CHAPTER III.

HISTORY OF THE THEORY OF HEREDITY—(*Continued*).

Some form of the evolution hypothesis a logical necessity—Darwin's pangenesis hypothesis—This is an evolution hypothesis, since all the characteristics of the adult are supposed to be latent in the germ—Miscellaneous objections to it—These objections do not show that it conflicts with fact—Difficulty in imagining detailed working is no reason for rejecting it—Galton's experimental disproof—There are many reasons for believing that the sexual elements have different functions—The evidence from parthenogenesis—Polar-cell hypothesis—The evidence from hybrids, from variation, and from structures confined to one sex—The pangenesis hypothesis recognizes no such difference in the functions of the reproductive elements—We must therefore distrust its absolute correctness—Summary of last two chapters.

Some Form of the Evolution Hypothesis a Logical Necessity.

Most of the hypotheses which have been proposed, of late years, to account for the phenomena of heredity, are like the two we have quoted, epigenesis hypothesis, for they are attempts to show that the ovum is in reality, as well as in form, an unspecialized cell. Analysis shows, however, that they all rest ultimately upon the assumption that this is not true, but that the ovum really contains, in some form or other, actually or potentially, the future organism, with all its hereditary characteristics.

We know that eggs which are to all appearances essentially alike, may, when artificially removed from the ovaries and artificially fertilized, and when kept under exactly the same conditions, develop into widely different organisms, and as like things cannot, under like conditions, give rise to different results, we are forced to conclude that these eggs are not essentially alike, but that each contains within itself in some form the organism to which it is to give rise—that individual development is, in some sense, the unfolding of a germ which already exists in the egg. There is no escape from this conclusion, at least there is none which can be accepted by the scientific student, and we see that logical thinkers like Prof. Huxley are driven to conclude that the process which in its superficial aspects is epigenesis, appears in essence to be evolution.

Darwin's Hypothesis of Pangenesis.

In contrast to the views already quoted we have the well-known pangenesis hypothesis of Darwin, an hypothesis which is thoroughly one of evolution, since Darwin believes that the whole organization of the species is present not only in the egg but in the male cell also; that each of these not only contains the complete organization of the parent, but an indefinite series of similar organizations, inherited from a long line of ancestors. It is true that Darwin does not believe that each of these ancestors is represented in the ovum and in the male cell by a minute but perfect animal, like those imagined by Bonnet, but he imagines what is essentially the same thing, that each of the cells of each parent, and every cell of each ancestor for a long and practically an unlimited series of generations, is represented in each ovum and each male cell by a germ capable of producing that particular cell with all its distinctive characteristics.

Darwin's original statement (*Variation*, chaps. xxvii.

and xxviii.) is readily accessible, but it will not be out of place to quote it before entering upon its critical discussion.

He says: "In the previous chapters large classes of facts, such as those bearing on bud-variation, the various forms of inheritance, the causes and laws of variation, have been discussed, and it is obvious that these subjects, as well as the several modes of reproduction, stand in some sort of relation to each other. I have been led, or rather forced, to form a view, which to a certain extent connects these facts by a tangible method. Every one would wish to explain to himself, even in an imperfect manner, how it is possible for a character possessed by some remote ancestor suddenly to reappear in the offspring; how the effects of increased use or disuse of a *limb can be transmitted to the child; how the male* sexual element can act not solely on the ovule, but occasionally on the mother form; how a limb can be reproduced on the exact line of amputation, with neither too much nor too little added; how the various forms of reproduction are connected, and so forth. I am aware that my view is merely a provisional hypothesis or speculation, but until a better one be advanced it may be serviceable by bringing together a multitude of facts which are at present left disconnected by any efficient cause. As Whewell, the historian of the inductive sciences, remarks, hypotheses may often be of service to science, when they involve a certain portion of incompleteness or even of error.

"Under this point of view I venture to advance the hypothesis of pangenesis, which implies that the whole organization, in the sense of every separate atom or unit, reproduces itself. Hence ovules and pollen grains—the fertilized seed or egg, as well as buds—include and consist of a multitude of germs thrown off from each separate atom of the organism."

From the extract we see that the hypothesis is an attempt to show that all the phenomena of generation and development, including those of variation as well as those of heredity, depend upon the fact that each structural unit of the body is the direct offspring of a similar unit in the body of a parent or of a more remote ancestor. The cells of the body of one of the higher organisms are not only morphologically but actually independent individuals, reproducing themselves directly in the next generation: and the germ of such an organism is in reality an aggregate of these cell-germs.

Stated more at length, the hypothesis is as follows:

"I assume that cells, before their conversion into 'form material,' throw off minute granules or atoms, which circulate freely throughout the system, and when supplied with proper nutriment, multiply by self-division, subsequently becoming developed into cells like those from which they were derived. These granules, for the sake of distinctness, may be called . . . gemmules. They are supposed to be transmitted from the parent to the offspring, and are generally developed in the generation which immediately succeeds, but are often transmitted in a dormant state during many generations and are then developed. Their development is supposed to depend on their union with other partially developed cells or gemmules, which precede them in the regular order of growth. Why I use the term union will be seen when we discuss the direct action of pollen on the tissues of the mother plant.

"Gemmules are supposed to be thrown off by every cell or unit not only during the adult state but during all stages of development. Lastly I assume that gemmules in their dormant state have a mutual affinity for each other, leading to their aggregation either into buds or into the sexual elements. Hence, speaking strictly, it is not the reproductive elements nor the buds which generate new organisms, but the cells themselves throughout the body. These assumptions constitute the provisional hypothesis of pangenesis."

Darwin's gemmules are, of course, entirely imaginary, that is, a belief in their existence does not rest upon direct observation. We cannot deny that the hypothesis furnishes an explanation of most of the phenomena which he attempts to interpret by it, although it seems possible that there may be a simpler explanation. If the existence of the gemmules were proven we could understand not only the wonderful facts of ordinary inheritance by sexual reproduction, but the various forms of asexual reproduction as well.

We should have a simple explanation of the manner in which the characteristics of a remote ancestor may suddenly reappear after they have been dormant for many generations. We should understand how the embryological history of a species may become simplified by the omission of larval forms or appendages. In a word, nearly all the phenomena of heredity admit of explanation by the hypothesis, and those who have criticised it have not usually attempted to show that it conflicts with fact, but have simply objected to it as a purely *imaginary explanation. It is urged that the transmission* of all the characteristics which we know to be inherited from near and remote ancestors demands that the number of gemmules should be almost unlimited and practically infinite; that not only are the gemmules imaginary, but that the aggregation of such numbers in masses as small as the reproductive elements requires that they shall be of inconceivable minuteness, and that nature furnishes no analogy for attributing to such small particles the vital properties which we know only in bodies which are comparatively gigantic. It is also urged that the gemmules must be endowed with entirely imaginary and wonderfully specialized elective affinities, in virtue of which each develops only at the proper time and place. In order to account for the manner in which the characteristics of each parent are mingled in the child we must regard each individual as the product of a struggle for existence among the gemmules, resulting in the selection and development of the fittest. The formation of several individuals asexually by budding from a parent stock demands that the gemmules themselves must be capable of multiplication, and that they must have the power to transmit their properties to their offspring. To explain alternation of generations we must suppose that the embryo receives several complete sets of gemmules, which are not duplicates, and it is almost impossible to follow out, in thought, the complicated relations which must exist between the gemmules of the egg-embryo of such an organism as a Siphonophore.

These and similar objections may be fairly urged, and while their great weight is obvious, we must not attach undue importance to them, for they do not show that the hypothesis conflicts with any known law or observed fact, and the great drafts made upon the imagination should not, alone, prevent its provisional acceptance so long as we have no simple explanation of the phenomena, for difficulty in imagining the details of an hypothesis is a purely subjective matter, which varies with the age and with the individual.

Galton's Experiments.

Besides these theoretical objections, we have the experimental disproof furnished by Galton. In order to test the hypothesis this experimenter selected the silver-gray rabbit—a variety which has, in itself, little tendency to vary, although it readily crosses with other varieties, and breeding freely with them gives birth to hybrid offspring. Into the bodies of eighteen of these silver-gray rabbits he transfused the blood of other varieties, in some cases replacing one half of the blood. From the eighteen rabbits thus operated upon eighty-six young were produced, and in no case did the offspring exhibit any of the characteristics of the variety from which the blood was taken, but all of the eighty-six were pure silver gray. From these experiments Galton concludes that "the doctrine of pangenesis, pure and simple, is incorrect;" and I think we must agree with him that this conclusion is justified by the results which he reached, although I hope to show that it is possible to restate the hypothesis in a form which is so modified as to escape this objection.

The Sexual Elements Perform Different Functions in Heredity.

There is another objection which seems to me to be of almost equal weight, but which has never, so far as I am aware, been pointed out. The early writers upon heredity attributed certain functions to the male cell and others to the ovum; but we now know that their means of observation were so inadequate, and their knowledge so limited, that their conclusions were of little value, and that both ovists and spermists were wide of the mark. The fact that they erroneously attributed certain functions to the ovum and certain others to the male cell does not, of course, prove that there is no difference in the functions of these elements; but in modern times we actually find that thinkers have gone to this opposite extremity of the subject, and have either tacitly implied or directly accepted the view that the two sexual elements play similar parts in heredity.

Neither Haeckel's hypothesis nor Jäger's recognizes any difference in their functions, while Jäger seems to believe, and Darwin explicitly states, that their shares in hereditary transmission are alike.

Many facts indicate that this view is, to say the least, very improbable, and I will give, briefly, a statement of some of the arguments against it, and will then devote a little space to a discussion of the reasons which have been given by Darwin and others for accepting it.

The structural difference between the ovum and the male cell is one of the most widespread and fundamental characteristics of organic beings, and it is found in all except the very lowest animals and plants. It is, to say the least, very improbable that a structural difference so fundamental and so nearly universal should have no functional significance, and the fact that in many marine animals, when the ripe unfertilized ova are thrown out into the ocean, like the male fluid, to be swept away by the tide, the sexual elements differ in the same way that they do in animals whose eggs are fertilized inside the body of the female, forbids us to believe that the difference depends simply upon the fact that the male cell must make its way to the ovum.

Many of the secondary characteristics of the ovum, such as its great size in birds and reptiles, and the presence in it of food-material in so many animals, are no doubt traceable to the fact that, in most animals, the egg is stationary, while the male cell can be conveyed from place to place; but we must believe that there is some more fundamental and primitive difference.

Even if the phenomena of Parthenogenesis did not show us that the part played by the ovum is more essential to the perpetuation of the race than the part played by the male cell, we should still be justified in the belief that the difference in form corresponds to some profound difference in function, and the possibility of Parthenogenesis shows beyond question that this is the case.

Parthenogenesis.

Siebold has proposed the term parthenogenesis for the power which is possessed by certain female animals, especially the arthropods, to produce descendants without sexual union with a male.

The existence of this power was first pointed out by Aristotle (*De Generatione Animalium, Lib. III., Cap.* 10, 21, 22, 23). As this remarkable observer had no means for exact research at his command, he was, of course, unable to make use of rigid tests, or to furnish the severely exact proofs which have been given us by more modern naturalists; but he gives many reasons for suspecting that the unfertilized eggs of the honey-bee may give rise to perfect animals without sexual union; and although we now know that some of the reasons he urges do not really prove the case, yet modern science has given the most convincing proofs of the correctness of his general conclusion.

I shall devote considerable space to this subject in order to show the unscientific reader that the existence of fertile virgin female animals is proved by the observations of a great number of competent naturalists; that the subject has been thoroughly and carefully studied, with every precaution against error, and that our belief in its existence does not rest upon the unverified statements of a few observers.

In this summary I shall give many references to authorities, but as my purpose is not to give a complete bibliography, but simply to show how thoroughly the subject has been studied, many names are omitted.

Most of the following facts are taken from Gerstaecker's history of the subject in Volume V. of Bronn's *Klassen und Ordnungen des Thierreichs,* although I have referred to many of the original papers and have added many facts which are not mentioned by Gerstaecker. The subject is perfectly familiar to most naturalists, and the amount of space devoted to it may seem unnecessarily great to such persons, but it is important to impress upon unscientific readers a sense of the exact and definite character of the evidence for the existence of parthenogenesis, and a short history of the subject seems the most effective means for accomplishing this purpose.

Among the crustacea and insects, parthenogenesis is by no means unusual. It occurs in some groups where impregnation by males is so nearly universal that naturalists have been slow to credit any exceptions. In other groups it is the general rule, and fertilization by a male is the exception. In some genera and species the power is shown only by a few individuals, while in others it is shared by all the females. In some cases the unfertilized eggs give rise to females only, in other cases to males, and in still other cases to both sexes.

In 1775, Schäffer, of Regensburg, discovered its occurrence in fresh-water crustacea, although Dr. Albrecht had made the same discovery in insects in 1701. Schäffer found ("Abhandlungen von Insecten") that when a female specimen of the common water-flea or *Daphnia*, a small fresh-water crustacean, is placed by itself immediately after it is born, and is kept throughout its whole life without any chance for union with a male, it gives birth to great numbers of young females, and that the isolation of these young specimens has no more effect upon their fertility than it had in the case of their mother, but that they continue to reproduce for an indefinite number of generations when all chance of access to a male is excluded.

This observation may be repeated by any one with the greatest ease, for Daphnia is very common in most fresh water ponds and streams, and it multiplies in confinement with great rapidity, so that there is no difficulty in verifying Schäffer's experiments, or in showing the correctness of his conclusions.

Certain authors have held that the parthenogenetic eggs of Daphnia are not true eggs at all, but simply internal buds (Lubbock, *Phil. Trans.*, 147, p. 88), and that the so-called "winter eggs," which seem, in most cases at least, to require impregnation, are the true ova; but Weismann, who has made a very thorough study of the origin of the ova in the ovary of Leptodora ("Ueber die Bildung von Wintereiern bei Leptodora hyalina," *Zeit. f. Wiss. Zool.*, xxxv.), has shown that while there are some minor differences in the mode of origin of the two kinds of eggs, both are real ova in the strictest sense, and cannot be compared with buds.

Schäffer's experiments were independently repeated in 1820 by Jurine, and this observer not only reached the same result, but also proved that fertile winter eggs may be produced by isolated females whose mothers and grandmothers have been isolated all their lives.

Claus has shown that the eggs begin to develop in the female Evadne, a form closely related to Daphnia, before the animal is born; and impregnation would here seem to be impossible.

In Daphnia and related forms the parthenogenetic eggs usually give rise to females only, but experiments have shown that the approach of winter or the failure of the supply of food causes males as well as females to be produced. Schäffer, the discoverer of parthenogenesis in Daphnia, also discovered that Apus, a crustacean which belongs to another order, lays eggs which give rise without impregnation to fertile females, and that this may go on for an indefinite number of generations. In Apus, and in most of its allies, the males are extremely rare, although the females may be very abundant, and one observer, Joly, found only one male specimen of Artemia salina among 3000 females.

Parthenogenesis is known to occur in many insects. It is rare and exceptional in some of them, while in others it is as frequent and normal as it is in Daphnia.

Among the butterflies and moths, sexual union is the rule, and parthenogenesis a rare exception, but in 1701 Dr. Albrecht made the remarkable discovery that a female Bombyx, which had escaped from its pupa under a glass shade, and which could not have been visited by a male, laid fertile eggs. As sexual union is known to be almost universal in the Bombycidæ, this observation was at first discredited, but the phenomenon has in more modern times been observed with every possible precaution in Bombyx mori by a number of most competent observers, among whom are Schmidt, Barthélemy, Jourdan, Siebold and others. They all agree that while parthenogenesis is rare in this species, it does sometimes occur, and it is known that the parthenogenetic eggs give rise to fertile males and fertile females, which may unite sexually and thus produce fertile eggs. Dr. Kipp has reared another form, *Smerinthus populi*, from eggs fertilized by a male which hatched from a parthenogenetic egg, and laid by a female which had been reared in the same way.

In Bronn's *Klassen und Ordnungen*, Gerstaecker gives the following list of moths in which parthenogenesis has been observed, with the name of the observer. The list might be greatly enlarged by the addition of cases which have been recorded since its compilation, but it is sufficient for our purpose, which is simply to show that the fact has been verified repeatedly by many observers.

Sphinx ligustri, once............................Treviranus.
Smerinthus populi, four times....Nordmann, Brown, Newnham, Kipp.
Smerinthus ocellatus, once.........................Johnston.
Euprepia caja, five times....Brown, Lehocq, Robinson, Schlapp, Barthélemy.
Euprepia villica, once..............................Stowell.
Saturnia Polyphemus, twice................Curtis, De Filippi.
Gastropacha pini, three times......Scopoli, Suckrow, Lacordaire.
Gastropacha quercifolia, once.........................Basler.
Gastropacha potatoria, once........................Burmeister.
Gastropacha quercus, once..........................Pleininger.
Liparis dispar, once...............................Carlier.
"Egger Moth" (Liparis dispar ?), once.................Tardy.
Liparis ochropoda, once..............................Popoff.
Orgyia pudibunda, once.............................Wernberg.
Psyche apiformis, once...............................Rossi.
Bombyx mori, many times..........Schmidt, Siebold, Jourdan, Barthélemy, and others.

Although these cases make a long list, which might be greatly increased, they are still exceptional, for in all these species almost all the eggs fail to develop unless they are fertilized by a male; but in some other groups of insects parthenogenesis occurs more frequently, and seems to be perfectly normal. The most remarkable instances are those which occur in the social insects, such as the bees.

It is well known that a community of honey-bees consists of individuals of three kinds—the workers or rudimentary females, which are the most numerous; the perfect females or queens, of which only one is usually present in a hive; and the drones or males.

In the workers, or as they are sometimes falsely called the neuter bees, the female reproductive organs are very imperfectly developed: the vagina is so small that union with a male is hardly possible, and the receptaculum-seminis is very rudimentary, yet it is well known to all bee-cultivators that they do sometimes lay eggs which are capable of development, not only in the honey-bee but in other species also. Among the honey-bees such fertile workers are always found in a hive which has lost its queen, and they have been called "drone mothers," from the fact that their eggs produce only drones or males.

The queen-bee is the only member of the hive which unites sexually with the males, and her reproductive organs are very large and well developed, as contrasted with those of the worker. Her receptaculum-seminis is large enough to retain a sufficient supply of the male fluid to serve for fertilizing great numbers of eggs, and it is usually found to contain a considerable quantity. Sexual union takes place during flight, and queens with imperfect wings are never impregnated, and Siebold, Leuckart, Berlepsch, and others have shown, by microscopic examination, that in such cases the receptaculum-seminis is empty, and the queen is a virgin. In such cases, as well as in hives, where the receptaculum-seminis of the queen has been exhausted by old age, or has been removed, it is well known to bee-cultivators that only drones are produced, while eggs destined to give rise to females, to workers or perfect queens, are produced only by queens which have been impregnated and have some of the male fluid in the receptacle. This fact, considered in connection with the fact that the eggs laid by workers produce only drones, indicates that the drone eggs laid by an impregnated queen are not fertilized; and Siebold has found active spermatozoa on newly laid worker-eggs, but has failed to find them on drone-eggs. We are, therefore, compelled to believe that the queen is able to lay both fertilized and parthenogenetic eggs. It is stated that when a queen of the common German variety is crossed with a drone of the Italian bee she produces hybrid workers, while her male offspring are all pure German bees.

In certain Lepidoptera, as in the bees, parthenogenesis seems to be normal, and it has been observed in Solenobia and Psyche by a great number of ancient and modern naturalists, including Schrank, Réaumer, Pallas, De Geer, Scriba, Speyer, Reutti, Siebold, Leuckart, Hofmann, and others. Their observations show—1st, that the wingless female is abundant and widely distributed at all seasons, while the winged males are seldom met with, and are found only in certain restricted localities; 2d, that there is only one form of female; those which unite with the male, as well as those who do not, have perfect reproductive organs which resemble those of other butterflies. Parthenogenesis is the rule, and the females lay eggs as soon as they have passed through the pupa stage. These parthenogenetic eggs give rise only to females, and these may give rise to female descendants in the same way for an indefinite number of generations; 3d, in at least one species (*Solenobia triquetrella*), the eggs which are laid by impregnated females give rise to both sexes.

Dufur, Kessler, Hartig, Walsh, and many other naturalists have shown that certain female gall-wasps are parthenogenetic; within recent years Bassett and Adler have made most interesting observations upon these wasps. In 1873 Bassett showed (*Canadian Entomologist*, 1873–75, p. 91) that great numbers of male and female wasps escape in June from certain galls which are found in very great abundance on the leaves of an oak. Late in the summer the females lay their eggs in the leaves of the same oak, and give rise to galls, which, however, are of quite a different character from those in which the insects were born. Early in the following spring a brood of females hatch from these winter galls, and at once lay parthenogenetic eggs, which give rise to the summer galls, and hatch in June into males and females.

Bassett and Adler have extended these observations to a great number of species, and the following account is taken from a paper by the latter writer ("Ueber den Generationswechsel der Eichen-Gallwespen," von Dr. H. Adler, *Zeit. f. Wiss. Zool.*, xxxv. 151), who has carried on a long series of the most painstaking experiments, using every precaution against error.

He reared a great number of small oak-trees under glass cases, and then, introducing the wasps, traced their whole life history, and he found that in many species there is a winter gall, which is produced in the fall by a fertilized female, and which gives rise early in the spring to a brood of females without males. These at once lay their eggs and form summer galls, from which both sexes are born.

In all cases the parthenogenetic forms are so different from the sexual forms that they had previously been described as distinct species, and in most cases they had been placed in distinct genera.

The following example selected from Adler's paper will give an idea of the character of his experiments: *Neuroterus lenticularis* is a wasp which is born within a small round gall which appears in July on the lower surfaces of oak leaves. The galls continue to grow until the end of September, when the leaves drop off and fall to the ground. In the spring the insects escape, and all of them are females, with their ovaries full of eggs, and the male of this species was unknown previously to Adler's experiments. He gathered the fallen leaves, and rearing the wasps in isolated captivity found that, soon after the female is born, she pierces the leaf buds of the oak, and lays her eggs. Adler marked by pieces of thread all the buds which the insect was actually seen to pierce, and in a few days he found on the leaves which expanded from these buds a great number of minute young galls, which soon became large enough to show that they were very different from the winter gall in which the parent was born.

This new gall proved to be one with which entomologists had long been familiar, as the birthplace of what had always been regarded as a wasp of quite a different genus—*Spathogaster baccarum*. It is a soft green gall, punctated with red spots, and it grows entirely through the leaf, so that part is on the upper and part on the lower surface. The oak trees with these galls were kept carefully protected from the access of other insects until about the middle of June, when male and female specimens of *Spathogaster baccarum* were produced. The sexes united at once, and the females were then isolated and placed in captivity, each with its little oak tree. They soon laid their eggs in the leaf buds, and thus gave rise to the winter galls, which, in the following spring, produced a brood of the parthenogenetic female *Neuroterus lenticularis.*

He has made similar careful observations on many other species, and he gives the following table to exhibit his results:

Parthenogenetive form born from a winter gall, and producing a summer gall.	Sexual form born from a summer gall, and producing a winter gall.
Neuroterus lenticularis.	Spathogaster baccarum.
Neuroterus læviusculus.	Spathogaster albipes.
Neuroterus neumismatis.	Spathogaster vesicatrix.
Neuroterus fumipennis.	Spathogaster tricolor.
Aphilotrix radicis.	Andricus noduli.
Aphilotrix Sieboldi.	Andricus testaceipes.
Aphilotrix corticis.	Andricus gemmatus.
Aphilotrix globuli.	Andricus inflator.
Aphilotrix collaris.	Andricus currator.
Aphilotrix fecundatrix.	Andricus pilosus.
Aphilotrix callidoma.	Andricus cirratus.
Aphilotrix Malpighii.	Andricus nudus.
Aphilotrix autumnalis.	Andricus ramuli.
Dryophanta scutellaris.	Spathogaster Taschenbergi.
Dryophanta longiventris.	Spathogaster similis.
Dryophanta divisa.	Spathogaster verrucosus.
Biorhiza aptera.	Terus terminalis.
Biorhiza renum.	Trigonaspis crustalis.
Neuroterus ostreus.	Spathogaster aprilinus ?

In the following four species no males were discovered, but the parthenogenetic females gave birth to females like themselves:

Aphilothrix seminationis.	Aphilothrix quadriliniatus.
Aphilothrix marginalis.	Aphilothric albopunctata.

These are all of them insects which form galls on oak leaves, but Adler finds that the same power to lay parthenogenetic eggs exists in some other wasps. *Pteromalus puparum* lays its eggs in the bodies of butterfly larvæ, and thus gives birth to both males and females. The sexes are so different that there is no difficulty in separating them as soon as they are born. Adler found that females which were thus isolated, and which were shown by microscopic examination to be virgins, nevertheless laid eggs as soon as a caterpillar was furnished them.

Among 206 females which hatched from these eggs there were only 9 males, so that there is, in this species, a strong tendency for parthenogenetic eggs to produce females.

In the rose-gall-wasps Adler finds that the males are very rare, about one to fifty females, and he believes that they are superfluous, since the females in two species, *Rhodites rosæ* and *Rhodites eglanteriæ*, are perfectly parthenogenetic, giving rise to parthenogenetic female offspring.

The instances of parthenogenesis in larval or immature insects are extremely interesting, but as they will be referred to at some length in another place I will not dwell upon them at present, as the cases which have been given are enough for our purpose, which is simply to show the satisfactory and exhaustive character of the proof that unfertilized eggs do in many animals develop and give rise to organisms which are in all respects like those born from fertilized eggs.

In *Nematus ventricosus* the males are not uncommon, but Adler has verified Siebold's statement that in this species parthenogenesis of the ordinary females is not at all infrequent.

Although parthenogenesis is more frequent among the insects and crustacea than it is in other animals, it is not confined to these groups.

Cohn has given good reasons (*Zeit. f. Wiss. Zool.*, xii., *1863*, p. *197) for believing that among the Rotif*era the summer eggs, which give rise to both males and females, are parthenogenetic; while the winter eggs, which hatch into females exclusively, are the only ones which are fertilized. There is no reason for doubting the correctness of this conclusion, but it has not been placed beyond the possibility of all doubt, as is the case with so many insects.

Many observers have thought that they have found evidences of parthenogenesis in groups of animals where such an occurrence would be very exceptional, but in most of these cases there is much chance for error. Thus it has been stated that the eggs of echinoderms sometimes develop without impregnation, but when we recollect that both male and female echinoderms in most cases discharge their reproductive elements into the water, we can see that it must be almost impossible to state that the sea-water in which the eggs are placed contains no spermatozoa of the same species. Dr. J. M. Wilson has recently undertaken some experiments on this point at my suggestion. He fertilized a lot of eggs from one of our common sea-urchins, Strongylocentrotus, with male fluid from another of a distinct genus, Arbacia. A lot of Arbacia eggs were fertilized with a male Strongylocentrotus,a lot from each form with fluid from a male of the same species, and eggs from each species were placed in water without fertilization.

In all six cases the eggs gave rise to normal embryos; but that this was really due to the presence of spermatozoa in the water, was shown by the fact that no such surprising result followed in a second set of experiments where especial effort was made to get pure sea-water. Many of the recorded cases are open to the same objection; and in other cases, as in the virgin sow referred to by Bischoff, there seems to be some doubt whether the ova were really undergoing development; but Oelacher's observations on the eggs of a virgin hen ("Die Veränderungen des unbefruchteten Keimes des Hühnereies im Eileiter und bei Bebrütungsversuchen," *Zeit. f. Wiss. Zool.*, xxii., 1872, p. 220) seem to show that the hen's egg does have the power to pass through the first stages of development whether it is impregnated or not.

The instances of parthenogenesis which I have given show that this power may be independently acquired by animals which cannot possibly inherit it from a common source. In the vast majority of insects, and in the majority of the crustacea, the egg does not show the slightest tendency to develop before it is fertilized. It is true that in the case of the crustacea the evidence for this statement is almost entirely of a negative character, for no one has ever shown by experiment on any considerable number of species that the female cannot lay fertile eggs when the access of a male is prevented, but in many insects we know from actual observation that the eggs die soon after they are laid, unless they are fertilized; and we know enough of the breeding habits of crustacea to feel confident that parthenogenesis is exceptional among them, just as it is among insects.

We must, therefore, conclude that if we could retrace the course of evolution of any parthenogenetic animal we should be led back to an ancestral form which never manifested any such power. It is impossible to believe that Daphnia and the honey-bee have inherited from a common parthenogenetic ancestor the power to produce fertile unimpregnated eggs, for the one form is much more closely related to normal insects and the other to normal crustacea than they are to each other. We may therefore state with confidence that the power has been independently acquired by many animals.

In the second place, we must admit that parthenogenetic ova are true ova in every sense: they are developed in an ovary like other eggs, and in many cases, as in those butterflies which are occasionally parthenogenetic, the very eggs which usually require impregnation may in rare instances develop without it. Weismann has made very careful examination as to the origin of both kinds of eggs in Leptodora, a water-flea related to Daphnia ("Ueber die Bildung von Wintereier bei Leptodora hyalina," *Zeit. f. Wiss. Zool.*, xxvii., 1876), and he finds that while there is some difference in the mode of origin of the winter eggs, which do not develop unless they are fertilized, and the summer eggs, which are parthenogenetic, the difference simply consists in the amount of nourishment which they receive in the ovary. In each case certain ova degenerate and are used up by the others as food, and a winter egg thus absorbs a greater number of these embryonic ova than a summer egg does; but Weismann's observations show that each of them is in all respects a true ovum, and that they are *perfectly homologous with each other.*

In some cases, as in some of the wasps described by Bassett and Adler, the animal which is born from a parthenogenetic egg differs considerably in structure from that which is born from a fertilized egg; but in other cases, as in butterflies and moths, there is no such difference. In some cases, as in Daphnia, all the parthenogenetic eggs hatch into females; in other cases, as in bees, they give rise to males alone; while in still other cases, as in the gall-wasps, some of the unfertilized eggs produce males and some females.

In many cases the animals which are thus produced are perfectly normal, and have nothing to distinguish them from those born from impregnated eggs. They have the ordinary structure of their species, and they are perfectly capable of propagating their kind. In some cases, as in the gallwasps, reproduction is preceded by the union of the sexes, and in other cases the animals born from parthenogenetic eggs are themselves parthenogenetic.

There is possibly one difference between ordinary and parthenogenetic eggs,—the presence of polar globules in the one case and their absence in the other; and I shall discuss this difference soon.

Except in this particular, the history of the development of the egg into the perfect animal is the same, whether the egg is fertilized or not. Weismann, who has studied the embryology of both parthenogenetic and fertilized eggs in insects ("Beiträge zur Kenntniss der ersten Entwicklungsvorgänge im Insectenei"), shows that all the minuter details in the process of building up the embryo are the same, whether the egg is fertilized or not.

We must therefore believe that an ovum has in itself the power to give rise to a new organism, and that although it does not usually manifest this power, unless the egg is fertilized, it may exhibit it under certain circumstances, as parthenogenesis. Of the character of the circumstances which lead to parthenogenesis we know little, except that such circumstances have thus acted in many groups of animals where the eggs ordinarily require to be fertilized.

Certain authors have suggested that there may be a connection between the extrusion of the "polar globules" from the ovum and the need of impregnation by a male cell.

The ripe ovarian ovum of an animal usually contains a transparent central body, the germinative vesicle, and when the egg is fully ripe the germinative vesicle approaches the surface and divides into two portions: one of these is discharged from the egg, thus forming the "polar globules." These take no part in the formation of the embryo. They become entirely separated from the egg, and soon die and disappear. The remainder of the germinative vesicle remains in the egg, as the "female pronucleus," which unites with the "male pronucleus" *formed from the male cell after impregnation*, and thus builds up a compound body, the first "segmentation nucleus."

The formation of these "polar globules" has been observed in all groups of the animal kingdom, except the rotifera and arthropods, and their functional significance is therefore a subject of the greatest interest. They obviously contain something which is not needed for the formation of the embryo, and they may be discharged from the egg before it is laid, or they may remain until it is laid, as seems to be the general rule, and may be discharged just before fertilization takes place, as is the case in the star-fish, or they may be discharged immediately after the egg is impregnated.

Within recent years an hypothesis regarding their significance has excited considerable notice. This hypothesis, which was first advanced by the late Prof. McCrady, and which is stated at length in Balfour's Treatise on

Comparative Embryology, is that each sexual element originally contains a male portion and a female portion; the ripe male cell is the male half of the male element, and the "polar globules" contain the male substance of the ovum, which is discharged in order that it may be replaced by the male element from the body of another organism. Balfour says: "I would suggest that in the formation of the polar cells part of the constituents of the germinal vesicle, which are requisite for its functions as a complete and independent nucleus, is removed to make room for the supply of the necessary parts to it again by the spermatic nucleus. My view amounts to the following, viz., that after the formation of the polar cells the remainder of the germinal vesicle within the ovum (the female pronucleus) is incapable of further development without the addition of the nuclear part of the male element (spermatozoon), and that if polar cells were not formed parthenogenesis might normally occur. A strong support for this hypothesis would be afforded were it to be definitely established that a polar body is not formed in the arthropoda and rotifera; since the normal occurrence of parthenogenesis is confined to these two groups in which polar bodies have not so far been satisfactorily observed. . . . To the suggestion already made with reference to the function of the polar cells, I will venture to add the further one, that the function of forming polar cells has been acquired by the ovum for the express purpose of preventing parthenogenesis. . . . There can be little doubt that the ovum is potentially capable of developing, by itself, into a fresh individual, and therefore, unless the absence of sexual differentiation was very injurious to the vigor of the progeny, parthenogenesis would most certainly be a very constant occurrence; and, on the analogy of the arrangements in plants to prevent self-fertilization, *we might expect to find* some contrivance both in animals and plants to prevent the ovum developing by itself without fertilization. . . . On my hypothesis the possibility of parthenogenesis, or at any rate its frequency in arthropoda and rotifera, is possibly due to the absence of polar cells" (*Comp. Emb.*, vol. i. p. 63).

The simplicity of this hypothesis renders it very fascinating, but even if it were possible to accept it without qualification, it would not affect our argument, for it would still remain true that "the ovum is potentially capable of developing, by itself, into a fresh individual," and must therefore be very different in function from the male cell, which under no circumstances exhibits a similar power.

My reasons for doubting the hypothesis are, first, that a failure to discover polar cells in the eggs of rotifera or of the arthropods may be due to the fact that they are discharged very early in the history of the ovarian ovum. We know that in some animals, as in hydra, the polar cells are discharged while the egg is still contained in the ovary, and we also know that the eggs of many arthropods undergo in the ovary very peculiar changes, which greatly obscure their fundamental similarity to ordinary uncomplicated eggs, so that it is quite possible that our failure to discover the polar cells may be due to something else than to the fact that they are never formed. The eggs of insects especially are very peculiar, and Weismann says that "nirgends im ganzen Thierreich die Ontogenese so verschoben und coenogenetisch entartet ist" as it is among the insects. This author has figured, in the fertilized egg of a species of Chironomus, certain bodies which are not present in the parthenogenetic eggs of Rhodites, and he suggests that these may be the long-sought polar cells, but he does not feel certain that this is the case, and examination of his paper will show that there is so much difference between the early stages of insect eggs and the corresponding stages of simpler and more typical eggs, that the identity of these bodies must remain open to some doubt, but there can be no doubt of the nature of the polar cells described by Grobben in the parthenogenetic eggs of Moina.

There is another objection to the hypothesis, which seems to me to be entitled to great weight. According to Balfour's statement we should expect that any egg which retained the polar cells might develop without impregnation. Observers have failed to discover their extrusion in the eggs of ordinary arthropods, as well as in those which are parthenogenetic, and we should therefore expect all the arthropods to be parthenogenetic, but this is not the case. In many other animals, as in the oyster, they are not discharged until the egg is fertilized, and the hypothesis would require us to believe that an unfertilized oyster egg contains a male element as well as a female element; but when perfectly ripe oyster eggs are placed, without fertilization, under conditions which are perfectly favorable to development: they show no signs of life, and soon die and decay. If a little male fluid is added, however, they quickly discharge their polar cells, and then rapidly pass through the changes which build up the embryo.

If the polar cell is really equivalent to a male cell, we certainly might expect these oyster eggs, which are perfectly ripe, and, according to the hypothesis, contain all that is necessary for development, to show some power to develop without impregnation. If the power to extrude polar cells "*has been acquired by the ovum for the express purpose of preventing parthenogen-*

esis," we certainly should look for the occurrence of parthenogenesis in ripe ova which have not extruded these bodies.

However this may be, the correctness or incorrectness of the polar-cell hypothesis has no bearing upon our present argument, for the phenomena of parthenogenesis show beyond question that an egg may develop without union with a male cell, and there is no evidence whatever that a male cell ever acts in a similar way.

Other reasons for believing that the ovum and the male cell perform different functions in heredity.

Even if the possibility of parthenogenesis did not show us that the part played in heredity by the ovum is different from that played by the male cell, there are many other reasons for believing that the difference in the form of the two sexual elements corresponds to some profound difference of function.

I shall devote several chapters of this book to the extended discussion and proof of the facts which drive us to this conclusion, and I shall show that the belief in the essential similarity of the functions of the reproductive elements cannot possibly be retained.

When the male of one species or variety is crossed with the female of another species or variety, the hybrid offspring is often very different from that which is produced when the female of the first species is crossed with the male of the second. If the function of the ovum is the same as that of the male cell, we should have exactly the same elements in each case, and should expect the same result. The fact that the result is not the same proves that the elements are not the same either.

In many cases the male of one species will breed freely with the female of the second species, while absolute sterility follows the union of a male of the second species with a female of the first species. The offspring of a male hybrid and the female of a pure species is much more variable than the offspring of a female hybrid and the male of a pure species. These facts are absolutely inexplicable, if the two sexual elements play similar parts in heredity.

A structure which is more developed or of more functional importance in the male parent than it is in the female parent is very much more apt to vary in the offspring than a part which is more developed or more important in the mother than it is in the father.

These facts, and many others which will be mentioned farther on, compel us to believe that there is some profound functional difference between the ovum and the male cell.

It is, therefore, only reasonable to distrust the absolute correctness and completeness of any hypothesis of heredity, which, like Darwin's Pangenesis hypothesis, recognizes no such difference.

Summary of last two Chapters.

The phenomena of heredity are certainly among the greatest marvels of the material universe, but there is no reason to believe that they lie outside the province of legitimate scientific inquiry. Our present purpose is not to trace them back to their origin or to show that they result from the properties of matter, but simply accepting them as vital phenomena, to trace the secondary laws to which their present form is due. The fact that the distinctive properties of the egg of any living species have been gradually acquired during the evolution of the race through the action of influences which are, to a certain extent, open to observation and study, gives us ground for believing that we may hope to discover what it is in the structure of the egg, which renders these properties possible. There have been many attempts to do this, but it is impossible to accept any hypothesis which has ever been advanced. The evolution hypothesis, as advocated by Bonnet and Haller, is directly contradicted by the discoveries in the modern science of embryology, and it is accordingly now regarded as having only an historical interest, but the modern epigenesis hypothesis is no more satisfactory, for the resemblance between the evolution of a species from an unicellular ancestor and the development of an individual animal from an unicellular egg is only an analogy.

The efficient cause in the first case, the slow modification of the race by the natural selection of the most favorable variations, is absent in the second case, and there is nothing whatever to take its place. The parallelism between embryology, or the ontogenetic development of the individual, and phylogeny, or the evolution of the race, is one of the most remarkable and instructive generalizations of modern science, and the very existence of the parallelism gives us every reason to hope that an explanation of heredity or of ontogenetic development may be discovered: but to point out the parallelism is, in no sense whatever, to explain heredity.

If the conclusion be true which is accepted by most of the modern advocates of epigenesis, the conclusion that the egg which is to become a man differs in no essential particular from the egg which is to become a starfish, heredity is an insoluble mystery, for we neither possess nor have any grounds for believing that we ever shall possess any knowledge of forces competent to produce from two essentially similar eggs adult animals which are so essentially dissimilar. We cannot attribute this result to natural selection, for this law can only act on successive individuals; we cannot attribute it to the direct action of external conditions, for we know that eggs may give rise to very different animals when placed under identical surrounding conditions. Haeckel's statement that heredity is memory, contains a profound truth, as we have already seen, but it does not help us to understand heredity.

We know memory only in connection with organization, and if we believe that an egg contains the memory of all the past experience of the race, we must believe that it contains a complex organization to correspond to the complexity of this past experience.

So far as Haeckel's hypothesis of perigenesis has any claim to be considered an *explanation* of heredity, it is an hypothesis of evolution, not of epigenesis.

Jäger's view that the ovum is at first unspecialized, and that it gradually assimilates from its developing parent all the specializations of the structure of the latter, fails to account for reversion or for the transmission of adult characters by immature parents, and the author is compelled to substitute for it an evolution hypothesis when he comes to treat of reversion.

There is no escape from the conclusion that the ovum of an animal actually contains in some form the potentiality of that particular animal, and Huxley acknowledges that the development of an egg is in essence a process of evolution.

We thus find ourselves driven back from the modern hypothesis of epigenesis to the long abandoned hypothesis of evolution, and we must therefore inquire whether our recent great advances in knowledge of the forces which have produced the various forms of animal and vegetable life, will guide us nearer to the truth than the speculations of the last century. Bonnet and Haller might fairly assume that each species had been what it is now "from the beginning," but we cannot nowaday make any such assumption, and we must believe that the structure of the germ, like the structure of the adult animal, has been gradually acquired by natural selection.

A modern hypothesis of evolution must therefore be a very different thing from the one which Bonnet furnished, and must account for the slow advancement of the germ from generation to generation.

In Darwin's pangenesis hypothesis we have a provisional explanation based upon the generalizations of modern science. It is a true evolution hypothesis, for Darwin believes that an ovum or a male cell is a wonderfully complex structure, and that it contains gemmules to represent each feature in the organization of the adult. One essential difference between this hypothesis and the original hypothesis of evolution as stated by Bonnet, is that Darwin believes that the ovum contains, not the perfect animal in miniature, but a distinct germ for each distinct cell or structural element of the adult. Darwin's hypothesis recognizes the gradual specialization of the ovum during the evolution of the race, for each cell of the body of the parent may at any time transmit to it new gemmules. Most of the objections to it are based upon its complexity, and on the almost infinite number of gemmules which it requires; but besides these objections we know from Galton's experiments that it is impossible to accept it without modification. We also have, in the fact that the functions of the two sexual elements are not alike, a reason for believing that, although it may be an approximation to the truth, it cannot be regarded as a complete and satisfactory explanation.

The object of this work is to present a new hypothesis which will be seen to bear a close resemblance to the one which has been advocated by Darwin, although careful examination will show that it is in reality very different. I hope to show that it is not open to the objections which are urged against the pangenesis hypothesis, while it contains all the features which give value to the latter.