

III B.Sc. ZOOLOGY

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UNIT II & III

REFERENCE

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2 | Gametogenesis

The production of gametes is called **gametogenesis**. It occurs in the gonads. Gametes are of two types, namely **spermatozoon** and **egg**. The production of spermatozoon is called **spermatogenesis**. It takes place in the testis. The production of egg (ovum) is called **oogenesis**. It occurs in the ovary.

Primordial Germ Cells

The cells which are destined to develop into gametes are called **primordial germ cells**. The gametes and the primordial germ cells constitute the **germplasm**. The germplasm is of paramount importance because the somatoplasm ceases to exist with the death of animals, but the germplasm continues to live on indefinitely in succeeding generations.

The Origin of Primordial Germ Cells

The germplasm of an individual has come from its parents by way of the ovum and the sperm. The future of the human race depends on the germplasm held in trust within the bodies of the individuals now living.

As the embryo develops from the gametes, it is clear that the primordial germ cells are present inside the embryo. Recent investigations indicate that the primordial germ cells can be recognized in the early embryonic stages itself.

There are two views regarding the origin of primordial germ cells in chordates. They are, 1. germinal epithelial origin and 2. extragonadal origin.

1. Germinal Epithelial Origin: *Waldeyer*, (1870) stated that the primordial germ cells arise from the germinal epithelium of gonads.

2. Extragonadal Origin: This theory says that the germ cells arise outside the gonad at an early period of embryonic development and then migrate to the gonads.

The Origin of Primordial Germ Cells in Different Chordates

1. Petromyzon: In *Petromyzon*, the primordial germ cells arise from coelomic epithelium (*Butcher*, 1929).

2. Fishes: In fishes like *Amia*, *Lepidosteus*, etc. the primordial germ cells arise from endoderm (*Allen*, 1911).

3. Amphibians: The urodele amphibians develop the primordial germ cells from the postero-ventral part of the lateral mesoderm (*Nieuwkoop*, 1946).

In anuran amphibians, the primordial germ cell materials are located in the vegetal half of the uncleaved egg. After cleavage these materials are traced in the endoderm cells located in the middle of the yolk-laden endoderm cells (*Mahowald* and *Hennen*, 1971).

4. Reptiles and Birds: In these animals, the primordial germ cells originate in the *endoderm* of the extra-embryonic part of the blastoderm, just anterior to the head region of the embryo.

5. Mammals: In almost all mammals, the primordial germ cells originate in the *endoderm*. But their place of origin differs in the different groups. For examples, in mouse it develops in the endoderm of caudal region; in man the cells develop from the endoderm of yolk sac in the vicinity of allantoic stalk.

Transportation of Primordial Germ Cells

As the primordial germ cells originate outside, they move to reach the gonads. They are transported in two ways:

1. By *blood stream* in chick embryo.
2. By *amoeboid movement* in human embryo.

Spermatogenesis

It refers to the *formation of spermatozoa*. Spermatozoa are formed in the testis. In each vertebrate, a pair of testes are found. Each testis is attached to the dorsal body wall by a

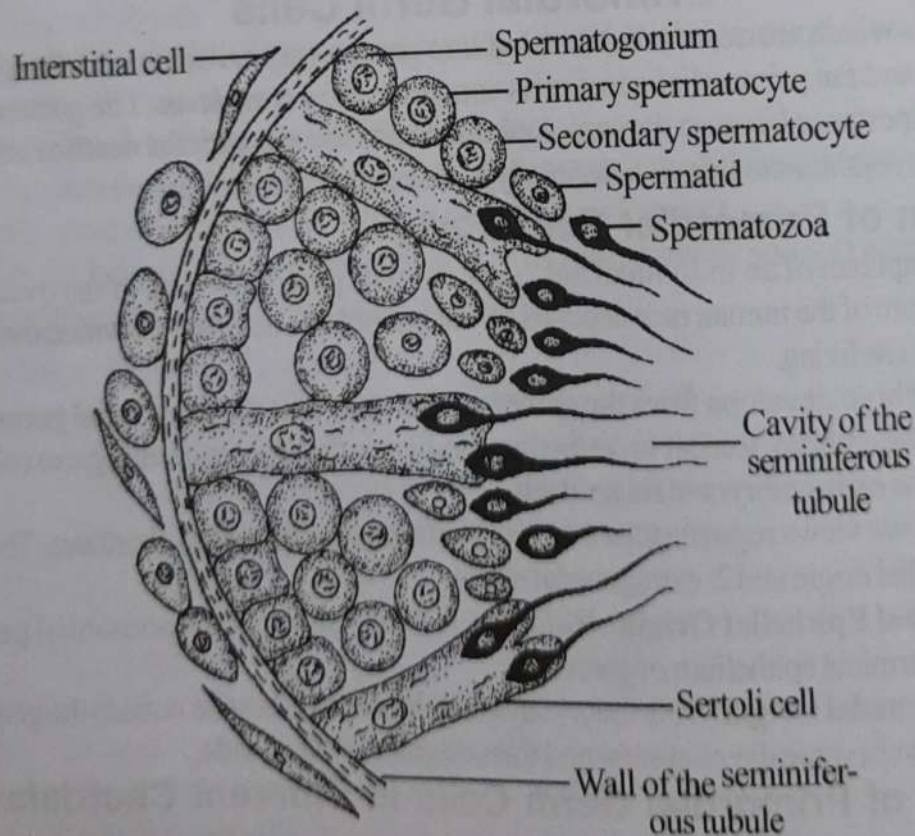


Fig.2.1: Transverse section of seminiferous tubule of mammalian testis.

connective tissue membrane called *mesorchium*. The testis is formed of thousands of minute tubules called *seminiferous tubules*. They lead into vasa deferentia. The seminiferous tubules are separated by *interstitial cells*.

Each seminiferous tubule is covered by a *basement membrane* and lined with *germinal epithelium*. The germinal epithelial cells are separated by giant cells called *Sertoli cells*. The germinal epithelial cells develop into spermatozoa and the Sertoli cells nourish the developing spermatozoa. The entire process of spermatogenesis has two stages, namely 1. the formation of spermatid and 2. the spermiogenesis.

1. Formation of Spermatid

The spermatid is formed from the epithelial cells of seminiferous tubules. The germinal cells which develop into spermatids are called *primordial germ cells*. There are three phases in the conversion of primordial germ cells into spermatids. They are

- a. *Multiplication phase*
- b. *Growth phase* and
- c. *Maturation phase*.

a. Multiplication Phase: The primordial germ cells are larger in size and their nuclei are distinct. They undergo repeated *mitotic* divisions. The resulting cells are called *spermatogonia* or *sperm mother cells*. Each spermatogonium has a diploid number ($2n$) of chromosomes.

b. Growth Phase: During this phase, the spermatogonium grows. The volume increases. Now the cell is called *primary spermatocyte*. It is also a diploid ($2n$) cell.

c. Maturation Phase: The primary spermatocyte, then enters the *maturation phase* where each cell divides by meiosis. Meiosis consists of two divisions. The first meiotic division produces two cells which are having *haploid* (n) number of chromosomes. These cells are called *secondary spermatocytes*. In the second meiotic division, each secondary spermatocyte divides into two cells called *spermatids*. The spermatid has only haploid number of chromosomes. Thus by meiosis each primary spermatocyte is converted into four spermatids. The spermatids differentiate into spermatozoa.

2. Spermiogenesis

The transformation of the spermatid into spermatozoon is called *spermiogenesis*. The spermatid is in the form of a typical cell containing the nucleus, Golgi bodies, mitochondria, centriole, etc. but it contains only haploid number of chromosomes. During the differentiation of the sperm, all these organelles undergo changes.

1. The nucleus gradually diminishes in its size by losing water.
2. The chromosomes become concentrated and are closely packed.
3. All the achromatic substances, *nucleolus* and *RNA* disappear.
4. The nucleus becomes elongated.
5. The *Golgi bodies* develop into the acrosome. In an early spermatid, the Golgi bodies are in the form of membranous vesicles, arranged around a group of vacuoles. The small vacuoles gradually fuse together to form large vacuoles. It is now called *acroblast*. Inside the acroblast, a dense body called *proacrosomal granule* is developed. The whole of the acroblast spreads over the front part of the nucleus. The proacrosomal granule enlarges to form the *acrosomal granule*. The acroblast is now called *acrosome* which forms the cap of the sperm. The acrosome and the nucleus together constitute the *head*. The remnants of the Golgi body degenerate and eventually get discarded.

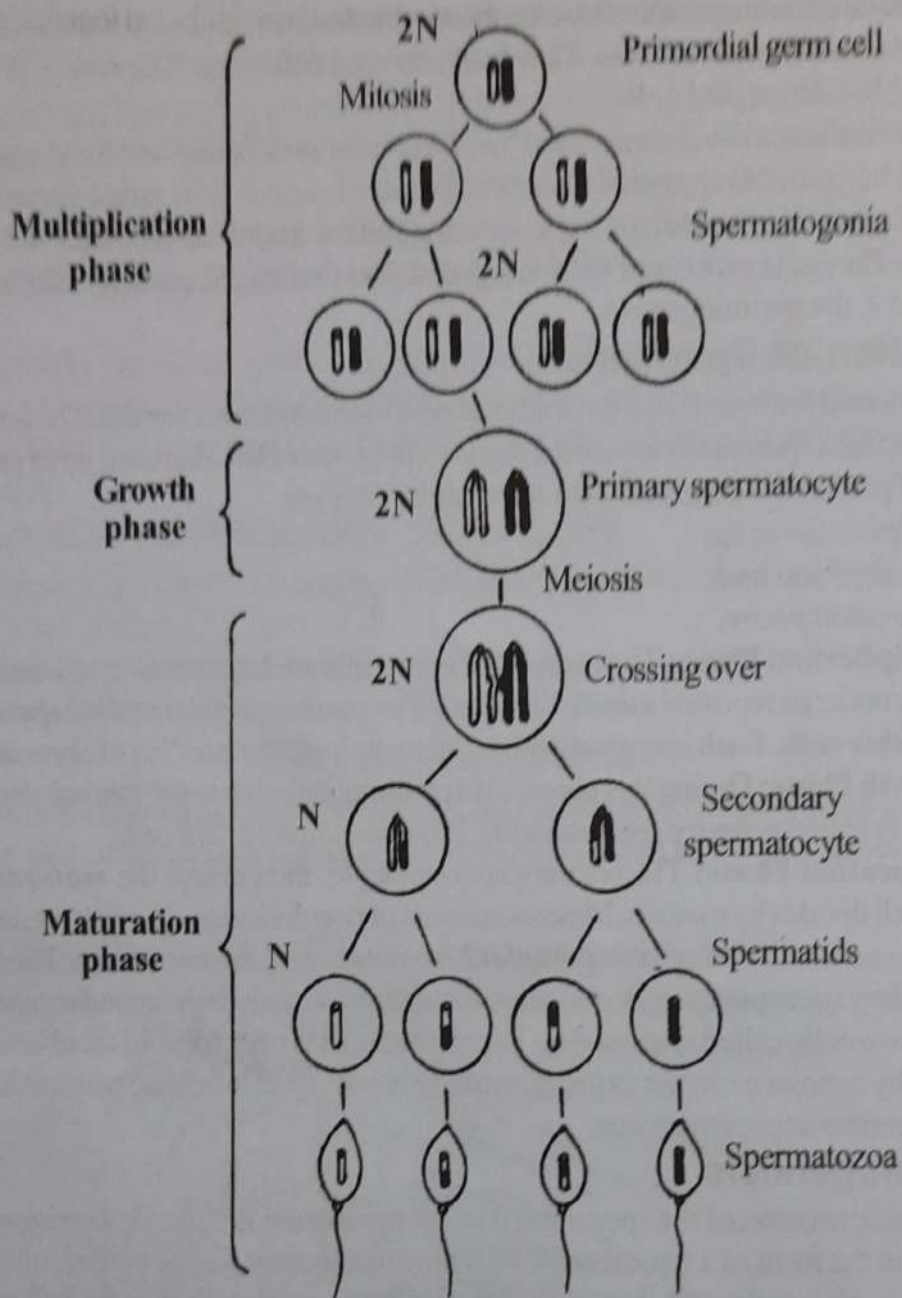


Fig.2.2: Spermatogenesis.

6. The centrosome of the spermatid contains two **centrioles**. They move towards the nucleus and occupy a position behind it. A depression is formed in the posterior surface of the nucleus and one of the two centrioles becomes placed in this depression. This is the **proximal centriole**. The other centriole is called the **distal centriole** takes up a position behind the proximal centriole.

7. The distal centriole develops a filament-like structure called **axial filament**. It gradually elongates and forms the tail by developing a cytoplasmic sheath. The distal end of the axial filament is free from the cytoplasmic sheath and it is named **end piece**.

8. The mitochondria of the spermatid are aggregated together to form a large mass in the region of the centrioles. This is called **mitochondrial cloud**. In mammals, the mitochondrial cloud becomes twisted spirally around the proximal part of the axial filament. However, in other animals the spiral arrangement of the mitochondria is not found and they may be arranged in two

bands on either side of the proximal part of the axial filament or clumped together in a compact mass. This region forms the *middle piece*.

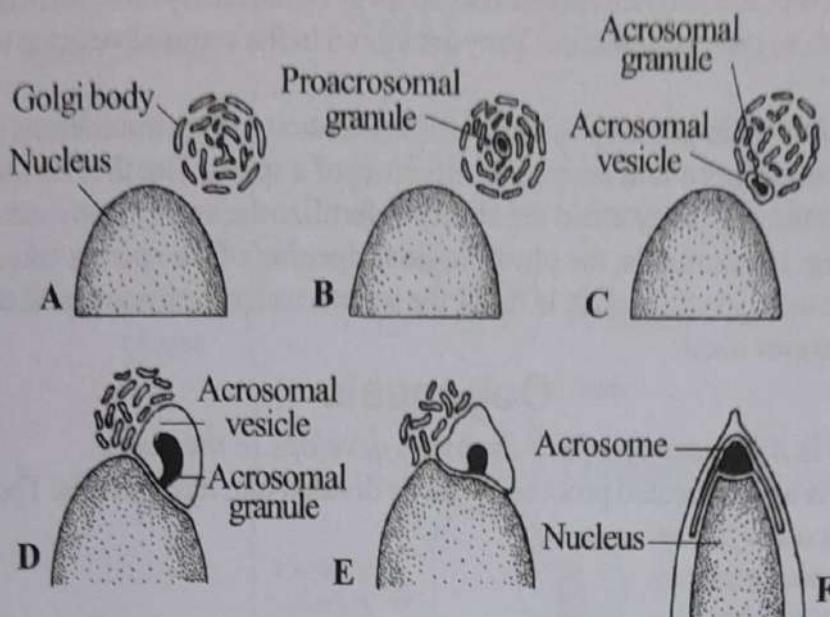


Fig.2.3: Spermiogenesis: Formation of acrosome and head.

9. Around the surface of the middle piece the cytoplasm forms a condensed sheath called *manchette*.

10. The cytoplasm flows backwards and forms a thin layer around the nucleus, middle piece and tail.

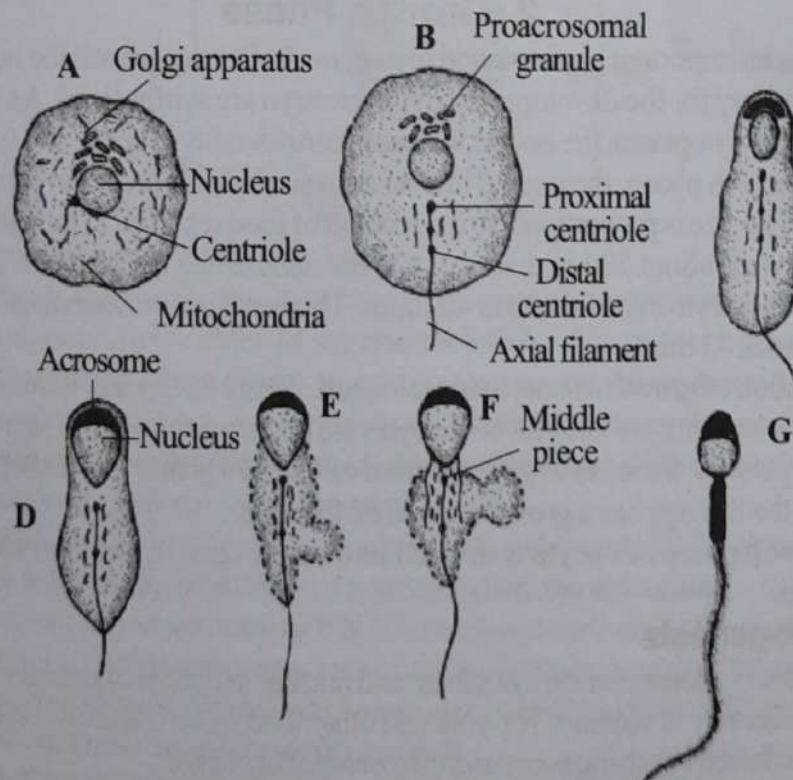


Fig.2.4: Spermiogenesis.

11. When the spermatozoa are developing, their heads are embedded in the cytoplasm of the *Sertoli cells* and their tails protrude into the lumen of the seminiferous tubules. When they are fully matured, they are released and are carried away by the ciliary movement of the lining of the vasa efferentia to the vas deferens. They are stored in the seminal vesicles to be released when required.

12. The sperms undergo morphological differentiation in the seminiferous tubules of the testis. By this change they attain the typical structure of a sperm. But they do not possess the ability to fertilize the egg. They attain the ability to fertilize the egg by a process called *physiological ripening*. In mammals, the physiological ripening of the sperms takes place in the epididymis while they pass through it. In frogs, the sperms undergo physiological ripening in the *seminiferous tubules* itself.

Oogenesis

Oogenesis is a process by which the ovum develops in the ovary.

Oogenesis is a complicated process. It can be divided into three phases. They are

1. Multiplication phase
2. Growth phase and
3. Maturation phase

1. Multiplication Phase

The germinal epithelial cells of the ovary detach themselves from the surface and enter the cortex of the ovary. These cells are called *primordial germ cells*. They divide repeatedly by mitosis and the resultant cells are called *oogonia* or *egg mother cells*. The oogonia again divide repeatedly by mitosis. When the division stops, the cells are named as *primary oocytes*. The nucleus of primary oocyte is diploid.

2. Growth Phase

Growth is an important phenomenon in *oogenesis*. During growth the nutrients and other materials necessary for the development of the embryo are synthesized. As these substances accumulate in the cytoplasm, the oocyte increases considerably in size.

During growth phase, the oocyte increases in size. The increase in size of the oocyte is considerable. The size is proportional to the amount of food reserved in the cytoplasm. In frogs, the young oocyte is about 50μ in diameter and the mature egg ranges from 1000 to 2000μ in diameter; so the oocyte increases 20 to 40 times. The hen's oocyte increases 200 times and in mouse it increases 43 times.

The duration of growth of oocyte is prolonged. It lasts for 3 years in frog.

In the new born human baby all her oocytes are already formed. The first ovum is released at the time of puberty. So it has a growth period of 12 to 14 years. The last egg released at the age of 45. So the last egg has a growth period of 45 years.

The growth phase of oocyte is divided into two stages, namely *previtellogenesis* and *vitellogenesis*.

1. Previtellogenesis

During previtellogenesis the cytoplasm and nuclear materials of primary oocyte grow and increase considerably in volume. The yolk and other food materials are not synthesized during this phase. The following changes occur during previtellogenesis:

1. The nuclear sap is produced in large amount. As a result, the nucleus increases in size. The large nucleus of the oocyte is called *germinal vesicle*.

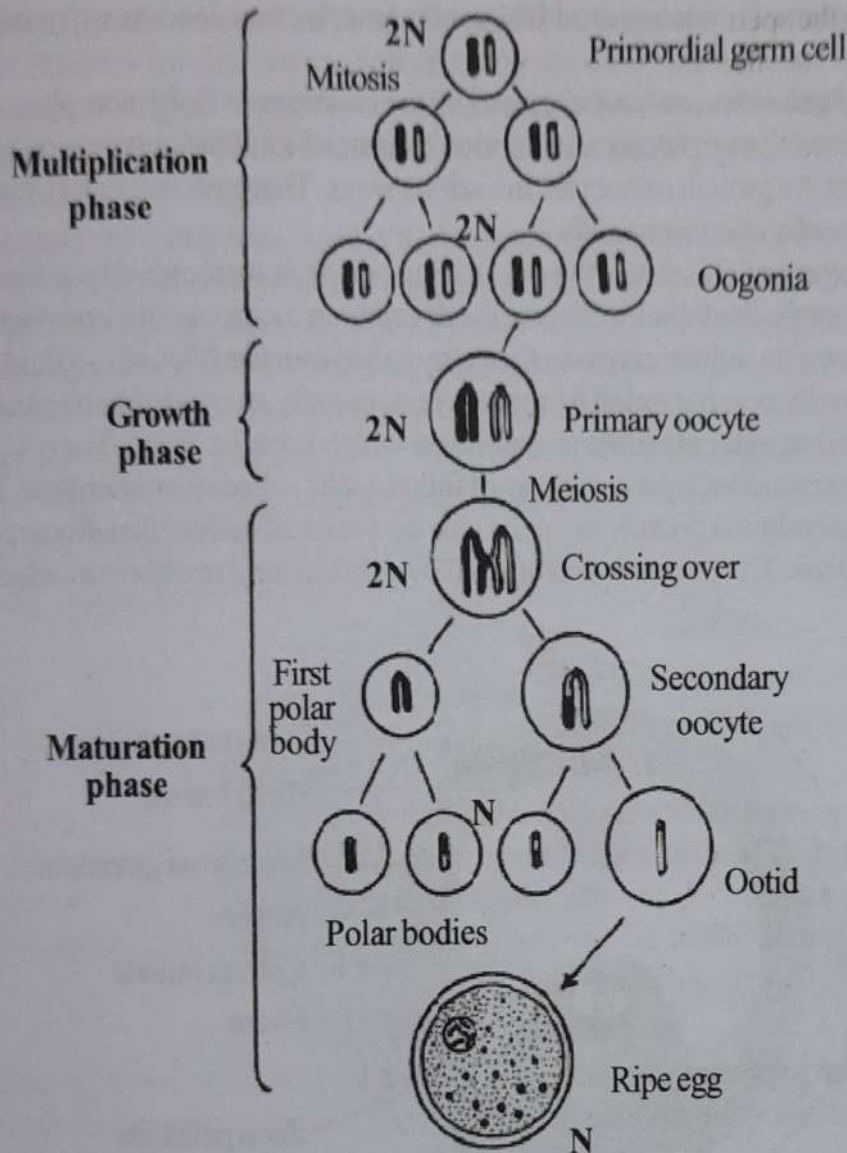


Fig. 2.5: Oogenesis.

2. Homologous chromosomes pair together.

3. In amphibians, the chromosomes of primary oocytes acquire a characteristic shape; thin loops or threads appear on the sides of the chromosomes. These loops give a **brush-like** appearance to the chromosomes. Hence the chromosomes are called **lamp-brush** chromosomes. The loops of these chromosomes are actively involved in the synthesis of mRNA.

4. The ribosomal RNAs are produced in a remarkable amount. They are produced by the nucleolus. As a result the nucleolus increases greatly in size.

5. The genes producing the rDNA are multiplied several times to facilitate the rapid synthesis of rDNA. This increase in the number of genes is called **amplification**.

6. In many cases, the production of RNA is increased further, by the development of a greater number of nucleoli. This phenomenon is more common in the egg of the amphibian. The *Triturus* (urodele) oocyte has 600 nucleoli; *Siredon* (urodele) has about 1000 nucleoli and the oocyte of *Xenopus* (anuran) has 900 to 1200 nucleoli.

7. The **mitochondria** increase in number. In some animals, like the amphibians and birds the mitochondria are aggregated to form **mitochondrial clouds**.

8. The amount of mitochondrial DNA increases. It exceeds even the amount of nuclear DNA.

9. **Cortical granules** are manufactured by the cisternae of Golgi complex.

10. The growing oocytes are surrounded by special kinds of nutritive cells. These cells immensely assist the growth of oocytes in various ways. There are two types of nutritive cells, namely **follicle cells** and **nurse cells**.

11. In the ovary of chordates, the developing oocyte is surrounded by **follicle cells**.

12. In mammals, the follicle cells and the developing ovum together constitute a **Graafian follicle**. Each Graafian follicle consists of a cavity called **antrum** filled with a fluid called **liquor folliculi**. The cavity is surrounded by three layers, namely an outer **theca externa**, a middle **theca interna** and an inner **membrana granulosa** which lines the cavity. The oocyte lies inside the antrum. It is surrounded by a few layers of follicle cells called **corona radiata**. The oocyte is attached to the membrana granulosa on the side by a stalk of cells called **discus proligerus** or **cumulus oophorus**. The oocyte is surrounded by a transparent membrane called **zona pellucida**.

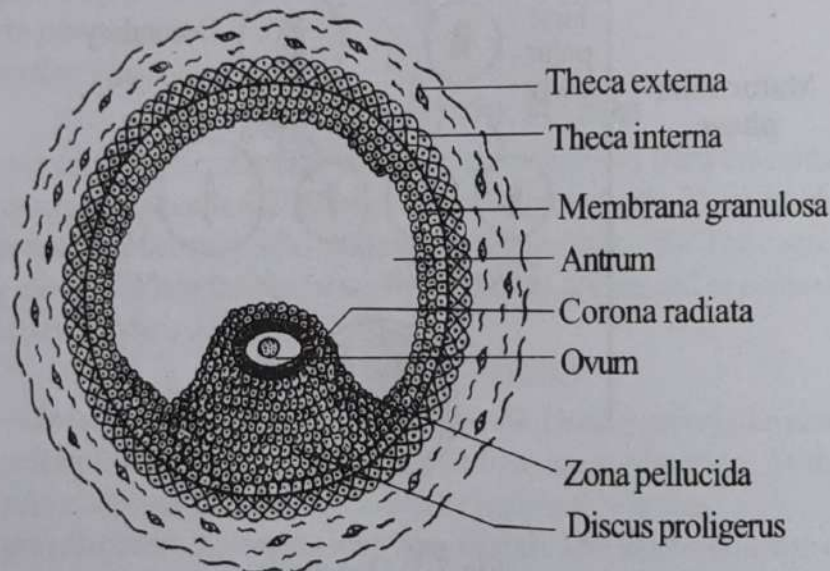


Fig.2.6: A mature Graafian follicle.

13. In annelids, insects and molluscs, the oocyte is surrounded, in addition to follicle cells, by a special type of cells called **nurse cells**. The nurse cells are derived by the division of oogonium. In *Drosophila*, an oogonial cell divides by four mitotic divisions into 16 cells. One of these cells develops into the oocyte and the remaining cells become the nurse cells. The oocyte grows at the expense of the nurse cells. In snail, *Helix*, the entire nurse cells are engulfed into the cytoplasm of the oocyte.

2. Vitellogenesis

The process of formation and deposition of yolk in the oocyte is called **vitellogenesis**. Yolk is the nutritive material of the ovum. It is present in the form of **platelets** or **granules**.

Origin of Yolk

Initially when an oocyte starts developing, it does not contain any nutrients. The nutrients are formed only during growth phase of oogenesis. There are two views regarding the place of the origin of yolk.

1. Insitu Origin: A very small amount of yolk is synthesized in the oocyte cytoplasm. For example, in vertebrates less than 1% is synthesized by the oocyte cytoplasm.

2. Exogenous Origin: A major part of the yolk is synthesized outside the oocyte. In vertebrates, it is synthesized in the liver; in insects it is synthesized in the fat body.

Transportation of Yolk

In vertebrates, the yolk synthesized in the liver, is in a soluble state. It is transported by the blood stream to the follicle cells present around the oocyte. The follicle cells deposit the yolk in the oocyte. The transport of yolk to the oocyte is facilitated by the development of finger-like structures called **microvilli** by the oocyte and **macrovilli** by the follicle cells.

The deposit of yolk and other nutrients like the lipid, glycogen, etc. begins close to the oocyte surface and fills the peripheral cytoplasm first. Gradually, the entire cytoplasm is deposited with yolk except the perinuclear zone. Thus the cytoplasm is progressively occupied from the peripheral zone inward.

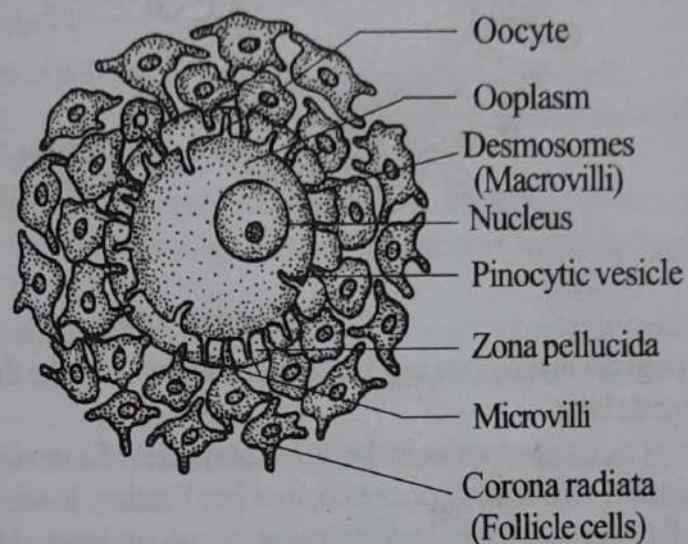


Fig.2.7: Developing mammalian oocyte with follicle cells.

The Processing of Yolk by the Oocyte

The liver does not produce the yolk directly. But it synthesizes a precursor called **vitellogenin** for the yolk. When it is brought to the oocyte, the vitellogenin is transformed into actual yolk.

The Golgi complex and the endoplasmic reticulum transport the yolk-components to the mitochondria. In mitochondria, the soluble yolk-components are made insoluble by a mitochondrial enzyme called **proteinkinase**. This enzyme crystallizes the soluble yolk into insoluble **yolk granules** or **yolk platelets**. During this process of crystallization, the mitochondrial cristae become dislodged and their membrane ultimately become arranged in concentric layers while the whole mitochondrial space is occupied by the main body of the yolk platelet.

3. Maturation Phase

The primary oocyte contains a **diploid** number of chromosomes. The diploid chromosome number is reduced to haploid number by **meiosis** or **reduction** division and the primary oocyte is changed into the **ovum** or **egg**. This is called **maturation**.

The meiotic divisions are unequal in oogenesis. As a result of the first meiotic division the primary oocyte divides into a very small and a large cell each with a haploid number of chromo-

somes. The smaller cell is always formed at the animal pole and is called the **first polar body** or **polarocyte**. It contains only a negligible amount of cytoplasm. The other cell contains the main bulk of the primary oocyte and is called the **secondary oocyte**. In the second meiotic division also, the secondary oocyte divides unequally into a small cell and a large cell. This small cell is called the **second polar body** or **second polarocyte**. The larger cell is the **ovum**. As the secondary oocyte is dividing, the first polar body divides into two polar bodies.

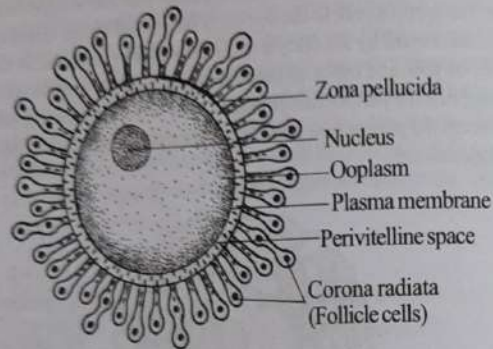


Fig. 2.8: Human ovum.

Thus in oogenesis only one egg is produced along with the three polar bodies. The polar bodies disintegrate later.

The time of maturation varies in the different species of animals. It may occur after fertilization or at the time of fertilization or even before fertilization. In sea urchin, maturation division occurs before fertilization. In all the vertebrates, the second maturation division occurs only after fertilization. In ascidians, in some molluscs and in some annelids, the maturation division occurs at the time of fertilization. In extreme cases, the maturation division occurs only after fertilization.

Hormonal Control of Oogenesis

Oogenesis is regulated by the concentrations of hormones. Hormonal regulation is significant in insects and vertebrates.

Hormonal Regulation in Insects

In insects, oogenesis is controlled by an endocrine gland called **corpus allatum**. It is attached to the brain. It secretes a hormone called **juvenile hormone**. The juvenile hormone has two functions in oogenesis. They are

1. The juvenile hormone stimulates the differentiation of oocytes.
2. It also promotes the synthesis of yolk protein, **vitellogenin**, by the fat body. The vitellogenin is released into the haemolymph and is taken up by the oocyte.

Hormonal Regulation in Vertebrates

In vertebrates, oogenesis is regulated by three hormones, namely **gonadotropins**, **progesterone** and **oestrogen**. Gonadotropins are secreted by the pituitary gland and they include **follicle stimulating hormone (FSH)** and **luteinizing hormone (LH)**. The progesterone and oestrogen are produced by the follicle cells of the ovary.

The FSH promotes the growth and development of the oocyte.

The LH triggers **ovulation** (release of egg from the ovary.)

The FSH and LH also promote **meiotic maturation** division of the oocyte.

The FSH and LH also stimulate the follicle cells to synthesize **oestrogen** and **progesterone**.

The oestrogen stimulates liver to synthesize **vitellogenin** (yolk protein).

Gonadotropin promotes the uptake of vitellogenin from the circulation by the oocyte.

Comparison of Spermatogenesis and Oogenesis

1. The development of sperm is called **spermatogenesis**. The development of ovum is called **oogenesis**. **Spermatogenesis** and **oogenesis** are together called **gametogenesis**.
2. Spermatogenesis occurs in the **testis**. But oogenesis occurs in the **ovary**.
3. Both spermatogenesis and oogenesis involve **meiosis** or **reduction division**.
4. During spermatogenesis and oogenesis, the chromosome number is reduced from **diploid (2N)** to **haploid (N)**.
5. Both sperm and ovum develop from diploid **primordial germ cells**.
6. Both spermatogenesis and oogenesis involve three phases, namely **multiplication phase**, **growth phase** and **maturation phase**.
7. During multiplication phase the primordial germ cells divide by mitosis and develop into **spermatogonia** (sperm mother cells) during spermatogenesis and **oogonia** (egg mother cells) during oogenesis.
8. The number of oogonia is limited; but the number of spermatogonia is not limited.
9. The spermatogonia further divide by mitosis to form **primary spermatocyte**. Similarly, the oogonia further divide to form **primary oocyte**.
10. During growth phase, nutritive materials accumulate into the primary spermatocyte and primary oocyte and they increase in size.
11. The growth period is short in spermatogenesis. But it is long in oogenesis. The growth period of oogenesis varies from a few days to many years. In frog, it lasts for 3 years. In human, the primary oocytes are completely formed during intrauterine development. From these, the first egg develops during puberty after 12 to 14 years. So the growth phase extends for 14 years. The last egg develops at the age of 45. So the growth phase of the last human egg is about 45 years.
12. The size of the primary spermatocyte increase very slightly. But the primary oocyte increase considerably. In frog, the increase is about 27,000 times. In man, the oocyte increase 7 times.
13. Yolk is deposited inside the oocyte during oogenesis. But yolk is not deposited in the spermatocyte.
14. Meiosis occurs during maturation phase.
15. During maturation, the primary spermatocyte produces **four haploid spermatids**. But the primary oocyte produces only one haploid **ovum**.
16. During oogenesis **3 polar bodies** are produced. Polar bodies are not produced in spermatogenesis.
17. The spermatid differentiates into sperm by **spermiogenesis** after maturation division. The differentiation of ovum takes place simultaneously with the growth rather than after maturation.

18. The sperm becomes motile. But the ovum is immotile.

Polar Bodies

Polar bodies are minute cells released during oogenesis. They are also called *polocytes*. They are released and attached at the animal pole of the ovum and hence they are called *polar bodies*. They are *haploid* cells. They contain very small amount of cytoplasm.

During oogenesis **three** polar bodies are produced. They are produced by *unequal meiosis*.

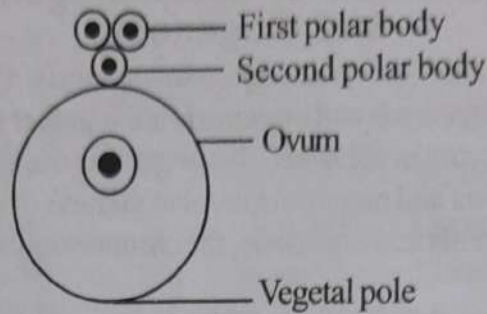


Fig.2.9: An ovum with its polar bodies.

The first polar body is produced when the primary oocyte divides by the first meiotic division.

The second polar body is released when the secondary oocyte divides by the second meiotic division. At the same time the first polar body divides into daughter polar bodies.

The polar bodies may be formed either before fertilization or after fertilization.

The polar bodies degenerate and disappear during embryogenesis.

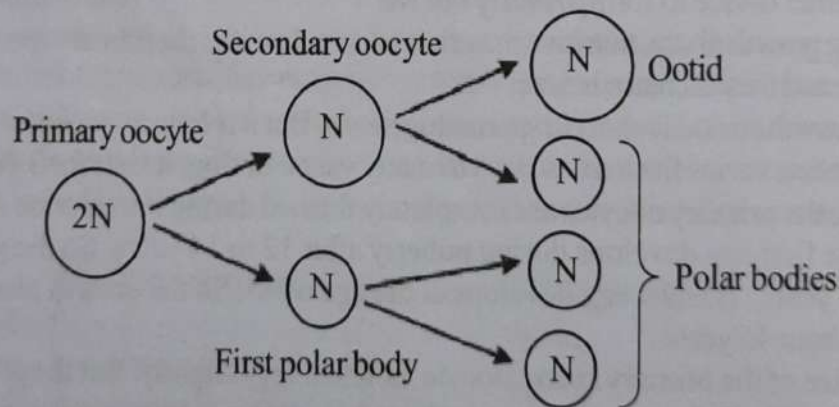


Fig.2.10: Oogenesis.

In some animals like *Artemia salina*, the egg fuses with the second polar body and the egg starts development by parthenogenesis. This type of fusion of egg with the polar body is called **autofertilization**.

The polar bodies do not contain yolk. They help to restore all the yolk inside a single ovum. This yolk is just sufficient for the development of a single embryo. If the meiotic division is equal, then the yolk will be distributed to all the 4 cells and the yolk will not be sufficient for the full development of an embryo. Hence the polar bodies are produced and wasted.

6 Fertilization

Fertilization is the union of spermatozoon and egg resulting in the formation of zygote.

Significance of Fertilization

1. Fertilization maintains the *diploid* number of chromosomes in the race.
2. Fertilization produces genetic variation by bringing together chromosomes from two different parents.
3. Fertilization *activates* the egg and thus development is initiated.

Physical Factors Involved in Fertilization

1. External Fertilization

In majority of aquatic animals, sperms and ova are released into the water where fertilization takes place. It is called *external fertilization*. It is the primitive type of fertilization. Eg. *Fishes, Frog, etc.*

2. Internal Fertilization

In amniotes, sperms are introduced into the female's genital tract, where fusion takes place. It is called *internal fertilization*. It is the advanced type. Eg. *Man*.

3. Life-span of the Gametes

Generally the eggs fertilized externally, have shorter life-span than those which are fertilized internally. For example, the human egg can live for more than twenty four hours after ovulation.

Spermatozoa have a comparatively long life span. For example, the spermatozoa of bat can live for 135 days in the female reproductive tract. The cock spermatozoon can live for two weeks in the oviduct. The life time of the human spermatozoon in the female genital tract is about 24 hours.

4. Production of Enormous Number of Sperms

The meeting of gametes is enhanced by the production of enormous number of sperms.

Table 6.1: The duration of survival of sperms in the female genital tract.

Sl.No.	Animal	Duration
1.	Turtle (<i>Malaclemys centrata</i>)	4 years
2.	Aquarium fish, guppy (<i>Lebistes</i>)	1 year
3.	Horse	144 days
4.	Bat	135 days
5.	Garter snake	4 months
6.	Hen	2 weeks
7.	Guinea pig	41 hours
8.	Man	24 hours
9.	Rat	17 hours
10.	Rabbit	14 hours

5. Random Collision

The egg and sperm are brought together by random collision. This is favoured by the large size of the egg and the enormous number of sperms.

6. Mechanical Juxtaposition of Gametes

Animals provide a number of mechanical agencies to bring together the eggs and spermatozoa. In mammals, the spermatozoa are injected deep into the female genital duct by *copulation*.

In birds, the spermatozoa are introduced into the cloaca of female by a process called '*cloacal kiss*'.

In cephalopods (*Sepia*, *Loligo*, etc.), one of the arms in the male modified to transfer the spermatozoa into the female genital duct. This arm is said to be *hectocotylus*. During courtship, the male carries a bundle of spermatophores from the genital duct in his hectocotylus arm and places it either in the mantle cavity or in the seminal receptacle of the female.

7. Synchrony in Production and Release of Gametes

The male and female gametes are produced at a particular time. In certain animals, eggs are released only after ovulation. This prevents wastage of sperms.

8. Capacitation

Capacitation is a process where the spermatozoa acquire the capacity to fertilize the eggs. After capacitation, the spermatozoa develop the ability to penetrate the membranes surrounding the egg. The spermatozoa obtain capacitation by the following methods:

1. The spermatozoa gets capacitation by remaining in the female genital tract for some time. The duration is six hours in man and one hour in mouse.
2. In some animals, sperms obtain capacitation by passing through *epididymis*.
3. During capacitation the coating substances on the surface of the sperm are removed. This helps the receptor sites on the sperm to recognize signals coming from the egg.

9. Entry of Sperm into the Egg

In some animals, such as nemertines, molluscs, echinoderms, insects and fishes, the egg is surrounded by a tough membrane called *chorion*. This membrane cannot be easily penetrated by the spermatozoa. Hence, the eggs are provided with one or more minute openings called *micropyles*. The spermatozoa enter the eggs only through these openings.

10. Time of Fertilization

The sperm fertilizes the egg at different stages of maturation in different species. It may occur after maturation or at the time of maturation or before maturation. In sea urchin, fertilization occurs after maturation divisions. In all vertebrates, the egg is fertilized after maturation division.

In ascidians, some molluscs and some annelids the egg is fertilized at the time of first maturation division. In nematodes and annelids, the egg is fertilized before the commencement of maturation division.

Chemical Factors Involved in Fertilization

1. Chemotaxis

In certain animals, sperms are attracted towards the eggs by chemicals. This happens in coelenterates, fishes, insects, etc. In fishes and insects, this chemical is present in the *chorion* lining the *micropyle*. When the chorion is removed from the egg, the activity of sperm slows down.

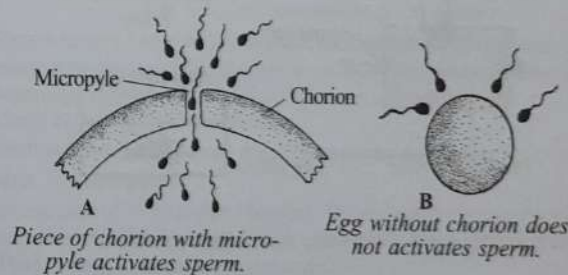


Fig. 6.1: Chemotaxis in the egg of fish.

2. Fertilizin-Antifertilizin Reaction

The sperm identifies the egg by the reaction between fertilizin and antifertilizin.

Fertilizin: The egg contains on its surface a chemical substance called *fertilizin*. It is a *glycoprotein*. It has a molecular weight of 3,00,000. The fertilizin molecule has *many receptor* or *binding sites* for antifertilizin. Fertilizins are *species specific* and there may be different fertilizins for different species.

The main source of the fertilizin is jelly coat or plasma membrane. The fertilizin present in the jelly coat and vitelline membrane is called *jelly coat fertilizin*. The fertilizin present in the plasma membrane is called *cytofertilizin*.

Antifertilizin: The surface of the sperm contains a chemical substance called *antifertilizin*. It is an *acid protein*. It is smaller than fertilizin. It has a molecular weight of 10,000. There may be different antifertilizins in the different species.

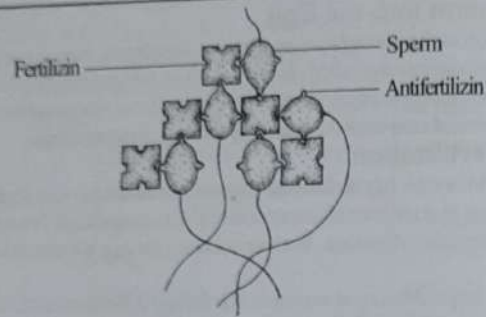


Fig. 6.2: Fertilizin-antifertilizin reaction.

Reaction: Fertilizin reacts with the antifertilizin in a manner comparable to the reaction between antigen and antibody. This reaction can also be compared to the *lock and key* system.

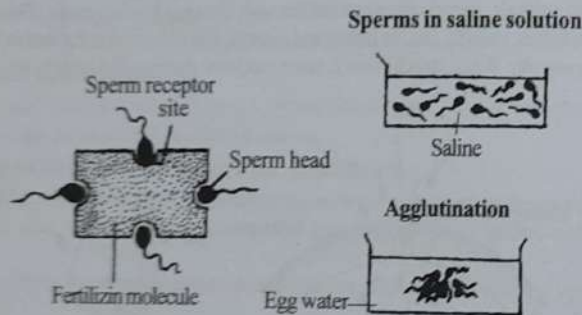


Fig. 6.3: Fertilizin and Antifertilizin reaction.

The fertilizin molecule has many *receptor sites* or *binding sites*. These receptor sites are complementary to the antifertilizin molecules.

When eggs and sperms are released in the water, the fertilizin particles embrace the antifertilizin particles. As a result, the sperms agglutinate or clump together. This reaction is strictly species specific.

Functions of Fertilizin-Antifertilizin Reaction: 1. The sperm identifies the egg by fertilizin-antifertilizin reaction.

2. The initial attachment of the sperm to the egg is the result of the linking between fertilizin particles and antifertilizin particles.

3. Certain amount of fertilizin is released from the egg into the surrounding water. These released fertilizins combine with the sperms. This leads to the *agglutination* of sperms. As a result of this, only a few sperms reach the surface of the egg. This prevents *polyspermy*.

4. As the reaction between fertilizin and the antifertilizin is *species-specific*, fertilization between different species of eggs and sperms is prevented.

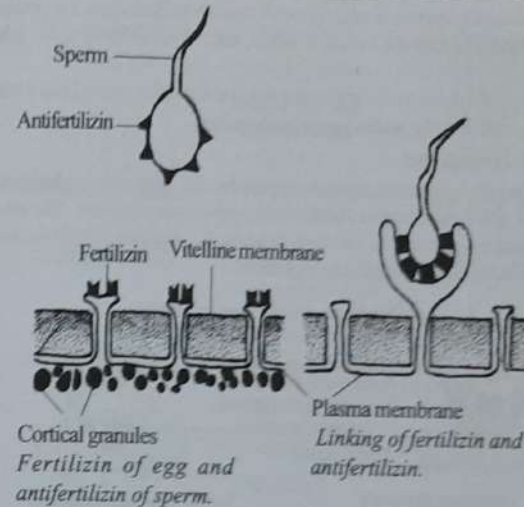


Fig. 6.4: Fertilizin-Antifertilizin reaction.

5. Sperms contain *lytic* substances which can break down the egg-coat. By holding together many sperms on the surface, the fertilizin-antifertilizin reaction ensures the production of sufficient quantities of lytic enzymes to dissolve the egg coverings.

6. It leads to the capacitation of sperm.

7. Fertilizin activates the *sperms* and initiates *acrosome reaction*.

3. Sperm Penetration

The mechanism of penetration is *chemical*. The spermatozoon liberates an enzyme called *sperm-lysin*. It is produced by the *acrosome* of the spermatozoa. It dissolves the egg-membrane and makes way for the entry of spermatozoa.

In mammals at the time of ovulation, the egg is surrounded by follicle cells. These cells are cemented together by a substance called *hyaluronic acid*. The mammalian sperm secretes a lytic enzyme called *hyaluronidase*. This enzyme dissolves the hyaluronic acid and the follicle cells are loosened. This paves the way for the entry of spermatozoa.

Cytological Factors Involved in Fertilization

1. Monospermy

Generally only one spermatozoon enters the egg and fuses with it. Such a fertilization is said to be *monospermy*. Monospermy is common in majority of animals like coelenterates, annelids, echinoderms, bony fishes, frogs, etc.

2. Polyspermy

In some animals, normally many sperms enter the egg. Such a fertilization is said to be *polyspermy*. Even though many sperms enter the egg, only one sperm nucleus fuses with the egg nucleus. Other sperm nuclei degenerate.

Polyspermy naturally occurs in animals with heavily yolked eggs. Eg. *Arachnids*, some insects, *elasmobranchs*, *urodeles*, *reptiles*, *birds*, etc. This is known as **physiological polyspermy**.

In other animals, polyspermy occurs during abnormal conditions and it is harmful. Such a type of polyspermy is said to be **pathological polyspermy**.

3. Acrosome Reaction

When the spermatozoon comes in contact with the egg, tremendous changes occur in the acrosome of sperm. All these changes constitute the **acrosome reaction**. The acrosome reaction has been studied extensively in a variety of animals. *Colwin* (1967) demonstrated the acrosome-reaction in the enteropneust *Saccoglossus*.

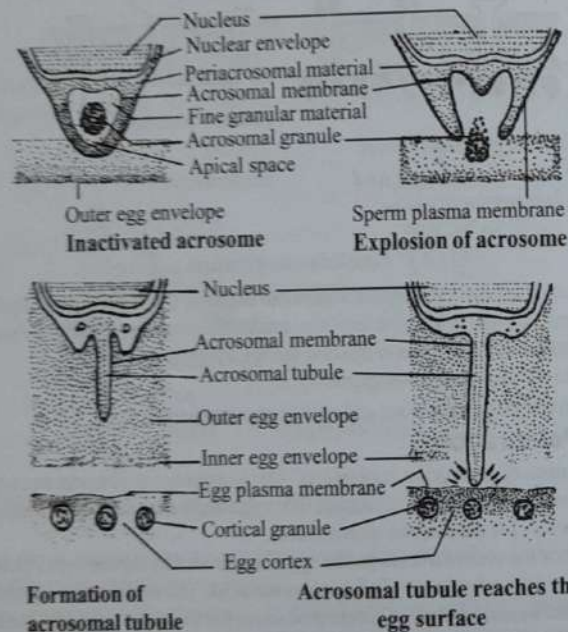


Fig. 6.5: Fertilization: Changes in the spermatozoon of *Saccoglossus* during fertilization.

1. When the spermatozoon's tip makes contact with the egg envelope, the sperm-plasma membrane and the acrosomal membrane rupture at the point of contact.
2. The acrosomal membrane then joins with the plasma membrane around the margin of the opening.
3. The **acrosomal granule** is released on the egg-envelope.
4. The acrosomal granule contains the **sperm lysin** which dissolves the egg envelope. Thus the egg surface is exposed at this spot.
5. Now, the centre of acrosomal membrane, nearer to the nucleus, grows towards the egg surface as a thin tube called **acrosomal tubule**.

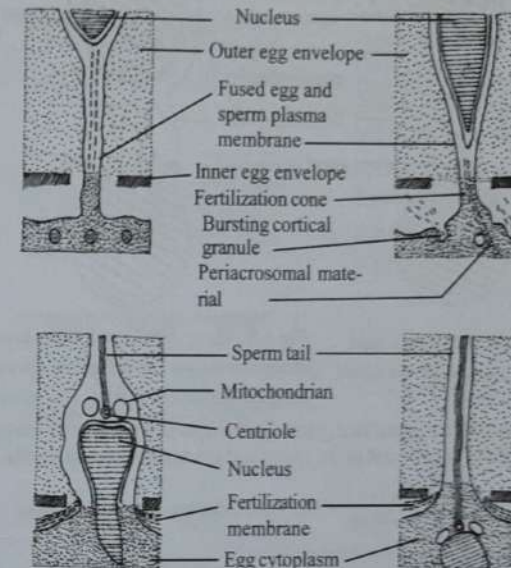


Fig. 6.6: Fertilization. Engulfment of spermatozoon by the fertilization cone.

6. As the acrosomal tube grows further, its tip comes in contact with the plasma membrane of the egg.

7. In some cases more than one acrosomal tubes develop. Eg. *Hydroides* (Polychaete).

4. Cytoplasmic Fusion

As the acrosomal tube comes in contact with the egg-surface, the egg is activated. At the point of contact, the plasma membranes of the egg and sperm fuse and the acrosomal tube opens into the egg-cytoplasm. As the fusion is made, the egg-cytoplasm at this point bulges out as a conical projection called **fertilization cone**. In *Saccoglossus*, only one fertilization cone develops. But in *Hydroides* many cones develop as there are many acrosomal tubes. The fertilization cone gradually engulfs the spermatozoon into the interior of the egg.

In mammals, the entire spermatozoon (nucleus, middle piece and tail) is engulfed by the egg-cytoplasm. In majority of animals, the nucleus and the middle piece enter the egg and the tail is excluded. In *Nereis*, the sperm nucleus along with the proximal centriole alone is engulfed; the tail and the middle piece are discarded.

5. Cortical Reaction

As the sperm enters the egg, the egg becomes activated. First of all, changes occur in the cortex (surface) of the egg. These changes, constitute the **cortical reaction**. The cortical reaction in the egg of sea urchin can be summarized as follows:

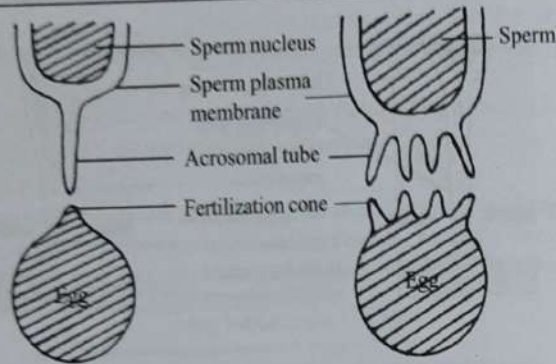


Fig. 6.7: An acrosomal tube and a fertilization cone.

Fig. 6.8: Many acrosomal tubes and fertilization cones develop during fertilization in *Hydroides*, a *Coelenterate*.

1. The colour of the egg-surface gradually changes from yellow to white. The change starts from the point of attachment of the sperm and gradually spreads over the surface of the egg.

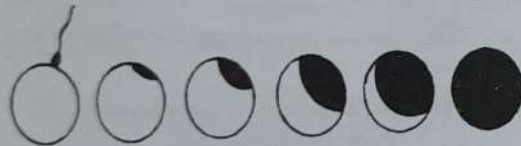


Fig. 6.9: Colour changes in the egg of sea urchin after fertilization.

2. The vitelline membrane gets lifted off. This membrane is then called **fertilization membrane**. The space between it and the surface of the egg is called **perivitelline space**. It is filled with a fluid called **perivitelline fluid**.

3. The cortical granules swell rapidly and explode. The cortical granules release three important components. They are,

a. Lamellar Folded Bodies: These are dark and dense bodies. On release, they unfold and fuse with the inner surface of the fertilization membrane. Thus the fertilization membrane is strengthened by the lamellar bodies.

b. Globules: The globular structures fuse together and form a new surface layer just outside the plasma membrane. This layer is called **hyaline layer**. It helps to keep the blastomeres intact during cleavage.

c. Liquid Component: The cortical granules contain mucopolysaccharides. They absorb water and become liquified. This liquid is released into the perivitelline space, and it is called **perivitelline fluid**. By imbibing more and more water, it assists in lifting the fertilization membrane still further.

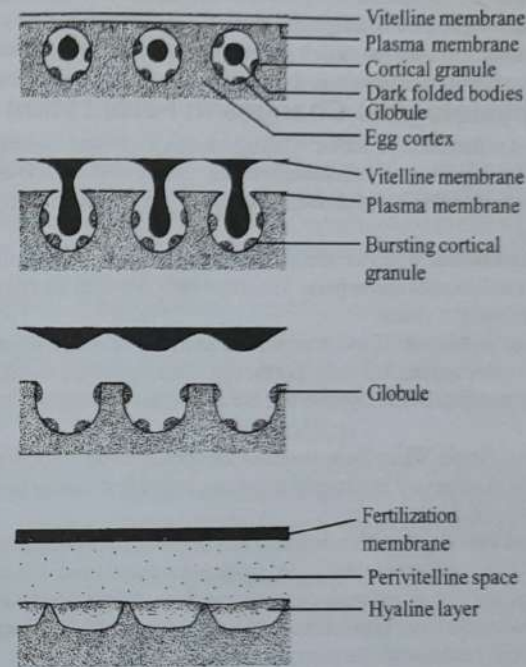


Fig. 6.10: Cortical reaction and the formation of fertilization membrane.

6. Sperm Nucleus

When the sperm is engulfed by the fertilization cone, it moves towards the **female pronucleus**. The sperm nucleus is followed by the centriole, the middle piece and the tail. Soon rotation of the nucleus and centriole occurs. As a result the centriole comes to occupy in front of the sperm nucleus. The other parts of the spermatozoon (the middle piece and the tail) get disconnected from the nucleus. They later disintegrate in the egg-cytoplasm.

The sperm nucleus is now termed as the **male pronucleus**. It moves through the egg-cytoplasm towards the female pronucleus. As the male pronucleus moves inwards, the path of the male pronucleus may be marked by pigment granule trailing along its path. The path taken by the sperm in the periphery of the egg (cortex) is called **penetration path**. Inside the egg the direction of movement of the sperm is slightly changed and the nucleus moves towards the female pronucleus. This changed path is called **copulation path**.

7. Amphimixis

Amphimixis refers to the **fusion of male and female pronuclei**. In sea urchin and in all vertebrates, the two nuclei come in contact, the nuclear membranes at the point of contact disappear and the contents of the two nuclei unite into one mass surrounded by a common nuclear membrane.

In *Ascaris*, molluscs and annelids, only after the completion of first cleavage, the male and female pronuclei fuse together. In *Cyclops*, the paternal and maternal nuclear components remain separate even after cleavage has started. As a result, each blastomere has a double nucleus consisting of two parts lying side by side, each surrounded by its own nuclear membrane.

Physiological Changes in Fertilization

1. Fertilizin-Antifertilizin Reaction: The egg releases a substance called *fertilizin*. The sperm contains a chemical substance called *antifertilizin*. The fertilizin binds to the antifertilizin. This reaction is called *fertilizin-antifertilizin reaction*. This reaction helps to attract the sperm near the egg.

2. Acrosome Reaction: When the sperm comes in contact with the egg, the acrosome of the sperm explodes and releases *sperm lysin*. The sperm lysin dissolves the egg membrane and makes a hole for the entry of sperm.

The acrosomal membrane of sperm grows out as a tube called *acrosomal tube*. The acrosomal tube elongates and reaches surface of the egg. Here the plasma membrane of the egg and the acrosomal membrane fuse together and the acrosomal tube opens into the egg cytoplasm.

3. Fertilization Cone: When the acrosomal tube opens into the egg cytoplasm, the egg cytoplasm at this point bulges out as a conical projection called *fertilization cone*. The fertilization cone gradually engulfs the sperm.

4. Elevation of Fertilization Membrane: The vitelline membrane is lifted off from the surface of the egg. This membrane is now called *fertilization membrane*. It is strengthened by the deposition of cortical granule materials on its inner surface. A fluid called *perivitelline fluid* gradually accumulates in the space between the surface of the egg and the fertilization membrane. The fertilized egg freely rotates inside the perivitelline fluid.

5. Explosion of Cortical Granules: When the sperm enters the egg, the cortical granules explode and release their contents. The cortical granules synthesize the *fertilization membrane*, *perivitelline fluid* and the *hyaline layer*.

6. Cytoplasmic Movements: The contact of sperms sets in the egg elaborate cytoplasmic movements. The movement of egg-cytoplasm is reflected in the violent activity of the pigment granules on the surface.

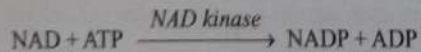
The cytoplasmic movement is best illustrated in amphibian eggs. As the sperm penetrates through the cortex of the egg, a trail of dark pigment from the egg's periphery flows in after the sperm. This initial path of the sperm constitutes the *penetration path*.

Then the sperm changes its direction and begins to travel towards the female pronucleus. This secondary path is the *copulation path*.

On the surface of the egg opposite to the point of sperm entry, the peripheral area of the egg becomes lighter in colour and assumes a grey appearance. This area is *crescentic* in shape and is known as the *grey crescent*.

7. Permeability of Plasma Membrane: The permeability of plasma membrane increases in the case of the molecules of water, ethylene, glycol, phosphate, etc.

8. Phosphorylation of Coenzymes: At fertilization, the coenzyme NAD is phosphorylated into NADP and NADPH in the presence of the enzyme *NAD kinase*.



9. Rate of Oxygen Consumption: The rate of oxygen utilization may increase or decrease or may not change. In frog and toad, there is a pronounced drop in *respiratory quotient*. In sea urchin and lamprey, oxygen consumption is increased during fertilization. In teleost fish, *Fundulus*, there is no change in the rate of oxygen consumption.

10. Rate of Protein Synthesis: In the unfertilized egg of sea urchin, there is no protein synthesis. During fertilization the rate of protein synthesis increases.

11. Initiation of Mitosis: Fertilization initiates mitosis in the egg resulting in cleavage. Mitosis requires the development of mitotic apparatus. It is produced exclusively by the centriole introduced by the sperm. The introduction of sperm centriole is a must for the egg to form a mitotic spindle. Thus the sperm stimulates the first mitotic division (cleavage) of the fertilized egg by contributing its centriole to the egg.

12. Breakdown of Polysaccharide: Immediately after fertilization a rapid breakdown of *polysaccharide* takes place. There is a corresponding increase in *lactic acid*.

13. Hexose Phosphate: It increases considerably after fertilization.

14. Dehydrogenase: This enzyme increases after fertilization.

Activation

The process of initiating the development in an egg is called *activation*. It is initiated or stimulated by the sperm. The egg responds to the sperm by forming fertilization cone and by undergoing the various surface and internal changes. All these changes collectively constitute activation. During activation the following changes occur in the egg.

1. The egg surface produces *fertilization cone*.
2. The vitelline membrane is lifted and is converted into *fertilization membrane*.
3. The cortical granules explode.
4. The cytoplasm exhibits movements.
5. The permeability of plasma membrane increases.
6. The coenzyme *NAD* is phosphorylated.
7. The rate of *protein synthesis* increases.
8. Mitosis is initiated.
9. The breakdown of polysaccharide occurs.
10. The enzyme *dehydrogenase* increases.

Theories of Activation

Many theories have been proposed to explain how the sperm activates the egg. A few are given below:

1. The Theory of Boveri (1887, 1895): The mature egg has no *division centre* (centriole). The egg has all the other factors, except the division centre for initiating the development. The sperm has an active division centre. So during fertilization the sperm introduces its active division centre into the egg. This division centre activates the egg to divide.

2. The Theory of Loeb (1913): *Loeb* suggested that the sperm brings in two principles. The first one is a lytic principle. It brings about cortical cytolysis which leads to a sudden increase in the oxidation process of the egg. The second principle regulates cytolysis and excess oxidation.

3. The Theory of Bataillon (1910, 11,13,16): *Bataillon* believed that the unfertilized egg is inhibited because of the accumulation of metabolic products. The entry of sperm leads to

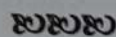
the release of these substances to the egg's exterior. This leads to the accumulation of perivitelline fluid and the elevation of the fertilization-membrane.

4. Fertilizin-Antifertilizin Theory: *F.R. Lillie* stated that the egg is activated by the fertilizin-antifertilizin reaction. Fertilizin is a *glycoprotein* present in the egg. Antifertilizin is an *acid protein* present in the sperm. Fertilizin activates, attracts and agglutinates the sperm at the egg's surface. As the sperm touches the egg, it unites with a part of fertilizin molecule. This union releases an activating principle within the egg. The activating principle activates the egg as a whole. The most important change in the egg is the *cortical reaction* including the formation of fertilization membrane. The fertilization membrane and fertilizin-antifertilizin reaction prevent *polyspermy*.

5. Change of Viscosity Theory: This theory was postulated by *Heilbrunn* (1915, 28, 43). During activation, calcium is released in the egg-cytoplasm. This leads to an increase in the viscosity of egg-cytoplasm. This change initiates development.

6. The Theory of Tyler (1967): This theory gives a molecular mechanism for the activation of the egg. In sea urchin egg, protein synthesis is initiated immediately after fertilization. In the mature, unfertilized egg, protein synthesis is nil, although it contains the entire machinery for protein synthesis. It has been demonstrated that mRNA in the unfertilized egg is '*masked*' or '*inactivated*'. The masking substance is supposed to be a *protein*. At fertilization, the masking protein is freed and mRNA is unmasked. Hence they participate in protein synthesis. The dissolution of masking protein is brought about by an enzyme liberated into the egg by the spermatozoon at the time of fertilization.

7. The Theory of Deinhibition: This theory is based on the observation of *Runnstrom* and *Brachet*. According to them, during maturation metabolic inhibitors accumulate in the oocyte. This is eliminated and the egg is deinhibited.

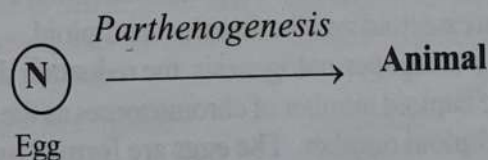


7 Parthenogenesis

Parthenogenesis is the development of an egg without fertilization. (Gr. *Parthenos* = virgin; *genesis* = birth).

The individuals formed by parthenogenesis are called **parthenotes**.

Parthenogenesis may be of two types. They are **natural parthenogenesis** and **artificial parthenogenesis**.



Natural Parthenogenesis

When parthenogenesis occurs spontaneously it is called **natural parthenogenesis**.

Parthenogenesis is a regular natural phenomenon in a few groups of animals. Some animals reproduce exclusively by parthenogenesis. In some other species, parthenogenesis alternates with sexual reproduction.

Natural parthenogenesis is divided into two groups, namely

1. **complete parthenogenesis** and 2. **incomplete parthenogenesis**.

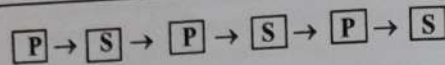
1. Complete Parthenogenesis

In certain animals, parthenogenesis is the only method of reproduction. This type of parthenogenesis is called **complete** or **total** or **obligatory** parthenogenesis. Populations exhibiting total parthenogenesis consist entirely of females. There are no males. Eg. *Lacerta* (lizard).

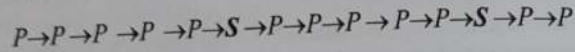
2. Incomplete Parthenogenesis

In some animals, parthenogenetic reproduction and sexual reproduction occur alternately. This is called **incomplete** or **cyclical** parthenogenesis.

Example: 1. In gallflies, parthenogenetic reproduction alternates with sexual reproduction; there is one parthenogenetic reproduction and one sexual reproduction per year.



2. In aphids, daphnids and rotifers, one sexual reproduction occurs in summer after many parthenogenetic reproductions.



Natural parthenogenesis is further classified into two types. They are haploid parthenogenesis or **arrhenotoky** and diploid parthenogenesis or **thelytoky**.

1. Arrhenotoky

Arrhenotoky is a type of parthenogenesis. In arrhenotoky, a haploid egg develops into a haploid animal without fertilization. It is also called **haploid parthenogenesis**.

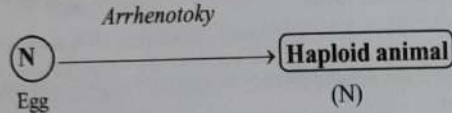


Fig.7.1: Arrhenotoky.

It is found in insects, arachnids and rotifers.

In honey bee, parthenogenetic eggs develop into males and fertilized eggs develop into females. Hence the males are haploid and the females are diploid.

The males are fertile. During spermatogenesis, the reduction division is omitted. Hence, the spermatozoa contain the haploid number of chromosomes as the parent.

The females contain diploid number. The eggs are formed by **meiosis**; hence, they are haploid.

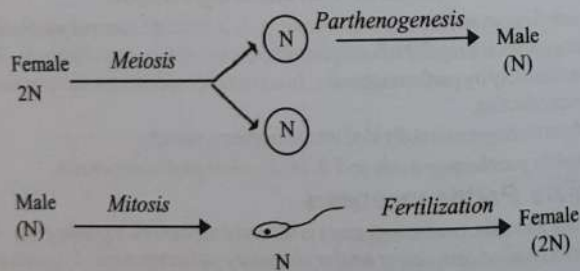


Fig.7.2: Haploid parthenogenesis in honey bee.

2. Thelytoky

Thelytoky is a type of parthenogenesis. In thelytoky, an unfertilized egg develops into a diploid animal. It is also called **diploid parthenogenesis**.

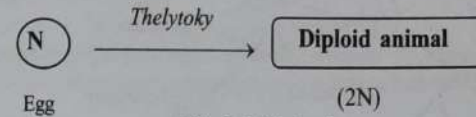


Fig.7.3: Thelytoky.

It is found in **crustaceans** and **insects**.

The diploid condition is maintained either by omitting the reduction division or by the fusion of one of the polar bodies with the haploid egg. Based on this, thelytoky is classified into two types, namely **ameiotic thelytoky** and **meiotic thelytoky**.

1. Ameiotic Thelytoky

In ameiotic thelytoky, meiosis is suppressed. The egg is produced by simple **mitosis**. As a result, the egg is diploid. It generally occurs in crustaceans and insects.

2. Meiotic Thelytoky

In meiotic thelytoky, meiosis occurs during oogenesis and the haploid eggs are produced. The diploid condition is achieved by the doubling of the chromosome. The doubling of the chromosome is called **diploisis**. Diploisis occurs in any one of the two ways, namely **restitution** and **autofertilization**.

a. Restitution: In this process, the first meiotic division is **incomplete**. The second meiotic division occurs normally. This results in the production of two diploid cells.

One cell is smaller and is called **polar body**. The other cell is large and it develops into the **egg**. This diploid egg develops into the embryo without fertilization. Eg. *Lepidopteran* insects.

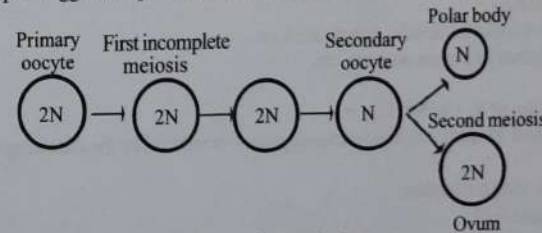


Fig.7.4: Thelytoky by restitution.

b. Autofertilization: In this process, meiosis occurs normally during oogenesis and haploid egg is produced.

The haploid egg then becomes diploid by fusing with one of the polar bodies. This process is called **autofertilization**. In *Artemia salina* (brine shrimp), diploisis occurs by the fusion of egg with the second polar body.

Parthenogenesis in Vertebrates

Natural parthenogenesis is rare in vertebrates. A few parthenogenetic vertebrates occur in nature. They are as follows:

1. In the case of lizard *Lacerta saxicola armeniaca*, there are no males. It produces diploid egg. The diploid egg develops into diploid females. Before gametogenesis, the chromosomes are duplicated in the sex cells.

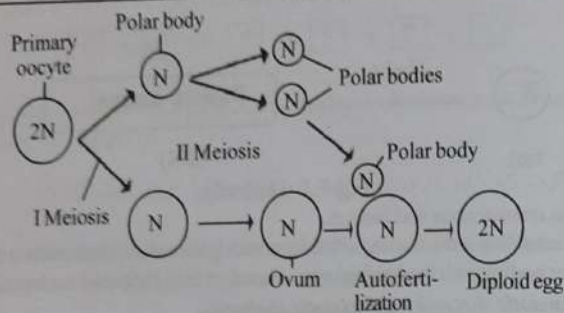


Fig.7.5: Thelytoky by autofertilization.

2. The fish *Carassius auratus gibelio*, reproduces parthenogenetically. Here also there are no males.

Artificial Parthenogenesis

Parthenogenesis produced experimentally in the laboratory is called **artificial parthenogenesis**. This has been demonstrated in annelids, molluscs, echinoderms, amphibians, birds and mammals. Parthenogenesis may be produced by mechanical or chemical means.

Chemical Means: Artificial parthenogenesis is induced by treating the eggs with the following chemical agents:

1. Hypotonic or hypertonic seawater
2. Chloroform
3. Blood serum
4. Fatty acids like lactic acid, butyric acid, etc.
5. Fat solvents like ether, acetone, etc.
6. Urea
7. Chlorides of K, Ca, Na, Mg, etc.

Mechanical Means: Artificial parthenogenesis is induced by the following mechanical methods:

1. High or low temperature
2. Ultraviolet light

Gynogenesis or Pseudo-fertilization

It is a special type of parthenogenesis occurring in a few turbellarians, nematodes and earthworms. In these animals, the egg is stimulated to develop by the penetration of the spermatozoon. After penetration, the sperm disintegrates without fusing with the egg nucleus. This process is said to be **gynogenesis** or **pseudo-fertilization**. Gynogenesis is more common in hermaphrodite animals.

Significance of Parthenogenesis

1. **As a Means of Reproduction:** Parthenogenesis is a simple and easier means of reproduction. It ensures the continuity of a race when fertilization fails to occur.

2. **Rapid Multiplication:** Parthenogenesis favours the production of large number of individuals within a short period.

3. **Persistence of Advantageous Characters:** Sometimes advantageous characters appear in the parthenotes by mutations.

4. **Elimination of Disadvantageous Characters:** Sometimes mutation produces unfavourable characters. These are not useful to the possessor. Such organisms cannot compete the fittest animals. Hence, parthenotes with unfavourable adaptations are eliminated from the population.

5. **Elimination of Variety:** As the offspring are formed by the contribution of only one animal, the possibility for the development of variation is reduced. Hence, parthenogenesis cannot produce new varieties.

6. **As a Means of Sex Determination:** As the sex is determined by chromosomes, parthenogenesis is very useful in determining the ratio of males and females in a population. For example, in aphids all the unfertilized eggs develop into males and fertilized eggs into females.

7. **Prevention of Wastage of Energy:** Mating is an essential phenomenon in sexual reproduction. It involves the wastage of energy. Parthenogenesis does not require mating. Hence, most of the energy can be saved.

8. **Polyploidy:** Parthenogenesis favours polyploidy.

9. **Fertility:** Parthenogenesis avoids sterility in the races.

10. **Inheritance:** Parthenogenesis supports the chromosome theory of inheritance.

□□□□