How many cell divisions in meiosis

3D image of a mouse cell in the final stages of cell division (telophase). (Image by Lothar Schermelleh)Sometimes you accidentally bite your lip or skin your knee, but in a matter of days the wound heals. Is it magic? Or, is there another explanation?Every day, every hour, every second one of the most important events in life is going on in your body—cells are dividing. When cells divide, they make new cells. A single cell divides to make two cells and these two cells then divide to make four cells, and so on. We call this process "cell division" and "cell reproduction," because new cells are formed when old cells divide. The ability of cells to divide is unique for living organisms. Why Do Cells Divide? Cells divide for many reasons. For example, when you skin your knee, cells divide to replace old, dead, or damaged cells. Cells also divide so living things can grow. When organisms grow, it isn't because cells are getting larger. Organisms grow because cells are dividing to produce more and more cells. In human bodies, nearly two trillion cells divide every day.Watch cells divide in this time lapse video of an animal cell (top) and an E. coli bacteria cell (bottom). The video compresses 30 hours of mitotic cell division into a few seconds. (Video by the National Institute of Genetics)How Many Cells Are in Your Body?You and I began as a single cell, or what you would call an egg. By the time you are an adult, you will have trillions of cells. That number depends on the size of the person, but biologists put that number around 37 trillion cells. Yes, that is trillion with a "T."How Do Cells Know When to Divide?In cell division, the cell that is dividing is called the "parent" cell. The parent cell divides into two "daughter" cells. The process then repeats in what is called the cell cycle. Cell division of cancerous lung cell (Image from NIH)Cells regulate their division by communicating with each other using chemical signals from special proteins called cyclins. These signals act like switches to tell cells when to start dividing and later when to stop dividing. It is important for cells to divide so you can grow and so your cuts heal. It is also important for cells to stop dividing at the right time. If a cell can not stop dividing when it is supposed to stop, this can lead to a disease called cancer. Some cells, like skin cells, are constantly dividing. We need to continuously make new skin cells to replace the skin cells we lose. Did you know we lose 30,000 to 40,000 dead skin cells every minute? That means we lose around 50 million cells every day. This is a lot of skin cells to replace, making cell division in skin cells is so important. Other cells, like nerve and brain cells, divide much less often. How Cells DivideDepending on the type of cell, there are two ways cells divide—mitosis and meiosis. Each of these methods of cell division has special characteristics. One of the key differences in mitosis is a single cell divides into two cells that are replicas of each other and have the same number of chromosomes. This type of cell division is good for basic growth, repair, and maintenance. In meiosis a cell divides into four cells that have half the number of chromosomes. Reducing the number of chromosomes by half is important for sexual reproduction and provides for genetic diversity.Mitosis Cell DivisionMitosis is how somatic—or non-reproductive cells—divide. Somatic cells make up most of your body's tissues and organs, including skin, muscles, lungs, gut, and hair cells. Reproductive cells (like eggs) are not somatic cells.In mitosis, the important thing to remember is that the daughter cells each have the same chromosomes and DNA as the parent cell. The daughter cells from mitosis are called diploid cells. Diploid cells have two complete sets of chromosomes. Since the daughter cells have exact copies of their parent cell's DNA, no genetic diversity is created through mitosis in normal healthy cells. Mitosis cell division creates two genetically identical daughter diploid cells. The major steps of mitosis are shown here. (Image by Mysid from Science Primer and National Center for Biotechnology Information)The Mitosis Cell CycleBefore a cell starts dividing, it is in the "Interphase." It seems that cells must be constantly dividing (remember there are 2 trillion cell divisions in your body every day), but each cell actually spends most of its time in the interphase. Interphase is the period when a cell is getting ready to divide and start the cell cycle. During this time, cells are gathering nutrients and energy. The parent cell is also making a copy of its DNA to share equally between the two daughter cells.The mitosis division process has several steps or phases of the cell cycle—interphase, prophase, prometaphase, metaphase, anaphase, telophase, and cytokinesis—to successfully make the new diploid cells.The mitosis cell cycle includes several phases that result in two new diploid daughter cells. Each phase is highlighted here and shown by light microscopy with fluorescence. Click on the image to learn more about each phase. (Image from OpenStax College with modified work by Mariana Ruiz Villareal, Roy van Heesheen, and the Wadsworth Center.)When a cell divides during mitosis, some organelles are divided between the two daughter cells. For example, mitochondria are capable of growing and dividing during the interphase, so the daughter cells each have enough mitochondria. The Golgi apparatus, however, breaks down before mitosis and reassembles in each of the new daughter cells. Many of the specifics about what happens to organelles before, during and after cell division are currently being researched. (You can read more about cell parts and organelles by clicking here.)Meiosis Cell Division Meiosis is the other main way cells divide. Meiosis is cell division that creates sex cells, like female egg cells or male sperm cells. What is important to remember about meiosis? In meiosis, each new cell contains a unique set of genetic information. After meiosis, the sperm and egg cells can join to create a new organism. Meiosis is why we have genetic diversity in all sexually reproducing organisms. During meiosis, a small portion of each chromosome breaks off and reattaches to another chromosome. This process is called "crossing over" or "genetic recombination." Genetic recombination is the reason full siblings made from egg and sperm cells from the same two parents can look very different from one another.The meiosis cell cycle has two main stages of division -- Meiosis I and Meiosis II. The end result of meiosis is four haploid daughter cells that each contain different genetic information from each other and the parent cell. Click for more detail. (Image from Science Primer from the National Center for Biotechnology Information.)The Meiosis Cell CycleMeiosis has two cycles of cell division, conveniently called Meiosis I and Meiosis II. Meiosis I halves the number of chromosomes and is also when crossing over happens. Meiosis II halves the amount of genetic information in each chromosome of each cell. The end result is four daughter cells called haploid cells. Haploid cells only have one set of chromosomes - half the number of chromosomes as the parent cell.Before meiosis I starts, the cell goes through interphase. Just like in mitosis, the parent cell uses this time to prepare for cell division by gathering nutrients and energy and making a copy of its DNA. During the next stages of meiosis, this DNA will be switched around during genetic recombination and then divided between four haploid cells. So remember, Mitosis is what helps us grow and Meiosis is why we are all unique!References: Bianconi E, Piovesan A, Facchin F, Beraudi A, Casadei R, Frabetti F, Vitale L, Pelleri MC, Tassani S, Piva F, Perez-Amodio S, Strippoli P, Canaider S. Ann. An estimation of the number of cells in the human body. Retrieved March 14, 2014 from animal cell and E. Coli cell video from National Institute of Genetics via Wikimedia. Movie_4._Cell_division.ogv For the figure of speech, see Meiosis (figure of speech). For the process whereby cell nuclei divide to produce two copies of themselves, see Mitosis. For excessive constriction of the pupils, see Miosis. For the parasitic infestation, see Myiasis. For muscle inflammation, see Myositis. Type of cell division in sexually-reproducing organisms used to produce gametes In meiosis, the chromosome or chromosomes duplicate (during interphase) and homologous chromosomes exchange genetic information (chromosomal crossover) during the first division, called meiosis I. The daughter cells divide again in meiosis II, splitting up sister chromatids to form haploid gametes. Two gametes fuse during fertilization, forming a diploid cell with a complete set of paired chromosomes. Play media A video of meiosis I in a crane fly spermatocyte, played back at 120× the recorded speed Meiosis (/maɪˈoʊsɪs/ (listen); from Greek μείωσις, meiosis, meaning "lessening", because it is a reductional division[1][2]) is a special type of cell division of germ cells in sexually-reproducing organisms used to produce the gametes, such as sperm or egg cells. It involves two rounds of division that ultimately result in four cells with only one copy of each chromosome (haploid). Additionally, prior to the division, genetic material from the paternal and maternal copies of each chromosome is crossed over, creating new combinations of code on each chromosome.[3] Later on, during fertilisation, the haploid cells produced by meiosis from a male and female will fuse to create a cell with two copies of each chromosome again, the zygote. Errors in meiosis resulting in aneuploidy (an abnormal number of chromosomes) are the leading known cause of miscarriage and the most frequent genetic cause of developmental disabilities.[4] In meiosis, DNA replication is followed by two rounds of cell division to produce four daughter cells, each with half the number of chromosomes as the original parent cell.[3] The two meiotic divisions are known as meiosis I and meiosis II. Before meiosis begins, during S phase of the cell cycle, the DNA of each chromosome is replicated so that it consists of two identical sister chromatids, which remain held together through sister chromatid cohesion. This S-phase can be referred to as "premeiotic S-phase" or "meiotic S-phase". Immediately following DNA replication, meiotic cells enter a prolonged G2-like stage known as meiotic prophase. During this time, homologous chromosomes pair with each other and undergo genetic recombination, a programmed process in which DNA may be cut and then repaired, which allows them to exchange some of their genetic information. A subset of recombination events results in crossovers, which create physical links known as chiasmata (singular: chiasma, for the Greek letter Chi (Χ)) between the homologous chromosomes. In most organisms, these links can help direct each pair of homologous chromosomes to segregate away from each other during Meiosis I, resulting in two haploid cells that have half the number of chromosomes as the parent cell. During meiosis II, the cohesion between sister chromatids is released and they segregate from one another, as during mitosis. In some cases, all four of the meiotic products form gametes such as sperm, spores or pollen. In female animals, three of the four meiotic products are typically eliminated by extrusion into polar bodies, and only one cell develops to produce an ovum. Because the number of chromosomes is halved during meiosis, gametes can fuse (i.e. fertilization) to form a diploid zygote that contains two copies of each chromosome, one from each parent. Thus, alternating cycles of meiosis and fertilization enable sexual reproduction, with successive generations maintaining the same number of chromosomes. For example, diploid human cells contain 23 pairs of chromosomes including 1 pair of sex chromosomes (46 total), half of maternal origin and half of paternal origin. Meiosis produces haploid gametes (ova or sperm) that contain one set of 23 chromosomes. When two gametes (an egg and a sperm) fuse, the resulting zygote is once again diploid, with the mother and father each contributing 23 chromosomes. This same pattern, but not the same number of chromosomes, occurs in all organisms that utilize meiosis. Meiosis occurs in all sexually-reproducing single-celled and multicellular organisms (which are all eukaryotes), including animals, plants and fungi.[5][6][7] It is an essential process for oogenesis and spermatogenesis. Overview Although the process of meiosis is related to the more general cell division process of mitosis, it differs in two important respects: recombination meiosis shuffles the genes between the two chromosomes in each pair (one received from each parent), producing recombinant chromosomes with unique genetic combinations in every gamete mitosis occurs only if needed to repair DNA damage; usually occurs between identical sister chromatids and does not result in genetic changes chromosome number (ploidy) meiosis produces four genetically unique cells, each with half the number of chromosomes as in the parent mitosis produces two genetically identical cells, each with the same number of chromosomes as in the parent Meiosis begins with a diploid cell, which contains two copies of each chromosome, termed homologs. First, the cell undergoes DNA replication, so each homolog now consists of two identical sister chromatids. Then each set of homologs pair with each other and exchange genetic information by homologous recombination often leading to physical connections (crossovers) between the homologs. In the first meiotic division, the homologs are segregated to separate daughter cells by the spindle apparatus. The cells then proceed to a second division without an intervening round of DNA replication. The sister chromatids are segregated to separate daughter cells to produce a total of four haploid cells. Female animals employ a slight variation on this pattern and produce one large ovum and two small polar bodies. Because of recombination, an individual chromatid can consist of a new combination of maternal and paternal genetic information, resulting in offspring that are genetically distinct from either parent. Furthermore, an individual gamete can include an assortment of maternal, paternal, and recombinant chromatids. This genetic diversity resulting from sexual reproduction contributes to the variation in traits upon which natural selection can act. Meiosis uses many of the same mechanisms as mitosis, the type of cell division used by eukaryotes to divide one cell into two identical daughter cells. In some plants, fungi, and protists meiosis results in the formation of spores: haploid cells that can divide vegetatively without undergoing fertilization. Some eukaryotes, like bdelloid rotifers, do not have the ability to carry out meiosis and have acquired the ability to reproduce by parthenogenesis. Meiosis does not occur in archaea or bacteria, which generally reproduce asexually via binary fission. However, a "sexual" process known as horizontal gene transfer involves the transfer of DNA from one bacterium or archaeon to another and recombination of these DNA molecules of different parental origin. History Meiosis was discovered and described for the first time in sea urchin eggs in 1876 by the German biologist Oscar Hertwig. It was described again in 1883, at the level of chromosomes, by the Belgian zoologist Edouard Van Beneden, in Ascaris roundworm eggs. The significance of meiosis for reproduction and inheritance, however, was described only in 1890 by German biologist August Weismann, who noted that two cell divisions were necessary to transform one diploid cell into four haploid cells if the number of chromosomes had to be maintained. In 1911, the American geneticist Thomas Hunt Morgan detected crossovers in meiosis in the fruit fly Drosophila melanogaster, which helped to establish that genetic traits are transmitted on chromosomes. The term "meiosis" is derived from the Greek word μείωσις, meaning 'lessening'. It was introduced to biology by J.B. Farmer and J.E.S. Moore in 1905, using the idiosyncratic rendering "maiosis": We propose to apply the terms Maiosis or Maiotic phase to cover the whole series of nuclear changes included in the two divisions that were designated as Heterotype and Homotype by Flemming.[8] The spelling was changed to "meiosis" by Koernicke (1905) and by Pantel and De Sinety (1906) to follow the usual conventions for transliterating Greek.[9] Phases Meiosis is divided into meiosis I and meiosis II which are further divided into Karyokinesis I and Cytokinesis I and Karyokinesis II and Cytokinesis II respectively. The preparatory steps that lead up to meiosis are identical in pattern and name to interphase of the mitotic cell cycle.[10] Interphase is divided into three phases: Growth 1 (G1) phase: In this very active phase, the cell synthesizes its vast array of proteins, including the enzymes and structural proteins it will need for growth. In G1, each of the chromosomes consists of a single linear molecule of DNA. Synthesis (S) phase: The genetic material is replicated; each of the cell's chromosomes duplicates to become two identical sister chromatids attached at a centromere. This replication does not change the ploidy of the cell since the centromere number remains the same. The identical sister chromatids have not yet condensed into the densely packaged chromosomes visible with the light microscope. This will take place during prophase I in meiosis. Growth 2 (G2) phase: G2 phase as seen before mitosis is not present in meiosis. Meiotic prophase corresponds most closely to the G2 phase of the mitotic cell cycle. Interphase is followed by meiosis I and then meiosis II. Meiosis I separates replicated homologous chromosomes, each still made up of two sister chromatids, into two daughter cells, thus reducing the chromosome number by half. During meiosis II, sister chromatids decouple and the resultant daughter chromosomes are segregated into four daughter cells. For diploid organisms, the daughter cells resulting from meiosis are haploid and contain only one copy of each chromosome. In some species, cells enter a resting phase known as interkinesis between meiosis I and meiosis II. Meiosis I and II are each divided into prophase, metaphase, anaphase, and telophase stages, similar in purpose to their analogous subphases in the mitotic cell cycle. Therefore, meiosis includes the stages of meiosis I (prophase I, metaphase I, anaphase I, telophase I) and meiosis II (prophase II, metaphase II, anaphase II, telophase II). Diagram of the meiotic phases During meiosis, specific genes are more highly transcribed.[11][12] In addition to strong meiotic stage-specific expression of mRNA, there are also pervasive translational controls (e.g. selective usage of preformed mRNA), regulating the ultimate meiotic stage-specific protein expression of genes during meiosis.[13] Thus, both transcriptional and translational controls determine the broad restructuring of meiotic cells needed to carry out meiosis. Meiosis I Meiosis I segregates homologous chromosomes, which are joined as tetrads (2n, 4c), producing two haploid cells (n chromosomes, 23 in humans) which each contain chromatid pairs (1n, 2c). Because the ploidy is reduced from diploid to haploid, meiosis I is referred to as a reductional division. Meiosis II is an equational division analogous to mitosis, in which the sister chromatids are segregated, creating four haploid daughter cells (1n, 1c).[14] Meiosis Prophase I in mice. In Leptotene (L) the axial elements (stained by SYCP3) begin to form. In Zygotene (Z) the transverse elements (SYCP1) and central elements of the synaptonemal complex are partially installed (appearing as yellow as they overlap with SYCP3). In Pachytene (P) it's fully installed except on the sex chromosomes. In Diplotene (D) it disassembles revealing chiasmata. CREST marks the centromeres. Schematic of the synaptonemal complex at different stages of prophase I and the chromosomes arranged as a linear array of loops. Prophase I Prophase I is by far the longest phase of meiosis (lasting 13 out of 14 days in mice[15]). During prophase I, homologous maternal and paternal chromosomes pair, synapse, and exchange genetic information (by homologous recombination), forming at least one crossover per chromosome.[16] These crossovers become visible as chiasmata (plural; singular chiasma).[17] This process facilitates stable pairing between homologous chromosomes and hence enables accurate segregation of the chromosomes at the first meiotic division. The paired and replicated chromosomes are called bivalents (two chromosomes) or tetrads (four chromatids), with one chromosome coming from each parent. Prophase I is divided into a series of substages which are named according to the appearance of chromosomes. Leptotene Main article: Leptotene stage The first stage of prophase I is the leptotene stage, also known as leptonema, from Greek words meaning "thin threads".[18]:27 In this stage of prophase I, individual chromosomes—each consisting of two replicated sister chromatids—become "individualized" to form visible strands within the nucleus.[18]:27[19]:353 The chromosomes each form a linear array of loops mediated by cohesin, and the lateral elements of the synaptonemal complex assemble forming an "axial element" from which the loops emanate.[20] Recombination is initiated in this stage by the enzyme SPO11 which creates programmed double strand breaks (around 300 per meiosis in mice).[21] This process generates single stranded DNA filaments coated by RAD51 and DMC1 which invade the homologous chromosomes, forming inter-axis bridges, and resulting in the pairing/co-alignment of homologues (to a distance of ~400 nm in mice).[20][22] Zygotene Leptotene is followed by the zygotene stage, also known as zygonema, from Greek words meaning "paired threads",[18]:27 which in some organisms is also called the bouquet stage because of the way the telomeres cluster at one end of the nucleus.[23] In this stage the homologous chromosomes become much more closely (~100 nm) and stably paired (a process called synapsis) mediated by the installation of the transverse and central elements of the synaptonemal complex.[20] Synapsis is thought to occur in a zipper-like fashion starting from a recombination nodule. The paired chromosomes are called bivalent or tetrad chromosomes. Pachytene The pachytene stage (/ˈpækɪtiːn/ PAK-i-teen), also known as pachynema, from Greek words meaning "thick threads".[18]:27 is the stage at which all autosomal chromosomes have synapsed. In this stage homologous recombination, including chromosomal crossover (crossing over), is completed through the repair of the double strand breaks formed in leptotene.[20] Most breaks are repaired without forming crossovers resulting in gene conversion.[24] However, a subset of breaks (at least one per chromosome) form crossovers between non-sister (homologous) chromosomes resulting in the exchange of genetic information.[25] Sex chromosomes, however, are not wholly identical, and only exchange information over a small region of homology called the pseudoautosomal region.[26] The exchange of information between the homologous chromatids results in a recombination of information; each chromosome has the complete set of information it had before, and there are no gaps formed as a result of the process. Because the chromosomes cannot be distinguished in the synaptonemal complex, the actual act of crossing over is not perceivable through an ordinary light microscope, and chiasmata are not visible until the next stage. Diplotene During the diplotene stage, also known as diplonema, from Greek words meaning "two threads",[18]:30 the synaptonemal complex disassembles and homologous chromosomes separate from one another a little. However, the homologous chromosomes of each bivalent remain tightly bound at chiasmata, the regions where crossing-over occurred. The chiasmata remain on the chromosomes until they are severed at the transition to anaphase I to allow homologous chromosomes to move to opposite poles of the cell. In human fetal oogenesis, all developing oocytes develop to this stage and are arrested in prophase I before birth.[27] This suspended state is referred to as the dictyotene stage or dictyate. It lasts until meiosis is resumed to prepare the oocyte for ovulation, which happens at puberty or even later. Diakinesis Chromosomes condense further during the diakinesis stage, from Greek words meaning "moving through".[18]:30 This is the first point in meiosis where the four parts of the tetrads are actually visible. Sites of crossing over entangle together, effectively overlapping, making chiasmata clearly visible. Other than this observation, the rest of the stage closely resembles prometaphase of mitosis; the nucleoli disappear, the nuclear membrane disintegrates into vesicles, and the meiotic spindle begins to form. Meiotic spindle formation Unlike mitotic cells, human and mouse oocytes do not have centrosomes to produce the meiotic spindle. In mice, approximately 80 MicroTubule Organizing Centers (MTOCs) form a sphere in the ooplasm and begin to nucleate microtubules that reach out towards chromosomes, attaching to the chromosomes at the kinetochore. Over time the MTOCs merge until two poles have formed, generating a barrel shaped spindle.[28] In human oocytes spindle microtubule nucleation begins on the chromosomes, forming an aster that eventually expands to surround the chromosomes.[29] Chromosomes then slide along the microtubules towards the equator of the spindle, at which point the chromosome kinetochores form end-on attachments to microtubules.[30] Metaphase I Homologous pairs move together along the metaphase plate: As kinetochore microtubules from both spindle poles attach to their respective kinetochores, the paired homologous chromosomes align along an equatorial plane that bisects the spindle, due to continuous counterbalancing forces exerted on the bivalents by the microtubules emanating from the two kinetochores of homologous chromosomes. This attachment is referred to as a bipolar attachment. The physical basis of the independent assortment of chromosomes is the random orientation of each bivalent along the metaphase plate, with respect to the orientation of the other bivalents along the same equatorial line.[17] The protein complex cohesin holds sister chromatids together from the time of their replication until anaphase. In mitosis, the force of kinetochore microtubules pulling in opposite directions creates tension. The cell senses this tension and does not progress with anaphase until all the chromosomes are properly bi-oriented. In meiosis, establishing tension ordinarily requires at least one crossover per chromosome pair in addition to cohesin between sister chromatids (see Chromosome segregation). Anaphase I Kinetochore microtubules shorten, pulling homologous chromosomes (which each consist of a pair of sister chromatids) to opposite poles. Nonkinetochore microtubules lengthen, pushing the centrosomes farther apart. The cell elongates in preparation for division down the center.[17] Unlike in mitosis, only the cohesin from the chromosome arms is degraded while the cohesin surrounding the centromere remains protected by a protein named Shugoshin (Japanese for "guardian spirit"), what prevents the sister chromatids from separating.[31] This allows the sister chromatids to remain together while homologs are segregated. Telophase I The first meiotic division effectively ends when the chromosomes arrive at the poles. Each daughter cell now has half the number of chromosomes but each chromosome consists of a pair of chromatids. The microtubules that make up the spindle network disappear, and a new nuclear membrane surrounds each haploid set. The chromosomes uncoil back into chromatin. Cytokinesis, the pinching of the cell membrane in animal cells or the formation of the cell wall in plant cells, occurs, completing the creation of two daughter cells. However, cytokinesis does not fully complete resulting in "cytoplasmic bridges" which enable the cytoplasm to be shared between daughter cells until the end of meiosis II.[32] Sister chromatids remain attached during telophase I. Cells may enter a period of rest known as interkinesis or interphase II. No DNA replication occurs during this stage. Meiosis II Meiosis II is the second meiotic division, and usually involves equational segregation, or separation of sister chromatids. Mechanically, the process is similar to mitosis, though its genetic results are fundamentally different. The end result is production of four haploid cells (n chromosomes, 23 in humans) from the two haploid cells (with n chromosomes, each consisting of two sister chromatids) produced in meiosis I. The four main steps of meiosis II are: prophase II, metaphase II, anaphase II, and telophase II. In prophase II, we see the disappearance of the nucleoli and the nuclear envelope again as well as the shortening and thickening of the chromatids. Centrosomes move to the polar regions and arrange spindle fibers for the second meiotic division. In metaphase II, the centromeres contain two kinetochores that attach to spindle fibers from the centrosomes at opposite poles. The new equatorial metaphase plate is rotated by 90 degrees when compared to meiosis I, perpendicular to the previous plate.[33] This is followed by anaphase II, in which the remaining centromeric cohesin, not protected by Shugoshin anymore, is cleaved, allowing the sister chromatids to segregate. The sister chromatids by convention are now called sister chromosomes as they move toward opposing poles.[31] The process ends with telophase II, which is similar to telophase I, and is marked by decondensation and lengthening of the chromosomes and the disassembly of the spindle. Nuclear envelopes re-form and cleavage or cell plate formation eventually produces a total of four daughter cells, each with a haploid set of chromosomes. Meiosis is now complete and ends up with four new daughter cells. Origin and function Main article: Origin and function of meiosis The origin and function of meiosis are currently not well understood scientifically, and would provide fundamental insight into the evolution of sexual reproduction in eukaryotes. There is no current consensus among biologists on the questions of how sex in eukaryotes arose in evolution, what basic function sexual reproduction serves, and why it is maintained, given the basic two-fold cost of sex. It is clear that it evolved over 1.2 billion years ago, and that almost all species which are descendants of the original sexually reproducing species are still sexual reproducers, including plants, fungi, and animals. Meiosis is a key event of the sexual cycle in eukaryotes. It is the stage of the life cycle when a cell gives rise to haploid cells (gametes) each having half as many chromosomes as the parental cell. Two such haploid gametes, ordinarily arising from different individual organisms, fuse by the process of fertilization, thus completing the sexual cycle. Meiosis is ubiquitous among eukaryotes. It occurs in single-celled organisms such as yeast, as well as in multicellular organisms, such as humans. Eukaryotes arose from prokaryotes more than 2.2 billion years ago[34] and the earliest eukaryotes were likely single-celled organisms. To understand sex in eukaryotes, it is necessary to understand (1) how meiosis arose in single celled eukaryotes, and (2) the function of meiosis. The new combinations of DNA created during meiosis are a significant source of genetic variation alongside mutation, resulting in new combinations of alleles, which may be beneficial. Meiosis generates gamete genetic diversity in two ways: (1) Law of Independent Assortment. The independent orientation of homologous chromosome pairs along the metaphase plate during metaphase I and orientation of sister chromatids in metaphase II, this is the subsequent separation of homologs and sister chromatids during anaphase I and II, it allows a random and independent distribution of chromosomes to each daughter cell (and ultimately to gametes);[35] and (2) Crossing Over. The physical exchange of homologous chromosomal regions by homologous recombination during prophase I results in new combinations of genetic information within chromosomes.[36] Prophase I arrest Female mammals and birds are born possessing all the oocytes needed for future ovulations, and these oocytes are arrested at the prophase I stage of meiosis.[37] In humans, as an example, oocytes are formed between three and four months of gestation within the fetus and are therefore present at birth. During this prophase I arrested stage (dictyate), which may last for decades, four copies of the genome are present in the oocytes. The arrest of ooctyes at the four genome copy stage was proposed to provide the informational redundancy needed to repair damage in the DNA of the germline.[37] The repair process used appears to involve homologous recombinational repair[37][38] Prophase I arrested oocytes have a high capability for efficient repair of DNA damages, particularly exogenously induced double-strand breaks.[38] DNA repair capability appears to be a key quality control mechanism in the female germ line and a critical determinant of fertility.[38] Occurrence In life cycles Diplontic life cycle Haplontic life cycle. Main article: Biological life cycle See also: Alternation of generations Meiosis occurs in eukaryotic life cycles involving sexual reproduction, consisting of the constant cyclical process of meiosis and fertilization. This takes place alongside normal mitotic cell division. In multicellular organisms, there is an intermediary step between the diploid and haploid transition where the organism grows. At certain stages of the life cycle, germ cells produce gametes. Somatic cells make up the body of the organism and are not involved in gamete production. Cycling meiosis and fertilization events produces a series of transitions back and forth between alternating haploid and diploid states. The organism phase of the life cycle can occur either during the diploid state (diplontic life cycle), during the haploid state (haplontic life cycle), or both (haplodiplontic life cycle, in which there are two distinct organism phases, one during the haploid state and the other during the diploid state). In this sense there are three types of life cycles that utilize sexual reproduction, differentiated by the location of the organism phase(s).[citation needed] In the diplontic life cycle (with pre-gametic meiosis), of which humans are a part, the organism is diploid, grown from a diploid cell called the zygote. The organism's diploid germ-line stem cells undergo meiosis to create haploid gametes (the spermatozoa for males and ova for females), which fertilize to form the zygote. The diploid zygote undergoes repeated cellular division by mitosis to grow into the organism. In the haplontic life cycle (with post-zygotic meiosis), the organism is haploid instead, spawned by the proliferation and differentiation of a single haploid cell called the gamete. Two organisms of opposing sex contribute their haploid gametes to form a diploid zygote. The zygote undergoes meiosis immediately, creating four haploid cells. These cells undergo mitosis to create the organism. Many fungi and many protozoa utilize the haplontic life cycle.[citation needed] Finally, in the haplodiplontic life cycle (with sporic or intermediate meiosis), the living organism alternates between haploid and diploid states. Consequently, this cycle is also known as the alternation of generations. The diploid organism's germ-line cells undergo meiosis to produce spores. The spores proliferate by mitosis, growing into a haploid organism. The haploid organism's gamete then combines with another haploid organism's gamete, creating the zygote. The zygote undergoes repeated mitosis and differentiation to become a diploid organism again. The haplodiplontic life cycle can be considered a fusion of the diplontic and haplontic life cycles.[39][citation needed] In plants and animals Overview of chromatides' and chromosomes' distribution within the mitotic and meiotic cycle of a male human cell Meiosis occurs in all animals and plants. The end result, the production of gametes with half the number of chromosomes as the parent cell, is the same, but the detailed process is different. In animals, meiosis produces gametes directly. In land plants and some algae, there is an alternation of generations such that meiosis in the diploid sporophyte generation produces haploid spores. These spores multiply by mitosis, developing into the haploid gametophyte generation, which then gives rise to gametes directly (i.e. without further meiosis). In both animals and plants, the final stage is for the gametes to fuse, restoring the original number of chromosomes.[40] In mammals In females, meiosis occurs in cells known as oocytes (singular: oocyte). Each primary oocyte divides twice in meiosis, unequally in each case. The first division produces a daughter cell, and a much smaller polar body which may or may not undergo a second division. In meiosis II, division of the daughter cell produces a second polar body, and a single haploid cell, which enlarges to become an ovum. Therefore, in females each primary oocyte that undergoes meiosis results in one mature ovum and one or two polar bodies. Note that there are pauses during meiosis in females. Maturing oocytes are arrested in prophase I of meiosis I and lie dormant within a protective shell of somatic cells called the follicle. At the beginning of each menstrual cycle, FSH secretion from the anterior pituitary stimulates a few follicles to mature in a process known as folliculogenesis. During this process, the maturing oocytes resume meiosis and continue until metaphase II of meiosis II, where they are again arrested just before ovulation. If these oocytes are fertilized by sperm, they will resume and complete meiosis. During folliculogenesis in humans, usually one follicle becomes dominant while the others undergo atresia. The process of meiosis in females occurs during oogenesis, and differs from the typical meiosis in that it features a long period of meiotic arrest known as the dictyate stage and lacks the assistance of centrosomes.[41][42] In males, meiosis occurs during spermatogenesis in the seminiferous tubules of the testicles. Meiosis during spermatogenesis is specific to a type of cell called spermatocytes, which will later mature to become spermatozoa. Meiosis of primordial germ cells happens at the time of puberty, much later than in females. Tissues of the male testis suppress meiosis by degrading retinoic acid, proposed to be a stimulator of meiosis. This is overcome at puberty when cells within seminiferous tubules called Sertoli cells start making their own retinoic acid. Sensitivity to retinoic acid is also adjusted by proteins called nanos and DAZL.[43][44] Genetic loss-of-function studies on retinoic acid-generating enzymes have shown that retinoic acid is required postnatally to stimulate spermatogonia differentiation which results several days later in spermatocytes undergoing meiosis, however retinoic acid is not required during the time when meiosis initiates.[45] In female mammals, meiosis begins immediately after primordial germ cells migrate to the ovary in the embryo. Some studies suggest that retinoic acid derived from the primitive kidney (mesonephros) stimulates meiosis in embryonic ovarian oogonia and that tissues of the embryonic male testis suppress meiosis by degrading retinoic acid.[46] However, genetic loss-of-function studies on retinoic acid-generating enzymes have shown that retinoic acid is not required for initiation of either female meiosis which occurs during embryogenesis[47] or male meiosis which initiates postnatally.[45] Flagellates While the majority of eukaryotes have a two-divisional meiosis (though sometimes achiasmatic), a very rare form, one-divisional meiosis, occurs in some flagellates (parabasalids and oxymonads) from the gut of the wood-feeding cockroach Cryptocercus.[48] Role in human genetics and disease Recombination among the 23 pairs of human chromosomes is responsible for redistributing not just the actual chromosomes, but also pieces of each of them. There is also an estimated 1.6-fold more recombination in females relative to males. In addition, average, female recombination is higher at the centromeres and male recombination is higher at the telomeres. On average, 1 million bp (1 Mb) correspond to 1 cMorgan (cm = 1% recombination frequency).[49] The frequency of cross-overs remain uncertain. In yeast, mouse and human, it has been estimated that ≥200 double-strand breaks (DSBs) are formed per meiotic cell. However, only a subset of DSBs (~5–30% depending on the organism), go on to produce crossovers,[50] which would result in only 1-2 cross-overs per human chromosome. Nondisjunction Main article: Nondisjunction The normal separation of chromosomes in meiosis I or sister chromatids in meiosis II is termed disjunction. When the segregation is not normal, it is called nondisjunction. This results in the production of gametes which have either too many or too few of a particular chromosome, and is a common mechanism for trisomy or monosomy. Nondisjunction can occur in the meiosis I or meiosis II, phases of cellular reproduction, or during mitosis. Most monosomic and trisomic human embryos are not viable, but some aneuploidies can be tolerated, such as trisomy for the smallest chromosome, chromosome 21. Phenotypes of these aneuploidies range from severe developmental disorders to asymptomatic. Medical conditions include but are not limited to: Down syndrome – trisomy of chromosome 21 Patau syndrome – trisomy of chromosome 13 Edwards syndrome – trisomy of chromosome 18 Klinefelter syndrome – extra X chromosomes in males – i.e. XXY, XXXY, XXXXY, etc. Turner syndrome – lacking of one X chromosome in females – i.e. X0 Triple X syndrome – an extra X chromosome in females Jacobs syndrome – an extra Y chromosome in males. The probability of nondisjunction in human oocytes increases with increasing maternal age,[51] presumably due to loss of cohesin over time.[52] Comparison to mitosis In order to understand meiosis, a comparison to mitosis is helpful. The table below shows the differences between meiosis and mitosis.[53] Meiosis Mitosis End result Normally four cells, each with half the number of chromosomes as the parent Two cells, having the same number of chromosomes as the parent Function Production of gametes (sex cells) in sexually reproducing eukaryotes with diplont life cycle Cellular reproduction, growth, repair, asexual reproduction Where does it happen? Almost all eukaryotes (animals, plants, fungi, and protists);[54][48] In gonads, before gametes (in diplontic life cycles); After zygotes (in haplontic); Before spores (in haplodiplontic) All proliferating cells in all eukaryotes Steps Prophase I, Metaphase I, Anaphase I, Telophase I, Prophase II, Metaphase II, Anaphase II, Telophase II Prophase, Prometaphase, Metaphase, Anaphase, Telophase Genetically same as parent? No Yes Crossing over happens? Yes, normally occurs between each pair of homologous chromosomes Very rarely Pairing of homologous chromosomes? Yes No Cytokinesis Occurs in Telophase I and Telophase II Occurs in Telophase Centromeres split Does not occur in Anaphase I, but occurs in Anaphase II Occurs in Anaphase Molecular regulation This section needs expansion. You can help by adding to it. (August 2020) How a cell proceeds to meiotic division in meiotic cell division is not well known. Maturation promoting factor (MPF) seemingly have role in frog Oocyte meiosis. In the fungus S. pombe. there is a role of MeiRNA binding protein for entry to meiotic cell division.[55] It has been suggested that Yeast CEP1 gene product, that binds centromeric region CDE1, may play a role in chromosome pairing during meiosis-I.[56] Meiotic recombination is mediated through double stranded break, which is catalyzed by Spo11 protein. Also Mre11, Sae2 and Exo1 play role in breakage and recombination. After the breakage happen, recombination take place which is typically homologous. The recombination may go through either a double Holliday junction (dHJ) pathway or synthesis-dependent strand annealing (SDSA). (The second one gives to noncrossover product).[57] Seemingly there are checkpoints for meiotic cell division too. In S. pombe, Rad proteins, S. pombe Mek1 (with FHA kinase domain), Cdc25, Cdc2 and unknown factor is thought to form a checkpoint.[58] In vertebrate oogenesis, maintained by cytostatic factor (CSF) has role in switching into meiosis-II.[56] See also Fertilisation Coefficient of coincidence DNA repair Oxidative stress Synizesis (biology) Biological life cycle Apomixis Parthenogenesis Alternation of generations Brachymeiosis Mitotic recombination Dikaryon Mating of yeast

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