

Unit-II (SEM-II)

Developmental biology is the study of the process by which [animals](#) and [plants](#) grow and develop. Developmental biology also encompasses the biology of [regeneration](#), [asexual reproduction](#), [metamorphosis](#), and the growth and differentiation of [stem cells](#) in the adult organism.

Perspectives

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The main processes involved in the [embryonic development](#) of animals are: tissue patterning (via [regional specification](#) and patterned [cell differentiation](#)); [tissue growth](#); and tissue [morphogenesis](#).

- [Regional specification](#) refers to the processes that create the spatial patterns in a ball or sheet of initially similar cells. This generally involves the action of [cytoplasmic determinants](#), located within parts of the fertilized egg, and of inductive signals emitted from signaling centers in the embryo. The early stages of [regional specification](#) do not generate functional differentiated cells, but cell populations committed to developing to a specific region or part of the organism. These are defined by the expression of specific combinations of [transcription factors](#).
- [Cell differentiation](#) relates specifically to the formation of functional cell types such as nerve, muscle, secretory epithelia, etc. Differentiated cells contain large amounts of specific proteins associated with cell function.
- [Morphogenesis](#) relates to the formation of a three-dimensional shape. It mainly involves the orchestrated movements of cell sheets and of individual cells. Morphogenesis is important for creating the three germ layers of the early embryo ([ectoderm](#), [mesoderm](#), and [endoderm](#)) and for building up complex structures during organ development.
- [Tissue growth](#) involves both an overall increase in tissue size, and also the differential growth of parts ([allometry](#)) which contributes to morphogenesis. Growth mostly occurs through [cell proliferation](#) but also through changes in cell size or the deposition of extracellular materials.

The development of plants involves similar processes to that of animals. However, plant cells are mostly immotile so morphogenesis is achieved by differential growth, without cell movements. Also, the inductive signals and the genes involved are different from those that control animal development.

Generative biology

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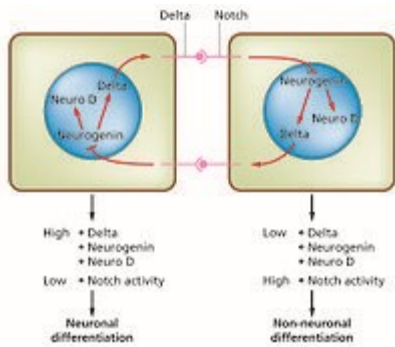
Generative biology is the [generative science](#) that explores the dynamics guiding the development and evolution of a biological morphological form.^{[1][2][3]}

Developmental processes

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Cell differentiation

[edit]



The Notch-delta system in neurogenesis (Slack Essential Dev

Biol Fig 14.12a)

[Cell differentiation](#) is the process whereby different functional cell types arise in development. For example, neurons, muscle fibers and hepatocytes (liver cells) are well known types of differentiated cells. Differentiated cells usually produce large amounts of a few proteins that are required for their specific function and this gives them the characteristic appearance that enables them to be recognized under the light microscope. The genes encoding these proteins are highly active. Typically their [chromatin](#) structure is very open, allowing access for the transcription enzymes, and specific transcription factors bind to regulatory sequences in the DNA in order to activate gene expression.^{[4][5]} For example, [NeuroD](#) is a key transcription factor for neuronal differentiation, [myogenin](#) for muscle differentiation, and [HNF4](#) for hepatocyte differentiation. Cell differentiation is usually the final stage of development, preceded by several states of commitment which are not visibly differentiated. A single tissue, formed from a single type of progenitor cell or stem cell, often consists of several differentiated cell types. Control of their formation involves a process of lateral inhibition,^[6] based on the properties of the [Notch signaling pathway](#).^[7] For example, in the neural plate of the embryo this system operates to generate a population of neuronal precursor cells in which NeuroD is highly expressed.

Regeneration

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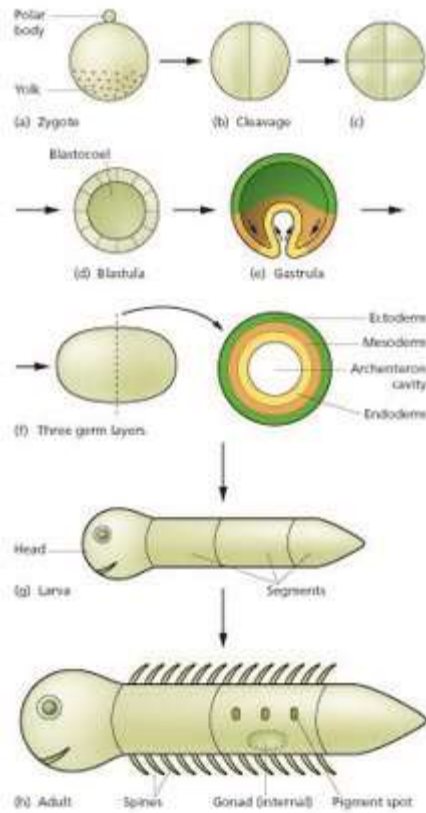
[Regeneration](#) indicates the ability to regrow a missing part.^[8] This is very prevalent amongst plants, which show continuous growth, and also among colonial animals such as hydroids and ascidians. But most interest by developmental biologists has been shown in the regeneration of parts in free living animals. In particular four models have been the subject of much investigation. Two of these have the ability to regenerate whole bodies: [Hydra](#), which can regenerate any part of the polyp from a small fragment,^[9] and [planarian](#) worms, which can usually regenerate both heads and tails.^[10] Both of these examples have continuous cell turnover fed by [stem cells](#) and, at least in planaria, at least some of the stem cells have been shown to be [pluripotent](#).^[11] The other two models show only distal regeneration of appendages. These are the insect appendages, usually the legs of hemimetabolous insects such as the cricket,^[12] and the limbs of [urodele amphibians](#).^[13] Considerable information is now available about amphibian limb regeneration and it is known that each cell type regenerates itself, except for connective tissues where there is considerable interconversion between cartilage, dermis and tendons. In terms of the pattern of structures, this is controlled by a re-activation of signals active in the embryo. There is still debate about the old question of whether regeneration is a "pristine" or an "adaptive" property.^[14] If the former is the case, with improved knowledge, we might expect to be able to improve regenerative ability in humans. If the latter, then each

instance of regeneration is presumed to have arisen by natural selection in circumstances particular to the species, so no general rules would be expected.

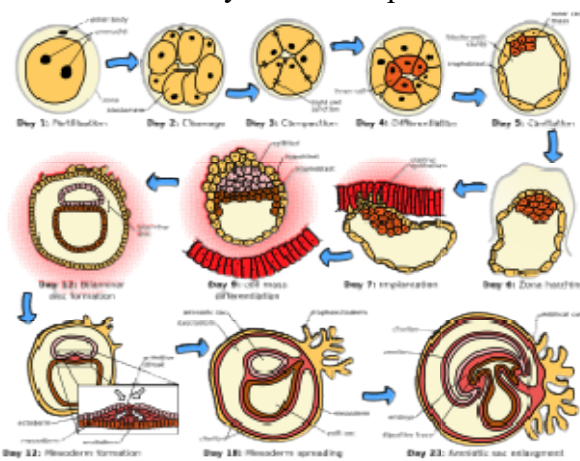
Embryonic development of animals

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Main article: [Embryogenesis](#)



Generalized scheme of embryonic development. Slack



"Essential Developmental Biology". Fig. 2.8. initial stages of [human embryogenesis](#)

The

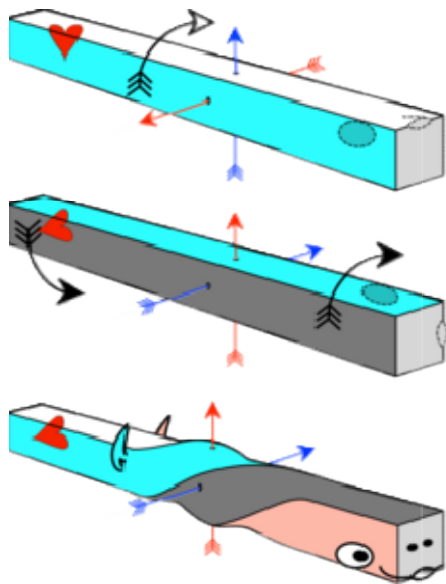
The sperm and egg fuse in the process of fertilization to form a fertilized egg, or [zygote](#).^[15] This undergoes a period of divisions to form a ball or sheet of similar cells called a [blastula](#) or [blastoderm](#). These cell divisions are usually rapid with no growth so the daughter

cells are half the size of the mother cell and the whole embryo stays about the same size. They are called [cleavage](#) divisions.

Mouse [epiblast](#) primordial [germ cells](#) (see Figure: “The initial stages of human [embryogenesis](#)”) undergo extensive [epigenetic](#) reprogramming.^[16] This process involves [genome](#)-wide [DNA demethylation](#), [chromatin](#) reorganization and [epigenetic](#) imprint erasure leading to [totipotency](#).^[16] DNA demethylation is carried out by a process that utilizes the DNA [base excision repair](#) pathway.^[17]

Morphogenetic movements convert the cell mass into a three layered structure consisting of multicellular sheets called [ectoderm](#), [mesoderm](#) and [endoderm](#). These sheets are known as [germ layers](#). This is the process of [gastrulation](#). During cleavage and gastrulation the first regional specification events occur. In addition to the formation of the three germ layers themselves, these often generate extraembryonic structures, such as the mammalian [placenta](#), needed for support and nutrition of the embryo,^[18] and also establish differences of commitment along the anteroposterior axis (head, trunk and tail).^[19]

[Regional specification](#) is initiated by the presence of [cytoplasmic determinants](#) in one part of the zygote. The cells that contain the determinant become a signaling center and emit an inducing factor. Because the inducing factor is produced in one place, diffuses away, and decays, it forms a concentration gradient, high near the source cells and low further away.^{[20][21]} The remaining cells of the embryo, which do not contain the determinant, are competent to respond to different concentrations by upregulating specific developmental control genes. This results in a series of zones becoming set up, arranged at progressively greater distance from the signaling center. In each zone a different combination of developmental control genes is upregulated.^[22] These genes encode [transcription factors](#) which upregulate new combinations of gene activity in each region. Among other functions, these transcription factors control expression of genes conferring specific adhesive and motility properties on the cells in which they are active. Because of these different morphogenetic properties, the cells of each germ layer move to form sheets such that the ectoderm ends up on the outside, mesoderm in the middle, and endoderm on the inside.^{[23][24]}



Schema of the development of the axial twist in vertebrates

Morphogenetic movements not only change the shape and structure of the embryo, but by bringing cell sheets into new spatial relationships they also make possible new phases of signaling and response between them. In addition, first morphogenetic movements of embryogenesis, such as gastrulation, [epiboly](#) and [twisting](#), directly activate pathways involved in endomesoderm specification through mechanotransduction processes.^{[25][26]} This property was suggested to be evolutionary inherited from endomesoderm specification as mechanically stimulated by marine environmental hydrodynamic flow in first animal organisms (first metazoa).^[27] Twisting along the body axis by a left-handed chirality is found in all [chordates](#) (including vertebrates) and is addressed by the [axial twist theory](#).^[28]

[Growth](#) in embryos is mostly autonomous.^[29] For each territory of cells the growth rate is controlled by the combination of genes that are active. Free-living embryos do not grow in mass as they have no external food supply. But embryos fed by a placenta or extraembryonic yolk supply can grow very fast, and changes to relative growth rate between parts in these organisms help to produce the final overall anatomy.

The whole process needs to be coordinated in time and how this is controlled is not understood. There may be a master clock able to communicate with all parts of the embryo that controls the course of events, or timing may depend simply on local causal sequences of events.^[30]

Metamorphosis

[\[edit\]](#)

Developmental processes are very evident during the process of [metamorphosis](#). This occurs in various types of animal. Well-known examples are seen in frogs, which usually hatch as a tadpole and metamorphoses to an adult frog, and certain insects which hatch as a larva and then become remodeled to the adult form during a pupal stage.

All the developmental processes listed above occur during metamorphosis. Examples that have been especially well studied include tail loss and other changes in the tadpole of the frog *Xenopus*,^{[31][32]} and the biology of the imaginal discs, which generate the adult body parts of the fly *Drosophila melanogaster*.

Fertilisation or **fertilization** (see [spelling differences](#)), also known as **generative fertilisation**, **syngamy** and **impregnation**,^[1] is the fusion of [gametes](#) to give rise to a [zygote](#) and initiate its development into a new individual organism or offspring.^[2] While processes such as [insemination](#) or [pollination](#), which happen before the fusion of gametes, are also sometimes informally referred to as fertilisation,^[3] these are technically separate processes. The cycle of fertilisation and development of new individuals is called [sexual reproduction](#). During [double fertilisation](#) in [angiosperms](#), the [haploid](#) male gamete combines with two haploid [polar nuclei](#) to form a [triploid](#) primary [endosperm](#) nucleus by the process of vegetative fertilisation.

History

[\[edit\]](#)

In antiquity, [Aristotle](#) conceived the formation of new individuals through fusion of male and female fluids, with form and function emerging gradually, in a mode called by him as [epigenetic](#).^[4]

In 1784, [Spallanzani](#) established the need of interaction between the female's ovum and male's sperm to form a zygote in frogs.^[5] In 1827, [Karl Ernst von Baer](#) observed a [therian](#) mammalian egg for the first time.^[4] [Oscar Hertwig](#) (1876), in Germany, described the fusion of nuclei of spermatozoa and of ova from [sea urchin](#).^[5]

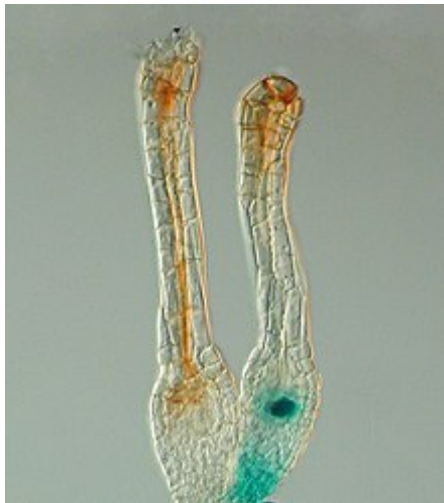
Evolution

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The evolution of fertilisation is related to the [origin of meiosis](#), as both are part of [sexual reproduction](#), originated in [eukaryotes](#). One hypothesis states that [meiosis](#) originated from mitosis.^[6]

Fertilisation in plants

[\[edit\]](#)



In the [bryophyte](#) land plants, fertilisation takes place within the [archegonium](#). This [moss](#) has been [genetically modified](#) so that the unfertilised egg within the archegonium produces a blue colour.

The gametes that participate in fertilisation of plants are the sperm (male) and the egg (female) cell. Various plant groups have differing methods by which the gametes produced by the male and female [gametophytes](#) come together and are fertilised. In [bryophytes](#) and [pteridophytic](#) land plants, fertilisation of the sperm and egg takes place within the [archegonium](#). In [seed plants](#), the male gametophyte is formed within a [pollen](#) grain. After [pollination](#), the [pollen](#) grain [germinates](#), and a [pollen tube](#) grows and penetrates the [ovule](#) through a tiny pore called a [micropyle](#). The sperm are transferred from the pollen through the pollen tube to the ovule where the egg is fertilised. In [flowering plants](#), two sperm cells are released from the pollen tube, and a second fertilisation event occurs involving the second sperm cell and the [central cell](#) of the ovule, which is a second female gamete.^[7]

Pollen tube growth

[\[edit\]](#)

Unlike animal sperm which is motile, the sperm of most seed plants is immotile and relies on the [pollen tube](#) to carry it to the ovule where the sperm is released.^[8] The pollen tube penetrates the [stigma](#) and elongates through the extracellular matrix of the style before reaching the ovary. Then near the receptacle, it breaks through the [ovule](#) through the micropyle (an opening in the ovule wall) and the pollen tube "bursts" into the embryo sac, releasing sperm.^[9] The growth of the pollen tube has been believed to depend on chemical cues from the pistil, however these mechanisms were poorly understood until 1995. Work done on [tobacco plants](#) revealed a family of [glycoproteins](#) called TTS proteins that enhanced growth of pollen tubes.^[9] Pollen tubes in a sugar free pollen germination medium and a medium with purified TTS proteins both grew. However, in the TTS medium, the tubes grew at a rate 3x that of the sugar-free medium.^[9] TTS proteins were also placed on various locations of semi [in vivo](#) pollinated pistils, and pollen tubes were observed to immediately extend toward the proteins. Transgenic plants lacking the ability to produce TTS proteins had slower pollen tube growth and reduced fertility.^[9]

Rupture of pollen tube

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The rupture of the pollen tube to release sperm in [Arabidopsis](#) has been shown to depend on a signal from the female gametophyte. Specific proteins called FER protein kinases present in the ovule control the production of highly reactive derivatives of oxygen called [reactive oxygen species](#) (ROS). ROS levels have been shown via [GFP](#) to be at their highest during floral stages when the ovule is the most receptive to pollen tubes, and lowest during times of development and following fertilisation.^[8] High amounts of ROS activate Calcium ion channels in the pollen tube, causing these channels to take up Calcium ions in large amounts. This increased uptake of calcium causes the pollen tube to rupture, and release its sperm into the ovule.^[8] Pistil feeding assays in which plants were fed diphenyl iodonium chloride (DPI) suppressed ROS concentrations in [Arabidopsis](#), which in turn prevented pollen tube rupture.^[8]

Flowering plants

[\[edit\]](#)

Main article: [Double fertilisation](#)

After being fertilised, the ovary starts to swell and develop into the [fruit](#).^[10] With multi-seeded fruits, multiple grains of pollen are necessary for syngamy with each ovule. The growth of the pollen tube is controlled by the vegetative (or tube) cytoplasm. Hydrolytic [enzymes](#) are secreted by the pollen tube that digest the female tissue as the tube grows down the stigma and style; the digested tissue is used as a nutrient source for the pollen tube as it grows. During pollen tube growth towards the ovary, the generative nucleus divides to produce two separate sperm nuclei (haploid number of chromosomes)^[11] – a growing pollen tube therefore contains three separate nuclei, two sperm and one tube.^[12] The sperms are interconnected and dimorphic, the large one, in a number of plants, is also linked to the tube nucleus and the interconnected sperm and the tube nucleus form the "male germ unit".^[13]

Double fertilisation is the process in [angiosperms](#) (flowering plants) in which two [sperm](#) from each pollen tube fertilise two [cells](#) in a female [gametophyte](#) (sometimes called an embryo sac) that is inside an ovule. After the pollen tube enters the gametophyte, the pollen tube nucleus disintegrates and the two sperm cells are released; one of the two sperm cells *fertilises* the egg cell (at the bottom of the gametophyte near the micropyle), forming a [diploid](#) (2n) [zygote](#). This is the point when fertilisation actually occurs; pollination and fertilisation are two separate processes. The nucleus of the other sperm cell fuses with two haploid polar nuclei (contained in the central cell) in the centre of the gametophyte. The resulting cell is [triploid](#) (3n). This triploid

cell divides through [mitosis](#) and forms the [endosperm](#), a [nutrient](#)-rich [tissue](#), inside the [seed](#).^[7] The two central-cell maternal nuclei (polar nuclei) that contribute to the endosperm arise by mitosis from the single meiotic product that also gave rise to the egg. Therefore, maternal contribution to the genetic constitution of the triploid endosperm is double that of the embryo.

One primitive species of flowering plant, *[Nuphar polysepala](#)*, has endosperm that is diploid, resulting from the fusion of a sperm with one, rather than two, maternal nuclei. It is believed that early in the development of angiosperm lineages, there was a duplication in this mode of reproduction, producing seven-celled/eight-nucleate female gametophytes, and triploid endosperms with a 2:1 maternal to paternal genome ratio.^[14]

In many plants, the development of the flesh of the fruit is proportional to the percentage of fertilised ovules. For example, with [watermelon](#), about a thousand grains of pollen must be delivered and spread evenly on the three lobes of the stigma to make a normal sized and shaped fruit.^[citation needed]

Self-pollination and outcrossing

[\[edit\]](#)

Main article: [Self-pollination](#)

See also: [Cleistogamy](#) and [Autogamy](#)

[Outcrossing](#), or cross-fertilisation, and [self-fertilisation](#) represent different strategies with differing benefits and costs. An estimated 48.7% of plant species are either dioecious or self-incompatible obligate outcrossers.^[15] It is also estimated that about 42% of flowering plants exhibit a mixed mating system in nature.^[16]

In the most common kind of mixed mating system, individual plants produce a single type of flower and fruits may contain self-fertilised, outcrossed or a mixture of progeny types. The transition from cross-fertilisation to self-fertilisation is the most common evolutionary transition in plants, and has occurred repeatedly in many independent lineages.^[17] About 10-15% of flowering plants are predominantly self-fertilising.^[17]

Under circumstances where [pollinators](#) or mates are rare, self-fertilisation offers the advantage of [reproductive assurance](#).^[17] Self-fertilisation can therefore result in improved colonisation ability. In some species, self-fertilisation has persisted over many generations. *[Capsella rubella](#)* is a self-fertilising species that became self-compatible 50,000 to 100,000 years ago.^[18] *[Arabidopsis thaliana](#)* is a predominantly self-fertilising plant with an [out-crossing](#) rate in the wild of less than 0.3%;^[19] a study suggested that self-fertilisation evolved roughly a million years ago or more in *A. thaliana*.^[20] In long-established self-fertilising plants, the masking of deleterious [mutations](#) and the production of genetic variability is infrequent and thus unlikely to provide a sufficient benefit over many generations to maintain the meiotic apparatus. Consequently, one might expect self-fertilisation to be replaced in nature by an ameiotic asexual form of reproduction that would be less costly. However the actual persistence of meiosis and self-fertilisation as a form of reproduction in long-established self-fertilising plants may be related to the immediate benefit of efficient [recombinational repair](#) of DNA damage during formation of germ cells provided by meiosis at each generation.^[citation needed]

Fertilisation in animals

[\[edit\]](#)

See also: [Sexual reproduction in animals](#) and [Animal sexual behaviour](#)

The mechanics behind fertilisation has been studied extensively in sea urchins and mice. This research addresses the question of how the [sperm](#) and the appropriate egg find each other and the question of how only one sperm gets into the egg and delivers its contents. There are three steps to fertilisation that ensure species-specificity:

1. Chemotaxis
2. Sperm activation/acrosomal reaction
3. Sperm/egg adhesion

Internal vs. external

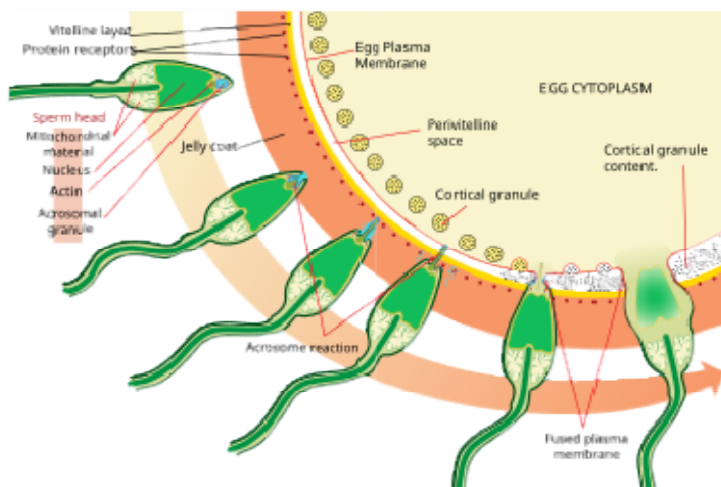
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Consideration as to whether an animal (more specifically a vertebrate) uses [internal](#) or [external fertilisation](#) is often dependent on the method of birth. [Oviparous](#) animals laying eggs with thick calcium shells, such as [chickens](#), or thick leathery shells generally reproduce via internal fertilisation so that the sperm fertilises the egg without having to pass through the thick, protective, tertiary layer of the egg. [Ovoviviparous](#) and [viviparous](#) animals also use internal fertilisation. Although some organisms reproduce via [amplexus](#), they may still use internal fertilisation, as with some salamanders. Advantages of internal fertilisation include minimal waste of gametes, greater chance of individual egg fertilisation, longer period of egg protection, and selective fertilisation. Many females have the ability to store sperm for extended periods of time and can fertilise their eggs at their own desire. ^{[\[citation needed\]](#)}

Oviparous animals producing eggs with thin tertiary membranes or no membranes at all, on the other hand, use external fertilisation methods. Such animals may be more precisely termed ovuliparous.^{[\[21\]](#)} External fertilisation is advantageous in that it minimises contact (which decreases the risk of disease transmission), and greater genetic variation.

Sea urchins

[\[edit\]](#)



Acrosome reaction on a sea

urchin cell.

Sperm find the eggs via [chemotaxis](#), a type of ligand/receptor interaction. Resact is a 14 amino acid peptide purified from the jelly coat of *A. punctulata* that attracts the migration of sperm.

After finding the egg, the sperm penetrates the [jelly coat](#) through a process called sperm activation. In another ligand/receptor interaction, an oligosaccharide component of the egg binds and activates a receptor on the sperm and causes the [acrosomal reaction](#). The acrosomal vesicles of the sperm fuse with the plasma membrane and are released. In this process, molecules bound to the acrosomal vesicle membrane, such as bindin, are exposed on the surface of the sperm. These contents digest the jelly coat and eventually the vitelline membrane. In addition to the release of acrosomal vesicles, there is explosive polymerisation of [actin](#) to form a thin spike at the head of the sperm called the [acrosomal process](#).

The sperm binds to the egg through another ligand reaction between receptors on the [vitelline membrane](#). The sperm surface protein bindin, binds to a receptor on the vitelline membrane identified as EBR1.

Fusion of the plasma membranes of the sperm and egg are likely mediated by bindin. At the site of contact, fusion causes the formation of a [fertilisation cone](#).

Mammals

[\[edit\]](#)

Mammals internally fertilise through [copulation](#).^[22] After a male [ejaculates](#), many sperm move to the upper vagina (via contractions from the vagina) through the [cervix](#) and across the length of the [uterus](#) to meet the ovum. In cases where fertilisation occurs, the female usually [ovulates](#) during a period that extends from hours before copulation to a few days after; therefore, in most mammals, it is more common for ejaculation to precede ovulation than vice versa.^[citation needed]

When sperm are deposited into the anterior vagina, they are not capable of fertilisation (i.e., non-capacitated)^[clarification needed] and are characterised by slow linear motility patterns. This motility, combined with muscular contractions enables sperm transport towards the uterus and [oviducts](#).^[23] There is a pH gradient within the micro-environment of the female reproductive tract such that the pH near the vaginal opening is lower (approximately 5) than the oviducts (approximately 8).^[24] The sperm-specific pH-sensitive calcium transport protein called CatSper increases the sperm cell permeability to calcium as it moves further into the reproductive tract. Intracellular calcium influx contributes to sperm capacitation and hyperactivation, causing a more violent and rapid non-linear motility pattern as sperm approach the oocyte. The [capacitated](#) spermatozoon and the oocyte meet and interact in the *ampulla* of the [fallopian tube](#). Rheotaxis, thermotaxis and chemotaxis are known mechanisms that guide sperm towards the egg during the final stage of sperm migration.^[25] Spermatozoa respond (see [Sperm thermotaxis](#)) to the temperature gradient of ~2 °C between the oviduct and the ampulla,^[26] and [chemotactic](#) gradients of [progesterone](#) have been confirmed as the signal emanating from the [cumulus oophorus](#) cells surrounding rabbit and human oocytes.^[27] Capacitated and hyperactivated sperm respond to these gradients by changing their behaviour and moving towards the cumulus-oocyte complex. Other chemotactic signals such as formyl Met-Leu-Phe (fMLF) may also guide spermatozoa.^[28]

The [zona pellucida](#), a thick layer of extracellular matrix that surrounds the egg and is similar to the role of the vitelline membrane in sea urchins, binds the sperm. Unlike sea urchins, the sperm binds to the egg before the acrosomal reaction. [ZP3](#), a glycoprotein in the zona pellucida,

is responsible for egg/sperm adhesion in humans. The receptor [galactosyltransferase](#) (GalT) binds to the N-acetylglucosamine residues on the ZP3 and is important for binding with the sperm and activating the acrosome reaction. ZP3 is sufficient though unnecessary for sperm/egg binding. Two additional sperm receptors exist: a 250kD protein that binds to an oviduct secreted protein, and SED1, which independently binds to the zona. After the acrosome reaction, the sperm is believed to remain bound to the zona pellucida through exposed ZP2 receptors. These receptors are unknown in mice but have been identified in guinea pigs. ^{[[citation needed](#)]}

In mammals, the binding of the spermatozoon to the GalT initiates the [acrosome reaction](#). This process releases the [hyaluronidase](#) that digests the matrix of [hyaluronic acid](#) in the vestments around the oocyte. Additionally, heparin-like glycosaminoglycans (GAGs) are released near the oocyte that promote the acrosome reaction. ^{[[29](#)]} Fusion between the oocyte [plasma membranes](#) and sperm follows and allows the sperm [nucleus](#), the typical [centriole](#), and atypical [centriole](#) that is attached to the [flagellum](#), but not the [mitochondria](#), to enter the oocyte. ^{[[30](#)]} The protein [CD9](#) likely mediates this fusion in mice (the binding homolog). The egg "[activates](#)" itself upon fusing with a single sperm cell and thereby changes its cell membrane to prevent fusion with other sperm. [Zinc](#) atoms are released during this activation. ^{[[citation needed](#)]}



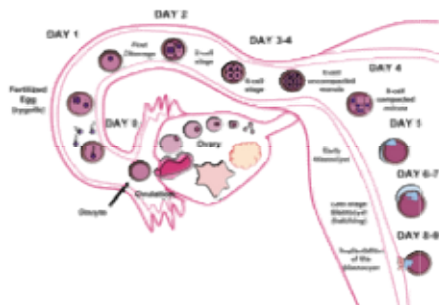
Wikimedia Commons has media related to [Mammalian fertilisation](#).

This process ultimately leads to the formation of a [diploid](#) cell called a [zygote](#). The zygote divides to form a [blastocyst](#) and, upon entering the uterus, [implants](#) in the endometrium, beginning [pregnancy](#). Embryonic implantation not in the [uterine](#) wall results in an [ectopic pregnancy](#) that can kill the mother.

In such animals as rabbits, coitus induces ovulation by stimulating the release of the pituitary hormone gonadotropin; this release greatly increases the likelihood of pregnancy.

Humans

[\[edit\]](#)



Fertilisation in humans. The sperm and ovum unite through fertilisation, creating a zygote that (over the course of 8-9 days) implants in the uterine wall, where it resides for nine months.

Main article: [Human fertilisation](#)

Fertilisation in humans is the union of a human [egg](#) and [sperm](#), usually occurring in the [ampulla of the fallopian tube](#), producing a single celled [zygote](#), the first stage of life in the development of a genetically unique organism, ^{[[31](#)]} and initiating [embryonic development](#). Scientists discovered the dynamics of [human fertilisation](#) in the nineteenth century.

The term *conception* commonly refers to "the process of becoming pregnant involving fertilisation or implantation or both".^[32] Its use makes it a subject of [semantic arguments about the beginning of pregnancy](#), typically in the context of the [abortion](#) debate. Upon [gastrulation](#), which occurs around 16 days after fertilisation, the implanted blastocyst develops three germ layers, the endoderm, the ectoderm and the mesoderm, and the genetic code of the father becomes fully involved in the development of the embryo; later twinning is impossible. Additionally, interspecies hybrids survive only until gastrulation and cannot further develop. However, some human developmental biology literature refers to the [conceptus](#) and such medical literature refers to the "products of conception" as the post-implantation embryo and its surrounding membranes.^[33] The term "conception" is not usually used in scientific literature because of its variable definition and connotation.

Insects

[\[edit\]](#)



Red-veined darters (*Sympetrum fonscolombii*) flying "in cop" (male ahead), enabling the male to prevent other males from mating. The eggs are fertilised as they are laid, one at a time.



This section **needs expansion**. You can help by [adding to it](#). (February 2015)

Insects in different groups, including the [Odonata](#) ([dragonflies](#) and [damselflies](#)) and the [Hymenoptera](#) ([ants](#), [bees](#), and [wasps](#)) practise delayed fertilisation. Among the Odonata, females may mate with multiple males, and store sperm until the eggs are laid. The male may hover above the female during egg-laying (oviposition) to prevent her from mating with other males and replacing his sperm; in some groups such as the darters, the male continues to grasp the female with his claspers during egg-laying, the pair flying around in tandem.^[34] Among social Hymenoptera, [honeybee](#) queens mate only on mating flights, in a short period lasting

some days; a queen may mate with eight or more [drones](#). She then stores the sperm for the rest of her life, perhaps for five years or more.^{[35][36]}

Fertilisation in fungi

[\[edit\]](#)

Main article: [Mating in fungi](#)

In many [fungi](#) (except [chytrids](#)), as in some protists, fertilisation is a two step process. First, the cytoplasm of the two gamete cells fuse (called [plasmogamy](#)), producing a [dikaryotic](#) or [heterokaryotic](#) cell with multiple nuclei. This cell may then divide to produce dikaryotic or heterokaryotic [hyphae](#). The second step of fertilisation is [karyogamy](#), the fusion of the nuclei to form a diploid zygote.

In [chytrid](#) fungi, fertilisation occurs in a single step with the fusion of gametes, as in animals and plants.

Fertilisation in protists

[\[edit\]](#)

Fertilisation in protozoa

[\[edit\]](#)

There are three types of fertilisation processes in protozoa:^[37]

- gametogamy;
- autogamy;^{[38][39]}
- gamontogamy.

Fertilisation in algae

[\[edit\]](#)

Algae, like some land plants, undergo [alternation of generations](#). Some algae are isomorphic, where both the sporophyte (2n) and gametophyte (n) are the same morphologically. When algae reproduction is described as oogamous, the male and female gametes are different morphologically, where there is a large non-motile egg for female gametes, and the male gamete are uniflagellate (motile). Via the process of syngamy, these will form a new zygote, regenerating the sporophyte generation again.

Fertilisation and genetic recombination

[\[edit\]](#)

[Meiosis](#) results in a random segregation of the genes that each parent contributes. Each parent organism is usually identical save for a fraction of their genes; each [gamete](#) is therefore genetically unique. At fertilisation, parental [chromosomes](#) combine. In [humans](#), $(2^{22})^2 = 17.6 \times 10^{12}$ chromosomally different [zygotes](#) are possible for the non-sex chromosomes, even assuming no [chromosomal crossover](#). If crossover occurs once, then on average $(4^{22})^2 = 309 \times 10^{24}$ genetically different zygotes are possible for every couple, not considering that crossover events can take place at most points along each chromosome. The X and Y chromosomes undergo no crossover events^[*citation needed*] and are therefore excluded from the calculation. The [mitochondrial DNA](#) is only inherited from the maternal parent.

The sperm aster and zygote centrosomes

[\[edit\]](#)

Shortly after the sperm fuse with the egg, the two sperm [centrioles](#) form the embryo first [centrosome](#) and microtubule [aster](#).^[40] The sperm centriole, found near the male pronucleus, recruit egg [Pericentriolar material](#) proteins forming the zygote first centrosome.^[41] This centrosome nucleates microtubules in the shape of stars called astral microtubules. The microtubules span the whole valium of the egg, allowing the egg pronucleus to use the cables to get to the male pronucleus. As the male and female pronuclei approach each other, the single centrosome split into two centrosomes located in the interphase between the pronuclei. Then the centrosome via the astral microtubules polarises the genome inside the pronuclei.^[42]

Parthenogenesis

[\[edit\]](#)

Main article: [Parthenogenesis](#)

Organisms that normally reproduce sexually can also reproduce via [parthenogenesis](#), wherein an unfertilised female gamete produces viable offspring. These offspring may be clones of the mother, or in some cases genetically differ from her but inherit only part of her DNA. Parthenogenesis occurs in many plants and animals and may be induced in others through a chemical or electrical stimulus to the egg cell. In 2004, Japanese researchers led by [Tomohiro Kono](#) succeeded after 457 attempts to merge the [ova](#) of two mice by blocking certain proteins that would normally prevent the possibility; the resulting embryo normally developed into a mouse.^[43]

Allogamy and autogamy

[\[edit\]](#)

[Allogamy](#), which is also known as cross-fertilisation, refers to the fertilisation of an egg cell from one individual with the male gamete of another.

Autogamy which is also known as self-fertilisation, occurs in such hermaphroditic organisms as plants and flatworms; therein, two gametes from one individual fuse.

Other variants of bisexual reproduction

[\[edit\]](#)

Some relatively unusual forms of reproduction are:^{[44][45]}

[Gynogenesis](#): A sperm stimulates the egg to develop without fertilisation or syngamy. The sperm may enter the egg.

[Hybridogenesis](#): One genome is eliminated to produce haploid eggs.

[Canina meiosis](#): (sometimes called "permanent odd polyploidy") one genome is transmitted in the Mendelian fashion, others are transmitted clonally.

Benefits of cross-fertilisation

[\[edit\]](#)

Main articles: [Allogamy](#) and [Heterosis](#)

The major benefit of cross-fertilisation is generally thought to be the avoidance of [inbreeding depression](#). [Charles Darwin](#), in his 1876 book [The Effects of Cross and Self Fertilisation in the Vegetable Kingdom](#) (pages 466-467) summed up his findings in the following way.^[46]

"It has been shown in the present volume that the offspring from the union of two distinct individuals, especially if their progenitors have been subjected to very different conditions, have an immense advantage in height, weight, constitutional vigour and fertility over the self-fertilised offspring from one of the same parents. And this fact is amply sufficient to account for the development of the sexual elements, that is, for the genesis of the two sexes."

In addition, it is thought by some,^[47] that a long-term advantage of out-crossing in nature is increased genetic variability that promotes adaptation or avoidance of extinction (see [Genetic variability](#)).

See also

[\[edit\]](#)

- [Cell fusion](#)
- [Conception cap](#)
- [Conception device](#)
- [Female sperm](#)
- [Fetal development](#)
- [In vitro fertilisation](#)
- [Kaquya \(mouse\)](#)
- [Parthenogenesis](#), a type of reproduction that does not involve fertilisation
- [Pollination](#)
- [Pre-embryo](#)
- [Pronucleus](#)
- [Superfecundation](#)
- [Superfetation](#)
- [Symmetry breaking and cortical rotation](#)
- [Cortical reaction](#)
- [Polyspermy](#)