CHAPTER I

THE DUALITY OF INHERITANCE

AT the outset we may with profit inquire what is meant by heredity. When a child resembles a parent or grandparent in some striking particular, we say it *inherits* such-and-such a characteristic from the parent or grandparent in question. *By heredity, then, we mean organic resemblance based on descent.*

Resemblances due to heredity may exist even between individuals not related as ancestor and descendant, as for example between uncle and nephew. Here the resemblance rests on the fact that uncle and nephew are both descended from a common ancestor, and they resemble each other simply because they have both inherited the same characteristic from that ancestor. This form of inheritance is sometimes spoken of as collateral in distinction from direct inheritance. In all cases alike community of descent is the basis of resemblances which can be ascribed to heredity, whether direct or collateral. Mother and child, no less than uncle and nephew, resemble each other because they have received a common inheritance from a common ancestor.

Three biological facts of fundamental importance to a right understanding of heredity were known imperfectly or not at all in the time of Darwin and Mendel. These are (1) the fertilization of the egg, (2) the maturation of the egg, which must precede its fertilization, and (3) the non-inheritance of "acquired" characters. These we may consider in order.

Every new organism is derived from a preexisting organism, so far as our present experience goes. It may not have been so always. Indeed, on the evolution theory, we must suppose that living matter originally arose from lifeless, inorganic matter. But if it did, this may have occurred, and probably did occur, under physical conditions quite different from those now existing. At the present time the most exhaustive researches fail to reveal the occurrence of spontaneous generation, that is, the origin of living beings other than from pre-existing living beings.

In asexual methods of reproduction a new individual arises out of a detached portion of the parent individual. Such methods of origin are varied and interesting, but do not concern us at present. In all the higher animals and plants a new individual arises, by what we call a sexual process, from the union of two minute bodies called the reproductive cells. They are an egg-cell furnished by the mother and a *sperm-cell furnished by the father.*

There is a great difference in size between egg and sperm. The egg is many thousand times greater in bulk, as seen in Fig. 1, for example, yet the influence of each in heredity appears to be equal to that of the other. This fact shows unmistakably that the bulk of the reproductive cell is not significant in heredity. A large part of the relatively huge egg can have no part in heredity. It serves merely as food for the new organism, furnishing it with building material until such a time as it can begin to secure food for itself. The essential material, so far as heredity is concerned, is evidently found in egg and sperm alike. It is plainly small in amount and possibly consists merely in ferment-like bodies which ini-

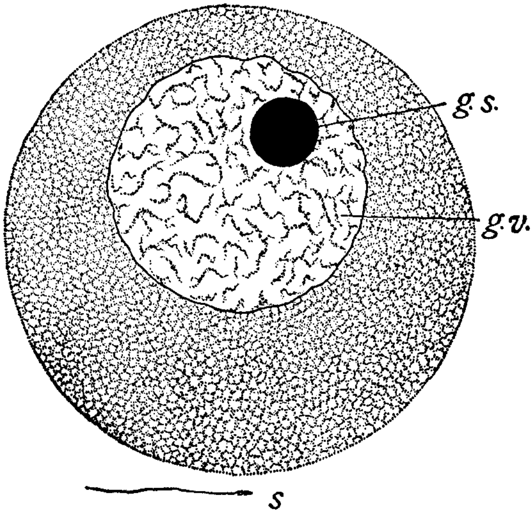

FIG. 1. — Egg and sperm (*s*) of the sea-urchin, *Toxopneustes*, both shown at the same enlargement. (After Wilson.)

tiate certain metabolic processes in a suitable medium represented by the bulk of the egg. The *amount* of a ferment used in starting a chemical change bears no relation, as is well known, to the amount of the chemical change which it can bring about in a suitable medium.

The equal share of egg and sperm in determining the character of offspring is well shown in the following experiment. An albino guinea-pig is one which lacks in large measure the ability to form black pigment. Apparently it does not possess some ingredient or agency necessary for the production of pigment. Now, if an albino male guinea-pig, such as is shown in Fig. 15, be mated with a black female guinea-pig of pure race, such as is shown in Fig. 14, young are produced all of which are black, like the mother, none being albinos, like the father. Fig. 16 shows black offspring produced in this way. Exactly the same result is obtained from the reverse cross, that is, from mating an albino mother with a black sire. It makes no difference, then, whether the black parent be mother or father, its blackness *regularly dominates* over the whiteness of the albino parent, so that only black offspring result. This fact, which has been repeatedly confirmed, shows that the black character is transmitted as readily through the agency of the minute sperm-cell as through the enormously greater egg-cell.

Let us now consider what happens when egg and sperm unite, in what we call the fertilization of the egg. The egg is a rounded body incapable of motion, but the sperm is a minute thread-like body which moves like a tadpole by vibrations of its tail. In the case of most animals which live in the water, egg and sperm-cells are discharged into the water and there unite and develop into a new individual, but in the case of most land animals this union takes place within the body of the mother. We may consider an illustration of either sort.

The fertilization of the egg of a marine worm, Nereis, is shown in Fig. 2. The thread-like sperm penetrates into the egg. Its enlarged head-end forms there a small nuclear body, which increases in size until it equals that of the egg-nucleus, with which it then fuses. The egg next begins to divide up to form the different parts of a new worm-embryo. To each of these parts the nuclear material of egg and sperm is distributed equally. Since this development takes place wholly outside the body of either parent it is necessary that the egg contain enough food to last until the young worm can feed itself. This food material is

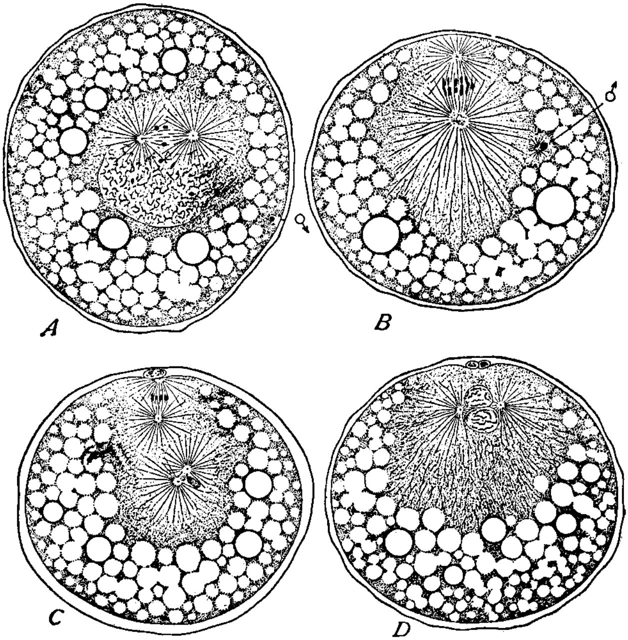

FIG. 2. — Fertilization of the egg of *Nereis*.

A. The sperm has entered the egg and is forming a minute nucleus at ♂. The egg-nucleus is breaking up preparatory to the first maturation division. *B*. The egg-nucleus is undergoing the first maturation division. Notice the conspicuous rod-like chromosomes separating into two groups. The sperm-nucleus (♂) is now larger and lies deeper in the egg. *C*. A small polar-cell has been formed above by the first maturation division of the egg. A second division is in progress at the same point. The sperm-nucleus is now deep in the egg and is preceded by a double radiation (amphiaster). *D*. Two polar-cells are fully formed. The matured egg-nucleus is now fusing with the sperm-nucleus. An amphiaster indicates that division of the egg will soon take place. (After Wilson.)

represented in part by the conspicuous oil-drops seen in the egg (the heavy circles in Fig. 2).

The egg of a mouse needs no such store of nourishment, since in common with the young of other mammals the mouse-embryo nourishes itself by osmosis from the body fluids of the mother. The mouse-egg is accordingly smaller. Stages in its fertilization are shown in Fig. 4. In *A* the sperm has already entered the egg. Remnants of its thread-like tail may still be seen there. Nearby is seen a nuclear body derived from the sperm-head. Opposite is seen the nuclear body furnished by the egg itself. The two nuclear bodies fuse and their united substance is then distributed to all parts of the embryo-mouse, just as happens in the development of the worm, Nereis.

There are reasons for thinking that the nuclear material is especially important in relation to heredity and that the equal share of the two parents in contributing it to the embryo is not without significance, for inheritance, as we have seen, is from both parents in equal measure. In cases where the inheritance from each parent is different it can be shown that the offspring possess two inherited possibilities, though they may show but one. Thus in the case of a black guinea-pig, one of whose parents was white, the other black, it can be shown that the animal transmits both qualities (black and white) which it received from its respective parents, and transmits them in equal measure. For, if the cross-bred black animal be mated with a white one, half the offspring are black and half of them white. The cross-bred black animal inherited black from one parent, white from the other. It showed only the former, but on forming its reproductive cells it transmitted black to half of these, white to the other half. Hence the cross-bred black individual was a duality, containing two possibilities, black and white, but its reproductive cells were again single, containing either black or white, but not both.

Now it has been shown in recent years that the nuclear material in the reproductive cells behaves exactly as do black and white in the cross just described. This nuclear material becomes doubled in amount at fertilization,

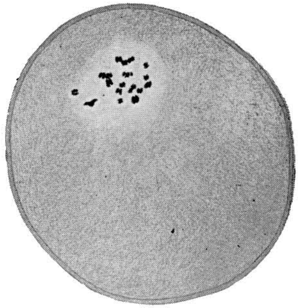

FIG. 3. — Egg of a mouse previous to maturation. (After Kirkham.)

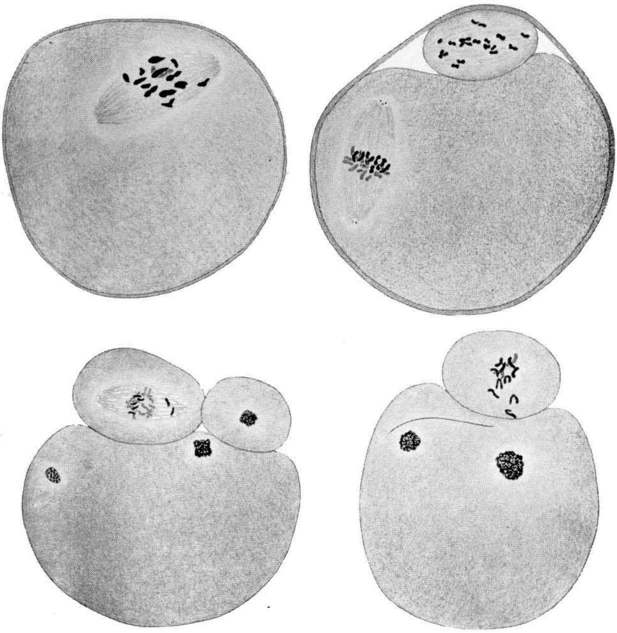

FIG. 4. — Maturation and fertilization of the egg of a mouse. *A*. The first maturation division in progress. *B*. The first polar-cell fully formed; the second maturation division in progress. *C*. The second maturation division completed; the second polar-cell is the smaller one; near it, in the egg, is the egg-nucleus, and at the left is the sperm-nucleus. *D*. A view similar to the last, but showing only one polar-cell, the second; note its twelve distinct chromosomes; near the sperm-nucleus in the egg, at the left, is seen the thread-like remains of the sperm-tail. (After Kirkham.)

equal contributions being made by egg and sperm. This double condition persists throughout the life of the new individual in all its parts and tissues. But if the individual forms eggs or sperm, these, before they can function in the production of a new individual, must undergo reduction to the single condition.

This reduction process is called maturation; it is well illustrated in the case of the mouse-egg, whose fertilization has already been described. The large nucleus of the egg-cell, as it leaves the ovary, is either broken up or about to break up preparatory to a cell-division. The most conspicuous of the nuclear constituents are some dense, heavily staining bodies called chromosomes, about twenty-four in number. In Fig. 3 each of these is split in two, preparatory to the first maturation division. The egg now divides twice, both times very unequally (Fig. 4), forming thus two smaller cells called polar cells, or polar bodies. They take no part in the formation of the embryo. The chromosomes left in the egg after these two divisions are only about half as numerous as before, or about twelve in number. These form the chromatin contribution of the egg to the production of a new individual. It is possible that other cell constituents undergo a similar reduction by half during maturation, but of this we have no present knowledge.

The known fact of chromosome reduction, of course, favors the current interpretation that the chromosomes are bearers of heredity, though it by no means proves the correctness of that interpretation. In the egg of Nereis, as well as in that of the mouse, two maturation divisions precede the fertilization of the egg. See Fig. 2. In *B* the first maturation division is in progress; in *C* the second is in progress; and in *D* both polar cells are fully formed, while egg and sperm nuclei are uniting. Similar processes occur in eggs generally, prior to their fertilization.

Like changes occur also in the development of the sperm-cells. In Fig. 5 the original or unreduced condition of the chromosomes in a cell of the male sexual gland is shown (at *A*) as one of four chromosomes to a cell. After a series of changes involving as in the maturation of the egg two cell-divisions, we find (at *H*) that the products of the original cell contain in each case two chromosomes, half the original number.

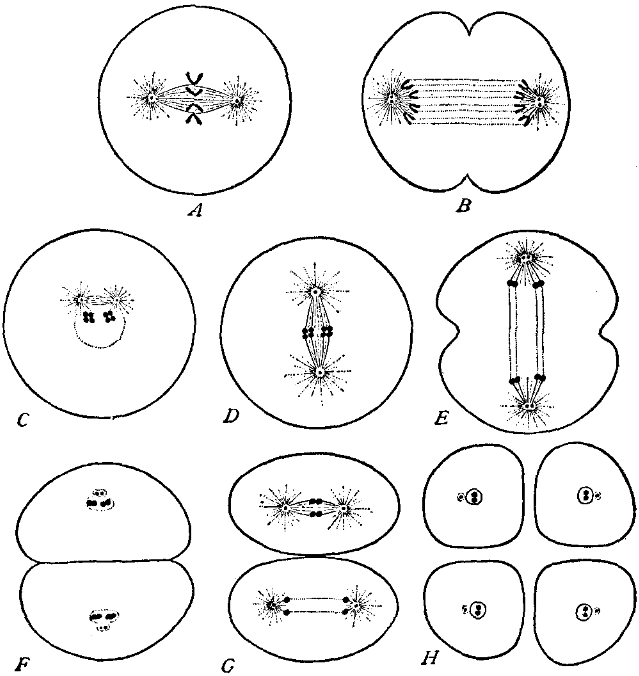

FIG. 5. — Diagrams showing the essential facts of chromosome reduction in the development of the sperm-cells. (After Wilson.)

These chromosomes make up the bulk of the head of the sperm which forms from each of these cells, its tail being derived from other portions of the cell.

It follows that not only eggs but also sperms, prior to their union in fertilization have passed into a reduced or single state as regards their chromatin constituents, whereas the fertilized egg, and the organism which develops from it, is in a double condition. It will be convenient to refer to the single condition as the N condition, the double as the 2 N condition.

From a wholly different source we have evidence strongly confirmatory of the conclusion that the fertilized egg contains a double dose of the essential nuclear material. By artificial means it has been found possible to cause the development of an unfertilized egg. The means employed may be of several different sorts, such as stimulation with acids, alkalies, or solutions of altered density. In such ways the development has been brought about of the eggs of sea-urchins, star-fishes, worms, and mollusks, which normally require fertilization to make them develop.

The sea-urchin egg has been made to develop more successfully than any other. This has occurred even after the egg had undergone maturation, being reduced to the N condition. From the development of such reduced but unfertilized eggs fully normal sea-urchins have been obtained which even contain developed sexual glands. On the other hand it has been found possible to break the egg into fragments by shaking it, or cutting it into bits with fine knives or scissors. It has also been found possible to bring about the development of an egg fragment so obtained, — a fragment which contained no egg nucleus. This result has been attained by allowing a sperm to enter it and form there a nuclear body. No adult organism has yet been reared from such a fertilized egg-fragment, but so far as the development has been followed it progressed normally.

There can accordingly be no doubt that the nuclear material of a sperm-cell has all the capabilities of that of an egg-cell and can indeed replace it in development. Accordingly, when, as in normal fertilization, both an egg nucleus and a sperm nucleus are present in the cell, a double dose of the necessary nuclear material is supplied. The second or extra dose is, however, not superfluous. It probably adds to the vigor of the organism produced, and in some cases at least, materially affects its form. For many animals and plants exist in two different conditions, in one of which the nuclear components are simple, N, while in the other they are double, 2 N. Thus in bees, rotifers, and small crustacea the egg may under certain conditions develop without being fertilized. If the egg develops before maturation is complete, that is in the 2 N condition, the animal produced is a female, like the mother which produced the egg. But if the egg undergoes reduction to the N condition before beginning its development, then it produces a male individual, an organism, so far as reproduction is concerned, of lower metabolic activity.

In many plants, too, individuals of N and of 2 N constitution occur, which differ markedly in appearance. Thus the ordinary fern-plant is a 2 N individual, but it never produces 2 N offspring. Fig. 6 shows an ordinary fern-plant, which produces spores on the under

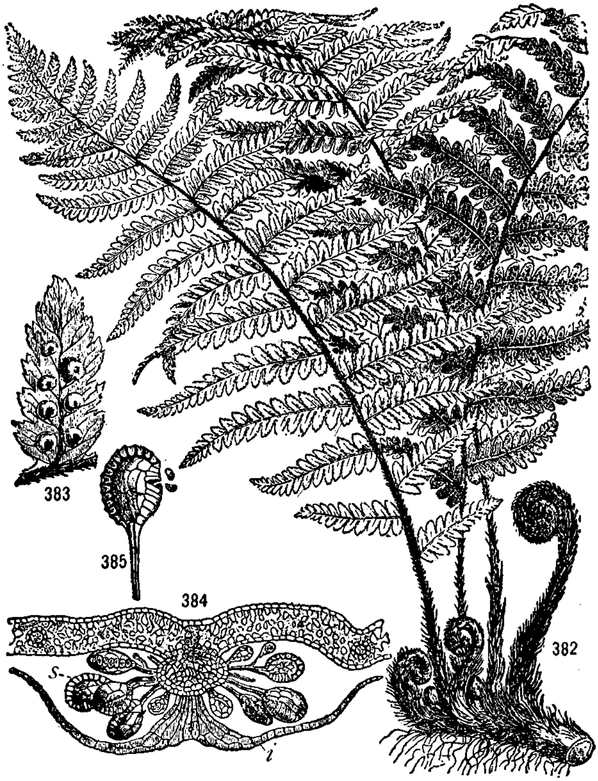

Fig. 6. — An ordinary fern, which reproduces by asexual spores. The fern is shown reduced in size at 382; a portion of a frond seen from below and slightly enlarged, at 383; a cross-section of the same more highly magnified, at 384. Notice in 384 the sporangia, and in 385 one of these discharging spores. (After Wossidlo, from Coulter Barnes and Cowle's Textbook of Botany.)

surface of its fronds. Each of those spores is a reproductive cell which, like the mature eggs and sperm of animals, is in a reduced nuclear condition (N). These spores germinate, however, without uniting in pairs and form a plant different from the parent, just as the mature egg of a bee, if unfertilized, develops into an individual different from the parent, in that case a male. The plant which develops from the spore of a fern is small and inconspicuous and is known as a prothallus. See Fig. 7. It produces sexual cells (eggs and sperm) which, uniting in pairs, form fern-plants, 2 N individuals. Thus there is a constant alternation of generations, fern-plants (2 N), which produce prothalli (N), and then these produce again fern-plants (2 N).

The fact is worthy of note that in an animal or plant which is in the single or N condition, there occurs no chromatin reduction at the formation of reproductive cells. Its cells are already in the single condition, and they probably cannot be further reduced without destroying the organism. The 2 N fern-plant forms reproductive cells, its spores, which are in the reduced condition, N, and these germinate into the prothallus, which accordingly is

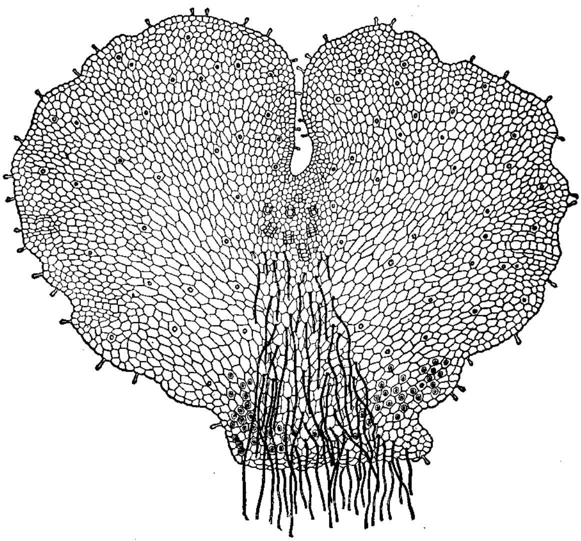

FIG. 7. — The prothallus of a fern, which reproduces by sexual cells, eggs and sperm. The eggs are borne in the sac-like "archegonia," just below the notch in the figure. They, like the sperm-forming "antheridia," lie on the under surface of the flattened prothallus which is here viewed from below. Notice the root-hairs or rhizoids by which the plant feeds. Highly magnified. (After Coulter, Barnes, and Cowles.)

N throughout. But when the prothallus forms reproductive cells, no reduction occurs. Its egg-cells and its sperm-cells in common with all other cells of the prothallus are already in the reduced condition without any maturation divisions. The result of their union in pairs, at fertilization, is the formation of 2 N combinations that germinate into fern-plants.

Similarly in the case of a male animal which

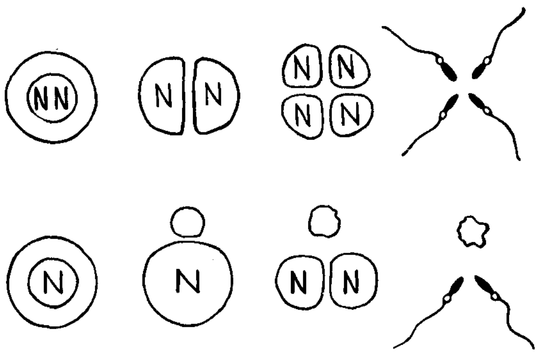

FIG. 8. — Diagram showing the chromosome number in the spermatogenesis of ordinary animals (upper line) and of the wasp (lower line).

has developed from a reduced but unfertilized egg, no reduction occurs at the formation of its sperm-cells. In an ordinary male animal, one which is in the double or 2 N state, the development of the sperms is attended by reduction to the N condition. In this process there occur two cell-divisions producing from each initial cell four sperms. See Fig. 5, and

Fig. 8, upper line. But in the male wasp, whose cells are in the N condition at the beginning, one of these divisions is so far suppressed that the resulting cell products are of very unequal size, and the smaller one contains no nuclear material. The other then gives rise to two sperm-cells, each possessing the original N nuclear condition, while the small non-nucleated cell degenerates. See Fig. 8, lower line.

In conclusion, I wish to introduce two technical terms, which it will be convenient for us to use in subsequent discussions. These are *gamete* and *zygote*. A reproductive cell (either egg or sperm) which is in the reduced condition (N) ready for union in fertilization is called a gamete. The result of fertilization is a zygote, a joining together of two cells each in the N condition. The result is a new organism, at first a single cell, in the 2 N condition.

BIBLIOGRAPHY

CASTLE, W. E.
1903. "The Heredity of Sex." *Bull. Mus. Comp. Zoölogy*, 40, pp. 189–218.

DELAGE, Y.
1898. "Embryons sans noyau maternel." *Compte rendu, Académie des sciences, Paris*, 127, pp. 528–531.
1909. "Le sexe chez les Oursins issus de parthénogenèse experimentale." *Compte rendus, Académie des sciences, Paris*, 148, pp. 453–455.

KIRKHAM, W. B.
1907. Maturation of the Egg of the White Mouse." *Trans. Conn. Acad. of Arts and Sciences*, 13, pp. 65–87.

LOEB, J.
1899. "On the Nature of the Process of Fertilization and the Artificial Production of Normal Larvae (Plutei) from the Unfertilized Eggs of the Sea-urchin." *Amer. Journ. of Physiol.*, 3, pp. 135–138.

LOTSY, J. P.
1905. "Die X-Generation und die 2 X-Generation." *Biologisches Centralblatt*, 25, pp. 97–117.

MEVES, F., und DUESBERG, J.
1908. "Die Spermatozytenteilungen bei der Hornisse (Vespa crabo L.)." *Arch. f. mik. Anat. u. Entwick.*, 71, pp. 571–587.

WILSON, E. B.
1896. "The Cell in Development and Inheritance," 370 pp., illustrated. The Macmillan Co., New York.