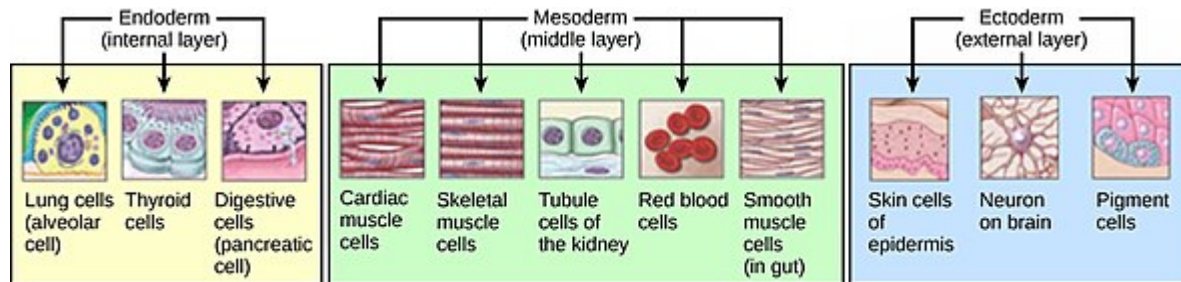


UNIT-III (SEM-II)

Organogenesis is the phase of [embryonic development](#) that starts at the end of [gastrulation](#) and continues until [birth](#). During organogenesis, the three [germ layers](#) formed from gastrulation (the [ectoderm](#), [endoderm](#), and [mesoderm](#)) form the [internal organs](#) of the organism.^[1]



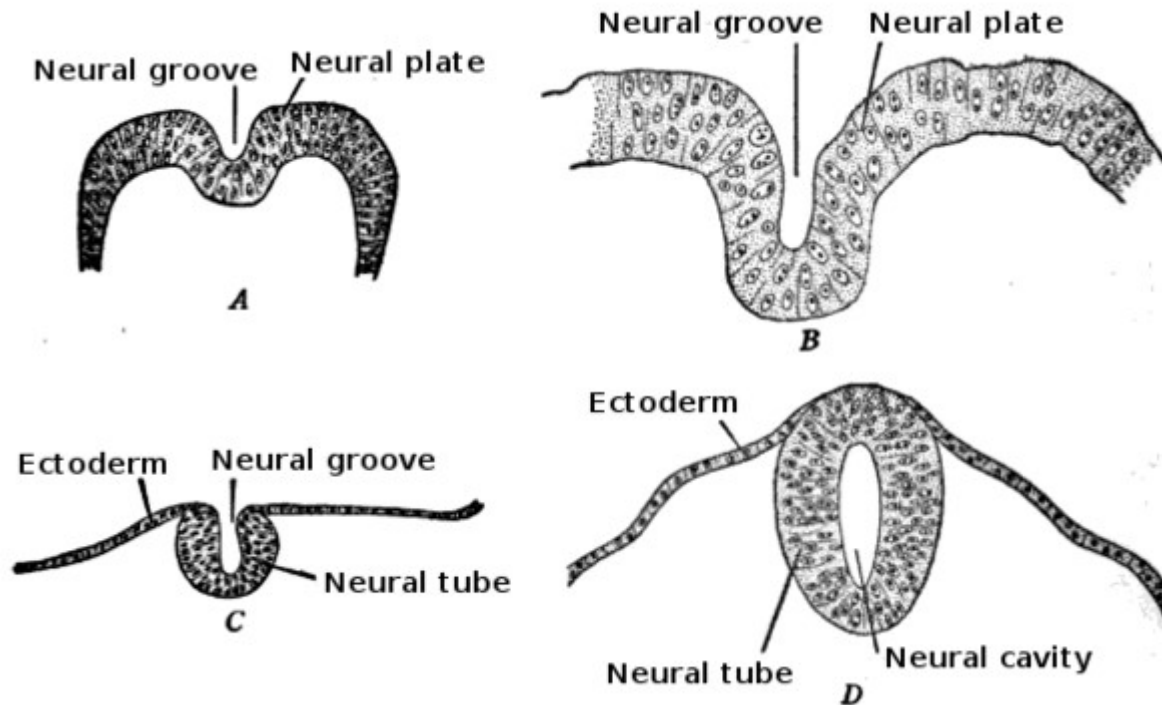
The [endoderm](#) of [vertebrates](#) produces tissue within the [lungs](#), [thyroid](#), and [pancreas](#).

The [mesoderm](#) aids in the production of [cardiac muscle](#), [skeletal muscle](#), [smooth muscle](#), tissues within the [kidneys](#), and [red blood cells](#). The [ectoderm](#) produces tissues within the [epidermis](#) and aids in the formation of [neurons](#) within the brain, and [melanocytes](#).

The cells of each of the three germ layers undergo [differentiation](#), a process where less-specialized cells become more-specialized through the expression of a specific set of genes. Cell differentiation is driven by cell signaling cascades.^[2] Differentiation is influenced by extracellular signals such as growth factors that are exchanged to adjacent cells which is called [juxtacrine signaling](#) or to neighboring cells over short distances which is called [paracrine signaling](#).^[3] Intracellular signals – a cell signaling itself ([autocrine signaling](#)) – also play a role in organ formation. These signaling pathways allow for cell rearrangement and ensure that organs form at specific sites within the organism.^[1] The organogenesis process can be studied using embryos and organoids.^[4]

Organs produced by the germ layers

[\[edit\]](#)



Neural precursor cells fold and elongate to form the neural tube. Mesoderm cells condense to form a rod which will send out signals to redirect the ectoderm cells above. This fold along the neural tube sets up the vertebrate central nervous system.

The endoderm is the inner most germ layer of the embryo which gives rise to gastrointestinal and respiratory organs by forming epithelial linings and organs such as the liver, lungs, and pancreas.^[5] The mesoderm or middle germ layer of the embryo will form the blood, heart, kidney, muscles, and connective tissues.^[5] The ectoderm or outermost germ layer of the developing embryo forms epidermis, the brain, and the nervous system.^[5]

Mechanism of organ formation

[\[edit\]](#)

While each germ layer forms specific organs, in the 1820s, embryologist [Heinz Christian Pander](#) discovered that the germ layers cannot form their respective organs without the cellular interactions from other tissues.^[4] In humans, internal organs begin to develop within 3–8 weeks after fertilization. The [germ layers](#) form organs by three processes: folds, splits, and condensation.^[6] Folds form in the germinal sheet of cells and usually form an enclosed tube which you can see in the development of vertebrates neural tube. Splits or pockets may form in the germinal sheet of cells forming vesicles or elongations. The lungs and glands of the organism may develop this way.^[6]

A primary step in organogenesis for chordates is the development of the [notochord](#), which induces the formation of the [neural plate](#), and ultimately the [neural tube](#) in vertebrate development. The development of the neural tube will give rise to the brain and spinal cord.^[4] Vertebrates develop a [neural crest](#) that differentiates into many structures, including bones, muscles, and components of the [central nervous system](#). Differentiation of the ectoderm into the neural crest, neural tube, and surface ectoderm is sometimes referred to as neurulation

and the embryo in this phase is the neurula. The [coelom](#) of the body forms from a split of the mesoderm along the [somite axis](#)^[1]

Plant organogenesis

[\[edit\]](#)

In plants, organogenesis occurs continuously and only stops when the plant dies. In the [shoot](#), the [shoot apical meristems](#) regularly produce new lateral organs ([leaves](#) or [flowers](#)) and lateral branches. In the [root](#), new [lateral roots](#) form from weakly differentiated internal tissue (e.g. the [xylem](#)-pole [pericycle](#) in the model plant *[Arabidopsis thaliana](#)*). *In vitro* and in response to specific cocktails of hormones (mainly [auxins](#) and [cytokinins](#)), most plant tissues can de-differentiate and form a mass of dividing [totipotent](#) stem cells called a [callus](#). Organogenesis can then occur from those cells. The type of organ that is formed depends on the relative concentrations of the hormones in the medium. Plant organogenesis can be induced in tissue culture and used to regenerate plants.^[7]

See also

[\[edit\]](#)

- [Ectoderm](#)
- [Embryogenesis](#)
- [Endoderm](#)
- [Eye development](#)
- [Gastrulation](#)
- [Germ layer](#)
- [Germ line development](#)
- [Gonadogenesis](#)
- [Heart development](#)
- [Histogenesis](#)
- [Limb development](#)
- [List of human cell types derived from the germ layers](#)
- [Mesoderm](#)
- [Morphogenesis](#)
- [Organoid](#)

The **kidneys** are a pair of [organs](#) of the [excretory system](#) in [vertebrates](#), which maintain the balance of water and [electrolytes](#) in the body ([osmoregulation](#)), filter the [blood](#), remove [metabolic waste products](#), and, in many vertebrates, also produce [hormones](#) (in particular, [renin](#)) and maintain [blood pressure](#).^{[1][2][3][4]} In healthy vertebrates, the kidneys maintain [homeostasis](#) of [extracellular fluid](#) in the body.^[5] When the blood is being filtered, the kidneys form [urine](#), which consists of water and excess or unnecessary substances, the urine is then excreted from the body through other organs, which in vertebrates, depending on the species, may include the [ureter](#), [urinary bladder](#), [cloaca](#), and [urethra](#).^[6]

All vertebrates have kidneys. The kidneys are the main organ that allows species to adapt to different environments, including [fresh](#) and [salt water](#), [terrestrial](#) life and [desert](#) climate.^[7] Depending on the environment in which animals have evolved, the functions and structure of the kidneys may differ.^[8] Also, between [classes](#) of animals, the kidneys differ in shape and anatomical location.^{[9][10]} In [mammals](#), they are usually bean-shaped.^[11] Evolutionarily, the kidneys first appeared in [fish](#) as a result of the independent evolution of the [renal glomeruli](#) and [tubules](#), which eventually united into a single functional unit.^[12] In some [invertebrates](#), the [nephridia](#) are analogous to the kidneys but nephridia are not kidneys.^[13] The [metanephridia](#), together with the vascular filtration site and [coelom](#), are functionally identical to the ancestral primitive kidneys of vertebrates.^[14]

The main structural and functional element of the kidney is the [nephron](#).^[15] Between [animals](#), the kidneys can differ in the number of nephrons and in their organisation.^[16] According to the complexity of the organisation of the nephron, the kidneys are divided into [pronephros](#), [mesonephros](#) and [metanephros](#).^[17] The nephron by itself is similar to pronephros as a whole organ.^[18] The simplest nephrons are found in the pronephros, which is the final functional organ in [primitive fish](#).^[19] The nephrons of the mesonephros, the functional organ in most [anamniotes](#) called [opisthonephros](#),^[20] are slightly more complex than those of the pronephros.^[19] The main difference between the pronephros and the mesonephros is that the pronephros consists of non-integrated nephrons with external glomeruli.^[7] The most complex nephrons are found in the metanephros of [birds](#) and [mammals](#).^{[19][21][22]} The kidneys of birds and mammals have nephrons with [loop of Henle](#).^[23]

All three types of kidneys are developed from the [intermediate mesoderm](#) of the [embryo](#).^[24] It is believed that the development of embryonic kidneys reflects the evolution of vertebrate kidneys from an early primitive kidney, the [archinephros](#).^[6] In some vertebrate species, the pronephros and mesonephros are functional organs, while in others they are only intermediate stages in the development of the final kidney, and each next kidney replaces the previous one.^[7] The pronephros is a functioning kidney of the embryo in [bony fish](#) and [amphibian larvae](#),^[7] but in mammals it is most often considered [rudimentary](#) and not functional.^[18] In some [lungfish](#) and bony fishes, the pronephros can remain functional in adults, including often simultaneously with the mesonephros.^[7] The mesonephros is the final kidney in amphibians and most fish.^[25]

Evolution

[\[edit\]](#)

[Evolutionary pressure](#) and the need to regulate body fluid [homeostasis](#) have led to pre-adaptation of the vertebrate kidneys to different environment conditions and to development of three kidney forms: the [pronephros](#), [mesonephros](#) and metanephros.^{[26][27]} The kidneys of [amniotes](#) are unique compared to other internal organs, since three different kidneys are sequentially developed during [embryogenesis](#), replacing each other and reflecting the evolution of the kidneys in vertebrates.^[28]

At the very beginning of vertebrates, when they evolved from marine [chordates](#), their evolution probably took place in fresh or slightly saline water. There is a hypothesis according to which [marine fish](#) received their kidneys after a previous adaptation of the kidneys to fresh water. As a result, early vertebrates developed [renal glomeruli](#) capable of filtering blood and perhaps tubules that reabsorbed [ions](#).^[29] Excretion of excess water from the body is the main characteristic of the pronephros in the case of species in which it develops into a functional excretory organ. In some species, the pronephros is functional during the embryonic stage of

development, representing the first stage of [kidney development](#), after which the mesonephros develops. The mesonephros probably appeared in the course of evolution in response to the increase in body mass of vertebrates, which also led to an increase in [blood pressure](#).^[28]

The evolution of the kidneys, along with the evolution of the lungs, allowed vertebrates called amniotes to live and reproduce in terrestrial environment.^{[30][28]} Metanephros, the permanent kidney of amniotes, has the unique ability to efficiently retain water in the body.^[28] In addition to water conservation, terrestrial life also required maintenance of salt levels in the body along with the excretion of waste products.^[30] The first class of animals to become fully terrestrial without a larval stage were the [reptiles](#), which were the first amniotes.^[21] The kidney takes a key role in maintenance of the constant internal environment. The relative ionic composition of the [extracellular fluid](#) is similar between marine fish and all subsequent species. Therefore, it can be said that the kidneys made it possible to preserve approximately the same composition of extracellular fluid in vertebrates as it was in the [primordial ocean](#).^[5]

Kidney forms

[\[edit\]](#)

Archinephros

[\[edit\]](#)

Main article: [Archinephros](#)

It is believed that the ancient primitive form of the kidney was the archinephros, which had series of segmental tubules through the entire length of the [trunk](#) part of the body,^[13] and each body segment had a pair of tubules.^[31] All tubules were opened [medially](#) (closer to the midline of the body) into the body cavity known as [coelom](#) and united [laterally](#) into the two common [archinephric ducts](#) which were located in opposite sides of the body.^{[13][31]} And the archinephric ducts were opened into the [cloaca](#).^[13] As an organ, the archnephros is still preserved in the larvae of [hagfishes](#) and some [caecilians](#), and is also found in the embryos of some more developed vertebrates.^[32]

Pronephros

[\[edit\]](#)

Main article: [Pronephros](#)

In [lower vertebrates](#), the pronephros is sometimes called the head kidney due to its anterior position behind the head.^[33] In [embryogenesis](#) it is usually a transitional structure and is subsequently replaced by the [mesonephros](#) in most vertebrates.^[7] In [mammalian](#) embryogenesis, the pronephros is usually considered to be [rudimentary](#) and non-functional. A functional pronephros develops in vertebrates that have a free-swimming [larval](#) stage in their development.^[7]

Pronephros functions in amphibians in the larval stage, in the adults of some bony fishes, and in the adults of some other fish species.^[7] The pronephros is a vital organ in animals that go through the aquatic larval stage. If in larvae the pronephros becomes non-functional, then they rapidly die from [edema](#).^[34]

The pronephros is a relatively large organ that has a primitive structure and usually consists of a single pair of bilateral [nephrons](#) with an external [glomerulus](#) or glomus.^{[34][15]} The typical pronephric nephron is non-integrated, and the wastes are filtered through the glomerulus or glomus directly to the [coelom](#), in the more advanced pronephros they are filtered into the nephrocoel, which is a cavity adjacent to the coelom. The coelom is connected to the [pronephric duct](#) through the ciliated [nephrostomes](#), which drain coelom fluid into the [cloaca](#).^[7]

Because of its small size and simple structure, the pronephros of fish and amphibian larvae has become an important experimental model for studying [kidney development](#).^[35]

Mesonephros and opisthonephros

[\[edit\]](#)

Main articles: [Mesonephros](#) and [Opisthonephros](#)

Mesonephros develops after the pronephros, replacing it. The mesonephros is the final kidney in [amphibians](#) and most [fish](#). In more advanced vertebrates ([amniotes](#)), mesonephros develops during [embryogenesis](#) and is then replaced by the [metanephros](#).^[36] In [reptiles](#) and [marsupials](#), it remains functional for some time after birth along with the [metanephros](#).^{[37][38]} When mesonephros degenerates in male [mammals](#), its remains are involved in the formation of the [reproductive system](#).^[39] Sometimes the [anamniote](#) mesonephros is called opisthonephros to distinguish it from the stage of development in [amniotes](#).^[40] In anamniotes, opisthonephros develops from a region of the nephric ridge, which is derived from [intermediate mesoderm](#), from which both the mesonephros and metanephros are developed in the [embryo](#) of amniotes.^{[41][42]}

Unlike the pronephros, the mesonephros consists of a set of nephrons, the glomeruli of which are enclosed in [Bowman's capsules](#), but in some marine fish glomeruli may be absent.^[36] In fish, mesonephric kidneys has no division into [cortex](#) and [medulla](#).^[43] Usually the mesonephros consists of 10–50 nephrons. The mesonephric tubules may have a connection to the coelom, however, the glomeruli of mesonephric nephrons still remain integrated. [Nephrostomes](#) are typically absent in the embryonic mesonephros of [birds](#) and [mammals](#).^[44] Mesonephros in fish has the ability to add new nephrons while body mass increases.^[45]

Metanephros

[\[edit\]](#)

In [amniotes](#), which include [reptiles](#), [birds](#), and [mammals](#), the pronephros and mesonephros are usually intermediate stages in the formation of metanephros during embryonic development, and metanephros is the final kidney.^[28] Genes that are involved in the formation of one form of kidney are reused in the formation of the next one.^[28] Metanephros differs from pronephros and mesonephros in development, position in the body, shape, number of nephrons, organization and drainage.^{[46][44]} Unlike mesonephros, after the end of its development process, metanephros has no longer the ability to add new nephrons through [nephrogenesis](#).^[5] although many reptiles show ongoing nephron formation in adults.^[47]

Metanephros is the most complex form of kidney.^[44] Each metanephric kidney is characterized by a large number of [nephrons](#) and a highly branched system of [collecting tubules and ducts](#),^[28] that open into the [ureter](#).^[48] Such branching in the metanephros is unique in relation to the pronephros and mesonephros.^[44] Depending on classes and species [urine](#) from the ureters can be excreted directly into the [cloaca](#), or collected in the [urinary bladder](#) and then excreted

into the cloaca, or collected in the urinary bladder and then excreted outside through the [urethra](#).^[46]

Metanephric kidneys

[\[edit\]](#)

Reptile kidney

[\[edit\]](#)

Reptiles were the first class of [animals](#) that had no larval stage and that were fully terrestrial animals.^[21] The [mesonephros](#) in reptiles functions for some time after birth simultaneously with the metanephros, while later the metanephric kidneys become permanent and the mesonephros degenerates.^[38]

The kidneys in reptiles are located mainly in the caudal part (away from the head) of the [abdominal cavity](#)^{[49][50]} or retroperitoneally (behind the [peritoneum](#)) in the [pelvic cavity](#) in the case of [lizards](#).^[49] Reptile kidneys are commonly elongated^[51] with color ranging from light to dark brown.^[52] The shape of the kidneys varies between reptiles due to variations of their body form.^[8] The kidneys of [snakes](#) are elongated, cylindrical^{[53][50]} and lobulated.^[52] [Turtles](#) and some lizards have [urinary bladder](#)^[50] that opens into the [cloaca](#)^[54] but snakes and crocodiles do not have it.^[50]

Compared with the metanephros of birds and mammals, the metanephros of reptiles is simpler in structure.^[21] Unlike mammals, the kidneys of reptiles do not have a clear distinction between cortex and medulla.^[43] The kidneys lack the [loop of Henle](#), have fewer nephrons (from about 3,000 to 30,000), and cannot produce hypertonic urine.^{[3][21]} Nitrogenous waste products excreted by the kidneys may include [uric acid](#), [urea](#) and [ammonia](#).^[55] Aquatic reptiles excrete predominantly [urea](#), while terrestrial reptiles excrete [uric acid](#), which allows them to conserve water.^[21]

Since the reptile kidneys are unable to produce concentrated urine due to the absence of the loop of Henle, [glomerular filtration rate](#) is decreased if water loss needs to be reduced.^[56] The glomeruli in reptiles have also decreased in size compared to [amphibians](#).^[52] In addition to the [renal artery](#) blood supply, reptiles also have a [renal portal system](#), which can redirect blood to the kidneys during periods of water deprivation, bypassing the glomeruli, to prevent [ischemic necrosis](#) of [tubular cells](#).^{[21][57]}

Mammalian kidney

[\[edit\]](#)

Main article: [Mammalian kidney](#)

See also: [Kidney](#)

In mammals, the kidneys are usually bean-shaped^[58] and located retroperitoneally^[59] on the dorsal (posterior) wall of the body.^[60] The outer layer of each kidney is made up of a fibrous sheath called the [renal capsule](#). The peripheral layer of the kidney is called the [cortex](#) and the inner part is called the [medulla](#). The medulla consists of one or more pyramids, the bases of which start from corticomedullary border. Medulla pyramid with overlying cortex comprises the [renal lobe](#).^[28] In multilobar kidneys, the pyramids are separated from each other by dipped

into the kidney areas of cortical tissue known as the [renal columns](#).^[61] [Blood](#) enters the kidney through the [renal artery](#), which in the multilobar kidney then branches in the region of the [renal pelvis](#) into large [interlobar arteries](#) that pass through the renal columns.^{[62][63]} The pyramids consist mainly of tubules that transport urine from the cortex, that produces it by blood filtration, to the tips of the pyramids, that form the [renal papillae](#). Urine is excreted through the renal papillae into the calyces and then into the [pelvis](#), [ureter](#), and [bladder](#).^{[62][28]} Then it is excreted outside through the [urethra](#).^[64] In [monotremes](#), the ureters open into the [urogenital sinus](#), which is connected to the urinary bladder and [cloaca](#),^[65] and urine is excreted into the cloaca instead of the urethra.^{[66][65]}

Structurally, kidneys vary between mammals.^[67] Which structural type a particular species will have depends mainly on the body mass of the [species](#).^[68] Small mammals have simple, unilobar kidneys with a compact structure and a single renal papilla, while large animals have more complex multilobar kidneys, such as those of [bovines](#).^{[67][69]} Kidneys can also be with a single renal papilla (the unipapillary kidneys),^[69] as in [mice](#) and [rats](#),^[70] with several, as in [spider monkeys](#), or with a large number, as in [pigs](#) or [humans](#).^[69] Most animals have a single renal papilla.^[69] In some animals, such as horses, the apices of the renal pyramids fuse with each other to form a common renal papilla, called the renal crest.^[71] The renal crest usually appears in animals larger than [rabbits](#).^[68] The kidneys of bovines are multilobar with external lobation.^[72] [Marine mammals](#), [bears](#) and [otters](#) have [reniculate kidneys](#) which are made of large amount of lobes called reniculi.^[73] Each reniculus can be compared to a simple unipapillary kidney as a whole.^[74]

[Nitrogenous waste](#) products are excreted by the kidneys of mammals primarily in the form of [urea](#),^[75] which is highly [soluble](#) in water.^[76] Each nephron is located in both the cortex and the medulla. The most proximal part of the nephron is [glomerulus](#), which is located in the cortex.^[28] The [nephrons](#) of the mammalian kidneys have [loops of Henle](#), which are the most efficient way to reabsorb water and produce concentrated urine to conserve water in the body.^[12] The mammalian kidneys combine both nephrons with a short and nephrons with a long loop of Henle.^[77] The medulla is divided into outer and inner regions. The outer region consists of short loops of Henle and collecting ducts, and the inner region consists of long loops of Henle and collecting ducts.^[28] After passing through the loop of Henle, the fluid becomes [hypertonic](#) relative to the [blood plasma](#).^[78] The [renal portal system](#) is absent in mammals.^[56]

Avian kidney

[\[edit\]](#)

In [birds](#), the kidneys are typically elongated^[79] and located dorsally in the [abdominal cavity](#) in the [pelvic](#) skeletal depressions.^{[80][81]}

The structure of the avian kidneys differs from the structure of the mammalian kidneys.^[67] The avian kidney is lobulated and usually consists of three lobes.^[80] The lobes are divided into lobules, each of which has a cortex and a medulla.^{[67][3]} The medulla of the each lobule is shaped like a cone, and, unlike mammals, it is not subdivided into the inner and outer regions, while structurally it is similar to the outer medulla of the mammalian kidney.^[67] In the avian kidney, the [renal pelvis](#) is absent,^[82] and each lobule has a separate branch to the [ureter](#).^[3] No birds, except for the [ostrich](#), have a [bladder](#); urine is excreted from the kidneys through the ureters to the [cloaca](#).^[83]

Avian kidneys combine so called reptilian-type nephrons, without the [loop of Henle](#), and mammalian-type nephrons, with the loop of Henle.^[23] Most nephrons are reptilian-type.^[84] The loop of Henle of birds is similar to that of mammals, the main difference is that the nephron of birds has only a short loop of Henle.^[77] Like mammals, although to a lesser extent,^[67] birds are able to produce concentrated urine, thus conserving water in the body.^[23] [Nitrogenous](#) waste products are excreted mainly in the form of [uric acid](#), which is a white paste that is poorly soluble in water, which also helps to reduce water loss.^[85] Additional water reabsorption occurs in the cloaca and distal intestine. Altogether, this allows birds to excrete their wastes without significant loss of water.^[9]

In birds, the arterial blood is supplied to the kidneys by the cranial, middle and caudal renal arteries.^[86] Like reptiles, birds have a [renal portal system](#), but it does not deliver blood to the loops of Henle, blood is delivered only to the proximal and distal tubules of the nephrons. When birds are in a state of [dehydration](#), nephrons without a loop of Henle stop filtering, while nephrons with a loop continue, but due to the presence of a loop, they can produce concentrated urine.[!]

The **kidneys** are a pair of [organs](#) of the [excretory system](#) in [vertebrates](#), which maintain the balance of water and [electrolytes](#) in the body ([osmoregulation](#)), filter the [blood](#), remove [metabolic waste products](#), and, in many vertebrates, also produce [hormones](#) (in particular, [renin](#)) and maintain [blood pressure](#).^{[1][2][3][4]} In healthy vertebrates, the kidneys maintain [homeostasis](#) of [extracellular fluid](#) in the body.^[6] When the blood is being filtered, the kidneys form [urine](#), which consists of water and excess or unnecessary substances, the urine is then excreted from the body through other organs, which in vertebrates, depending on the species, may include the [ureter](#), [urinary bladder](#), [cloaca](#), and [urethra](#).^[6]

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Evolution

[\[edit\]](#)

[Evolutionary pressure](#) and the need to regulate body fluid [homeostasis](#) have led to pre-adaptation of the vertebrate kidneys to different environment conditions and to development of three kidney forms: the [pronephros](#), [mesonephros](#) and metanephros.^{[26][27]} The kidneys of [amniotes](#) are unique compared to other internal organs, since three different kidneys are sequentially developed during [embryogenesis](#), replacing each other and reflecting the evolution of the kidneys in vertebrates.^[28]

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The evolution of the kidneys, along with the evolution of the lungs, allowed vertebrates called amniotes to live and reproduce in terrestrial environment.^{[30][28]} Metanephros, the permanent kidney of amniotes, has the unique ability to efficiently retain water in the body.^[28] In addition to water conservation, terrestrial life also required maintenance of salt levels in the body along with the excretion of waste products.^[30] The first class of animals to become fully terrestrial without a larval stage were the [reptiles](#), which were the first amniotes.^[21] The kidney takes a key role in maintenance of the constant internal environment. The relative ionic composition of the [extracellular fluid](#) is similar between marine fish and all subsequent species. Therefore, it can be said that the kidneys made it possible to preserve approximately the same composition of extracellular fluid in vertebrates as it was in the [primordial ocean](#).^[5]

Kidney forms

[\[edit\]](#)

[Archinephros](#)

[\[edit\]](#)

Main article: [Archinephros](#)

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Pronephros

[\[edit\]](#)

Main article: [Pronephros](#)

In [lower vertebrates](#), the pronephros is sometimes called the head kidney due to its anterior position behind the head.^[33] In [embryogenesis](#) it is usually a transitional structure and is subsequently replaced by the [mesonephros](#) in most vertebrates.^[7] In [mammalian](#) embryogenesis, the pronephros is usually considered to be [rudimentary](#) and non-functional. A functional pronephros develops in vertebrates that have a free-swimming [larval](#) stage in their development.^[7]

Pronephros functions in amphibians in the larval stage, in the adults of some bony fishes, and in the adults of some other fish species.^[7] The pronephros is a vital organ in animals that go through the aquatic larval stage. If in larvae the pronephros becomes non-functional, then they rapidly die from [edema](#).^[34]

The pronephros is a relatively large organ that has a primitive structure and usually consists of a single pair of bilateral [nephrons](#) with an external [glomerulus](#) or glomus.^{[34][15]} The typical pronephric nephron is non-integrated, and the wastes are filtered through the glomerulus or glomus directly to the [coelom](#), in the more advanced pronephros they are filtered into the nephrocoel, which is a cavity adjacent to the coelom. The coelom is connected to the [pronephric duct](#) through the ciliated [nephrostomes](#), which drain coelom fluid into the [cloaca](#).^[7]

Because of its small size and simple structure, the pronephros of fish and amphibian larvae has become an important experimental model for studying [kidney development](#).^[35]

Mesonephros and opisthonephros

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Main articles: [Mesonephros](#) and [Opisthonephros](#)

Mesonephros develops after the pronephros, replacing it. The mesonephros is the final kidney in [amphibians](#) and most [fish](#). In more advanced vertebrates ([amniotes](#)), mesonephros develops during [embryogenesis](#) and is then replaced by the [metanephros](#).^[36] In [reptiles](#) and [marsupials](#), it remains functional for some time after birth along with the [metanephros](#).^{[37][38]} When mesonephros degenerates in male [mammals](#), its remains are involved in the formation of the [reproductive system](#).^[39] Sometimes the [anamniote](#) mesonephros is called opisthonephros to distinguish it from the stage of development in [amniotes](#).^[40] In anamniotes, opisthonephros develops from a region of the nephric ridge, which is derived from [intermediate mesoderm](#), from which both the mesonephros and metanephros are developed in the [embryo](#) of amniotes.^{[41][42]}

Unlike the pronephros, the mesonephros consists of a set of nephrons, the glomeruli of which are enclosed in [Bowman's capsules](#), but in some marine fish glomeruli may be absent.^[36] In fish, mesonephric kidneys has no division into [cortex](#) and [medulla](#).^[43] Usually the mesonephros consists of 10–50 nephrons. The mesonephric tubules may have a connection to the coelom, however, the glomeruli of mesonephric nephrons still remain integrated. [Nephrostomes](#) are typically absent in the embryonic mesonephros of [birds](#) and [mammals](#).^[44] Mesonephros in fish has the ability to add new nephrons while body mass increases.^[45]

Metanephros

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In [amniotes](#), which include [reptiles](#), [birds](#), and [mammals](#), the pronephros and mesonephros are usually intermediate stages in the formation of metanephros during embryonic development, and metanephros is the final kidney.^[28] Genes that are involved in the formation of one form of kidney are reused in the formation of the next one.^[28] Metanephros differs from pronephros and mesonephros in development, position in the body, shape, number of nephrons, organization and drainage.^{[46][44]} Unlike mesonephros, after the end of its development process, metanephros has no longer the ability to add new nephrons through [nephrogenesis](#),^[5] although many reptiles show ongoing nephron formation in adults.^[47]

Metanephros is the most complex form of kidney.^[44] Each metanephric kidney is characterized by a large number of [nephrons](#) and a highly branched system of [collecting tubules and ducts](#),^[28] that open into the [ureter](#).^[48] Such branching in the metanephros is unique in relation to the pronephros and mesonephros.^[44] Depending on classes and species [urine](#) from the ureters can be excreted directly into the [cloaca](#), or collected in the [urinary bladder](#) and then excreted into the cloaca, or collected in the urinary bladder and then excreted outside through the [urethra](#).^[46]

Metanephric kidneys

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Reptile kidney

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Reptiles were the first class of [animals](#) that had no larval stage and that were fully terrestrial animals.^[21] The [mesonephros](#) in reptiles functions for some time after birth simultaneously with the metanephros, while later the metanephric kidneys become permanent and the mesonephros degenerates.^[38]

The kidneys in reptiles are located mainly in the caudal part (away from the head) of the [abdominal cavity](#)^{[49][50]} or retroperitoneally (behind the [peritoneum](#)) in the [pelvic cavity](#) in the case of [lizards](#).^[49] Reptile kidneys are commonly elongated^[51] with color ranging from light to dark brown.^[52] The shape of the kidneys varies between reptiles due to variations of their body form.^[8] The kidneys of [snakes](#) are elongated, cylindrical^{[53][50]} and lobulated.^[52] [Turtles](#) and some lizards have [urinary bladder](#)^[50] that opens into the [cloaca](#)^[54] but snakes and crocodiles do not have it.^[50]

Compared with the metanephros of birds and mammals, the metanephros of reptiles is simpler in structure.^[21] Unlike mammals, the kidneys of reptiles do not have a clear distinction between cortex and medulla.^[43] The kidneys lack the [loop of Henle](#), have fewer nephrons (from about

3,000 to 30,000), and cannot produce hypertonic urine.^{[3][21]} Nitrogenous waste products excreted by the kidneys may include [uric acid](#), [urea](#) and [ammonia](#).^[55] Aquatic reptiles excrete predominantly [urea](#), while terrestrial reptiles excrete [uric acid](#), which allows them to conserve water.^[21]

Since the reptile kidneys are unable to produce concentrated urine due to the absence of the loop of Henle, [glomerular filtration rate](#) is decreased if water loss needs to be reduced.^[56] The glomeruli in reptiles have also decreased in size compared to [amphibians](#).^[52] In addition to the [renal artery](#) blood supply, reptiles also have a [renal portal system](#), which can redirect blood to the kidneys during periods of water deprivation, bypassing the glomeruli, to prevent [ischemic necrosis](#) of [tubular cells](#).^{[21][57]}

Mammalian kidney

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Main article: [Mammalian kidney](#)

See also: [Kidney](#)

In mammals, the kidneys are usually bean-shaped^[58] and located retroperitoneally^[59] on the dorsal (posterior) wall of the body.^[60] The outer layer of each kidney is made up of a fibrous sheath called the [renal capsule](#). The peripheral layer of the kidney is called the [cortex](#) and the inner part is called the [medulla](#). The medulla consists of one or more pyramids, the bases of which start from corticomedullary border. Medulla pyramid with overlying cortex comprises the [renal lobe](#).^[28] In multilobar kidneys, the pyramids are separated from each other by dipped into the kidney areas of cortical tissue known as the [renal columns](#).^[61] [Blood](#) enters the kidney through the [renal artery](#), which in the multilobar kidney then branches in the region of the [renal pelvis](#) into large [interlobar arteries](#) that pass through the renal columns.^{[62][63]} The pyramids consist mainly of tubules that transport urine from the cortex, that produces it by blood filtration, to the tips of the pyramids, that form the [renal papillae](#). Urine is excreted through the renal papillae into the calyces and then into the [pelvis](#), [ureter](#), and [bladder](#).^{[62][28]} Then it is excreted outside through the [urethra](#).^[64] In [monotremes](#), the ureters open into the [urogenital sinus](#), which is connected to the urinary bladder and [cloaca](#),^[65] and urine is excreted into the cloaca instead of the urethra.^{[66][65]}

Structurally, kidneys vary between mammals.^[67] Which structural type a particular species will have depends mainly on the body mass of the [species](#).^[68] Small mammals have simple, unilobar kidneys with a compact structure and a single renal papilla, while large animals have more complex multilobar kidneys, such as those of [bovines](#).^{[67][69]} Kidneys can also be with a single renal papilla (the unipapillary kidneys),^[69] as in [mice](#) and [rats](#),^[70] with several, as in [spider monkeys](#), or with a large number, as in [pigs](#) or [humans](#).^[69] Most animals have a single renal papilla.^[69] In some animals, such as horses, the apices of the renal pyramids fuse with each other to form a common renal papilla, called the renal crest.^[71] The renal crest usually appears in animals larger than [rabbits](#).^[68] The kidneys of bovines are multilobar with external lobation.^[72] [Marine mammals](#), [bears](#) and [otters](#) have [reniculate kidneys](#) which are made of large amount of lobes called reniculi.^[73] Each reniculus can be compared to a simple unipapillary kidney as a whole.^[74]

[Nitrogenous waste](#) products are excreted by the kidneys of mammals primarily in the form of [urea](#),^[75] which is highly [soluble](#) in water.^[76] Each nephron is located in both the cortex and the medulla. The most proximal part of the nephron is [glomerulus](#), which is located in the

cortex.^[28] The [nephrons](#) of the mammalian kidneys have [loops of Henle](#), which are the most efficient way to reabsorb water and produce concentrated urine to conserve water in the body.^[12] The mammalian kidneys combine both nephrons with a short and nephrons with a long loop of Henle.^[77] The medulla is divided into outer and inner regions. The outer region consists of short loops of Henle and collecting ducts, and the inner region consists of long loops of Henle and collecting ducts.^[28] After passing through the loop of Henle, the fluid becomes [hypertonic](#) relative to the [blood plasma](#).^[78] The [renal portal system](#) is absent in mammals.^[56]

Avian kidney

[\[edit\]](#)

In [birds](#), the kidneys are typically elongated^[79] and located dorsally in the [abdominal cavity](#) in the [pelvic](#) skeletal depressions.^{[80][81]}

The structure of the avian kidneys differs from the structure of the mammalian kidneys.^[67] The avian kidney is lobulated and usually consists of three lobes.^[80] The lobes are divided into lobules, each of which has a cortex and a medulla.^{[67][3]} The medulla of the each lobule is shaped like a cone, and, unlike mammals, it is not subdivided into the inner and outer regions, while structurally it is similar to the outer medulla of the mammalian kidney.^[67] In the avian kidney, the [renal pelvis](#) is absent,^[82] and each lobule has a separate branch to the [ureter](#).^[3] No birds, except for the [ostrich](#), have a [bladder](#); urine is excreted from the kidneys through the ureters to the [cloaca](#).^[83]

Avian kidneys combine so called reptilian-type nephrons, without the [loop of Henle](#), and mammalian-type nephrons, with the loop of Henle.^[23] Most nephrons are reptilian-type.^[84] The loop of Henle of birds is similar to that of mammals, the main difference is that the nephron of birds has only a short loop of Henle.^[77] Like mammals, although to a lesser extent,^[67] birds are able to produce concentrated urine, thus conserving water in the body.^[23] [Nitrogenous](#) waste products are excreted mainly in the form of [uric acid](#), which is a white paste that is poorly soluble in water, which also helps to reduce water loss.^[85] Additional water reabsorption occurs in the cloaca and distal intestine. Altogether, this allows birds to excrete their wastes without significant loss of water.^[5]

In birds, the arterial blood is supplied to the kidneys by the cranial, middle and caudal renal arteries.^[86] Like reptiles, birds have a [renal portal system](#), but it does not deliver blood to the loops of Henle, blood is delivered only to the proximal and distal tubules of the nephrons. When birds are in a state of [dehydration](#), nephrons without a loop of Henle stop filtering, while nephrons with a loop continue, but due to the presence of a loop, they can produce concentrated urine.!