GAMETOGENESIS

SPERMATOGENESIS & OOGENESIS

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Gametogenesis

In multicellular eukaryotic organisms, the reproductive process begins with the generation of gametes by the process of gametogenesis. The gametes are formed from **germ cells** in the embryo. The germ cells are referred to collectively as the **germ line**, consisting of cells that will or can become the future gametes, and all other cells of the body are referred to as the somatic tissues or soma. During embryonic development germ cells undergo multiplication and will also often undergo a migration from the site of their formation to the gonad, which may be some distance away. The gonads arise from mesoderm and are initially composed entirely of somatic tissues. After the germ cells arrive they become fully integrated into its structure, and in postembryonic life undergo gamete formation. The sperms in males are produced by the process of **spermatogenesis** while the ova in the females are produced by the process of **oogenesis. These two processes are collectively known as gametogenesis.**

12.3 SPERMATOGENESIS

The process of spermatogenesis produces mature male gametes, commonly called sperms but more specifically known as spermatozoa. In humans, the entire process of spermatogenesis is variously estimated as taking 74 days. The paired testes of human males produce 200 to 300 million spermatozoa daily. However, only about half or 100 million of these become viable sperm.

We had said earlier that the primordial germ cells (PGC) migrate from their site of origin to the site where gonads in case of males, the testes (Fig.12.1a), are formed. They lie in the germinal epithelium, near the outer edge of the testes .This germinal epithelium also contains the Sertoli's cells (Fig.12.1b) which are supporting cells and play a role in sex differentiation.

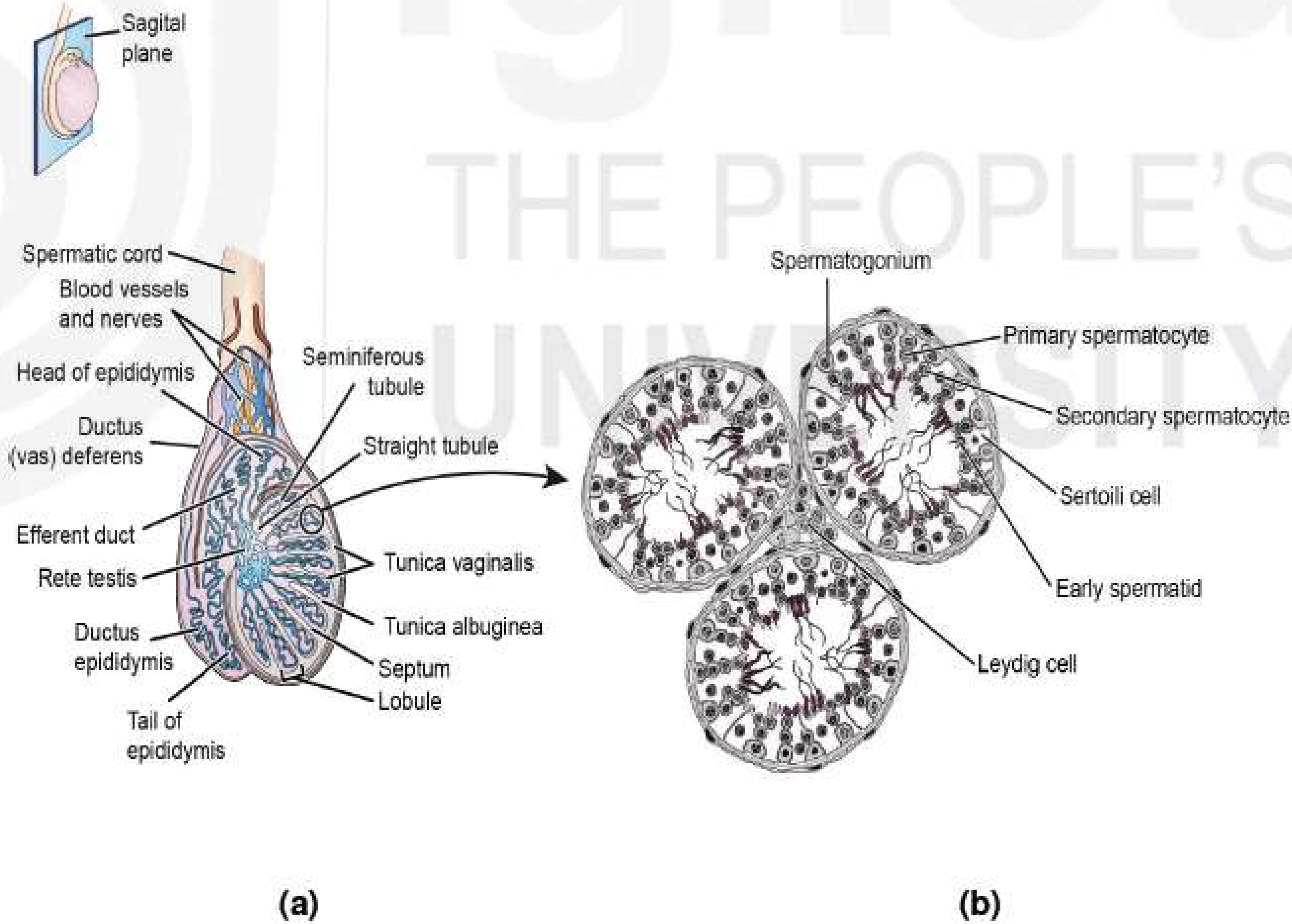


Fig.12.1: a) Saggital section of human testis showing seminiferous tubules; b) cross section of seminiferous tubules, showing Sertoli's cells, developing stages of sperms and Leydig cells between adjacent seminiferous tubules.

Spermatogenesis is a continuous process of various physical, chemical and morphological changes by which the spermatozoon is developed from the undifferentiated mother cells known as the **spermatogonia**. Spermatogenesis takes place within the seminiferous tubules of the testis, through cell division and differentiation. Spermatogenesis in humans is initiated in the paired male testis at the beginning of puberty and usually continues uninterrupted until death; although a slight, decrease in the quantity of production of sperms is seen with an increase in age. With the start of spermatogenesis at puberty, the germinal lining of the coiled seminiferous tubules exhibit two differing cell populations: (i) some are the Sertoli's cells while (ii) the majority are the germ cells in various stages of division and differentiation (refer to Fig 12.1 b again).

The Sertoli's cells in addition to playing a role in sex differentiation are also responsible for the barrier between "blood and testicles"(testicle refers to the testis present in men and other male mammals when enclosed in the scrotal sac) in the seminiferous tubules of human testes. This is of practical importance because haploid cells in the inner part of the tubule exhibit surface antigenic properties, different from all other body cells. Thus, they must thus be kept secluded from the immune system of the organism.

12.3.1 Phases of Spermatogenesis

The process of spermatogenesis (Fig. 12.2) can be broadly divided into three phases- (1) multiplication phase, (2) growth phase and (3) maturation phase.

1. Multiplication phase

Multiplication phase or the mitotic phase is the stage of multiplication or proliferation of the immature primordial germ cells within the seminiferous tubules of the testes.

The primordial germ cells which are located in the outer wall of the of the seminiferous tubules divide mitotically to give rise to the stem cells which further divide mitotically to produce spermatagonial cells, also called spermatogonia. Two types of spermatogonia are produced during the multiplication phase: i) "A type spermatogonia" and ii) "B type spermatogonia". A type spermatogonia, lack heterochromatin in their nucleus and continue to divide mitotically throughout the life span of the male human being, in order to provide additional spermatogonia so that there is a constant source of germ cells. Type B spermatogonia contain heterochromatin in the nucleus and are known as **primary sperm cells**. They are the prototypes of male sex cells that are destined to develop into mature sperm cells.

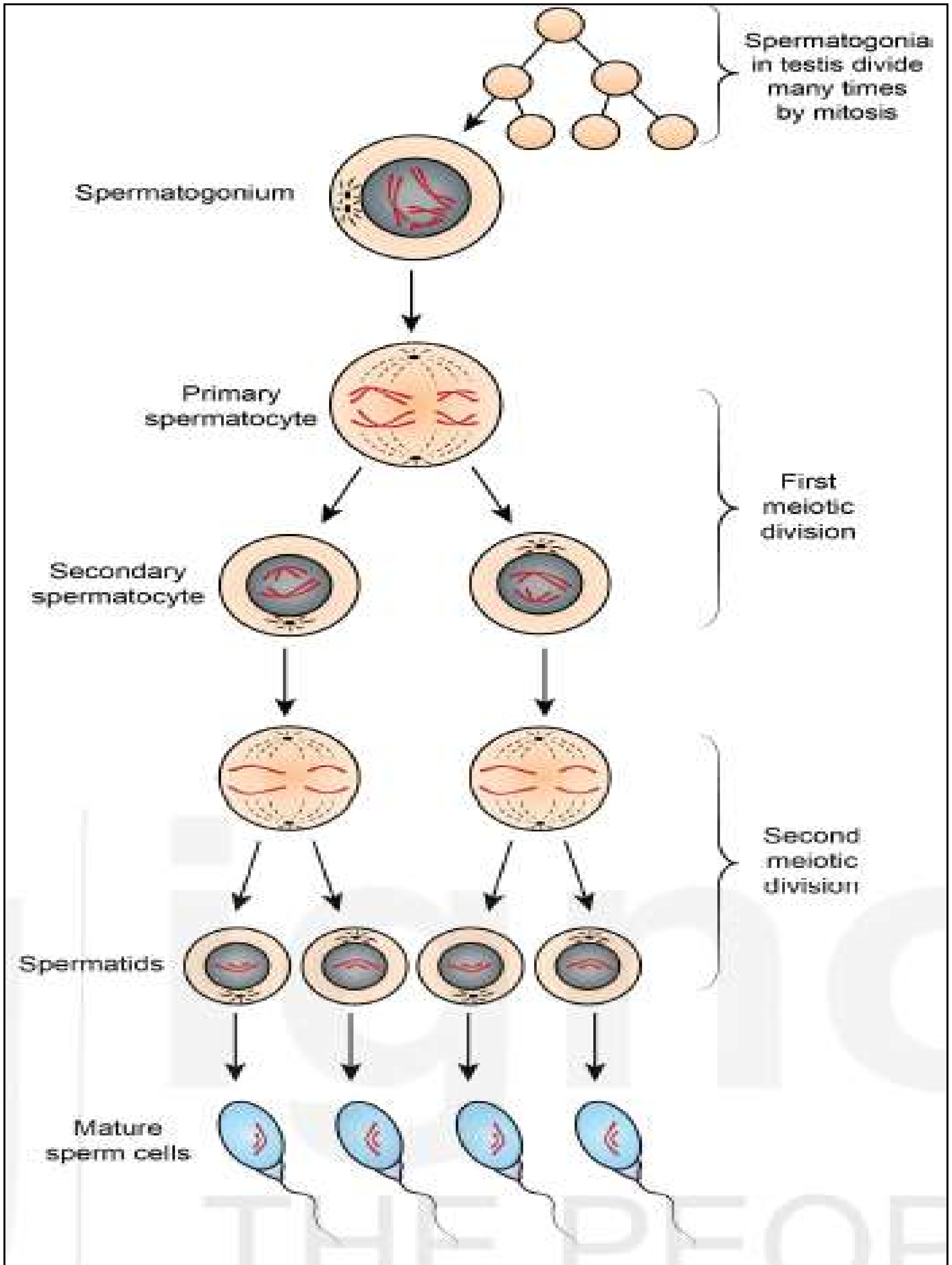


Fig.12.2: Stages in spermatogenesis

2. Growth Phase

Growth phase is characterized by the development of structural and functional features of the distinct sex cells. The primary sperm cells develop during this phase by increasing the amount of cytoplasm and developing the organelles within the cytoplasm. These **large, B Type spermatagonial cells** are now known as **primary spermatocytes** and their cytoplasmic and the nuclear contents become ready for subsequent changes. The primary spermatocytes now move towards the lumen of the seminiferous tubule and duplicate their DNA. The Growth phase is then followed by the maturation stage.

3. Maturation Phase

The maturation phase is the stage in which the diploid primary spermatocytes get transformed into haploid spermatids (Fig.12.2) by two successive meiotic divisions. The primary spermatocyte divides meiotically to produce two **secondary spermatocytes** each with a haploid nucleus. Each of the secondary spermatocytes undergoes second meiotic division, thus giving rise to four haploid **spermatids**. Each spermatid undergoes an intracellular differentiation to produce a spermatozoa. Maturation then takes place under the influence of testosterone. Humans have a diploid number of 46 chromosomes, while their haploid gametes have half the number of chromosomes ($n = 23$).The haploid spermatids undergo extensive changes in order to differentiate into sperms.

During maturation the unnecessary cytoplasm and organelles are removed. The excess cytoplasm, known as residual bodies, are phagocytosed by the surrounding Sertoli's cells in the testes. The mature haploid spermatids formed at this stage however, lack motility and are still not capable of functioning as male gametes. They are transformed into the motile, active spermatozoa or sperms by the process of spermiogenesis about which we will study in more detail in the next subsection.

12.3.2 Spermiogenesis

At the end of the meiosis the spermatids appear as simple spherical cells with a centrally located nucleus. Their differentiation into sperm requires an extensive morphological transformation. The various cellular organelles like mitochondria, Golgi body and centrosome contribute to such a transformation. The transformation of a spermatid into a spermatozoon is essential so that it (1) attains motility and (2) its motility and movement is improved by reduction of unnecessary or superfluous materials present in it.

The number of programmed steps needed to transform an ordinary looking round spermatid into a dynamically shaped spermatozoon varies from species to species. The steps range from six to eight steps in man; to 19 steps in rats and rabbits.

The fully formed sperm (Figs.12.3 and 12.4.) consists of the head and flagellum. The flagellum can be divisible into the following regions which consist of neck piece/ the middle or mid piece, principle piece which is usually the longest part of the flagellum and the tail end. The axoneme is the central cytoskeletal structure of the flagellum. It has the typical structure of a cilium and is composed of an array of microtubules, typically consisting of nine pairs surrounding two single central ones. You will be reading about the structure of

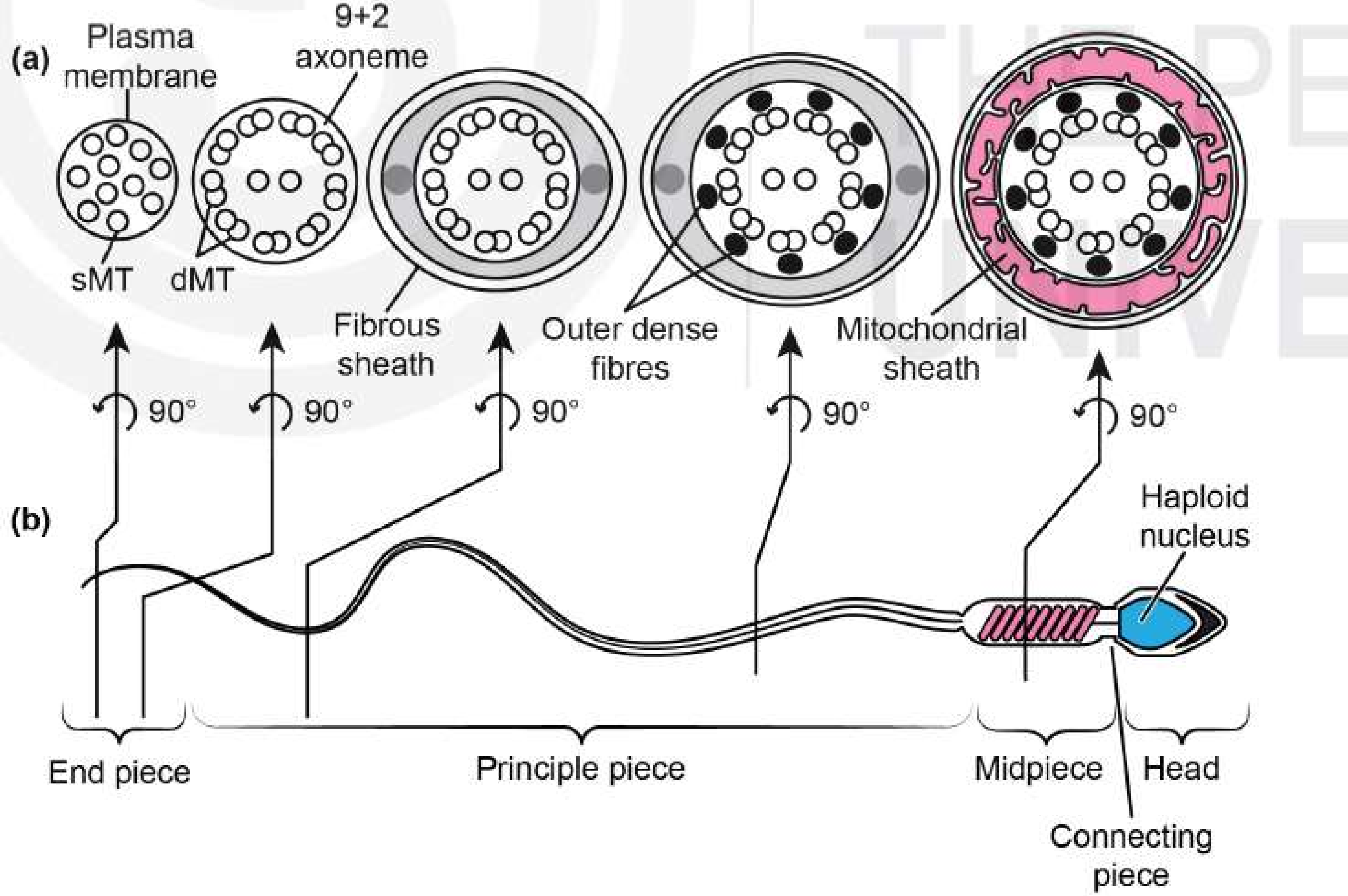


Fig. 12.3: Mature spermatozoon. The genetic information is packaged in a tight bundle in the haploid nucleus in the head region. Surrounding it is an acrosomal vesicle that helps the sperm penetrate the ovum. The spermatozoa's motility is derived from its flagellum, which is powered by a group of mitochondria in the midpiece.

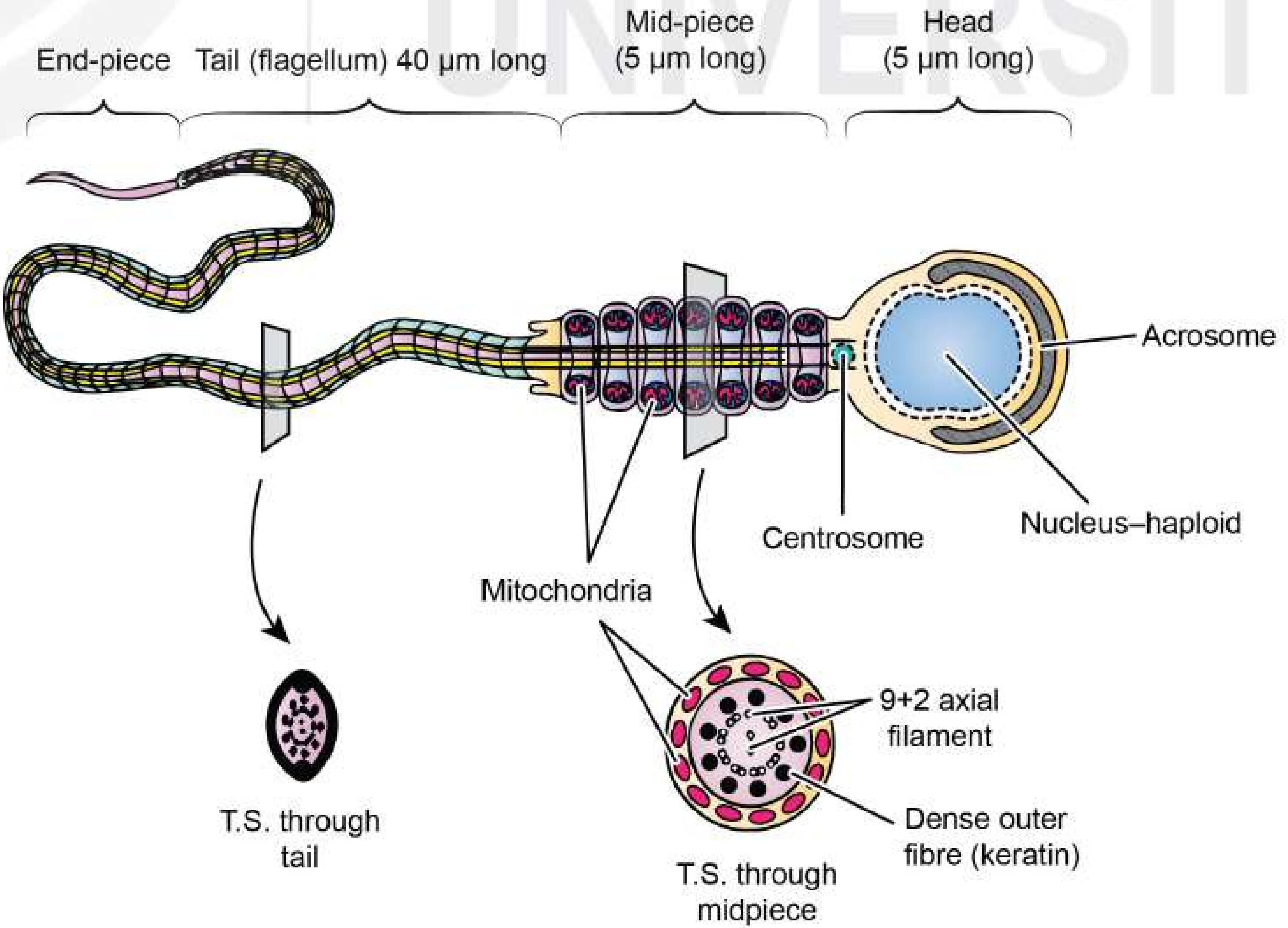
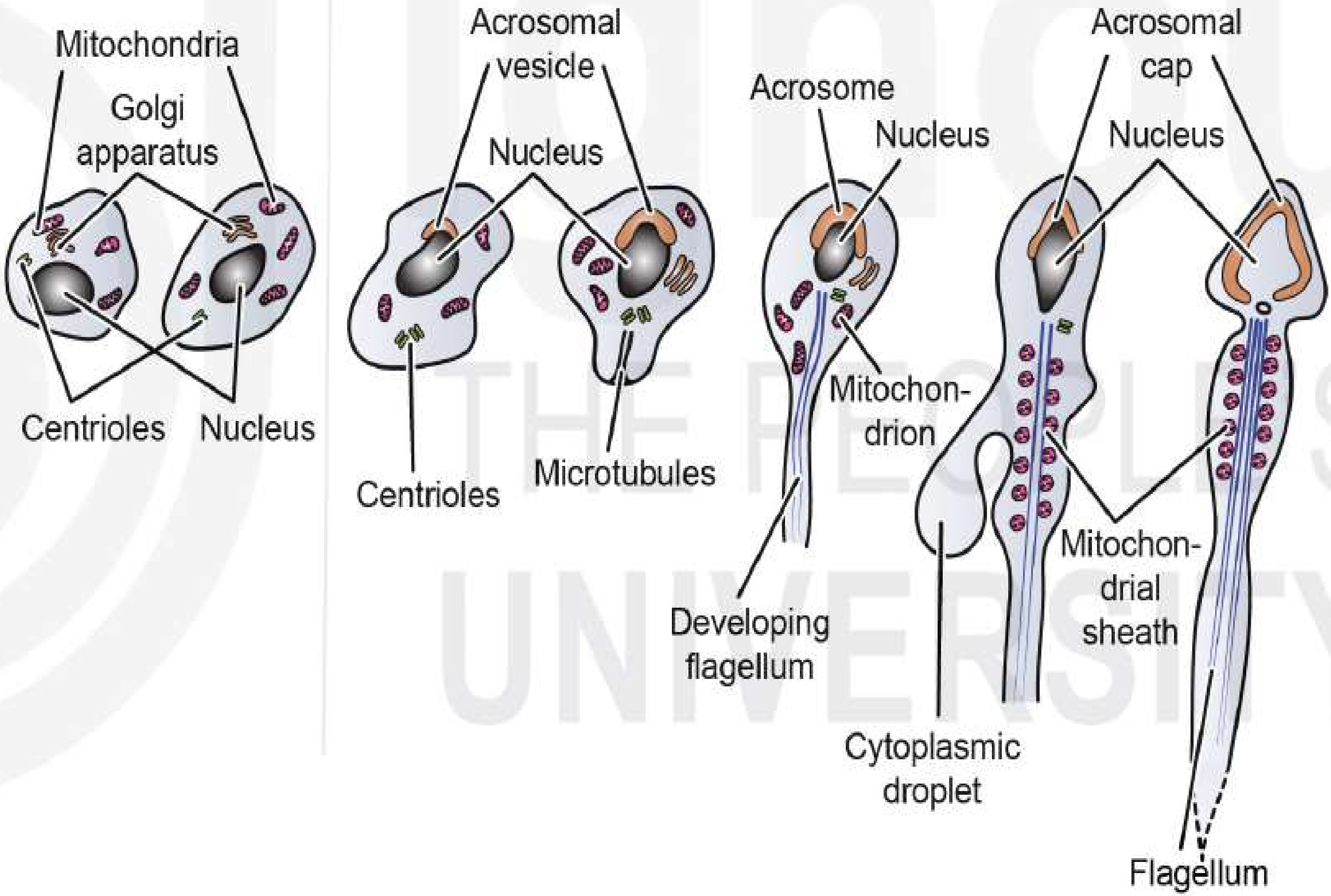


Fig12.4: Structure of a human sperm showing cross section of the flagellum at its different segments.

Figure 12.6 shows the transformation of the spermatid into a sperm.



12.3.3 Spermiation: Activation of Sperm

The mature though inactive, non-motile spermatozoa or sperms contained in the testicular fluid which is secreted by the Sertoli's cells, move inwards towards the fluid-filled lumen (cavity) of the seminiferous tubules and are released in it. After which the spermatids are transported from the lumen of the seminiferous tubule into the epididymis (highly convoluted duct behind the testis) and then via the vas deferens to the outside of the body through the penis, by means of peristaltic contractions. While travelling in the epididymis, the non-motile spermatozoa transform into the motile spermatozoa or sperms, by the process of spermiation and become capable of fertilizing the ovum.

The motile sperms are microscopic, remain alive, and have the capability to fertilize an ovum from 24 to 48 hours, right after they the female genital tract.

In humans the whole process of spermatogenesis, from spermatogonia to spermatozoa takes approximately 74 days (Fig.12.7) while in mouse it takes 34.5 days to complete the whole process of spermatogenesis.

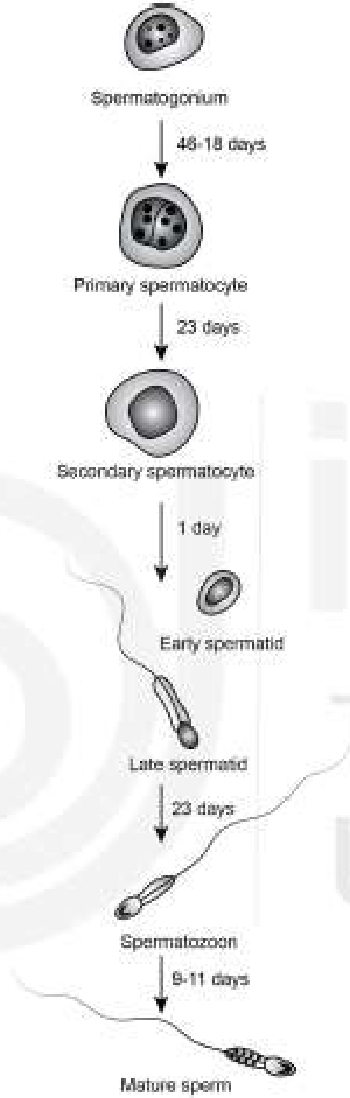


Fig. 12.7: Development of human spermatozoa: Each of the stage of spermatogenesis in humans, has its own specific duration. The spermatogonia take 16–18 days to form the primary spermatocytes; the primary spermatocytes take 23 days to make the secondary spermatocytes; the secondary spermatocytes take only one day to become spermatids, and the spermatids spend another 23 days maturing into spermatozoa. This does not add up to 74 days because after release of the spermatozoa into the lumen of the seminiferous tubules, the spermatozoa still require maturation. The released spermatozoa are not yet motile, and they are transferred to the epididymis by movement of the luminal fluid, and not by motility of the sperm. In the epididymis, the spermatozoon undergoes maturation processes that progressively enable it to bind to the zona pellucida of the ovum and to fertilize the ovum.

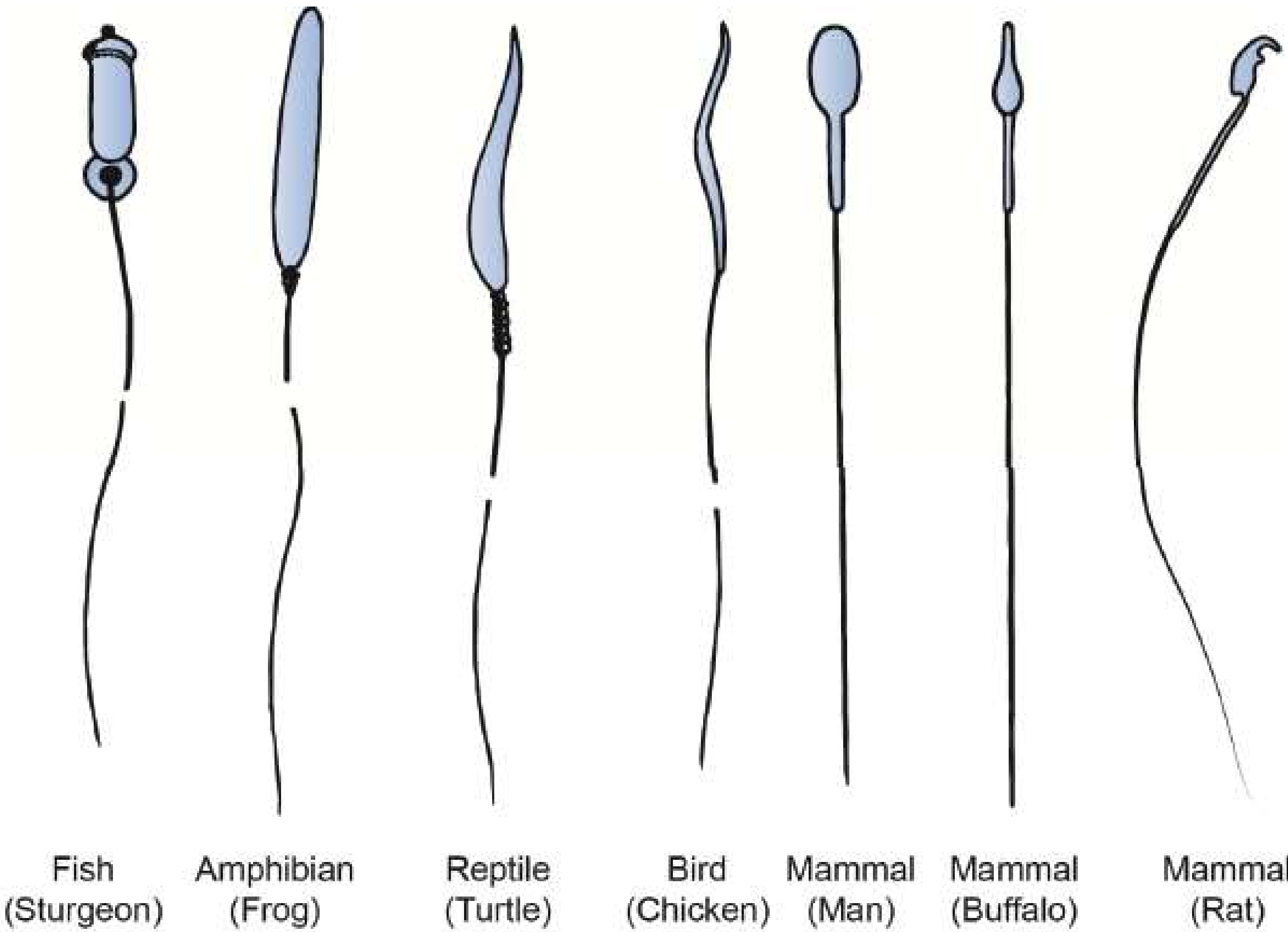


Fig.12.8: Sperms of some vertebrates (the break in the flagellum of sperm indicates that a portion is omitted), showing the head which varies in size and shape. The flagellum also varies in length.

12.4 OOGENESIS

Oogenesis begins in the ovary of the female embryo. The embryonic ovary contains primordial germ cells, which as you have read in section 12.2 migrate to the ovary in the same manner as the primordial germ cells of the males. The primordial germ cells give rise to the **diploid oogonial cells, or oogonia** which are also known as the mother cells. These give rise to the haploid ovum. The mechanism of oogenesis varies much more among animal species as compared to spermatogenesis. In some species, hundreds and thousands of eggs are produced routinely as seen in the sea urchin and frog. Whereas in mammals only a few eggs are produced. Oogenesis like spermatogenesis involves meiosis to produce the haploid ovum. Oogenesis is a complex process as the ovum (egg) acquires its developmental potentialities from the molecular information, encoded in its DNA and the accumulation of materials present in it, which is required for building the structures of the early embryo as well as for providing energy till the embryo becomes self-sufficient. You have learnt in the subsection on spermatogenesis that the differentiation of sperms occur after meiotic events .In oogenesis the process of the first meiotic division is very prolonged and it is during this process that growth and differentiation of oocyte takes place. In many animals most events related to oocyte differentiation occur during prophase I of the first meiotic division. Even though the mechanisms for oogenesis vary in animal species the basic mechanism of formation and maturation of ovum is more or less similar in all organisms (Fig. 12.9).It essentially includes the same steps as in spermatogenesis but the steps and the products of the process are modified.

12.4.1 Formation and Maturation of Ova

Oogenesis (Fig.12.9) mainly involves 3 phases: I) proliferative or pre-meiotic phase; II) meiotic phase and III) cell growth phase.

I) Proliferative or pre-meiotic phase

The primordial germ cells that enter into the ovary divide mitotically and produce oogonial cells, which as a result, increase in number. This is the proliferative or pre-meiotic phase as there is increase in the number of oogonial cell, within the ovary, usually during embryonic life. These oogonial cells grow in size and become the **primary oocytes**. The proliferative phase occurs in all vertebrates but the timing is different for different groups of animals. For example, in higher animals like reptiles, birds, and mammals, the proliferative phase is completed long before sexual maturity whereas, in amphibians, each year, a new crop of egg is generated by mitotic proliferation from a population of **gametogenic stem cells**.

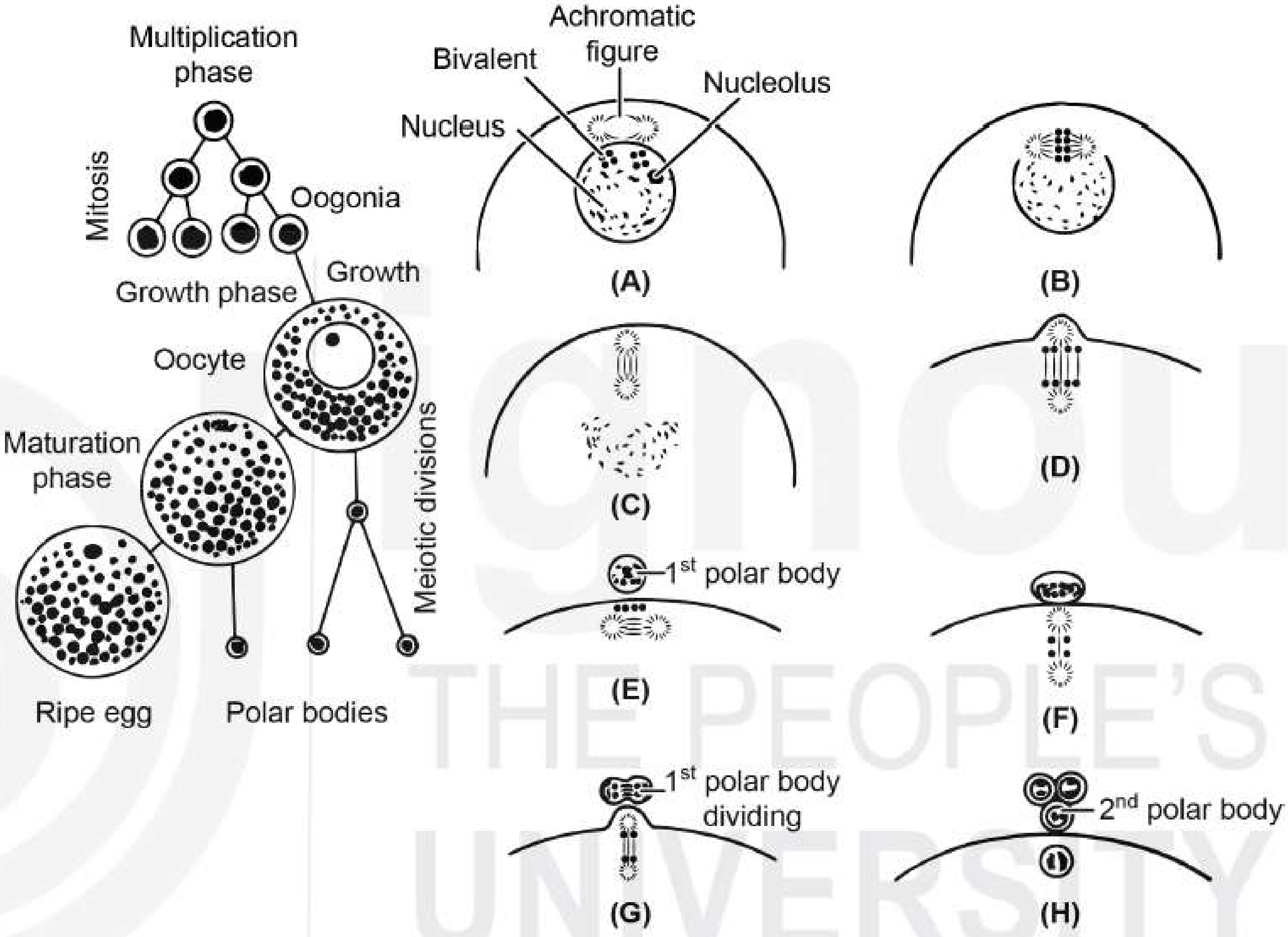


Fig.12.9: Diagrammatic representation of (1) stages in oogenesis and (2) of the first (A to E) and second (F to H) meiotic divisions in the oocyte.

II) Meiotic phase

The primary oocytes after attaining their full size undergo, a meiotic division. For this process, the chromosomes present in the primary oocytes replicate. Shortly after prophase I of the first meiotic division the replicated chromosomes condense and remain in an arrested stage of division for a prolonged period. This period of arrested division may last for months and even years. In many animals most events related to oocyte differentiation occur during prophase I of the first meiotic division. In human females, each primary oocyte is contained within a small follicle, which is a cavity lined with protective cells. At birth, the paired ovaries together contain about 1-2 million primary oocytes, of which about 500 mature between puberty and menopause.

In most vertebrates and many invertebrates, the egg does not actually complete the meiotic division before fertilization. The second meiotic division may be completed only outside the ovary after fertilization. The general rule is that development is arrested during prophase I of the first meiotic division (in the primary oocyte phase). Meiosis resumes and is completed either at the time of ovulation (birds and most mammals) or shortly after fertilization (many invertebrates, teleost fishes, amphibians, and reptiles). In humans, the ova begin the first meiotic division at about the thirteenth week of foetal development. Then their development arrests in prophase I until puberty, at which time one of these primary oocyte typically develops into a secondary oocyte in each month for ovulation. When the first meiotic division or maturation (reduction) division is completed, the cytoplasm is divided unequally. One of the two daughter cells, called the **secondary oocyte**, is large and receives most of the cytoplasm; the other is very small and is called the first polar body. Each of these daughter cells, however, receives half of the chromosomes and so are haploid cells.

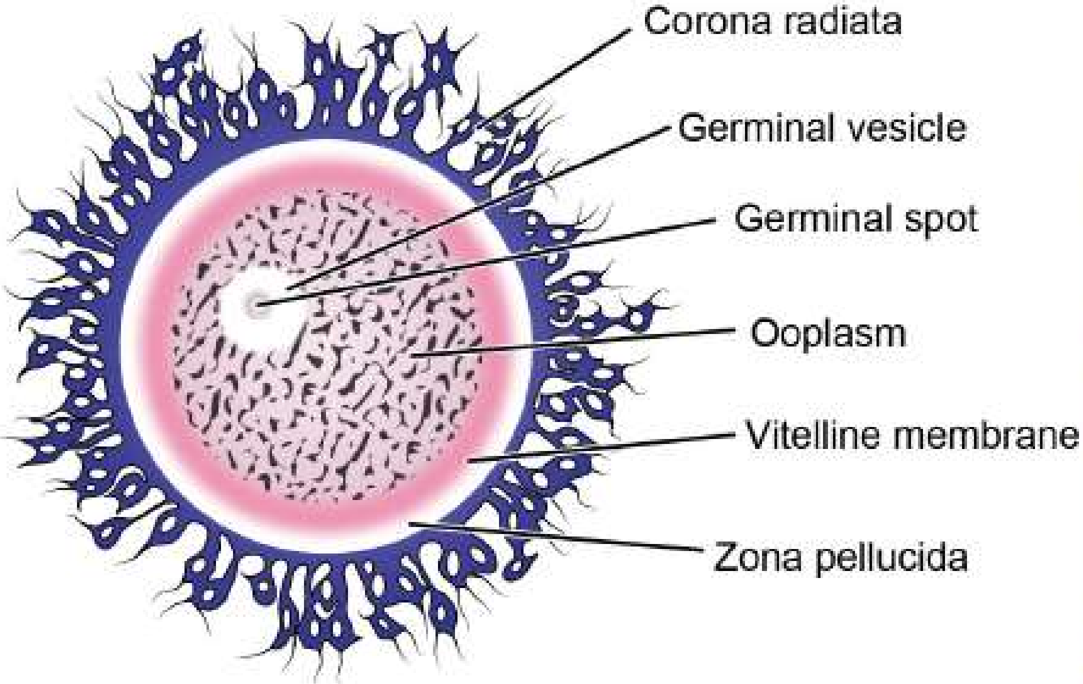
The secondary oocyte undergoes the second meiotic division to produce a large **ovum** called **ootid** and another small polar body. In humans, meiosis II is completed only when a spermatozoon penetrates the secondary oocyte. If the first polar body also divides in this division, which sometimes happens then there are three polar bodies and one ootid (Figure 12.9). The ootid develops into a functional, haploid ovum. Polar bodies are nonfunctional, and they eventually degenerate.

The formation of polar bodies during ova production is necessary as the excess chromosomes that result from each nuclear division during meiosis, is disposed off through them. In addition, the unequal cytoplasmic division results in the formation of a large cell with the cytoplasm that contains a full set of cytoplasmic components needed for early development. Thus, a mature ovum or egg has N (haploid) number of chromosomes, the same as a sperm. However, each primary oocyte gives rise to only one functional ova instead of four as in spermatogenesis.

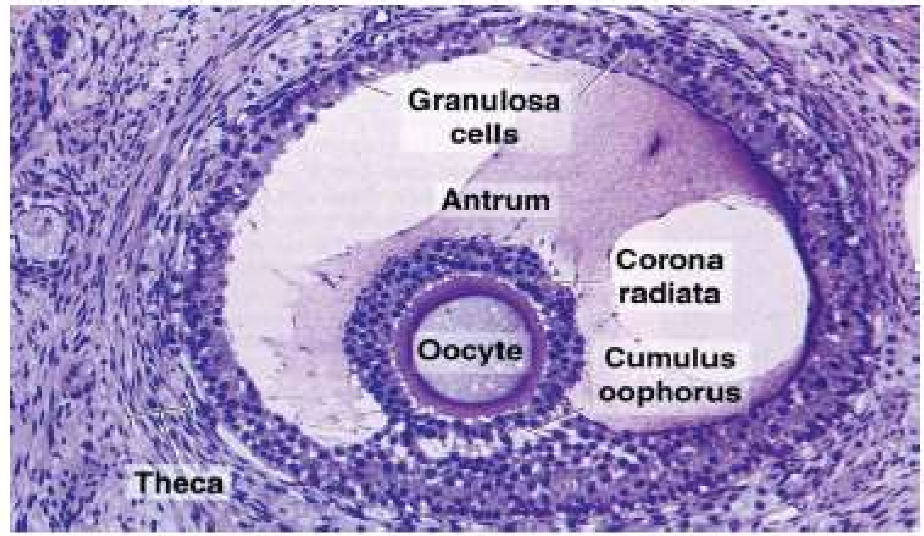
III) Growth Phase of Oocyte

During the **growth phase** period of the oocyte the gene products and nutrients are stored and accumulated in the oocyte. The growth of oocyte is so enormous that it becomes almost the largest of the body cells. For example, it ranges in size from 10µm to 200µm in mammals; it is 2000µm in frog *Lithobates pipiens* (earlier known as *Rana pipiens)* and is 40,000µm in birds. The time required for this growth varies with species. A greater amount of RNA polymerase enzymes, histone proteins, mitochondria, ribosomes etc. are also formed as they are required for cell division. During this growth phase, both qualitative and quantitative changes occur in the nucleus as well as cytoplasm.

In many animals, the most obvious feature of egg maturation is deposition of yolk. We shall discuss oogenesis in two groups of animals, (1) the amphibians as an example of organisms, which produce moderately yolky eggs and (2) mammals, as an example of organisms whose eggs do not contain any yolk.



(a)



(b)

Fig.12.13: (a) Young oocyte of a mammal surrounded by follicle cells and; b) photograph from a histological slide of a mature Graafian follicle or tertiary follicle, in which the oocyte is present on one side of the secondary oocyte.