

A REVIEW OF PARTHENOGENESIS.<sup>1</sup>

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## GENERAL INTRODUCTION.

In the great majority of cases the sex cells disintegrate unless they unite with the products of the opposite sex of the same species, but in many cases in the animal kingdom cells are given off from the germinal epithelium which, without fertilization, are able to undergo development, as is manifested by cell division. That these are true ova is evident from their origin, appearance, behavior and fate, and the only difference between these and eggs requiring fertilization is that they have in them the ability to divide mitotically without receiving the external stimulus given by the male sex cell. To this phenomenon the name Parthenogenesis is applied.

The importance of facts of this kind cannot be overestimated, especially from the standpoint of cytological investigation. The various ways in which these eggs behave during maturation and the sex relations connected with the different kinds of Parthenogenesis give us most valuable guides in our study and afford invaluable material toward the solution of that much debated problem—the determination of sex.

In view of the importance of the subject and the scattered condition of the literature, it has seemed desirable to give a brief summary of the most important work done, together with a literature list of all important papers. Most attention has been given to the case of the Honey Bee, since it was on this form that Dzierzon worked and especially since the most conflicting theories have been advanced concerning it. A somewhat lengthy discussion of this one case will make clearer what follows concerning other species, but it is hoped that this will not make it appear that I consider this the most important case, but that it is simply used as a basis for the later discussion.

The preparation of this paper was begun at the suggestion of Prof. E. G. Conklin to fill partially the need of some such review. I wish at this time to express my appreciation of the help

<sup>1</sup> Contribution from the Zoological Laboratory of the University of Pennsylvania.



and suggestions given me by Dr. Conklin all through the work. I wish also to state that I have referred constantly to the review of Taschenberg (1892) and especially to his long literature list. His paper is an excellent review up to the time of its publication.

#### HISTORICAL SKETCH OF THE THEORY.

The word Parthenogenesis (Greek *παρθένος*, a virgin, *γένεσις*, production) was first used by Owen<sup>1</sup> in the sense of Alternation of Generations.

In 1856, in his classic paper, "Wahre Parthenogenesis bei Schmetterlingen und Bienen," Carl Th. Ernst v. Siebold used the word in the sense of the development of eggs without fertilization, in which sense it has since been universally adopted. Previous to 1856 the phrase *lucina sine concubitu nulla* and similar terms were used in practically the same sense in which the word parthenogenesis is now used.

For the first observations on parthenogenetic development we must go back to Aristotle, as is true for the beginnings of so many lines of observation. This old Greek scientist recorded extensive observations on the Honey Bee which will be referred to in another place.

The next writer who gave any intimation of a belief in such phenomena was Goedart (1667) who succeeded in raising larvæ from eggs laid by an unfertilized female of *Orgyia gonostigma*. After that Leenwenhoek (1695), Blancard (1696), Albrecht (1706) and Réamur (1737 and 1741) recorded somewhat similar results.

In 1745 Bonnet, of *emboîtement* fame, described, rather fully, parthenogenetic development in plant lice. Oscar Hertwig, in his "Historical Account of Embryology," in the *Entwicklungslehre*, speaks of Bonnet's work in the strongest terms and does not hesitate to designate it as marking one of the milestones in the history of embryology.

Just one hundred years after this, Dzierzon (1845) announced his theory on the parthenogenetic development of the drone eggs of the common bee, *Apis mellifica*, which will be treated more fully in a later section. During this period of one hundred years a

<sup>1</sup> V. v. Prosch, in 1851, in *Om Parthenogenesis og Genexationsvexel, et Bidrag til Generationstaeren* (Kjobenhavn, Trijkt hos J. C. Scharling), used the word in the same sense.



number of papers appeared in which the development of unfertilized eggs was described, but the importance of the observations was not recognized fully until after Dzierzon published his first paper. This paper, published in a bee journal, may well be looked on as the starting-point of the Theory of Parthenogenesis, since it started a very important discussion and marks the beginning of a host of work along similar lines.

The most important papers of the period between 1745 and 1845 will be found in the literature list at the end of this paper. It does not seem desirable to go into a detailed account of these earlier papers since, while they are valuable, the greatest additions to our knowledge of these phenomena have been made since the time named.

As stated on a preceding page, more attention has been paid to the parthenogenesis of the Honey Bee, in the preparation of this paper, than to any other form. A full statement of the present state of our knowledge of the phenomena in this species will make clearer what follows concerning other species.

#### THEORIES ON THE HONEY BEE PREVIOUS TO 1845.

Before discussing the various theories and experiments on the parthenogenetic development of the drone eggs of the common bee, it may be of interest, from the historical standpoint, to review briefly the various theories put forth previous to 1845 which were used to explain the peculiar phenomena observed in the hive in regard to the sex of the bees. Since the bee is of economic value it has been the object of much investigation for centuries, and for this reason the peculiarities of its development have long been known.

Aristotle, in his *Historia animalium*, wrote: "All persons are not agreed as to the generation of bees, for some say that they neither produce young nor have sexual intercourse; but that they bring their young from other sources. . . . Other persons affirm that they collect the young of the drones from any of the substances we have named (flowers of the honeysuckle, reed or olive), but that the rulers (queens) produce the young of the bees (workers). . . . Unless the ruler (queen) is present drones only are produced. Others affirm that they have sexual intercourse, and that the drones are males and the bees females." In his *De generatione animalium* he wrote: "The drones develop in a queenless



stock'' and ''The bees produce drones without copulation.'' Here we get a rather clear statement of what was rediscovered centuries later.

Huish gives an account of other theories advanced, and a large part of the information from which these summaries of the earlier work were made is from his paper.

1. Schirach says that the hive consists of three kinds of bees: (1) queens, the mother of the hive, (2) drones or males, and (3) workers, a middle sex with greater affinity to the queen but destitute of procreating powers. The parts which belong to the queen lay concealed in imperceptible minuteness, and just as soon as they receive the necessary space for their expansion, increase takes place in size and a queen is developed. Drones from fertile workers and queens arise from false or corrupted eggs, to which the name ''abortion'' is applied. Some of the opponents of Schirach held that all workers lay eggs, the view being based on the fact that in queenless hives drones are produced by the ''fertile workers.''

2. Herold was one of the greatest opponents of Schirach, maintaining that the queen copulates with a male worker, producing male and female workers. The true workers, male workers, perform their duties outside the hive, collect honey and pollen and copulate with the queen and female workers which remain inside the hive. The female workers lay eggs (fertilized by male workers) which produce drones of no sex whatever. This was at once proven false by an anatomical examination showing that the drones are males. The hive was then considered as an Amazon republic with drones raised to the rank of males or husbands, a view that had many supporters up to the time of Heinmetz.

3. Heinmetz proposed a double genealogical tree for the bee family, symmetrically for both the male and female lines. (1) The queen as the great mother bee copulates with a male worker and lays eggs producing insects like their sire (male workers). If laid in large cells they produce great male bees, if the rudiments of a great male exists in the egg.<sup>1</sup> ''But as only small male workers are the issue, although they may be bred in large cells, the conclusion must be drawn that in these male eggs the rudiment was only existing for small workers and that from these no great male bees are pro-

<sup>1</sup> Quotation from Huish. See former reference.



duced.” (2) The queen also lays eggs producing females which resemble the queen or are female workers or mothers of the drones. The working bees are partly male and partly female and are derived from the queen. On the other hand the drones are from a mother drone, as follows: A mother drone copulates with a great male drone and lays only drone eggs which develop as small drones or as great drones (like their sire). Needless to say, a theory of this kind had many opponents.

4. Voigt and Lucas. These men separately maintained that the queen is the mother of all the bees, laying in six months of the year an almost incredible number of fertilized eggs, from which in twenty to twenty-four days are produced common workers which are both male and female. The males *by their mouths* fructify not only the queen but common female workers or mother drones, and from eggs laid by the latter in May and June drones are developed. This fructifying or vivification of all these eggs is performed and executed by the principle of life or by the animating creative spiritual power, *aura seminalis*, contained in the spittle, the process of which is so very visible in the frequent application of the proboscis of the common male bees to that of the queen. This theory was based on the facts that workers and queens can compose a perfect hive without adding drones and that workers produce drones.

5. Haumann maintained that the queen is the only mother of her like and of workers and drones. The bees (workers) are nurses and co-operate in breeding, and without them the eggs prove abortive. In the small cells the sex property of female eggs is lost and the egg becomes a common bee, but in a royal cell a queen or fertile mother, and in drone cells a spurious mother drone. The male eggs in common cells become bees devoid of sex, and in drone cells a male or drone. Hummel attacked this most violently on the principle that it is at variance with every analogy of nature to invest an insect with the power of altering the sex character of an egg after laying, and impart to it a power which did not belong to it in its original nature. From Hummel's argument was founded one of the chief objections to the hypothesis advanced by Huber, that a common bee is possessed of the power of generating a queen from a common egg.

6. Strube held that the queen with a double-branched ovarium lays male and female eggs. The male eggs are placed in small cells and become male workers. The female eggs become queens



in queen cells or degraded queens. The remaining workers are those which can breed only drones; they are fertilized by the male workers and not by drones. The eggs of drones of May are laid by degraded queens. The ovaria of these queens cannot develop in the small cells and are weakened. During honey flow these degraded queens lay eggs. The eggs from which early drones arise are laid in the autumn and are outside the heat of the hive in winter, developing in spring. It is only when there is a deficiency of male workers that the queen is fertilized by a drone.

### HABITS OF THE BEE.

In order to appreciate fully the experimental work done on the subject of the parthenogenetic development of the male bee, it is necessary to know something of the habits of the different members of the hive or colony. The habits of no insect are better known to zoologists, but a very brief statement may not be out of place here, although necessarily incomplete.<sup>1</sup>

At the age of about five days the queen takes what is commonly spoken of as her "marriage flight," flying from the hive to meet a drone. She returns in about half an hour with the organs of the male generally hanging to her; the copulation taking place on the wing and the male being killed in the operation. Before the marriage flight the spermatheca is filled with a clear fluid and afterward it contains a white liquid, the seminal fluid, the number of spermatozoa having been estimated at several millions. Since a queen lays during her lifetime, averaging three or four years, a total of possibly 500,000 eggs, it will be seen that the apparatus for preserving sperm cells is very perfect. The spermatheca opens by a tube into the oviduct, the tube being surrounded by highly enervated muscles and accompanied by accessory glands which probably nourish the spermatozoa. These muscles must contract during the laying of a

<sup>1</sup> The facts here given regarding bees are gathered from various sources and from personal observation, and only such facts are here introduced as seem necessary to a better understanding of the discussion following. For more detailed accounts any book on apiculture may be consulted, of which the following are some of the well known examples:

Root, *A B C of Bee Culture*, Medina, O.

Cook, *Manual of the Apiary*, Lansing, Mich.

Benton, *The Honey Bee*, U. S. Dept. of Agriculture, Washington, D. C.



drone egg, so that no sperm cell can reach the oviduct to fertilize the egg.<sup>1</sup>

During the active season the queen can under stress of circumstances lay eggs at the rate of four a minute, although generally much slower, and in twenty-four hours can lay over 4000 eggs, the total weight of which is more than the weight of her own body. The eggs are laid at the bottom of the cells, the abdomen of the queen being put into the cell during the oviposition, and the eggs are attached to the middle point of the base of the cell by the end opposite the micropyle. In the hive the eggs are laid in what are known as brood cells, generally situated near the middle of the hive, these cells being used for the storing of honey when not used for larvæ. The cells from which the workers hatch are about one-fifth of an inch across, while those from which drones hatch measure about one-fourth inch; these being spoken of as worker and drone cells respectively. The royal or queen cells, in which queens develop, are shaped like an acorn and occupy about the space of three ordinary cells, these being built naturally only when the hive is queenless, when the queen is to be superseded by another on account of her age, or at the swarming season when the hive is to be divided. The queen passes quickly from one cell to another, laying in each an egg which almost invariably develops according to the size of the cell. This necessitates a very fine manipulation of the entrance of the spermatheca or seminal receptacle, as the sex is dependent upon whether a spermatozoon is allowed to escape or not.

Various theories have been advanced to explain the power of the queen to control the escape of the spermatozoa since we cannot believe that it is a conscious act, in spite of statements to that effect. A very plausible one is that the difference in the size of cells causes a difference in the pressure of the abdomen, and by a reflex nervous action, of the nature of which we know nothing, the muscles are contracted when the abdomen is put into a drone cell. Kückenmeister was probably the first to advance this theory. In opposition to this Cook (1881) and many others cite the fact that queens lay fertile eggs in cells where the walls have not yet been built up, and in such cases pressure on the abdomen could play no part. We have not as yet been able to account for the nearly

<sup>1</sup> For a description of these parts of the queen see Cheshire, F. R. (1886).



infallible ability of the queen to determine the sex of each egg. Probably queens never lay eggs in queen cells, but when a new queen is desired the workers build out a queen cell over a cell containing a very young worker larva (less than one day old). At any rate, this is the general method of procedure, although I have seen a drone-laying queen lay eggs in a partly built queen cell.

When a hive becomes hopelessly queenless it frequently happens that certain of the workers begin to lay eggs, which of course produce nothing but drones since a worker never copulates with a drone. These are called Fertile or Laying Workers, and are far more easily produced in the races of bees found in Eastern Asia than in the Italian bees.

The species *Apis mellifica* is divided into several races, the principal differences being in the coloration of the segments of the abdomen, although the instincts differ slightly, especially as regards the production of queens. The two races on which experiments on parthenogenesis have been performed are the Germans and Italians. The former are almost entirely black, while the latter have bands of yellow on the abdomen, three to five in number, or occasionally six. This difference has been used as a means of determining the truth of the parthenogenetic development of the males.

#### THE THEORY OF DZIERZON.

The parthenogenetic development of the male eggs of the bee, *Apis mellifica*, was first observed by Johannes Dzierzon, a priest of Karlsmarkt, Germany. He was a bee-keeper of many years' experience and a good observer. The theory was first announced in the *Eichstadt Bienenzeitung* in 1845, and in 1852 was published in book form. His arguments were briefly as follows:

(1) <sup>1</sup> A queen to be of any value must be fertilized by a drone. This takes place on the wing, high in the air. Drone eggs are not fertilized, but worker and queen eggs always are. “<sup>2</sup> In copulation the ovaries are not fecundated, but the seminal receptacle, that little

<sup>1</sup> The results of his investigations and his conclusions appeared in the *Eichstadt Bienenzeitung* and other journals, most of which were not accessible in the preparation of this paper. They were recorded in a very large number of short papers and it does not seem desirable to refer to all of them at this time. A complete list of the writings of Dzierzon can be found in *Bibliotheca Zoologica*, II, O. Taschenberg, to which the reader is referred.

<sup>2</sup> The quotations from Dzierzon are translations made by Lowe (1867).



vesicle or knot which in the young queen is filled with watery moisture, is saturated with semen, after which it is more clearly distinguishable from its white color." The supply of semen is enough for a lifetime. No clipped queen can be fertilized, as copulation never takes place in the hive. "The power of the fertile queen, accordingly, to lay worker or drone eggs at pleasure is rendered very easy of explanation by the fact that the drone eggs require no impregnation, but bring the germ of life with them out of the ovary; whilst otherwise it would be inexplicable and incredible. Thus the queen has it in her power to deposit an egg just as it comes from the ovary, and as the unfecundated mothers lay it; or by the action of the seminal receptacle, past which it must glide, to invest it with a higher degree, a higher potency, of fertility and awaken in it the germ of a more perfect being, namely a queen or a worker bee."

(2) The most important point in the theory is that "All eggs which come to maturity in the two ovaries of the queen bee are only of one and the same kind, which when they are laid without coming in contact with the male semen become developed into male bees, but on the contrary when they are fertilized by male semen produce female bees."

This, as v. Siebold expresses it, "strikes at the root of and completely abolishes the time-honored physiological law that an egg which is to be developed into a male or female individual must always be fertilized by male semen." Dzierzon refers to Riem, a French naturalist, for the fact that fertile workers lay only drone eggs (a fact now well known from many sources), and Mme. Jurin found on anatomical investigation that these fertile workers were queens with the spermatheca aborted and the ovaries not fully developed. Dzierzon also asserted that a queen must be able to lay either drone or worker eggs *at will*.

v. Siebold wrote: "We might beforehand expect that by the copulation of a unicolorous black-brown German and reddish-brown Italian bee the mixture of the two races would only be expressed in the hybrid females or workers but not in the drones, which are produced from unfecundated eggs. They must remain purely German or purely Italian according as the queen selected for the production of hybrids belongs to the German or Italian race." In 1854 Dzierzon wrote: "Continued observations of the hybrid hives also must be no less adapted to raise the veil, more and more to penetrate into the obscurity and finally bring the mysterious



truth to light. If the drone egg does not require fertilization, Italian mothers must always produce Italian drones and German mothers, German drones, even when they have been fertilized by drones of another race." His faith in this proposition was so strong that when in a few years he found one case in which it did not seem to hold good he gave up his theory, just when it was becoming generally accepted, and as an explanation took up the old exploded theory of Swammerdam of the vivifying action of an *aura seminalis*. Either the experiments of Count v. Berlepsch<sup>1</sup> or the work of v. Siebold reconverted him, for in 1861 he reiterated his belief in his theory.

#### EXPERIMENTS AND LATER INVESTIGATION ON BEES.

Owing to the fact that the phenomena connected with parthenogenetic development of the Drone Bee are so striking, even to a person not used to scientific methods of investigation, many experiments have been tried to test the Theory of Dzierzon. Journals devoted to Bee Culture as well as more strictly scientific publications have recorded a large number of experiments, of which but a few can be mentioned here.

Lowe (1867), after several years of experimenting with hybrid hives, denied the truth of Dzierzon's Theory. With Italian queens fertilized by common black drones he could get no definite results, but with Egyptian queens fertilized by black bees he obtained many drones which appeared to have characteristics of the male parent. His work was not so carefully recorded as was that of Perez which will be mentioned later.

Landois (1867) put worker eggs in drone cells and drones were produced, and *vice versa*. This he did many times and his results were verified by the presence of the little piece of wax, to which the eggs had been attached, sticking to the cocoons. He in every case cut out a little piece of the wax at the base of the cell and stuck this with the egg attached into the new cell, so that the egg was not injured by the transfer. His earlier experiments were not successful, due to imperfect manipulation. His conclusion then was that sex in the bee is determined by the food given the larva

<sup>1</sup> v. Berlepsch upheld the theory in a large number of papers in the *Eichstadt Bienenzeitung*. For a list of his writings see *Bibliotheca Zoologica*, O. Taschenberg, Zweiter Band, pp. 252-3.



and not by fertilization. It is known that after the eggs are hatched, at about the third day, the workers pour into the cell a food paste for the nourishment of the larva. Great quantities of this are eaten for six days and then the workers cap the cell, and in ten or eleven days the bee in its adult form comes out. The cap put over the smaller worker cells is flat; that over drone cells, arched. v. Siebold (1868), in answer to this theory, points out that sex is differentiated early in insect larvæ. Herold, for *Pieris rapæ*, was able to tell sex early. On the other hand Meyer did not see this in caterpillars only a few days old. Weismann, in *Musca vomitoria* and *Sarcophaga carnaria*, confirms Herold, but is not so sure in the case of *Corethra plumicornis*. Leuckart (1865) found first traces of external genitalia on the sixth day in *Apis*. v. Siebold insists that all embryos (queens included) up to the sixth day get food paste (digested chyle paste). The queens continue to get this, and from that time on the workers and drones get undigested honey and pollen. The food of the drones and workers is therefore the same. Landois thinks the drones of unfertile queens and of fertile workers are due to scanty nourishment or weak larvæ, for in *Vanessa urticæ* only males are produced if badly fed. v. Siebold (1871) does not find this true in *Polistes gallica*, for in the spring, when food is scarce, workers are produced; and Cuenot (1899) denies the truth of all such statements which make the sex depend upon nutrition.

Sanson and Bastian (1868) attempted to repeat the experiments of Landois, but in every case when the egg was put in a different cell the workers in the hive carried it outside. Never in a single case was the egg allowed to develop and they were therefore led to deny the experiments of Landois. The reason for their failure, as pointed out later by Landois, was imperfect manipulation. They cut out the entire bottom of the cell and stuck it in place by melting the edge with a hot needle, and this made such a bad job as compared with the work of the workers that they cleaned it out. Sanson (1868), in opposition to Landois, also cites cases of the production of drones in worker cells. This is now well known, as is also the converse, and this fact alone is enough to overthrow all of the work of Landois.

Perez (1878) put a pure Italian queen fertilized by a French drone into a hive with pure French workers and no drones. Later in the season he collected and examined carefully three hundred



drones from this hive. If these drones were produced from unfertilized eggs then they should, since the queen was pure Italian, show no trace of French characteristics. Perez first examined pure Italian and pure French drones from other colonies and determined what were the varietal markings in each case; and with these characteristics well mapped out examined the three hundred drones, and found one hundred and fifty-one pure Italians, eighty-three pure French and sixty-six showing various gradations between the Italian and French varieties, indicating that one hundred and forty-nine, almost half, had some French characteristics, which he held must have been derived from the French drone that had fertilized the queen.

Arviset (1878) announces a similar case, and Matter (1879) writes of three hundred black drones taken from the hive of an Italian queen fertilized by a black African drone.

Sanson (1878), in a reply to this paper, criticised the experiments of Perez, claiming that in this case the results had been modified by atavism, all bees having been derived from an original black variety. The possibility of the impurity of the queen was also suggested. He insisted that the purely parthenogenetic origin of drones was undoubted. It cannot be claimed that the contraction of the spermathecal opening is due to the pressure of the side of the cell on the abdomen of the queen, since drones often develop from unfertilized eggs in worker cells and workers from fertilized eggs in drone cells. He insisted that in the ovary all eggs are male and impregnation is necessary to produce female characters. If a queen is frozen and revived it is found that she afterward lays only drone eggs, and an examination of her spermatheca shows only dead spermatozoa.

Girard (1878) thinks that probably these hybrid drone eggs were laid by the hybrid workers which would result from the union of the Italian queen and French drone, and Hamit (1878) also takes the same stand; but according to the testimony of bee-keepers fertile workers are rare in a well-regulated hive, except in the cases of the Eastern varieties (Syrian, Palestine, etc.).

Perez replies to these criticisms in a later paper. The queen was obtained from a well-known firm of Italian apiarists and there can be no doubt of her purity, since the mother of the queen used in the experiment later produced many pure Italian queens. The possibility that the hybrids and French drones might be visitors



from other hives is denied by Perez on the ground that such visitations are not usual between hives, but this argument is not substantiated by other investigators. The hive used for the experiment had been used formerly for a pure French queen, but she could not have laid any of these eggs since considerable time had elapsed, and at any rate she would not have produced any of the sixty-six hybrids. The hybrids and French drone eggs could not have been laid by fertile workers since the drones all appeared at the same time.

Cook (1879) claims that these experiments are not wide enough to overthrow a theory which has so many arguments on the other side. Queens reared in autumn, when there are no drones, pass the winter as virgins and always after produce only drone eggs. Deformity and clipping of wings to prevent the marriage flight and consequent fertilization produces the same result. He suggests that possibly the queen used by Perez was a hybrid. (This is emphatically denied by Perez.)

The argument of atavism used by Sanson is such that a positive denial is impossible. One cannot but get the idea that Sanson was trying to make the facts fit his theory, however valid the argument may be.

In the face of the careful work of Perez it was evident that there must be some other explanation for these results, and it occurred to me that perhaps the mistake in the work came in when Perez mapped out the racial markings. In a recent number of a bee journal I noticed a letter from a novice at bee raising, complaining that some queens guaranteed to be pure Italians produced black drones, although the workers were yellow. I consequently decided to leave the matter to a bee-keeper of many years' experience, and wrote to Mr. E. R. Root, one of the editors of *Gleanings in Bee Culture*, and the following, by permission, is quoted from his letter: "We have repeatedly had queens direct from Italy that were supposed to be as pure as any stock could be; yet the drones from these queens varied greatly in their markings. Some of their sons would have a great deal of yellow on them, while others would be quite dark. If Perez had seen these drones he would have concluded some of them were French, some German and some Italian. Now the remarkable fact is that *bees* (workers) from these queens were all uniformly marked. They showed all the characteristics of pure stock."



"Pure Italian queens vary all the way from a jet black to a bright yellow. We had one daughter from an imported Italian that was very black ; but her bees (workers) were uniformly well marked and showed all the characteristics of pure Italians. Some of the queen daughters of the imported queen are quite yellow and some quite dark. Any one who attempts to judge of the purity of drones or queens by their markings has much to learn about bees."

I put a great deal of confidence in the statements of Mr. Root, since he is thoroughly informed in things relating to bees from a practical standpoint and is a man of high standing in his line of work. We must conclude then that in the honey bee we have a case in which certain racial characters are constant only in the abortive females, although they do not normally enter into the reproduction of the species. Since these markings are not a constant character, even in pure drones, any attempt to use them as tests of hybridism is not warranted.

A comparatively large number of cases have been recorded of hermaphroditic or androgynous bees. This fact was long since noticed by Lucas, more recently by Doenhoff, Menzel and Engster, and in 1864-5 by v. Siebold and Leuckart. There is a mixture of male and female characters, varying in different individuals, in both internal and external organs. Very often on each side of the body a few testicular cords and a few ovarian tubes, a well-developed male copulatory apparatus and a sting are developed, or one side of the body may be entirely male, the other side female. According to Leuckart all these must be regarded as workers with some male characteristics. The explanation offered is that fertilization did not take place here until after the male characters had become too well fixed to be thrown aside by female characteristics.

Boveri (1901) in a late paper suggests that such cases are due to the late fertilization of the egg, after mitosis has commenced, and as a result part of the cells have paternal characters and are therefore female, while the unfertilized portion remains male. This would, of course, easily explain the great differences in hemaphroditic bees.

There are numerous cases on record of queens which have taken their marriage flights and on their return to the hive, and during the rest of their lives, have laid eggs which never develop. The opponents of the theory of parthenogenesis eagerly take up a case



of this kind, claiming that for some reason the queen has not been fertilized and that on this account her eggs will not develop. v. Berlepsch was probably one of the first to make any observations on this line, and his conclusion was that it was due to some pathological condition of the queen.

Claus and v. Siebold (1873) took up this subject and carefully studied several cases that came to their notice. One of the cases was that of an Italian queen, born May 15, began to lay June 15 and continued until October 5, when she was killed. Her eggs did not hatch and an examination showed that her oviducts were normal, spermatozoa present in the spermatheca, but the ovarian tubes were degenerate. The conclusion, from this and other cases examined, was that all such cases of sterile queens are probably due to some irregularity in the formation of the ovum, and especially of the vitellus. Leuckart (1875) reports other cases examined and corroborates Claus and v. Siebold.

Of the opponents of the theory of Dzierzon, none perhaps are as radical as Ulivi (1874-82). His views were briefly as follows: Queens are usually fertilized in the hive, and he claims to have witnessed the act of copulation several times. The spermatheca, on the return from the so-called "marriage flight," is clear and contains no spermatozoa, as was demonstrated by numerous examinations. The marriage flight is explained as being merely for exercise. Drones are not mutilated in copulation, and on examination the white appendage which is always seen on the queen on her return from the marriage flight is found to be excreta. Every egg, male or female, is fertilized. Queens that were never allowed to fly (their wings being clipped) were put in hives without drones and laid no egg or eggs that did not hatch. Every queen whose spermatheca is distended has been fertilized. None of the eggs of a queen that has never met a drone will hatch. There is no such thing as a fertile worker. Fertilized eggs will keep through the winter and hatch out in the spring. He also claims that there can be no true parthenogenesis when a fertile copulation is admitted. The effect of the spermatheca does not consist of a simple excitement of the supposed vital germ preëxisting in the egg, but of a real infusion of the absolute principle of life. No transformation of sex can be effected by spermatheca injection. It need scarcely be added that such views have found no supporters.

For the past two or three years Dickel has been advancing a new



theory in regard to the determination of sex in the bee and he has some supporters, although the number of these seems to be decreasing. His views are briefly the following: Eggs laid by unfertilized queens or fertile workers produce drones, but these differ from the drones of a colony with a fertile queen. The egg before fertilization contains only male elements, the sperm cell only female, and after union of the two these are equally balanced. A fertile queen can lay only fertilized eggs since she cannot withhold sperm cells. The workers, in crawling over the brood cells just after the eggs are laid, pour out a secretion which penetrates the chorion of the egg. The wax, in the formation of brood cells, is kneaded in the mouths of workers and is impregnated from the salivary glands with a secretion characteristic of drone or worker cells, and this determines the kind of cell made and consequently the nature of the secretion poured out over the egg when laid. The two sexes are equally balanced in the newly-laid egg and the workers pour out a secretion from one of two glands in the head, the secretion from one causing the egg to develop into a male; of the other, into a female. The secretion of the "salivary" gland of the workers is comparable to a sexual act and probably produces similar emotions. Sex cannot be determined by mere size of cell or by food. These glands have been observed in the queen in a rudimentary state and in wasps. It is further claimed that experiments (performed by Dickel himself) on hybrid hives have clearly shown paternal characteristics in male offspring.

Weismann and his students, Petrunkevitch and Paulcke, have pointed out the errors in this theory and, from work of their own, strongly reaffirm the view of Dzierzon, that sex is here determined by fertilization.

#### OTHER CASES OF PARTHENOGENESIS.

*Classification.*—Parthenogenetic development manifests itself in a variety of ways and many synonymous terms have been applied to the different kinds of parthenogenesis. The following classification will serve to make clear the relations of the different phenomena to one another and to show the synonymous terms used:

#### PARTHENOGENESIS (Agamogenesis).

##### 1. Partial.

Development to early cleavage or larva.

*e.g.*, Vertebrates (?) and Echinoderms.



## 2. Complete—to adult condition.

(a) Occasional—exceptional—Tychoparthenogenesis (Henneguy).

*e.g.*, *Bombyx mori*.

(b) Normal—Isoparthenogenesis (Hatschek).

(1) No Alternation of Generations.

*e.g.*, *Apis*, *Nematus*.

(2) Alternation of Sexual and Parthenogenetic Generations—Heteroparthenogenesis (Hatschek), Heterogeny (Leuckart), Pseudoparthenogenesis (Spencer).

*e.g.*, *Aphis*, *Daphnia*.

The following classification of Complete Parthenogenesis is based on the sex of the resulting individuals:

## 1. Homoparthenogenesis (Henneguy), Complete Parthenogenesis (Spencer).

One sex only produced from unfertilized eggs.

(a) Arrhenotoky (Leuckart), Androgenetic (Breyer).

Males produced. *e.g.*, *Apis*.

(b) Thelytoky (v. Siebold), Gynogenetic (Breyer).

Females produced. *e.g.*, *Psyche*.

## 2. Heteroparthenogenesis (Henneguy), Mixed Parthenogenesis (Stein).

Amphoterotoky (Taschenberg), Amphotoky (Lankester).

Both sexes produced parthenogenetically. *e.g.*, Aphidæ.

An Alternation of Generations often accompanies parthenogenetic development, and in the literature considerable confusion occurs by a mixing of the terms. For this reason the following classification is given so that the occurrence of Parthenogenesis in relation to Alternation of Generations may be made clear:

*Alternation of Generations (Metagenesis Owen).*

## 1. Sexual Generation alternating with a Budding Generation.

(a) Buds remain attached to form colonies.

*e.g.*, Medusæ and Polyps.

(b) Buds separate.

*e.g.*, *Salpa*.

## 2. Sexual Generation alternating with Parthenogenetic Generation.

Heteroparthenogenesis (Hatschek), Heterogeny (Leuckart).



## 3. Two Sexual Generations differing in form—Alloigony (Leuckart).

(a) One free generation, one hermaphroditic and parasitic.

*e.g.*, *Rhabdonema*, *Allantonema*.

(b) Seasonal Dimorphism.

*e.g.*, *Lophyrus pini*.

Pædogenesis or the parthenogenetic reproduction by larval forms is frequently met with (*e.g.*, Diptera). This term was introduced by v. Baer (1864), but unfortunately it has since been applied by Seidlitz (1872), Dilling (1880) and others to all cases of sexually mature larvæ, even though the reproduction be truly sexual. Thus they would include under this term the reproduction of Axolotl and of Gyrodactylus. v. Siebold (1869) used the term pædogenesis for the reproduction of the Strepsiptera, but in this case the sexually mature female is simply a degenerate adult and not a larval form as v. Siebold supposed, and the reproduction is sexual as far as the evidence at present goes. To aid in the clearing up of this confusion of terms, Taschenberg (1892) suggests the term Proiogony for all cases of sexually mature larvæ, so that the word Pædogenesis can be used in its original and proper meaning. Chun (1892) uses the term Dissogonie for cases like those found by him in *Cydippe*, where the same individual at different stages of development is sexually mature, and these stages are separated by a metamorphosis.

The word Pseudoparthenogenesis has been applied by some writers to cases in which the eggs are fertilized from a seminal receptacle (*e.g.*, female eggs of *Apis*), and in which copulation does not take place for each egg. The use of such a word is unfortunate since it implies that there is a similarity to parthenogenesis, while there is really a very fundamental difference.

## INSECTA.

HYMENOPTERA.—Besides the case of the Honey Bee referred to at some length on preceding pages, numerous other cases of parthenogenesis occur among the Hymenoptera.

*Tenthredinidæ*.—The first case described in this family was that of *Nematus ventricosus* (= *N. ribesii*) by Robert Thom (1820) who wrote: "The insect is male and female, but the ova of the female produce caterpillars, even when the male and female flies are kept separate. How long this offspring would continue to



breed has not been ascertained. . . . There is some reason to suspect that there is a connection between male and female caterpillars, for I have frequently observed them twisted together for some time after they have ceased eating, and a little before they cast their skins to go into the pupa state." This same form was investigated by Kessler (1866) and especially by v. Siebold (1871). Other papers on this family are those of Cameron (1885), Fletcher, (1880), v. Stein (1881-83) and Brischke (1887). Taschenberg (1892) gives a long list of members of this family for which parthenogenetic development has been recorded. The various members of the group afford examples of Arrenotoky, Thelytoky and Amphoterotoky.

*Cynipidæ*.—In this family many species are known only from females, males being entirely absent or very rare. Leon Dufour (1841) found no males in two hundred individuals of *Diplolepis gallæ tinctoriæ* collected, and Hartig (1843) no males in nine thousand examples of *Cynips divisa*. Osten-Sacken (1861) attempted to explain this by claiming that the males live in different galls from the females and are not recognized as the same species. Such a dimorphism is known for some *Cynipidæ* and it is probably true for many more. Taschenberg (1892) gives a list of nineteen cases in which males and females have been described as different genera and are now known to be but cases of sexual dimorphism. *Cynips quercus-ærculata* (Osten-Sacken) which produces a large gall in the autumn, in the spring of the next year lays eggs which produce galls of another form, originally named *C. q. spongifica*. The autumn brood of this *Cynips* consists of parthenogenetic females, while the spring brood is of both males and females.

*Neuroterus lenticularis* produces galls of a certain form on the under side of oak-leaves and the flies appear in the early spring. These deposit their eggs on the buds of the oak which produce galls unlike those of the autumn and the fly, of both sexes, which emerges from the second gall has been referred to a separate genus (*Spathegaster baccarum*). This in turn lays eggs which produce the original form of *Neuroterus*, all females.

In the families of Ants and the family Vespidae parthenogenesis similar to that of *Apis* is very common, as is also true for other species of the family Apidae. The best known cases are those investigated by v. Siebold (1870-71), *Vespa germanica* and *Polistes gallica*.



*Andrenidæ*.—In *Halictus*, according to Fabre (1880), a mixed brood results from the development of the unfertilized eggs, Amphoterotoky. Cf. Perez (1895).

*Ichneumonidæ*.—v. Siebold (1884) describes Thelytoky for *Paniscus glaucopterus*.

*Chalcididæ*.—Adler (1881) describes an alternation of generations and probable Arrhenotoky for *Pteromalus puparum*.

COLEOPTERA.—Few cases of parthenogenesis are recorded for this sub-order, Osborne (1879–81) and Jobert (1882) being the only observers who record such phenomena. The cases recorded are *Eumolpus (Adoxus) vitis* and *Gastrophysa raphani* (*Gastroidea viridula*). Osborne considered parthenogenesis in *G. raphani* to be as frequent as in *Nematus ribesii*, while Jobert suggests that the form studied by him (*Adoxus*) is hermaphroditic. v. Siebold (1869) described pädogenesis for the Strepsiptera, the females of which are wingless and worm-like with a flattened triangular head and live in the abdomen of bees and wasps. The female is viviparous, producing hundreds of young, but is not a larval form at the time of reproduction, and there is no evidence that fertilization does not take place.

LEPIDOPTERA.—In *Bombyx mori* occasional parthenogenesis has been observed. Constans de Castellet (1795) first recorded this, and it was confirmed by Herold (1838) and Leuckart (1855). v. Siebold (1856) and a pupil Schmid got both sexes from unfertilized eggs. Verson (1873) showed that reproduction in this case is generally sexual and (1888) claimed that parthenogenetic development for this species is usually partial. Tichomiroff (1886–91) produced partial parthenogenesis in this form by mechanical excitement (1886) and by putting the eggs in 65 per cent. sulphuric acid for two and one-half minutes (1889). Nussbaum (1898) found that two per cent. of the eleven hundred unfertilized eggs examined showed segmentation but never hatched, and in similar observations on the eggs of *Parthesia* and *Liparis* he did not get cleavage in any case.

In *Solenobia triquetrella*, *S. lichenella*, and *Psyche helix* true Thelytoky occurs and we have a succession of parthenogenetic females, and only occasionally in *P. helix* is a male produced.<sup>1</sup> Much of the early work on parthenogenesis was done on Lepidop-

<sup>1</sup> Described by Claus, 1866. No males are known for *Solenobia*.



tera, some of the workers being Réaumur (1738), Pallas (1767), Degeer (1771), Kühn (1775), Schiffermüller (1776), Schrank (1776 and 1802), Scriba (1790) and Reutti (1810). v. Siebold was at first (1849) inclined to doubt the existence of parthenogenesis in these species, but in 1856 published the results of elaborate experiments in which it was fully proven. Speyer (1847), Wocke (1853) and Reutti (1853) reached similar conclusions, and Leuckart (1858) examined the females of *Solenobia* and found no spermatozoa in the seminal receptacle, although there was a micropyle on the egg. Hartmann (1871) raised many successive generations of individuals parthenogenetically.

HEMIPTERA.—The first to investigate the reproduction of Aphids was Leeuwenhoek (1695). He found that the young are produced vivaparously and that there are few males, and Réaumur (1737) from like observations, on theoretical grounds, held that they are protandric. Bonnet (1745), who generally gets the credit of having first observed the reproduction of the group, raised nine generations of viviparous females in two and one-half months in summer, and in the fall males appeared which copulated with the females, and eggs were laid which hatched out in the following year. Degeer (1773) worked on *Lachnus pini* and *Aphis rosæ*, and concluded that sexual individuals could be entirely done away with by keeping the insects protected from cold, and in this he was confirmed by Kybér (1815), who raised fifty successive generations of viviparous individuals in four years. Most of these earlier workers thought that the viviparous individuals were larval forms, which would afterward develop into the oviparous individuals.

Similar experiments led Duvau (1825) to believe that the oviparous and viviparous individuals are entirely distinct and that they never have the power of reproducing in both ways, and later Morren (1836), for *Aphis persicæ*; Ratzeburg (1844), for *Aphis oblonga*, and Newport (1847), for *Aphis rosæ*, came to similar conclusions.

Dufour (1841) repeated the experiments of Bonnet and referred the reproduction of *Diplolepis gallæ tinctoriæ* to "spontaneous or equivocal generation, in which impregnation is in no way concerned." Morren (1836) also believed in this spontaneous generation and thought that Aphids are developed in the body of the virgin parent: "Comme chez quelques entozoaires par individualisation d'un tissu précédemment organisé."<sup>1</sup>

<sup>1</sup> Page 90, *loc. cit.*



v. Siebold (1839) examined the viviparous and oviparous females and found that there is no appreciable difference between the ovaria of the two, but that the former lack a receptaculum seminis, and are, therefore, incapable of copulation. In the former point he was confirmed by Owen (1849), but not by Steenstrup (1842), who insisted that the viviparous individuals do not have ovaries but a well-developed uterus; to these he gave the name "Ammen" or nurses.

A most important step in advance was made by Steenstrup (1842) when he introduced the idea of an Alternation of Generations in Aphid development, as well as for other forms. He and Carus (1849) concluded that the viviparous development is comparable to the Cercaria stage of the Fluke worm, and the theory, first suggested by Duvau (1825), that here we have two generations, each distinct from the other, but each in turn giving rise to the other, was strengthened. Steenstrup would not, however, admit that the viviparous development is at all comparable to the oviparous, for he wrote: "No true ovary has been discovered in the larval and larviparous Aphids, but the germs, as soon as they are perceptible, are situated in organs which must be regarded as oviducts and uteri."<sup>1</sup>

About this time the theory of Dzierzon (1845) was advanced for the parthenogenetic development of the drone eggs of the Honey Bee, but such an explanation was not accepted for Aphids, and even v. Siebold, in his celebrated paper, "Wahre Parthenogenesis bei Schmetterlingen und Bienen" (1856), although advocating parthenogenesis for the forms on which he worked, refused to admit it for plant lice, for he wrote: "Die viviparen Blattläuse keine Weibchen sind, welche sine concubitu im jungfräulichen Zustande entwicklungsfähige Eier hervorbringen, sondern geschlechtlose mit Keimstöcken ausgestattete Ammen-oder larvenartige Individuen, welche von den wirklich jungfräulichen Blattläuse-Weibchen himmelweit verschieden sind."<sup>2</sup>

Owen (1849) applied the term Parthenogenesis to the development of Aphids, not in the sense in which it is now used, but as an equivalent of the term Alternation of Generations used by Steenstrup. Owen thought that the fertilization which takes place in

<sup>1</sup> Page 112, English translation.

<sup>2</sup> Page 14, *loc. cit.*



the fall was enough to furnish what he designated as "spermatic force" for the development of the numerous summer generations. "In the vertebrated and higher invertebrated animals only a single individual is propagated from each impregnated ovum. Organized beings might be divided into those in which the ovum is uniparous and those in which it is multiparous. This is the first and widest or most general distinction which we have to consider in regard to generation, and in proportion as we may recognize its cause will be our insight into the true condition on which Parthenogenesis depends." <sup>1</sup>

The next step in advance was made when it was discovered by Leydig that there is no observable fundamental difference between the ova of the viviparous and oviparous females. There is, of course, a great difference between the summer eggs which develop parthenogenetically and the winter eggs as to size and amount of yolk, but this is only such a difference as may be observed between the eggs of various species and in no way argues for a dissimilar origin. This, then, put the Aphid development in the same class with that of *Solenobia*, *Apis* and other species known to develop from unfertilized eggs; but so firm a hold had the idea that fertilization is necessary to the development of a true egg that Huxley (1858) and Lubbock (1857) gave the name "Pseudova" to the eggs of the viviparous females. From this time on it has been held that the viviparous development was a case of true parthenogenesis.

The Alternation of Generations and parthenogenetic development is further complicated by other factors. Thus in Aphids the last of the viviparous generations is a generation known as the *sexupara*, the parthenogenetic and viviparous descendants of which are winged males and wingless females. After copulation, these females lay the fertilized winter eggs. This cycle of development is still further complicated by migrations from one plant host to another. A winged parthenogenetic generation frequently appears, and then may migrate to a different plant there to reproduce itself, and in a later generation return to the original host (Lichenstein, 1875). These generations have been distinguished by Blochmann (1889) as emigrants, alienocolæ and remigrants. Thus *Pemphigus terebinthi* (Derbes, 1872) gives rise to a wingless parthenogenetic generation (*a*), which produces another winged

<sup>1</sup> Page 62, *loc. cit.*



generation (*b*), the emigrants. This generation goes to another plant and produces a third generation (*c*), the remigrants and sexupara, which hibernate, return to the original plant and produce the small wingless sexual forms (*d*), the "sexuales." Here the sexual generation occurs in the spring rather than in the fall, as in most other forms.

Similar conditions are found in the Chermetidæ, except that here the parthenogenetic generations as well as the generations arising from fertilized eggs are oviparous (see the works of Blochmann, Dreyfuss and Cholodovsky). In *Chermes abietis* the fertilized egg develops into a wingless parthenogenetic female (*a*), which hibernates at the base of the buds of *Abies balsamia* and produces galls. In the spring winged females (*b*) are produced, which migrate to the Larch and give rise parthenogenetically to a wingless generation (*c*), which hibernates under the bark. These alienocolæ in the following spring produce parthenogenetic winged females (*d*), remigrants or sexupara, which return to *Abies* and produce wingless males and females, the eggs of which produce the first generation named in the cycle. Here two years is required to complete the cycle.

In *Phylloxera quercus* (Lichenstein) the winter eggs are laid on *Quercus coccifera* and give rise to females, which produce parthenogenetically a winged generation (emigrants), which fly to *Q. pedunculata* and *Q. pubescens*. These parthenogenetically produce several generations of alienocolæ and finally produce the remigrating sexupara, which return to *Q. coccifera* and produce the sexual generation. In *Phylloxera vastatrix* the generation which develops from fertilized eggs laid under the bark of the grapevine wander to the roots and there produce parthenogenetically several generations of wingless forms, which cause the swellings of the roots. This series is closed by the production of winged sexupara which go to the surface and swarm. Their eggs, which develop without fertilization, vary in size according to the sex, and the resulting individuals again begin the cycle.

The physiological difference between fertilized and parthenogenetic eggs is often accompanied by difference in appearance. The parthenogenetic ones are generally small and poor in yolk and develop in a shorter time and in greater number, while those requiring sexual cell union are larger and develop more slowly. The former are called summer eggs or *Subitaneier*; the latter winter



eggs or, because of the fact that they remain undeveloped for some time after fertilization, *Dauereier* or retarded eggs.

DIPTERA.—This group furnishes some excellent examples of pædogenesis or pædoparthenogenesis, and the phenomena as shown in various genera grade into each other in such a manner that it becomes evident that no line of demarcation can be drawn between parthenogenetic development from eggs laid by adult females and pædogenesis. While it is perhaps well to make a distinction between the phenomenon of parthenogenesis as exhibited by eggs of adult females and the same phenomenon as shown by the eggs of females which have not yet reached the last or adult stage of their development, yet the fundamental principle is the same in each case and it is not well to put too much stress on the degree of development of the parent when such a distinction tends to hide the similarity of the two kinds of reproduction.

Wagner (1862), in a Russian paper, reported cases of fly *larvæ* which bring forth young viviparously and, as he thought, from a transformation of the fat body, the parent dying at the birth of the offspring. This was in opposition to every principle of zoology and was, of course, not accepted on account of the announced method of formation of the embryos. In a short time, however, v. Baer (1863) and Meinert (1864) confirmed Wagner in all points except the source of the young, and later Wagner came to the conclusion that the viviparous young, are developed from true eggs. These conclusions were confirmed by Ganin (1865). The forms worked on were *Miastor* and *Cecidomyia*.

The next phenomenon of the series is that shown in *Chironomus* (Grimm, 1870). Here the *pupæ* lay eggs which develop parthenogenetically. This case comes nearer to what is observed in Hymenoptera, and the next step, which completes the series, is that of *Chironomus Grimmii* (Schneider, 1885) in which the *imago* lays parthenogenetic eggs.

Without going into a discussion of other forms on which work has been done, it will be evident that here we have a series of cases in which the Cecidomyidæ have reached the most specialized condition, they being able to bring forth young viviparously from a larval parent without waiting for the parent to reach the adult condition before acquiring sexual maturity. The case reported by Grimm for *Chironomus* would then appear to be one in which this power of bringing forth young very soon had not been so com-



pletely acquired, since the female must here wait until she reaches the pupal stage before she is sexually matured, and then she has not the power of viviparity but must lay her eggs; viviparous reproduction being undoubtedly an advantage to a species from the standpoint of increasing their numbers. It would then seem that some Diptera have not only acquired the advantage of parthenogenetic development but have shifted this power back to the pupa, or even larva, so that they may still more profit by this specialized method of reproduction.

ORTHOPTERA.—The development of eggs without fertilization has recently been described for this group by several persons. Dominique (1899) obtained parthenogenetic development (thelytoky) in *Bacillus gallicus*, while Heymons got one male to every twenty to twenty-five females in the parthenogenetic offspring of *B. Rossii*; and Azam (1898) and Stadelman (1898) also got some parthenogenetic individuals in the last-named species. Bolivar (1897 and '99) got three cases out of ten in which isolated larvæ of *Heptynia hespanica* produced eggs which developed; but he is not sure that they were not fertilized, although Pautel describes parthenogenesis as occurring in this species [cf. also Brunn (1898)].

From the evidence now at hand it would appear that parthenogenesis in this group is exceptional.

#### CRUSTACEA.

Next to plant lice, our earliest knowledge of the development of unfertilized eggs was for cases among the Crustacea. Schäffer (1755) described the development of eggs from unfertilized females of Daphnids, and by isolation he succeeded in producing several generations without fertilization and described this as being similar to what was known to take place in Aphids. Ramdohr (1805) raised ten successive generations parthenogenetically, and Jurine (1820) also confirmed the work. Ramdohr, however, did not look on these forms as true females but as hermaphrodites. These observations were on summer eggs, there being practically the same difference in this group as we find in Hemiptera. The summer eggs as in Aphids develop parthenogenetically, while the winter eggs require fertilization.

v. Siebold (1856) stated that he thought that *Apus cancriformis*, *Limnadia gigas* and *Polyphemus oculis*, in which no males had been



observed, showed true parthenogenesis, and Leuckart (1857) expressed the same opinion for *Daphnia*. In 1858 males of *Apus* were discovered and were examined by v. Siebold and he thus learned that some broods can go on developing parthenogenetically, like the Lepidoptera (Thelytoky), while other broods have both sexes present. For several years he watched a small pool near Munich, and at one time with great care removed every individual and found no males in 5796 individuals. In pools where both sexes occurred the proportion of males and females was very variable, and v. Siebold was led to believe that in these cases the males are disappearing, since from examinations in different years he found a constantly increasing proportion of females.

v. Siebold foresaw the objection that males might have been present previous to the examination of the pools, and consequently examined the male genital organs and spermatozoa and then the ovaries and their development. He never succeeded in finding any spermatozoa in the female genital organs. The structure of the ovum made this observation decisive since he found a hard egg-shell formed in the uterus and no micropyle, so that if fertilization takes place it must be before the egg is laid. Brauer (1872) found that fertilized eggs of *Apus* produced males.

Several other groups of Crustacea show a similar method of development, but do not differ to any extent from *Apus*. Parthenogenesis has been observed in the Phyllopods, Ostracods and Copepods, but in none of the Malacostraca.

In *Artemia salina*, Joly (1840) found no males in 3000 individuals examined and explained this as due to hermaphroditism, but Gerstäcker (1867) and especially v. Siebold (1871) established this as a case of true parthenogenesis. In *A. Milhausenii*, Fischer v. Waldheim (1834), Rathke (1836) and Fischer (in Middendorff's *Reise, Zoologie*) found that males are rare, and the same is true for *Limnadia Hermanii*, both cases being explained like that of *A. salina*. The maturation of the parthenogenetic egg of *A. salina* (Brauer, 1893) is discussed in another place.

A case worthy of note is that of *Leptodora hyalina*, a Daphnid, in which the winter eggs follow the usual plan of Crustacean development and form a Nauplius stage, while the summer eggs develop directly into an adult form with all limbs present. This is one of the striking cases which indicate that parthenogenesis is acquired



where it is desirable to produce individuals quickly, since here the larval stages are omitted.

Unisexual and bisexual generations alternate with each other in various ways in Crustacea and the mode of the alternation is remarkably related to their environment, as has been shown by Weismann. According to whether the causes of destruction visit a colony once or several times during the year we find forms which have one or several cycles of parthenogenetic and bisexual generations, and finally species are known which show no alternation. These are designated as monocyclical, polycyclical and acyclical respectively.

#### TREMATODES.

The development of the *cercaria* and *redia* stages of *Distomum* has been the subject of much discussion for a long time. Leuckart, in his *Parasiten des Menschen*,<sup>1</sup> gives an historical account of our knowledge of the development of these forms up to the date of its issue (1879). That there is a development without fertilization is admitted on all sides, but the question as to whether the *redia* develop from true germ cells is still a point of dispute. Leuckart (1882) and Schwarz (1886) consider this as a true case of pædogenesis, the internally developing *redia* being looked on as arising viviparously from cells of the germinal epithelium. On the other hand, Wagener (1857) and Biehringer (1885) maintain that they arise from cells of the body wall and are therefore not produced sexually but by budding. Korschelt and Heider, in their *Text-Book of Embryology* (1890), do not consider this difference of great significance. “<sup>2</sup>This difference does not seem to us to be important, for we have already seen that the parietal cells and the germ cells are embryologically of the same origin. In a portion of the cells of the body wall even, a differentiation into separate histological elements appears not to have taken place, and for this reason they may continue to develop in the same way as the real germ cells. In harmony with this view is the statement of Thomas,<sup>3</sup> who derives the *redia* from both the germ cells and the cells of the body wall; if the supply of the former were exhausted, then the latter might take their place.”

<sup>1</sup> II. Bd., p. 488 and following pages.

<sup>2</sup> Page 183, Vol. I, English Translation.

<sup>3</sup> Thomas (1883).



If such an explanation be the true one, then it would appear that the difference between sexual and asexual reproduction is not so great as is generally supposed.

### ROTIFERS.

The phenomena of development are very complicated in the Rotifers. In most cases the males differ from the females in being smaller and in the absence of an alimentary canal. The eggs are of two kinds, the same difference being seen here between summer and winter eggs as in Aphids. Cohn (1856-58) first worked out the development of this group and found that the winter eggs are fertilized, while the summer eggs are not. Huxley (1857) looked on these summer eggs as sexless buds, but the work of Joliet (1883), Plate (1884-85) and Maupas (1889-90) established this as true parthenogenesis. Here, as in Aphids and Daphnids, the males appear at the beginning of an unfavorable period in the life cycle.

Under the subject of the Maturation of Parthenogenetic Eggs the work on Rotifers is mentioned, and the results there recorded are the most interesting features in connection with the phenomenon of parthenogenesis in the group. The principal point of interest is that the male and female eggs behave differently during their maturation, although eggs of both sexes have the power of development without fertilization.

Lauterborn (1898) found that the Rotifers could be classified into three groups as follows: (1) Species found all the year around; (2) Species found in summer, and (3) Species found in winter. In the summer and winter species the fertilized and yolk-laden eggs appear after a long series of parthenogenetic generations; they are monocyclic. In the species found during all seasons of the year the appearance of the males and the consequent fertilized eggs may occur twice or more times during the year; they are polycyclic. Probably some species are acyclic; that is parthenogenetic forms can be produced indefinitely and "winter" eggs are unknown. The determination of the appearance of males in Rotifers has been variously explained, the amounts of heat (Maupas) and nutrition (Nussbaum) being often considered as the causes. Lauterborn concludes that such external causes do not fully explain this but that some internal factor is the principal cause. The cyclic appearance



of fertilized eggs recalls the periodic occurrence of conjugation among protozoa, and according to Wesenberg-Lund (1898) and Lauterborn (1898) senility is an important factor in determining the length of the cycle. That lack of nutrition and the appearance of a senile condition are intimately connected seems very probable, if we may be permitted to reason from analogy on work done on *Paramœcium caudatum*. Calkins, in a recent paper,<sup>1</sup> records that he has been able to raise Paramœcia for six hundred and sixty-five generations by fission, and they were rejuvenated five successive times by change of food rather than by conjugation, or as he expresses it "parthenogenetically."

#### VERTEBRATES.

The question as to whether there is a parthenogenetic development among any of the Vertebrates is one which has been much discussed. If there are any cases at all they are cases of partial parthenogenesis, since in no case is it claimed that development goes farther than the first few cleavage stages. Bonnet (1899) discusses at some length the evidence on this subject, and since he has so well reviewed the literature it is not necessary to do more here than state the general conclusions to be reached from a survey of what has been reported.

Eggs of *Amphioxus lanceolatus* (van der Stricht, 1895) show a tendency to divide if not fertilized. This is not pronounced.

Cleavage of unfertilized eggs in the ovary are reported among the Gadidæ by Burnett and Agassiz (cited by Oellacher, 1869), for the Sturgeon by Bellonci (1885), and for the Trout by Oellacher (1872). Oellacher attributed this to the retention of the eggs for too long a time.

For the Frog and other Amphibia many investigators have claimed parthenogenetic cleavage, since it frequently happens that eggs which pass from the female when she is not copulating with a male show cleavages, but these are generally irregular. Pflüger (1882) was able to show rather conclusively that such cases are due to fertilization of these eggs by spermatozoa in the water which are nearly dead, and consequently the development is short and irregular. Kulagur (1895) and Bataillon (1900) did some experiments

<sup>1</sup> Calkins, Gary N., 1902, "Studies on the Life History of Protozoa," III. The Six Hundred and Twentieth Generation of *Paramœcium caudatum*, *Biol. Bull.*, III, No. 5, pp. 192-205.



on artificial parthenogenesis, but these must not be considered as arguing for a true natural parthenogenesis.

Among Reptiles, Strahl (1892) reports irregular parthenogenetic cleavages.

In the Birds, the evidence for a parthenogenetic development is perhaps the strongest of that for any vertebrates. It frequently happens that a blastoderm is formed on an egg which is apparently not fertilized. Cases of this kind are found in the Chick (Coste, 1859; Oellacher, 1869; Koelliker, 1879, and others), in the Turtle Dove (Motta Maja, 1877; cited by Duval, 1884), and for several other birds (Duval, 1884). Balfour (1880) pointed out that care must be exercised in passing judgment on these cases, since it is known that spermatozoa can live for a considerable time in the female and that possibly these are really cases of fertilized eggs. This is entirely upheld by the later work of Lau (1895) and Barfurth (1895), who show that eggs from virgin hens do not show cleavage in the same way as do those from hens which have copulated with a cock even a considerable time before. In eggs from virgin hens the blastomeres do not have a cellular character, since all but a few lack nuclei, and when nuclei are present they do not divide mitotically. The blastoderm lacks all power of assimilation, the blastomeres are irregular and the whole shows no thickening at the posterior end. There is never a segmentation cavity. Lau and Barfurth looked on such cases as due to a physico-chemical process, caused partly by evaporation and partly by coagulation of the protoplasm. Cases in which the female has previously copulated would then appear to be similar to those of the frog, in which there is a fertilization accomplished by a partially devitalized male cell.

Even in Mammals, cases are recorded of the cleavage of the egg while still in the Graffian follicle. Janosik (1896) reports several cases (Rabbit) in which a cleavage has taken place, a semblance of a cleavage cavity formed and the whole mass has broken away from the membrana pellucida as in normal development; but the phenomenon is so evidently connected with disintegration from the very beginning that it must not be considered as parthenogenesis.

The question as to whether Dermoid cysts are due to the parthenogenetic development of an egg has received a great deal of attention, and the exceptional case reported by Répin (cited by Duval, 1895) would point strongly to such an explanation as the true one. This cyst had four limbs and terminated in a kind of



head composed of bones arranged in a cube and surmounted by three teeth. The bones of the feet and hands were perfectly recognizable. There was no alimentary canal in the body, but beside it was a tube which histologically resembled an intestine.

It would appear then that these phenomena are not true parthenogenesis, unless it be that we consider that as the explanation of the cysts. The fact that the cleavages do not follow the regular plan of fertilized eggs would not of itself bar these cases as being classed as a true development from an unfertilized egg, since in other cases, where there is undoubtedly a parthenogenetic development, the method of growth differs from that of the fertilized egg of the same species, *e.g.*, *Leptodora*. Neither must we bar these cases because the development goes but a short distance, since the life of an individual must be considered as beginning with the unsegmented egg, and if that egg shows a power of development without fertilization, that phenomenon is as truly parthenogenesis as if an adult animal resulted. However, since in these cases we find the segmentation of the egg to be more in the nature of a physico-chemical change than a true cleavage, we must consider it as entirely different, and we must, of course, bar out all cases in which the proper amount of care has not been taken in proving that fertilization has not been affected by a half-dead spermatozoon.

#### ARACHNIDS.

But one well authenticated case is known to exist in Spiders (Campbell, 1883). Parthenogenesis in this group has recently been discussed by Montgomery (1903), and it is not necessary to repeat his discussion since it has been done so recently.

In many other animals there is a marked tendency for the mature egg to go on dividing if fertilization does not take place. This is often observed in Echinoderms, some Annelids and Molluscs. Such eggs never develop beyond a very early stage, and only a very small proportion of eggs show this cleavage. A point worthy of note is that these very forms are the ones which have yielded the best results in work done in Artificial Parthenogenesis, and the explanation which seems to follow from this is that such eggs normally require a very small amount of stimulus from the male cell, and the addition of some chemical to the water is enough to take the place of the male stimulus. In fact the results of artificial



parthenogenesis differ from what is normally found only in the greater proportion of parthenogenetic eggs.

### THE MATURATION OF PARTHENOGENETIC EGGS.

The main point of interest in parthenogenesis is perhaps that of the maturation of the parthenogenetic eggs, on account of its general bearing on the theory of fertilization and on account of its support of the theory of the individuality of chromosomes.

Minot (1877), in an article on the theoretical meaning of maturation, suggests that parthenogenesis may be due to failure to form polar bodies, and since the entire mass of chromatin remained in the egg it would be hermaphrodite and capable of development without the addition of any chromatin from the male cell. Balfour (1880) follows out the same line of thought in suggesting that the function of forming polar bodies has been acquired by most ova to prevent parthenogenesis, and van Beneden (1883) held a nearly similar view.

Weismann (1886) found that one polar body is given off in the case of *Polyphemus* (Daphnid), and he later determined the same thing for parthenogenetic Ostracodes and Rotifers.<sup>1</sup> Blochmann (1888) found in Aphids that one polar body is given off in the case of eggs which develop parthenogenetically, while two are produced in eggs which require fertilization. Weismann was thus led to the view that the second polar body is of special significance in parthenogenesis. In insects (Blochmann and others) the polar bodies are not thrown out of the egg as in most other animals, but the chromatin masses remain embedded in a vesicle in the protoplasm of the egg, near the periphery, and are called "polar nuclei."

Boveri (1887) found in *Ascaris megalocephala* that the second polar body might remain in the egg (as is normally the case in insects) and give rise to a nucleus indistinguishable from the pronuclei. He, therefore, suggested that parthenogenesis might be due to the retention of the second polar body in the egg and its use as a male pro-nucleus.<sup>2</sup> "The second polar body would thus, in a certain sense, assume the rôle of the spermatozoon, and it might

<sup>1</sup> Compare Lenssen (1899), Erlanger u. Lauterborn (1897) and Mrazek (1897).

<sup>2</sup> Boveri (1887), p. 73.



not without reason be said: Parthenogenesis is the result of fertilization by the second polar body."

This conclusion was in part confirmed by Brauer (1893) on the parthenogenetic egg of *Artemia salina*. There are two types of maturation in parthenogenetic eggs occurring in the same animal, one in accordance with the idea of Boveri and the other not irreconcilable with it. For a brief description of the two methods in *Artemia* the statement of Wilson<sup>1</sup> is quoted:

"In both modes typical tetrads are formed in the germ-nucleus to the number of eighty-four. In the first and more frequent case but one polar body is formed, which removes eighty-four dyads, leaving eighty-four in the egg. There may be an abortive attempt to form a second polar spindle but no division results, and the eighty-four dyads give rise to a reticular cleavage-nucleus. From this arise eight-four thread-like chromosomes and *the same number appears in later cleavage stages.*

"It is the second and rare mode that realizes Boveri's conception. Both polar bodies are formed, the first removing eighty-four dyads and leaving the same number in the egg. In the formation of the second, the eighty-four dyads are halved to form two daughter groups, each containing eighty-four single chromosomes. *Both these groups remain in the egg and each gives rise to a single reticular nucleus, as described by Boveri in Ascaris. These two nuclei place themselves side by side in the cleavage figure, and give rise each to eighty-four chromosomes, precisely like two germ-nuclei in ordinary fertilization.* The one hundred and sixty-eight chromosomes split lengthwise and are distributed in the usual manner, *and reappear in the same number in later stages.* In other words, the second polar body here plays the part of a sperm-nucleus precisely as maintained by Boveri.

"In all individuals arising from eggs of the first type, therefore, the somatic number of chromosomes is eighty-four; in all those arising from eggs of the second type, it is one hundred and sixty-eight. This difference is clearly due to the fact that in the latter case the chromosomes are single and univalent, while in the former they are bivalent (actually arising from dyads or double chromosomes). The remarkable feature, on which too much emphasis cannot be laid, is that the numerical difference should

<sup>1</sup> Wilson, *The Cell in Development and Inheritance*, pp. 281-284.



persist despite the fact that the mass and, as far as we can see, the quality of the chromatin is the same in both cases."

Blochmann (1889) studied the maturation of drone and worker eggs in *Apis mellifica* with the following results: The first polar nucleus is given off normally and remains undivided, but the second polar nucleus often appears to divide. The fact that these three nuclei are not, as in some cases, due to a division of the first polar nucleus is proven by the position of this nucleus, which is always found just under the surface of the egg and separated by some distance from the other two. The female pro-nucleus soon becomes vesicular in form and goes to the axis of the egg, where it forms a spindle and gives rise to the blastoderm cells. The polar nuclei change as in *Musca vomitoria*, but do not become vesicular in form, approach one another and are enclosed by a rather large vacuole of the superficial protoplasm, which is free from yolk. In this vacuole they break up into fine chromatin granules, which become scattered through the whole cavity of the vacuole. We may suppose that the contents are later removed from the egg. In fertilized eggs the ovarian nucleus undergoes the same divisions as the unfertilized.

Platner (1887) also found two polar nuclei in *Liparis dispar*, a parthenogenetic Lepidoptera. These two cases, the first two recorded, are not in accord with the previous views of Weismann, and in 1891 he sought to explain these cases as follows: "Das Kernplasma einzelner Eier einer Art das Vermögen des Wachstums in grösserern Masse als die Majorität derselben besitze, oder, im Falle der Biene, jedes Ei besitze die Fähigkeit, sein auf die Hälfte reducirtes Kernplasma, wenn es nicht durch Befruchtung wieder auf das Normalmass gebracht wird, durch Wachstum wieder auf die doppelte Masse zu bringen."

Petrunkewitsch (1901), studying *Apis*, found that eggs laid by the queen in drone cells never showed any signs of having been fertilized. As in a fertilized ovum the first polar nucleus is separated by an equatorial division, in the second maturation there is a reduction of chromosomes to one-half. Similarly the first polar nucleus always divides with a reduction and the peripheral half is liberated and perishes. The restoration of the number of chromosomes in non-fertilized eggs probably occurs by a longitudinal splitting of the chromosomes, but with a suppression of the corresponding division into two daughter nuclei. The central half of



the first polar nucleus conjugates regularly with the second polar nucleus and forms a "Richtungscopulationkern," with the normal number of chromosomes. This nucleus in the drone egg gives rise by three divisions to eight cells with double nuclei. In fertilized ova and in drone eggs laid by fertile workers this nucleus forms a spindle, which either simply disappears or gives rise to a number of nuclei, one to four; but these always show disruption phenomena in the chromosomes and ultimately disappear. In a later paper the same author (Petrunkewitsch, 1902) asserts that the products of the Richtungscopulationkern ultimately become the testes of the adult drone.

Paulcke (1899) found that in drone eggs there are four groups of chromosomes. Of these two seem to be the result of division of the first polar nucleus, one of the second polar nucleus and the fourth the egg nucleus. In twelve eggs examined from worker cells, fifteen minutes after they were laid, eight show sperm nuclei with their radiating systems. In eight hundred drone eggs examined no sperm nuclei were seen, but in three cases dark corpuscles were observed, which might have been sperm nuclei. In fertile worker eggs there were no indications of male pro-nuclei.

Mrazek (1897) and Erlanger und Lauterborn (1897) studied the maturation of the eggs of *Asplanchna*, a Rotifer. They find in this genus three kinds of eggs: (1) Parthenogenetic male eggs; (2) parthenogenetic female eggs, and (3) female eggs which require fertilization. When the female eggs requiring fertilization begin to develop, all other eggs begin to show cleavages of a degenerative nature, not like the normal cleavage, probably due to lack of nutrition (Mrazek). The parthenogenetic female eggs give off *one* polar body which never divides, while the parthenogenetic male eggs give off *two* polar bodies, the first of which normally divides. The female eggs requiring fertilization act like the parthenogenetic male eggs. In the parthenogenetic male eggs there is no indication of a union of the second polar body with the egg. The number of chromosomes is not determined (Erlanger und Lauterborn).<sup>1</sup>

Rückert (1895) found that in *Cyclops sternuus* the second maturation division cuts off a polar nucleus which remains in the egg, in a direction tangential to the second division figure. It does not

<sup>1</sup> See also Lenssen, 1899, "Contribution à l'Etude du développement et de la maturation des œufs chez *Hydatina sexta*," *Cellule*, xiv, pp. 421-51, 2 pl.



form the primordial germinal cells. The first maturation division gives off a true polar body.

*Causes of Parthenogenesis.*—When we consider the difference in behavior of various parthenogenetic eggs during maturation and the differences in sex relations exhibited by the various groups, together with the wide range of the scattered cases where such development occurs, it is evident that parthenogenesis has had a separate origin in many places in the animal scale. All that is necessary in the maturation of a parthenogenetic egg is that the normal number of chromosomes shall be retained, and this may be brought about by the retention of the second polar body, fertilization by the second polar body or perhaps by the division of the chromosomes without the corresponding cell division.

In seeking for a cause for the appearance of parthenogenesis in a group of animals, it must be borne in mind that we are dealing with a phenomenon that to all practical purposes is like asexual reproduction, in that the species is not dependent on the union of the two sexes for the propagation of all the individuals of the species and that the causes for the appearance of asexual and parthenogenetic reproduction are practically identical, it being merely a question as to which method of agamic reproduction is most readily acquired by a given form when the necessity for such a thing arises. And, too, it is probable that the cause is not the same in all cases, since the environments and habits of the various forms possessing this power are so varied.

In the first place, parthenogenesis is generally associated with and probably caused by the necessity of the appearance of a great many individuals suddenly at a certain period of the year or of the life cycle. A large part of the forms exhibiting this method of reproduction are small short-lived animals which are represented during the winter or some adverse time in the life cycle by a very few individuals and, in order that the species may survive, are compelled to acquire some method of rapid agamic reproduction.

In the case of the Aphids the necessity is for females and we find thelytoky evolved; in the case of the Honey Bee the necessity is for males, so that the queens may not go unfertilized, and we find arrhenotoky.

The question of economy enters very largely into the problem and is, in fact, almost identical with the preceding cause. In many



cases males are exceedingly rare at all times or except at certain seasons, and it is manifestly to the advantage of the species if it is able to survive without the presence of any but propagating individuals. Thus in the case of the bee, previously mentioned, it would be detrimental to the species to have countless drones feeding on the hive supplies during the winter; but for the purpose of increasing the hereditary influence, it is beneficial to the race to feed these males for a brief period when food is plentiful, in order that the fertilization may bring about the results known to come in all cases from such a union.

In still other cases the very habits of the animal make the chance of the occurrence of a sexual union too small, and in consequence the females have acquired the agamic methods of reproduction. The case of *Cercaria* offers a good example of this. If we accept the conclusions of Thomas, we see that here we get a transition from unisexual to asexual reproduction; and while these two processes are usually widely separated, yet the same difficulty of a sexual union may be looked upon as the probable cause of either phenomenon.

*Determination of Sex.*—From what has gone before we see that the problem of sex determination is very closely related to that of parthenogenesis, since parthenogenetic eggs so frequently show such peculiar sex relations. In some groups unfertilized eggs produce only males (arrenotoky), in others only females (thelytoky), while in some both sexes are produced (amphoterotoky). Taking as an example the Honey Bee, we know that the male eggs are not fertilized and the female eggs are; and reasoning from this, it seems true that the act of fertilization is the one determining factor, since no one has yet been able to find any other fundamental point of difference. As was shown under another heading, other explanations, such as differences in food or size of cell, have been advanced, but these have already been answered. Such work as that of Mrs. Treat (1873) on Caterpillars, of Born (1881) and Yung (1881) on Amphibia, and of Nussbaum (1897) on Rotifers would seem to indicate that lack of nourishment favors the production of males; but until we have more evidence we are perfectly justified in explaining these cases as simply survivals of the more fit sex under trying conditions, and cannot use them as arguing for theories like those of Dickel. In fact Cuénot (1899) did not succeed in verifying the results of Mrs. Treat, for he found that the proportions of



males and females remained approximately the same under all food conditions, and concluded that sex is determined in the ovary in insects.

There have recently appeared two papers of interest in this connection as offering suggestions for future work. Beard (1902) and v. Lenhossek (1903) conclude, on theoretical grounds, that sex is determined in the ovary of the mother and that there are in all cases two kinds of eggs, male and female, fundamentally differing from one another. Cases where such a state of affairs is known to exist are *Phylloxera*, *Dinophilus*, some Rotifers and possibly in *Raja batis* (Beard, 1902). According to these views, the sex is determined before leaving the ovary and consequently fertilization can have no influence, but at present we cannot look on these theories as more than interesting suggestions. It must be admitted that the determination of sex by fertilization is in direct opposition to what we know to be true for the great majority of animals where both sexes alike arise from fertilized eggs, and on *a priori* grounds the theory of Cuénot, Beard and von Lenhossek seems probable; but in this instance, as in all others in zoology, *a priori* reasoning is unsafe and we must wait for future investigations to decide whether there is any truth in these suggestions.

*Comparison of Various Sex Relations.*—As has been pointed out by several investigators, the process of fertilization has two distinct purposes—the giving of a stimulus for development to the mature egg, and the increasing of the number of hereditary tendencies of the offspring by giving it a blending of hereditary traits from two parents. The power of parthenogenetic development possessed by some animals takes the place of the stimulation of the male sex cell, since the ovum has given to it in the ovary enough vital force to go on dividing mitotically even after it becomes a part of another generation.

The second office of fertilization is simply omitted where fertilization does not occur, the advantage of agamic development more than balancing the advantage to be gained by the meeting of two lines of heredity. During ordinary maturation the egg gives off in its polar bodies one-half of the number of its chromosomes, the heredity carriers, and by the acquisition of an equal number from the male cell, carrying hereditary tendencies from the male parent, the original number is regained; and in order that the normal num-



ber may be retained in parthenogenetic eggs the reduction division is omitted, or in some other way the same result is accomplished.

This omission of a mixing of two lines of ancestry in the reproduction of a species is, if our conception of its significance is correct, a very important one. There is, however, a great difference in the extent of this omission in the various kinds of parthenogenesis. In Arrenotoky at every second generation a crossing occurs *of necessity*, since the females are produced from fertilized eggs. In Thelytoky, on the other hand, a mixing may be very rare or even entirely wanting; while in Amphoterotoky it generally occurs at regular intervals, as in the fall in Aphids. On the other hand, Thelytoky and Amphoterotoky are much more beneficial to a species from the standpoint of its propagation, since at no time is fertilization an absolute necessity, while in Arrenotoky fertilization is necessary for the production of the individuals which do the most toward the reproduction of the species. What the species loses in hereditary influences is more than made up by the increased advantage of these two most specialized kinds of parthenogenesis.

*Pædogensis*.—If we look on parthenogenesis as a phenomenon which has arisen in various groups of animals so that the species may be reproduced rapidly and without so much dependence on chance, then it is but another step in the same direction to find this process shifted back to an embryonic stage of development so that the reproduction would not be delayed until the female reached the adult state. The same precocious segregation of the reproductive process is met with in forms which always require the fertilization of the egg, *e.g.*, *Amblystoma* (Axolotl), but in these cases the coincident phenomenon of parthenogenic development has not been necessary or desirable and we distinguish such cases as Proiogony. We may look on certain groups of the Diptera as in a transition stage, between the parthenogenesis like that observed in *Chironomus Grimmii* and that of *Miastor*. The species of *Miastor* has still further acquired the advantage of viviparity for the protection of the youngest embryonic stages, and seems almost to have reached the limit of advantage that a species can acquire for the propagation of its kind.

*Partial Parthenogenesis*.—As has been seen, eggs which have not been fertilized often begin to develop, but after a short time die. On this account it has been argued that such cases are not really parthenogenesis, since an adult or a sexually mature individual does not



result from the division. Such an argument cannot hold, since the fundamental principle involved is the same whether an adult results or not. We must consider that the life of the individual begins with the unsegmented egg, and if that egg has in itself the power of growth, manifested by cell division, then we must class it as a parthenogenetic egg; the only difference between such cases and examples like the male eggs of the bee being that there is in the former not so much of the power of unisexual development: it is merely a difference in degree and not in kind. It would seem that many of the cases of artificial parthenogenesis described are exactly similar to these cases of partial parthenogenesis, and that the change in environment produced artificially simply allows the egg the power of growth already in it to go on for a short time exactly as if fertilized.

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*Stated Meeting, November 6, 1903.*

President SMITH in the Chair.

A letter was read from the Schlesische Gesellschaft für Vaterländische Cultur, announcing the celebration of its one hundredth anniversary on December 17, and inviting the Society to send a representative to take part in the celebration. The Hon. Charlemagne Tower was thereupon appointed as such representative.

The decease was announced of Prof. Robert Henry Thurston, at Ithaca, on October 25, æt. 64.

Prof. Charles F. Chandler, of New York, read a paper on "The Electro-Chemical Industries at Niagara Falls."

Dr. Hans Goldschmidt, of Essen, Germany, explained his method for producing intense heat by his Thermite process.

A paper on "Dying American Speech-Echoes from Con-





Phillips, Everett Franklin. 1903. "A Review of Parthenogenesis." *Proceedings of the American Philosophical Society held at Philadelphia for promoting useful knowledge* 42(174), 275–345.

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