T H Morgan

THOMAS HUNT MORGAN

1866–1945

THOMAS HUNT MORGAN, born 25 September 1866 at Lexington, Kentucky, was the elder son of Charlton Hunt Morgan of that State. His mother, Ellen Key Howard, was from Baltimore. There were two younger children in the family, of whom his sister Ellen survives him. From the University of Kentucky, Morgan graduated B.S. 1886 and proceeded to postgraduate work in the same University, later removing to Johns Hopkins University, Baltimore, where he took his Ph.D. in 1890. From that date his academic career falls into three periods: From 1891 to 1904 he was Professor of Zoology at Bryn Mawr College for women ; 1904 to 1928, Professor of Experimental Zoology at Columbia, New York ; while from 1928 to 1945 he was Professor of Biology at the California Institute of Technology, Pasadena, as director of the William G. Kerckhoff laboratories.

Morgan's interest in natural history, an abiding trait in his rich and many-sided character, was well marked as a child. Before he was ten he was collecting birds, birds' eggs and fossils, and enjoying the opportunities of country life. In the first year after his graduation he visited the seashore laboratory of Alpheus Hyatt at Annisquam, Massachusetts. During the summers of 1888 and 1889 he was doing research work at the U.S. Fish Commission Laboratory at Woods Hole ; and in 1890 the Adam Bruce Fellowship gave him his first opportunity of visiting Europe and especially Naples, where his meeting Hans Driesch, with whom he later collaborated, doubtless turned his thoughts to experimental embryology. He was at Naples again in 1895 and 1900, and was associated with the Marine Biological Laboratories at Woods Hole continuously from 1902, taking an active part in biological expeditions to the Bahamas and Jamaica. In his later years he characteristically established a private laboratory at Corona del Mar, California.

As a student Morgan had shown himself boldly critical, sceptical and of independent judgment. Before moving to Columbia his work in experimental embryology and regeneration had won him a high reputation. He was President of the American Morphological Society in 1900. He was habitually an intent worker, impatient of unnecessary interruptions; a prolific and sometimes a hasty writer, but with a growing passion for experimental elucidation. He seems not to have written on genetics before 1905, and his early papers show considerable distrust of the simplicity of current Mendelian conceptions. In 1905 he was challenging the assumed purity of the germ cells: 'for, once crossed always contaminated'. In the same year he voiced the current scepticism, represented in this country by William Bateson, of the origin of species by

natural selection: 'Nature makes new species outright'. Even in 1909, the year in which his department started work with Drosophila, and when he had already some personal experience in breeding mice, he had not clearly distinguished the problems of heredity from those of development. He quotes and endorses the following remarkable passage from Oscar Riddle (*Biol. Bull.* **16,** 1909):

'Here is then a *possible* picture of the basis of Mendelian segregation and proportion, but without recourse to hypothetical "particles" or to immutable and immortal factors. An apparently very specific end-result of an oxidation would be traceable in the germ only in the strength or pitch of a general vital process, and not at all in mnemons or representative particles packed with unthinkable precision, order and potentiality into (presumably) the chromosomes. . . . The nature of present Mendelian interpretation and description inextricably commits to the "doctrine of particles" in the germ and elsewhere. It demands a "morphological basis" in the germ for the minutest phase (factor) of a definitive character. It is essentially a morphological conception with but a trace of functional feature. Although heredity is quite surely a functional process of major complexity, it may be recalled that the primary and fundamental Mendelian conception of this process utilizes not a single finding of the science of biochemistry.'

It was then no preconception, but the experimental facts, brought unmistakably under his eyes by his work with Drosophila, which won Morgan to the simple and concrete interpretation of genetic phenomena, thereafter associated with his name. The brilliant band of younger workers, Sturtevant, Muller and Bridges, gathered round him at this time, not only made possible the extension of the work, on a scale new to genetic research, but no doubt contributed very actively to the clarification of ideas. Morgan always insisted that his epoch-making research with Drosophila was that of a team, in which full credit must be given to his collaborators. The fact that the very diverse talents of each of these able assistants found in the work with Drosophila the ideal field for their expression may perhaps be ascribed to the genius of Morgan himself.

Drosophila seems to have been first bred in quantity through successive generations by C. W. Woodworth. In the winter of 1900–1901 Woodworth studied at Harvard, and there suggested to W. E. Castle that the material might be useful for genetic study. Castle and his students used it for studies on the effects of inbreeding. Through them F. E. Lutz became interested in the material; and it was Lutz who introduced it to Morgan. He began intensive studies with Drosophila in 1909, and began publishing on it in 1910.

So early as 1902 W. S. Sutton had cogently put forward the theory that the chromosomes were the bearers of the Mendelian units. At this period the cytological observations available, though suggestive, were in some respects misleading, and Sutton naturally knew nothing of linkage as an observable fact, though foreseeing departures from Mendel's rule of independent segregation. By 1909 and 1910 English workers with the Sweet Pea had clear evidence of associations, recognized under the names of coupling and repulsion, but

speculating on the lines of 'The reduplication hypothesis' had formed no clear notion of linkage. The importance of the early work with Drosophila lay in demonstrating that coupling and repulsion were but the obverse and reverse aspects of the same phenomenon, later known as linkage, and that the rules of linkage with more than two linked factors implied a linear structure for the germ plasm, as well as correspondence of the linkage groups with the chromosome pairs. For the first point the fact of importance is that Morgan was using a bisexual animal, in which backcrossing was as easy as intercrossing heterozygotes, whereas with self-fertilizing plants the intercross is the usual and convenient procedure. The backcross technique exhibits the perfect symmetry of coupling and repulsion, whereas the intercross results are not only superficially unlike but, for the same number of plants grown, differ intrinsically in their precision.

Morgan's early papers with Drosophila focused attention principally by the prompt demonstration of sex linkage of the gene for white eye, showing the male fly to be heterogametic. Geneticists, too, were quickly impressed by the very large progenies which could be bred, and by the rapid accretion of fresh mutants arising in the stocks. Morgan's scepticism as to the validity of Mendel's concepts and notation seem to have fallen quickly away; and by 1911, with the aid of Janssen's cytological observation of chiasmata, a short letter in *Science* puts forward the theory of linear arrangement in the chromosomes, in essentials as it is now accepted, and as it was more fully expanded in *The Mechanism of Mendelian Heredity*.

To the large numbers in which Drosophila can be bred Morgan always attached great importance, and it is indeed to this circumstance that we owe another group of facts vital to the correct understanding of genetical and evolutionary theories, namely the knowledge which accumulated as to the nature and frequency of the spontaneous mutations arising in culture. It is to the energy of the early Drosophilists that we owe it, not only that Drosophila was bred by the million, but that this enormous mass of material was keenly scrutinized, aberrations followed up, and as time went on published in full detail. The extensions in the types of genetical research now pursued, with X-rays, for example, or the chromosomes of the salivary glands, spring from the enterprise and thoroughness of the early period.

Morgan's output of published matter was enormous, and it is only the central theme, to which he owes in particular his world-wide recognition, that can be mentioned here. A full bibliography, which I owe to Professor Sturtevant is, however, attached to this notice. Apart from other honours, in 1919 Morgan became a foreign member of the Royal Society, delivered the Croonian Lecture in 1922, received the Darwin Medal in 1924 and the Copley Medal in 1939. He presided at the Genetical Congress at Ithaca in 1932, and travelled to Sweden in 1933 to receive the Nobel Prize for Medicine.

In 1904 he married Lilian Vaughan Sampson, a former research student of Bryn Mawr College, and a frequent associate in his laboratory work. He leaves a son and three daughters. Always open-minded in scientific discussion, full

of humour and generous in his references to others, many will remember him as a most charming host.

For many personal particulars in this obituary notice I am indebted to Mrs L. Morgan, who has also kindly supplied the photograph; to Professor Conklin and to Dr Sturtevant.

R. A. Fisher

Thomas Hunt Morgan, Experimental Embryologist

It is not always realized that in addition to his work in genetics, Morgan made contributions of first importance to the study of experimental embryology and regeneration. The 'classical' experiment in experimental embryology was that in which Roux killed one of the blastomeres in the frog at the 2-cell stage and obtained the development of half-embryos. This was the basis for the Roux-Weismann theory of differentiation, which claimed that the blastomeres received unequal contributions from their parent blastomere, and formed a 'mosaic'. These views were hard to reconcile with the results of Driesch's work on sea-urchin larvae, in which he showed that separation of blastomeres at the 2-cell or even at the 4-cell stage, did not prevent them from developing into perfect diminutive larvae; the typical 'regulation' eggs.

Next it was found by Schulze that if frogs' eggs are turned upside down at the 2-cell stage, they do not develop into single embryos but into double monsters.

This is the background against which Morgan's investigation of frog development should be considered. He killed one blastomere at the 2-cell stage of the frog, and instead of leaving the preparation right way up, he turned it upside down. The living blastomere underwent a reorganization and developed into a perfect embryo. By this beautiful and simple experiment Morgan showed that the frog's egg was not, after all, the 'mosaic' which it had been thought to be.

Other experiments of Morgan's on amphibian development were concerned with the establishment of the correlation between the planes of the first cleavage-furrow, the plane of symmetry, and the sagittal plane; the production of abnormalities by low temperatures, lithium salts and oxygen-lack; and the non-importance of gravity for normal development (confirming Roux).

On Echinoderm larvae, Morgan obtained results independently of Loeb in his experiments on artificial parthenogenesis and induction of asters. He also confirmed that larvae obtained by artificial parthenogenesis by Loeb's method developed with the haploid number of chromosomes. He investigated the factors determining the fixation of the plane of bilateral symmetry, the developmental potencies of isolated ectoderm and endoderm, and the fertilization of non-nucleated eggs.

In collaboration with Driesch, he showed that the Ctenophore egg develops as a mosaic, for its blastomeres when isolated are unable to regulate to form a perfect larva.

In the field of regeneration he showed that in Oligochaete worms the nerve

cord was necessary for regeneration to take place at a cut surface, and similarly in the frog he demonstrated the necessity for the notochord at the cut surface if a tail was to be regenerated. In the flat-worm Bipalium he showed that the reconstitution of a complete worm from a fragment was brought about by the transformation of all the tissues of the fragment (morphallaxis). But perhaps Morgan's most important contribution to the study of regeneration was his demonstration that parts not subject to injury (such as the appendages of the abdomen of the hermit-crab) would nevertheless regenerate. This showed that regeneration is not an adaptive phenomenon evolved in response to liability to loss.

Centrifuge experiments enabled him to distinguish between common raw materials (albeit visibly distinct) and true organ-forming substances in Arbacia and Cumingia, by showing that the former could be disarranged without impairing normal development. The axis of polarity could not be altered by the centrifugalization.

He investigated the phenomenon of self-sterility in Ciona and found that there is evidence for the existence of pairs of genes for self-sterility in more then one pair of chromosomes.

In addition to a large number of papers, Morgan published several books on experimental zoology, all of them indispensable to students of the subject. These books were *The development of the frog's egg—An introduction to Experimental Embryology* (1897); *Regeneration* (1901); *Experimental Zoology* (1910) and *Experimental Embryology* (1927).

In spite of the magnificence of his contributions to genetics and the universal recognition which they brought to him, Morgan never forsook his interests in experimental embryology, and in his last years he paid increasing attention to the field of research in which, during his earlier days, he had laboured so hard and unobtrusively and successfully.

G. R. DE BEER

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