Linear arrangement

One of the most important points defended by Morgan's group was the proposal that the factors are linearly arranged along the length of the chromosomes and that the proportion of crossing-over gametes was an indirect measurement of the distances between the factors along the chromosomes. This momentous claim should have been substantiated by a wealth of data. However, they offered scarce information about each one of the four linked groups and about the factors mentioned by them. The lack of observational information may be regarded as a serious flaw in the book. This is not an anachronistic criticism, since William Bateson indicated it shortly after the publication of *The Mechanism*. Although Bateson regarded the linear arrangement hypothesis as a promising one, he stated that the book offered only a glimpse of the evidence from which it has been deduced, that is, the documentation for an examination of the theory was not contained in the book:

> We are told that the breeding numbers prove the factors to be in four linked groups. We would like to take each one separately and follow the proof regarding its linkage. [...]. The book tells us that more than 40 factors have been located in it and arranged in order. Respecting the great majority we have no details at all and as to most of the remainder very few. There are, however, six that we can examine in the light of the data summarised by Sturtevant in *Zeits. f. Vererbungsl.,* 1914, the last considerable body of evidence to hand. (Bateson, 1916, p. 540)

When Morgan and his associates omitted information, presenting only a few results, they prevented the reader from finding inconsistencies and gave the impression that everything was simple and clear.

3.3 Sex linkage

The book goes on to discuss the inheritance of one pair of factors in *Drosophila*, trying to explain it by the chromosome theory (Morgan *et al.*, 1915, pp. 8-13). The authors assumed the relation between sex and chromosomes from the very beginning, without discussing the doubts that existed at that time on this subject. Sex-linked inheritance is introduced by the white-eyes fly example (*ibid,* pp. 14-20). It is well known that, between 1905 and 1912, several studies on sex determi-

nation in insects had been developed by E. B. Wilson, Nettie Maria Stevens and others, including Morgan himself (see for instance: Stevens, 1906; Stevens, 1907; Stevens, 1909; Wilson, 1906; Wilson, 1909a; Wilson, 1909b, Wilson, 1909c; Morgan, 1909a; Morgan, 1909b). Although to some extent they could substantiate the relation between sex and some definite chromosomes, they faced several difficulties mainly due to the plurality of models of sex determination: the chromosome difference between males and females could vary according to the insect that was considered. There were lots of problems that led those authors, in some cases, to suggest several hypotheses to explain the relation between sex and chromosomes, without choosing any one of them. As late as 1914 Leonard Doncaster showed that the evidence that related sex determination to chromosomes was still incomplete (Martins, 1997, pp. 4:1-4:2; Doncaster, 1909). Moreover, Morgan did not mention his own previous difficulties when dealing with sex determination in *Phylloxera* (Morgan, 1909b, p. 275) and he also omitted them in building the explanation he presented in the *Mechanism* (see Morgan, 1910b, for instance).

We can see once more that omitting difficulties and creating the impression that the situation was clear and established was a convincing strategy used by the authors.

In the discussion of the inheritance of two or more independent pairs of factors, the experimental material is also *Drosophila*. Everything is explained from the point of view of the chromosome hypothesis. The authors did not even mention other possible explanations that existed at that time. Several diagrams depict chromosomes that were "painted" in different ways, suggesting that it was possible to establish a relationship between the factors and definite chromosomes to which they were associated (Morgan *et al.*, 1915, pp. 20-26). Of course, this was not possible at that time.

3.4 The explanation of development

In chapter 2 of *The Mechanism*, Morgan and his associates discussed the environmental conditions that could influence the development of characters[7] and they briefly mentioned the problem of cell

[7] They included among them "age" and gave the example of a white flower that may

differentiation. It is worth remembering that five years before Morgan considered that the chromosome theory could not explain cell differentiation (Morgan, 1910a, p. 453). He doubted that different animal organs and tissues could contain the same assemblage of chromosomes and, at the same time, to exhibit different properties (*ibid,* p. 477). However, the authors presented this point in the book as if it was devoid of problems, without showing the evidence upon which their ideas were grounded:

> There is extensive evidence from cytology, experimental embryology, and regeneration, to show that all the different cells of the body receive the same hereditary factors. We must suppose, then, that the Mendelian factors are not sorted out, each to its appropriate cell, so that factors for color go only to pigment cells, factors for wing-shape to cells of the wing, etc., **but that differentiation is due to cumulative effect of regional differences in the egg and embryo, reacting with a complex factorial background that is the same in every cell** [...] (Morgan *et al.*, 1915, p. 43; our emphasis)

This was an inaccurate description of the situation. First, because it was known at that time that the body cells were not all equal, in hereditary terms. Some plant experiments showed the possibility of obtaining, by graft, different plants from the same tree (see, for instance, Bateson, 1913, p. 312; Bateson & Pellew, 1915). The evidence of regeneration only showed that it could take place in *some simple organisms*, but this was not a general phenomenon. Why was it not general, if all the cells of every organism contained all the factors? Experimental embryology showed that, in some definite cases, from the beginning of the egg division, there was an irreversible differentiation that led the cells to change (Wilson, 1905).

Secondly, even if the facts described by Morgan and associates in the paragraph cited above were real, their *explanation* would be problematic. If the wing and the eye have the same chromosomes that carry the same factors, the properties of different kinds of cells are

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change to purple as the plant gets old. In *Drosophila*, they explained that in young flies it is possible to distinguish the factor for pink eyes from the factor for purple eyes. However, as they grow old the eyes of both of them assume a purplish shade and it is very difficult to distinguish one from the other (Morgan *et al.*, 1915, p. 420).

not determined by their chromosomes. Consequently, chromosomes and factors do not induce the existence of different organs that have different properties. So the basic organic structure could be determined by another cause. Certainly this presented a problem to the chromosome theory, and this was not only realised but also pointed out by several scholars, during the first decade of the twentieth century, such as Bateson (Bateson, 1907, pp. 165-166; Martins, 1997, p. 3:80) and Morgan himself (Morgan, 1910a). Although Morgan was aware of the difficulties and had no answers, he tried to conceal them, writing as if no doubts had arisen on the subject.

3.5 Linkage and crossing-over

In chapter 3 of *The Mechanism*, Morgan and his associates introduced linkage and crossing-over as necessary consequences of the theory and not as experimental results that could be interpreted in several ways. The chapter begins thus:

> If two factors lie in the same member of a chromosome pair we should expect them always to be found together in successive generations of a cross unless an interchange can take place between such a chromosome and the homologous chromosome derived from the other parent. [...] But if pieces of homologous chromosomes are interchanged, then some of the gametes will contain one of the factors in question, and an equal number will contain the other factor. The process of interchange between chromosomes is called crossing-over; the tendency of factors to stay together is called linkage. (Morgan *et al.*, 1915, p. 48)

The term "crossing-over" was first introduced as a description of the macroscopic phenomenon that could be observed in experimental crossings. The exchange of pieces between homologous chromosomes was the microscopic *explanation* of crossing-over, according to the chromosome hypothesis. However, by starting from a *cytological* definition of crossing-over it becomes almost impossible to believe that the recombination of factors could have had another different cause. In spite of this, at that time there was an alternative explanation for the recombination of the factors – the reduplication hypothesis – which had been previously proposed by Bateson and Reginald C. Punnett (Bateson & Punnett, 1911). It tried to explain why there were more gametes presenting the parental or maternal

combination of factors than gametes presenting the other combinations. Based on the evidences they got from their studies on sweet peas as well as from Edith Saunders' observations on *Matthiola* and *Petunia*[8], they suggested that after segregation the cells containing mixed factors would split only once, each one producing two cells. On the other hand, the cells that were similar to those of the parents would split several times. In this way, there would be more plants, which looked like their parents than plants that did not look like them. Whereas the chromosome hypothesis suggested that segregation would take place during the reduction division (meiosis), the reduplication hypothesis proposed that it could occur earlier than gametogenesis (Bateson & Punnett, 1911, p. 211).

Morgan and his colleagues introduced the exchange of chromosome pieces as a very simple concept, without presenting any problem. They did not discuss whether chromosomes could really exchange factors between them and how it could happen, for instance. Instead of discussing this, they presented several examples of macroscopic crossing-over (got from *Drosophila* experiments) without dealing with the microscopic evidence related to the *Drosophila* chromosomes. This was problematic since, although they had some genetic evidence (macroscopic) that suggested that crossing-over could take place in the female *Drosophila*, they had no available cytological evidence got from *Drosophila*. Besides that, they were only dealing with one single organism.

As the text unfolds we detect no references concerning papers where we could find the data and computations upon which the authors founded their claims[9]. In fact, the whole of chapter 3 is full of *fake or theoretical* examples. For instance, concerning crossings of black vestigial wing flies with grey, long wing flies, they presented the result shown in Table 2 (Morgan *et al.*, 1915, p. 50).

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[8] Bateson and Punnett referred to Saunder's articles published in the *Royal Society Evolution Committee Reports*, vol. 4, 1908 and the article published in the *Journal of Genetics* vol. 1, 1911 (Bateson & Punnett 1911, p. 211).

[9] Although the authors mentioned that they studied around 40 factors in *Drosophila,* the data or calculations related to them did not appear in the book. Even in the extensive bibliography presented at the end of the *Mechanism,* that should include all the works of the group, there is only one reference to specific papers in which we can find the data about 17 factors studied by the group (Morgan *et al.* 1915, pp. 232-233).

Without crossing over :		With crossing over	
Black, vest.	Grey, long	Black, long	Grey, vest.
41.5%	41.5%	8.5%	8.5%
83%		17%	

Table 2. A "theoretical" or "ideal" set of experimental values, according to Morgan.

Of course no real experiment would show the result of Table 2, with exactly equal numbers for "black, vestigial" and "grey, long". The table presented for backcrossings (Morgan *et al.*, 1915, p. 52) showing exactly the same percentages, could not also present real data. Let us compare them to a *real* set of data (Table 3) that was published by Morgan himself, dealing with the same factors (Morgan, 1914, pp. 196-197).

Without crossing over:		With crossing over :	
Black, long	Grey, vest.	Black, vest.	Grey, long
1.552	1.315	294	338
44.3%	37.6%	8.5%	9.6%
81.9%%		18.1%	

Table 3. A "real" set of experimental values, according to Morgan.

We can notice that this "real" table is a little bit different from the ideal one presented in the book.

The authors used several persuasive strategies in the cases mentioned above. First of all, they created the impression that the only explanation available for their experimental results involved the chromosome interpretation of linkage and crossing-over. They did not clarify that there were other possibilities, including the reduplication hypothesis, for instance. Besides that, they described crossing-over in *Drosophila* as if they had observed it in cytological terms, and that was not the case. They did not exhibit their real data or calculation, but only theoretical examples that displayed "perfect" numbers. This conveyed the impression that everything was crystal clear and established upon a solid basis.

When discussing linkage, the authors commented *en passant* that there was no crossing-over in the male *Drosophila* (Morgan *et al.*, 1915,

pp. 49, 50, 54). Morgan had published an article one year before about the absence of crossing-over in the male of *Drosophila* for genes in the second and third pairs of chromosomes, without discussing its implications to the theory (Morgan, 1914). The authors neither emphasised nor discussed this point as if it deserved no explanation, giving the impression that this was not a problem for the theory. However, the only cytological evidence for crossing-over at that time was related to *Batracoseps*, and in the case of that organism this phenomenon could only be observed in the males. This was pointed out by some of their coeval scientists.

Bateson regarded the absence of crossing-over in the male *Drosophila* as very difficult to conciliate with the theory and was surprised that there was no discussion of the difficulties thus created, either in the book or in the material previously published by Morgan and his associates (Bateson, 1916, p. 539). This same point was discussed elsewhere by another author (Anonymous, 1916, p. 118). He argued that the absence of any crossing-over in the male for any character should be cleared up and that this was a weak point in the theory. However, it could be turned into a strong one if the cytologist could show that the behaviour of the chromosomes during the maturation divisions was different in the two sexes. It is relevant to point out that two historians of science with a scientific background, Ernest Mayr and John A., when dealing with the context of the establishment of chromosome theory, did not mention this problem (Mayr, 1982, chapter 17; Moore, 1986).

Mentioning briefly, without any discussion, some problems of the theory, such as the absence of crossing-over in the male *Drosophila,* the authors led the reader to think that they were unimportant, contrary to the actual situation.

3.6 The cytological mechanism of crossing-over

In chapter 3 of *The Mechanism*, where the authors discussed linkage, they also dealt with the cytological mechanism of crossing-over. They presented cytological data in a very superficial and simplified way. The main point – the interchange of pieces between chromosomes – was treated in the following way:

> There has been much controversy as to how this union takes place, but in some cases at least, the united chromosomes twist around each other as they come together. This is illustrated to the left in figure [...]. As a consequence, parts of one chromosome will come to lie now on one, now on the other side of the mate. If when the twisted chromosomes separate, the parts on the same side go to the same pole the end result will be that shown to the right in figure [...]. Each chromosome has interchanged a part with its mate. This process has been called crossing-over. It is, of course, also possible that the twisted chromosomes do not break and reunite where they cross, and if they do not then when they begin to separate they simple pull apart irrespective of the side on which they lie. When this occurs each chromosome remains intact and no crossing over takes place (Morgan *et al.*, 1915, pp. 60-61).

As time went by Morgan changed his mind about the way in which he imagined the exchange of pieces between homologous chromosomes. At first, following Janssens' hypothesis, he supposed that two chromosomes twisted around each other. After that, they split longitudinally. In this way there would remain several pieces of each on one side, that would join forming a new chromosome. However, later Morgan changed his mind. It is possible that he had realised that crossing-over was not as frequent as it should be according to this previous model. From here onwards Morgan and his group considered only a single twist between homologous chromosomes (Figure 5).

Was this acceptable, at that time?

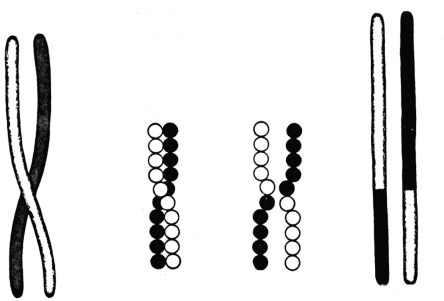

Fig. 5. The mechanism of crossing-over, as shown in *The Mechanism of Mendelian Heredity* (Morgan *et al.*, 1915, p. 60).

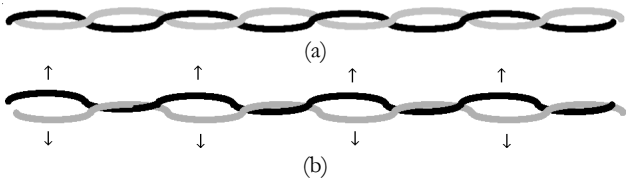

Fig. 6. If two chromosomes were twisted several times around each other, as it was described by some cytologists (a), they would necessarily break at several points, when they separated by a transversal motion (b).

Let us suppose that two chromosomes were really twisted several times around each other, as it was described by some cytologists (Figure 6a). It was possible that the chromosomes, instead of fusing at the points where they get in touch, were only rolled up. Up to this point Morgan's reasoning presented no problems. However, let us imagine that the two chromosomes would split by a movement perpendicular to their length, without unrolling. Morgan and colleagues thought that sometimes this could happen without the exchanging of pieces between chromosomes. This is impossible as we can see in Figure 6b. There are some pieces from one chromosome that should pass through the pieces of the other. This could not happen without breakage. If there is breakage, why do some pieces of the chromosomes not fuse? On the other hand, if chromosomes passed through each other, why do they sometimes exchange pieces?

We can see how important was the role of diagrams in the dissemination of the chromosome theory. The drawings presented in *The Mechanism* conveyed a false impression of what was observed in the cell division.

3.7 The cytological evidence of crossing-over

In chapter 5, entitled "The chromosomes as the bearers of heredity" the authors presented in a few pages the cytological evidence related to synapsis and the exchange of pieces between chromosomes. They admitted that there were doubts concerning those processes: "When we come to consider how this union of chromosomes is brought about, there is much divergence of the opinion, for the evidence is fragmentary or contradictory on almost every point"

(Morgan *et al.*, 1915, p. 122). Despite this statement they presented a favourable description of the chromosome hypothesis. How was this possible, if the evidence was contradictory? "For any information that is worth while we have to rely on the best material available" (*ibid,* p. 123). "The best material available" corresponded to two studies. The first was Janssens' study of spermatogenesis in the salamander *Batracoseps attenuatus*. The second one was Marechal's study of oogenesis in the shark *Pristiurus melanostomus*. Was it sensible to generalise the conclusions got from these *two cases* to all living beings?

The book reproduced some of drawings made by Janssens describing some stages of meiosis, emphasising that the leptotene chromosomes appeared as threads twisted around each other (Morgan *et al.*, 1915, p.124). Janssens' drawings not only showed this twisting, but also gave the impression that homologous chromosomes *twisted several times around each other,* and not once as it appears in the crossing-over diagrams presented in the book. After the period in which the chromosomes were united, Janssens' drawing showed a longitudinal split of the threads, and cross connections uniting the halves of the threads, looking like a rope ladder: "Later, *j,* the threads become fused throughout their length (pachytene stage). Still later the thick threads begin to show a longitudinal split (diplotene stage), and cross connections, uniting the halves of the threads, appear in different places" (*Ibid,* p.125). However, according to this description, if the exchanges between chromosomes took place in these stages, there should *always* be an exchange between *several* pieces of chromosomes. However, the authors only described Janssens' observation, without commenting on them. At another point of the same chapter they considered Janssens' representation as consistent with the model presented by them, in which homologous chromosomes twisted around each other only once:

> It is not necessary to assume that crossing over takes place at every node, but only that it may sometimes take place. In fact, our work on Drosophila shows for the sex chromosome in the female that crossing over takes place in only about half of the cells, and double crossing over is a rather rare event. (Morgan *et al.*, 1915, p. 132)

In short, instead of being guided by cytological studies, Morgan and his associates were guided by their own experimental results that

were *incompatible* with the idea of the existence of several exchanges of pieces between chromosomes.

For Bateson it was very difficult to judge to what extent Janssens' hypothesis (that chromosomes could twist, anastosomose and again break, exchanging parts of their substance) was in accord with the observed facts:

> That twisting takes place in many types, especially Amphibia, is clear; but neither the figures reproduced from Janssens nor the originals from which they are taken – still less the very fragmentary observations of both Stevens and Metz from *Drosophila* – provide more than a slender support for this most critical step in the argument. It is to be hoped that the authors will before long tell us exactly upon what evidence they are here relying (Bateson, 1916, p. 538).

Bateson's criticism was plausible since the figures presented showed only a twisting. This was not a guarantee of the occurrence of crossing-over. Besides that, there was no microscopic evidence of the occurrence of crossing-over.

In an anonymous critical review published in *Nature*, the author pointed out as a gap in the argument built by Morgan and his colleagues the fact that, at that time, one did not know whether or not *Drosophila* showed the peculiar twisting of the homologous chromosomes round one another, such as was described by Janssens in *Batracoseps*, and the existence of such a twisting was essential to the "crossing-over" explanation of the linkage characters in heredity (Anonymous, 1916, pp. 117-118). Another scientist of that time, Leonard Doncaster, commented:

> The twisting of the chromosomes round each other in synapsis appears undoubtedly, to occur in certain cases, but until the splitting across the twist postulated by Morgan has been shown with certainty to occur, his hypothesis must be regarded as almost speculative. (Doncaster, 1914, p. 492)

Morgan and his associates did not comment that there was no crossing-over in the male *Drosophila*, whereas Janssens, through his studies in the spermatogenesis of *Batracoseps,* found some signs that indicated that there could be an exchange between parts of homologous chromosomes. They could have argued that in *Drosophila* the phenomena could be different. But to what extent would it be rele-

vant to describe Janssens' observations if it could not be applied to other species?

There were several problems concerning the cytological evidence of crossing-over, which was a vital feature of the theory. However, the authors conveyed the impression that everything was clear and established. First of all, they used as evidence of their theory the cytological study made by Janssens in *Batracoseps* (salamander) although they were dealing with *Drosophila*, another organism. They did not present any cytological study made in *Drosophila* in their book but they had got genetic evidence (from experimental crossings) that there was crossing-over only in the female *Drosophila*. Janssens studied the male salamander. Morgan and his associates did not make this clear to the reader, that is, in those two organisms the situation was different and in *Drosophila* they were dealing with indirect evidence. Secondly, Janssens' drawings showed homologous chromosome threads twisting around each other twice or more times. In the model presented by Morgan and his colleagues in the book, this happened only once. They did so in order to conciliate the model with their experimental results. They also did not make any comment about this issue. To make things worse, although one could see homologous chromosome threads twisting around each other in Janssens' drawings, there was no cytological evidence of the exchange of pieces between them at that time, either in the salamander or any other organism. This was only a possibility. So, the authors did not present the real situation to the reader.

3.8 Discrepancies between prediction and observation

In chapter 3 the authors explained that it was possible to calculate the distance between factors from the frequency of crossing-over. They commented:

> In this way the diagram shown in the frontispiece has been constructed. Not only can all the facts of linkage so far studied be explained on this basis, but, as will now be shown, certain further results can be predicted. (Morgan *et al.*, 1915, p. 61)

The authors claimed that the frequency of crossing-over was proportional to the distance between the factors. If we consider three factors (A B C) arranged linearly on the same chromosome, the dis-

tance between A and B (AB) plus the distance between B and C (BC), would be the distance between A and C (dist. AB+ dist. BC = dist. AC). This could only be the case if the percentage of crossing-over between A and B plus the percentage of crossing-over between B and C was equal to the percentage between A and C (%AB + %BC = %AC). However, that is not the case. Except for very short distances, it was observed that %AB+%BC>%AC.

Before clarifying that (for long distances) the observed percentage of crossing-over was smaller than that which was calculated from the diagrams, Morgan and his colleagues introduced the concept of double-crossing-over. They presented this discrepancy as a (corollary) consequence foreseen by the theory and not as a problem:

> In fact, the sum of the two crossover percentages 33 and 22 (55) is much greater than the apparent amount (44) of crossing-over when only white and bar [factors] are involved. Here then we have an explanation of why long distances taken as a whole give too little crossing over, as compared with the same distances taken section by section. The lowered percentage is an actual **mathematical necessity** owing to the occurrence of double crossing over. (Morgan *et al.*, 1915, p. 63, our emphasis)

Well, if this reduction was a foreseen "mathematical necessity", and the simple rule did not hold in this case, how was it possible to calculate the percentages of crossing-over for long distances? Neither the book, nor the works published at that time offered any elucidation of this point. However, at another point the authors stated that it was possible *to calculate* this discrepancy:

> [...] given the distance between any two factors on the map, the per cent of crossing-over between them can always be *calculated* from this distance (since the amount of discrepancy due to the double crossing over also depends on the distance); this shows that the amount of crossing-over between them is an expression of their position in a *linear series*. (Morgan *et al.*, 1915, p. 65; original emphasis)

It would be nice if they could really present a way of determining the double crossing-over as well as conciliating the observed frequencies with the distances on the maps. Whether they did not know how to make this calculation or decided to hide this important feature of the theory, we do not know. In the book their main focus was upon the examples that "worked", such as the cases of short distances:

> In the construction of the maps shown in the frontispiece the distance taken as a unit is that within which 1 per cent. of crossing over will occur. Thus, yellow and white are placed one unit apart, since there is 1 per cent. of crossing over between yellow and white. White and bifid give 5 per cent. of crossing over, hence they are placed five units apart; and since yellow and bifid give 6 per cent., bifid must be on the other side of white from yellow. (Morgan *et al.*, 1915, p. 64)

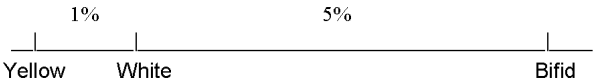

Fig. 7. A diagram representing the supposed relation between the distances between the three factors yellow, white, and bifid (Morgan *et al.*, 1915, p. 64).

In this example (Figure 7) there is a perfect correspondence between experimental data and theoretical prediction. Nonetheless, did the data really show this? At that time there was no published data on the bifid factor[10]. As regards the factors for yellow body and white eye, the percentage of crossing-over was 1.1% (354 cases in 32218) and not exactly 1% (see Sturtevant, 1915, p. 238). It is scarcely likely that the percentages of crossing-over for white/bifid and yellow/bifid were *exactly* 5% and 6%. This was again a theoretical example, with no real data. This example could lead the reader to think that the theory was able to make exact predictions.

In short, Morgan and his collaborators stated not only that it was possible to calculate the distance between factors from the frequency of crossing-over, but also to make predictions in this respect. However, they found discrepancies between what was predicted and what was observed. They created the impression that this was not a problem and focused their attention on the cases that worked.

4 OTHER PIECES OF EVIDENCE FOR THE CHROMOSOME THEORY

In chapter 5 the authors presented more evidence for the chromosome theory. It begins in this way:

[10] It is curious that the factor "bifid" did not appear in later chromosome maps. Thus, it is not possible to learn about the experimental data related to it.

> The evidence in favor of the view that the chromosomes are the bearers of hereditary factors comes from several sources and has continually grown stronger, while a number of alleged facts, that seemed opposed to this evidence, have either been disproved, or else their value has been seriously questioned. We propose now to examine in some detail the observations and experiments that bear on the chromosome theory of heredity. (Morgan *et al.*, 1915, p. 108)

The evidence presented by the authors came from several sources:

- Boveri experiments with sea urchins that showed the influence of the nucleus in the offspring, as well as Boveri's studies upon dispermic fertilisation of the egg of the sea urchins.
- Boveri's studies in *Ascaris* that led to the view that chromosomes retained their individuality from one cell division to the next.
- When different species are crossed and anomalous chromosomes are introduced in an egg, they may be identified and shown to reappear after several cell divisions, showing their continuity.

The evidence presented above was not new. The authors did not mention any of Morgan's previous embryological experiments that brought results that substantiated the role of the cytoplasm in heredity and that had led him to deny that the nucleus was the bearer of hereditary factors (Morgan, *The frog's egg*, *apud*, Gilbert, 1978, pp. 315-316). In a similar way, they did not refer to Morgan's previous doubts concerning the individuality of chromosomes:

> If [the chromatin threads] fuse, what guarantee is there that they will separate again along the exact lines of union? If the separation is not exact the materials of the chromosome would, before long, become completely intermixed. It is this difficulty that has created a presumption against the theory of the individuality of the chromosomes. (Morgan, 1910a, p. 455)

To sum up, in general, the evidence presented by Morgan and his associates was not new, and a few years before it was not regarded by Morgan as consistent enough to substantiate the chromosome theory. His old scientific objections had not been answered. However, in the book the authors did not discuss Morgan's previous objections, but presented the same evidence that was considered problematic by Morgan as being conclusive. In short, depending on his necessity

Morgan used the same evidence against or in favour of the chromosome theory.

5 DECISIVE POINTS OF THE THEORY

According to the authors the strongest features of the chromosome theory was the evidence of sex-linked inheritance and non-disjunction:

> In the case of sex and sex linked factors it can even be shown that they have the *same* distribution as the sex chromosomes. [...] Not to interpret this evidence to mean that factors are contained in and carried by the chromosomes is to reject a mechanistic basis known to exist in the cell [...] (Morgan *et al.*, 1915, p. 148).

> The advantage of the chromosomal interpretation as applied to sex chromosomes is nowhere better illustrated than in the history of a process called non-disjunction, which was discovered by Bridges. Furthermore this case, supported on the one hand by extensive and definite experimental breeding and on the other by cytological investigation, offers the most direct evidence yet obtained concerning the relations of particular characters and particular chromosomes, for in this case an abnormal distribution of sex chromosomes goes hand in hand with an identical abnormal distribution of all sex linked factors [...] (Morgan *et al.*, 1915, p. 149).

In fact, we must agree that these two points provided strong evidence for the theory.

In the same year when Sturtevant created the first chromosome map, Bridges provided a very important piece of evidence in favour of the chromosome theory (Bridges, 1913a). He realised that some crossings did not give the expected results and tried to explain this fact through the non-disjunction of sexual chromosomes, which was observed in a definite percentage of eggs during maturation. He stated that ordinarily when a *Drosophila* female with white eyes (XwXw) is mated to a wild male with red eyes (XWY), the daughters have red, and the sons, white eyes – a typical case of the criss cross inheritance characteristic of sex linkage. However, he found an exceptional case where 5% of the daughters were similar to their mothers and 5% of the sons were similar to their fathers (*ibid*). He explained that in such mothers "a certain per cent of maturations are of

a type characterized by non-disjunction, i.e., eggs are formed which contain two sex chromosomes instead of the normal one, and other eggs corresponding to them contain no sex chromosome" (*ibid,* p. 588). In this way some eggs, instead of presenting one X chromosome, would present two X (XX), and others would contain no X chromosome. There would be three classes of eggs: X; XX and no X. However, Bridges pointed out that, at this time there was no cytological evidence of non disjunction in *Drosophila* (*ibid,* p. 604). The cytological evidence came later in the 1930's (Moore, 1986; Martins, 1997, p. 10:8).

When *The Mechanism* was published there was, however, a problem related to Bridges' studies on non-disjunction: neither the experimental data about the experiments, nor the cytological information related to them had been published yet. It was in the *Mechanism* that there appeared for the first time a drawing that represented the chromosomes of the anomalous female (XXY) (Morgan *et al.*, 1915, p. 152). Even Bateson was very well impressed with Bridges' work on non-disjunction in *Drosophila*, which was afterwards published in *Genetics* in 1916. He considered it as bringing remarkable evidence not only concerning experimental crossings but also regarding cytological demonstration:

> [...] Of the discovery that may perhaps come hereafter to be regarded as the most illuminating of all – the phenomenon of "non-disjunction" – we have still to speak. The exploration of this group of facts has been made by Bridges, who, since the brief note contained in the book, has published in *Genetics* a detailed account of his experiments. With this publication it must be admitted we are lifted on to something like solid ground. (Bateson, 1916, p. 541)

We can say that the studies of sex-linked inheritance in *Drosophila* had brought quite good results. If we suppose that the female possessed two X chromosomes and the male only one as well as the sex linked factors were carried by these chromosomes, it was possible to make several predictions about what could occur or could not occur in definite crossings. In general the predictions could be confirmed – but there were a considerable amount of "impossible cases" that were explained away by Morgan and his associates as experimental errors, although Leonard Doncaster considered them as a serious difficulty (Doncaster, 1914, p. 510). The number of cases in which the theory

"worked" was impressive. In this way, at that time, it was possible to suppose that the "impossible cases" could be experimental errors.

Even when we regard the existence of the strong evidence of sex-linked inheritance and non-disjunction, we can say that the authors used some convincing strategies in presenting them. In the first quotation, for instance, they tried to relate the sex linked factors as having the same distribution as the sex chromosomes to the mechanistic basis known to exist in the cell, giving the impression that this was the only possibility – and that was not the case. Besides that, they did not mention the empirical observation of "impossible cases". Concerning the relationship between particular characters and particular chromosomes, they presented Bridges' non-disjunction in *Drosophila*, as if it was supported not only by experimental crossings, but also by cytological evidence. In this second case, there was no information nor in the book, neither in the papers available at that time. In spite of this, the authors gave the impression that this material was available.

In 1916 there appeared in *Nature* an anonymous critical review of *The Mechanism*. Its author pointed out some favourable aspects of the theory:

- Chromosome distribution corresponds to Mendelian factors distribution.
- In some cases there is a relationship between sex and definite special chromosomes.
- The factors found in Drosophila may be divided in four linkage groups.
- Only the factors that belong to one of these groups show sex-linked inheritance
- It is possible to build chromosome maps from the studies of crossing-over (Anonymous, 1916, p. 117).

The author acknowledged that *The Mechanism* presented strong arguments for the chromosome theory of heredity. However, the author also perceived some gaps in it (Anonymous, 1916, p. 117).

6 CRITICISMS ABOUT BATESON'S WORK MADE BY THE BOOK

At several points of the book the authors attacked directly or indirectly some features of Bateson's work, such as the presence-absence

hypothesis (Morgan *et al.*, 1915, pp. 208-222), the reduplication hypothesis (Morgan *et al.*, 1915, pp. 74-76) or even Bateson's careful analysis of the combs of fowls (Bateson, Saunders & Punnett, 1905; Bateson & Punnett, 1905). In this last case, they not only strongly criticised the nomenclature used by Bateson, but also suggested that it should be substituted by the one used by them in their studies of *Drosophila* (Morgan *et al.*, 1915, pp. 216-220).

Bateson was quoted only at four points in the book

- Bateson and Punnett made the discovery of linkage, which they called gametic coupling, *although they did not relate such a discovery to chromosomes* (Morgan *et al.*, 1915, p. 5)
- Bateson and Punnett interpreted linkage on a basis entirely different from that adopted in this book (chromosome theory*). It was based on questionable or even wrong suppositions* about 'gametic ratios', egg's polarity, somatic (prereductional) segregation and the gametogenesis process (Morgan *et al.*, 1915, pp. 74-76).
- Bateson pointed out that a complex character like stature must depend on multiple factors (Morgan *et al.*, 1915, p. 173).
- Bateson defended the idea that multiple alleles could be explained by a process of fractionation of factors, *but this suggestion is not acceptable* (Morgan *et al.*, 1915, pp. 214-216).

From the beginning of the 20th century Bateson had exhaustively dedicated himself to the Mendelian research program. Until 1915 he was considered the leader of Mendelian research not only in the UK, but also in the other English-speaking countries. Of course the authors were acquainted with Bateson's research. In their bibliography they included 8 of his works. Why did the authors present Bateson's work in such a negative way?

Was there a scientific incompatibility between the works of Bateson and Morgan's group? It does not seem so. Bateson's experimental studies were compatible with the chromosome theory except for some anomalies, which could not be explained at that time. Only the reduplication hypothesis (see section 7) was in conflict with chromosome theory, but it was proposed before the publication of Morgan's chromosomal interpretation of linkage, and not as an alternative to it.

The attitude of Morgan's group could be interpreted as a strategy for appropriating the authority in the field of genetics, by lowering

the importance of one of the main characters in the area. A kind of "struggle for authority in the field" was studied by Jan Sapp, though referring to other characters in the field of Genetics (Sapp, 1983; Sapp, 1987).

7 DISCUSSION AND COMMENTS

The present study led to the conclusion that although the theory presented in the *Mechanism* by Morgan and his associates could be deemed reasonably well grounded in some respects (see section 5), there were lots of gaps, problems and obscure points. We can try to follow Bruno Latour's suggestion that "we need to look at the way in which someone convinces someone else to take up a statement, to pass it along, to make it more a fact, and to recognise the first authors ownership and originality" (Latour, 1990, p. 24). We realised that when dealing with these obscure points they used several types of persuasive strategies to create the impression that the situation was clear and established.

First of all, the authors were not completely sure about the potential of the chromosomal interpretation of Mendelian theory. Therefore, they tried to guarantee their results even if in the future chromosomes could be denied as the bearers of hereditary factors. It was a strategy to protect their work against possible criticisms and to save at least a part of it, although they were adopting the chromosome theory throughout the whole book.

Morgan and his collaborators tried to convince the reader that since 1900 chromosomes furnished the adequate explanation for Mendelian theory, and that was not the case.

- The authors presented some points that were thought by Morgan five years ago as not explained by chromosome theory (such as cell differentiation) as devoid of problems, with no discussion and where no new scientific evidences was brought forward.
- The authors introduced linkage and crossing-over as a consequence of their theory and not as experimental results that could also be interpreted in another way.
- The authors presented several ideal numerical examples. They presented no real experimental data.

- The group attacked Bateson's ideas, even the ones that did not conflict with the theory supported by them in the book.

Morgan and his colleagues created the impression that there was a considerable amount of sex linked factors as well as other groups associated to definite chromosomes of Drosophila which were known at that time, when in fact there was evidence that suggested only a few ones.

We can see that in general throughout the book the authors focused their attention upon the main points of the chromosome theory and its successes, without mentioning the difficulties they faced. The same attitude was adopted by Morgan in two of his articles which were published in the same year as *The Mechanism* (Morgan, 1915a; Morgan, 1915b). He presented some diagrams describing the theory, which were not got from the cytological observation. Moreover, those papers, although they were published in academic periodicals, were devoid of bibliography (Martins, 1997, pp. 5:77–5:78).

The authors used some diagrams and drawings directly related to the Mendelian chromosome theory[11] that showed things that were not observed, conveying the impression that some points of the theory were clear and established.

These are some of the persuasive strategies used by the authors.

Despite of all these problems the authors succeeded in convincing many biologist that the Mendelian chromosome theory was already firmly established at that time. The way they presented some points gives the reader the false impression that their theory arose ready and devoid of problems, transmitting a wrong view about the theory and the very nature of the scientific endeavour. Although Morgan and his collaborators could have elucidated some previous difficulties, such as the relationship between the number of chromosomes and the number of factors, the chromosome theory was not established. They could neither present the cytological evidence that chromosomes

[11] But they did not make use of photographs or photo-diagram pairs, which are, according to Michael Lynch another pictorical mode of argumentative persuasion (Lynch, 1991, p. 219). In this sense, Morgan and his associates acted in a different way from E. B. Wilson, who in his early cytological work presented his data in photographs and only later, when he was more confident in his interpretations, adopted abstract diagrams (Maienschein, 1991, p. 227).

exchanged pieces in *Drosophila*, nor could they point out at which stage of meiosis it took place. In this sense, the criticisms made by Bateson, Doncaster and others lead them to improve and to make the theory not only more elegant, but also more consistent.

This case study also showed that the same problems found in the transposition of scientific subjects by teachers and in dealing with pseudo-history may be found sometimes when scientists disseminate an unduly simplified science accompanied by unjustified claims of established foundations. This kind of attitude may deceive readers and students and will transmit a wrong view about the theory and about the very nature of the scientific endeavour.

However, as Jean-Louis stated:

> It is necessary, especially at the secondary level, to give an accurate view of science, not an oversimplification. To present the good sides of science, and the less glorious ones. To give a fair report of history, not a childish or idealistic view. (Heudier, 2001, p. 23)

8 EDUCATIONAL STRATEGIES

We can ask what could be done in order to avoid – or, at least, to reduce – such kind of problem. Certainly it is not an easy task. We think that scientists, even when they address a broader public, should submit their work to a critical reading by their colleagues (people who are experts in that subject). It is up to this people to be critical and to point out problems and shortcomings. And it is up to the scientist to improve his work. In the case of the *Mechanism* a very careful criticism was made by Bateson but, unfortunately, after its publication. We imagine that the adoption of that kind of attitude could possibly help in reducing this problem.

Of course we do not expect that every reader will be an expert in the subject of the book. In our particular case, the book was not addressed to the specialist in Genetics. However, we may advice teachers, students and the reader in general to be careful concerning some respects. Students should be *trained* to have a critical view concerning the textbook presentation of "ideal science".

First of all, we think that the reader must be extremely cautious as regards scientific novelties that are usually presented in a simplified and exalted way. It is commonly the case that the evidence for new

theories is very scarce. In our case study, Morgan and his associates were proposing something new and they based their studies on one single organism: *Drosophila.* Secondly, the reader must distrust perfect numbers and exact fitting between theory and observation, such as the ones presented by Morgan and his associates, because in practice we seldom find such results. Moreover, he shall be cautious regarding perfect drawings representing difficult or obscure observations, such as the Morgan's drawings representing microscopic "facts", especially at a time when they were so ambiguous. The reader should also pay attention to the absence of any discussion of alternative explanations to the facts. Surely they may exist, and that was the case concerning the facts discussed in the book. Bateson and Punnett's reduplication hypothesis still remained a viable alternative at that time. Furthermore, in real science there are habitually exceptions, unexplained facts, difficulties of several kinds. The want of a discussion of problems such as the absence of crossing-over in the male *Drosophila* is also a serious symptom since they are always present in every theory.

By considering those points, educators, students or readers in general could learn to analyse a new scientific contribution more critically. This will contribute to form and impart a more accurate view of the complexity of the scientific endeavour.

A sound scientific education should exhibit case studies of "real science", such as the case described here. Of course, it is impossible to discuss every scientific subject showing its detailed history. However, the presentation of a few typical case studies will be enough to convey a more satisfactory view of the actual practice of science.

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