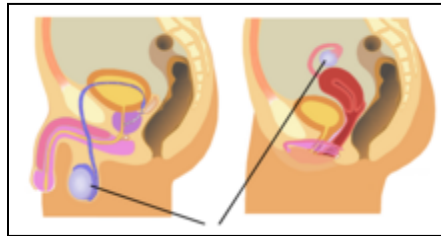


A **testicle** or **testis** (pl.: **testes**) is the male **gonad** in all **bilaterians**, including humans. It is **homologous** to the female **ovary**. The functions of the testicles are to produce both **sperm** and **androgens**, primarily **testosterone**. Testosterone release is controlled by the anterior pituitary **luteinizing hormone**, whereas sperm production is controlled both by the **anterior pituitary follicle-stimulating hormone** and gonadal testosterone.

## Structure

### Appearance



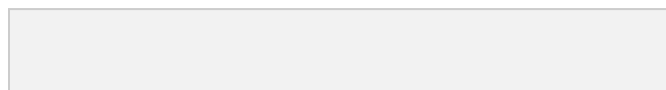
Male gonad (testes, left) and female gonad (**ovaries**, right)

Males have two testicles of similar size contained within the **scrotum**, which is an extension of the **abdominal wall**.<sup>[1]</sup> Scrotal asymmetry, in which one testicle extends farther down into the scrotum than the other, is common. This is because of the differences in the vasculature's anatomy.<sup>[1]</sup> For 85% of men, the right testis hangs lower than the left one.<sup>[1]</sup>

### Measurement and volume

The volume of the testicle can be estimated by palpating it and comparing it to **ellipsoids** (an **orchidometer**) of known sizes. Another method is to use calipers, a ruler, or an **ultrasound** image to obtain the three measurements of the x, y, and z axes (length, depth and width). These measurements can then be used to calculate the volume, using the formula for the volume of an ellipsoid:

$$\text{Volume} = \frac{4}{3} \cdot \pi \cdot \text{length} \cdot \text{width} \cdot \text{depth}$$



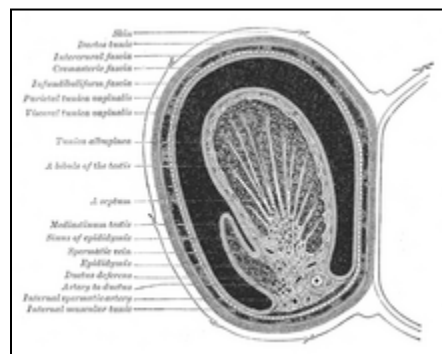
$$\approx \text{length} \cdot \text{width} \cdot \text{depth} \cdot 0.52$$

+

$\frac{1}{4}$  in). The [Tanner scale](#), which is used to assess the maturity of the male genitalia, assigns a maturity stage to the calculated volume ranging from stage I, a volume of less than 1.5 cm<sup>3</sup>; to stage V, a volume greater than 20 cm<sup>3</sup>. Normal volume is 15 to 25 cm<sup>3</sup>; the average is 18 cm<sup>3</sup> per testis (range 12–30 cm<sup>3</sup>).<sup>[1]</sup>

The number of spermatozoa an adult human male produces is directly proportional to testicular volume, as larger testicles contain more seminiferous tubules and [Sertoli cells](#) as a result.<sup>[3]</sup> As such, men with larger testicles produce on average more sperm cells in each [ejaculate](#), as testicular volume is positively correlated with semen profiles.<sup>[4]</sup>

## Internal structure



Transverse section through the left side of the scrotum and the left testis

## Duct system

The testes are covered by a tough fibrous shell called the [tunica albuginea](#).<sup>[5]</sup> Under the tunica albuginea, the testes contain very fine-coiled tubes called [seminiferous tubules](#).<sup>[5]</sup> The tubules are lined with a layer of cells ([germ cells](#)) that develop from [puberty](#) through old age into [sperm cells](#) (also known as [spermatozoa](#) or male [gametes](#)).<sup>[5]</sup> The developing sperm travel through the seminiferous tubules to the [rete testis](#) located in the [mediastinum testis](#), to the [efferent ducts](#), and then to the [epididymis](#) where newly created sperm cells mature ([spermatogenesis](#)).<sup>[6]</sup> The sperm move into the [vas deferens](#), and are eventually expelled through the [urethra](#) and out of the [urethral orifice](#) through muscular contractions.<sup>[6]</sup>

### Primary cell types

Within the seminiferous tubules, the germ cells develop into [spermatogonia](#), [spermatocytes](#), [spermatids](#) and spermatozoa through the process of spermatogenesis. The gametes contain DNA for fertilization of an [ovum](#).<sup>[7]</sup> Sertoli cells – the true epithelium of the seminiferous epithelium, critical for the support of germ cell development into spermatozoa. Sertoli cells secrete [inhibin](#).<sup>[8]</sup> [Peritubular myoid cells](#) surround the seminiferous tubules.<sup>[9]</sup>

Between tubules (interstitial cells) exist [Leydig cells](#)<sup>[10]</sup> – cells localized between seminiferous tubules that produce and secrete [testosterone](#) and other [androgens](#) important for [puberty](#) (including [secondary sexual characteristics](#) like facial hair), [sexual behavior](#), and [libido](#). Sertoli cells support spermatogenesis.<sup>[11]</sup> Testosterone controls testicular volume.

Immature Leydig cells and interstitial [macrophages](#) and [epithelial cells](#) are also present.

### Blood supply and lymphatic drainage

The testis has three sources of arterial blood supply: the [testicular artery](#), the [cremasteric artery](#), and the [artery to the ductus deferens](#).<sup>[12]</sup> Blood supply and [lymphatic drainage](#) of the testes and scrotum are distinct:

- The paired testicular arteries arise directly from the [abdominal aorta](#) and descend through the [inguinal canal](#), while the scrotum and the rest of the external genitalia is supplied by the [internal pudendal artery](#) (a branch of the [internal iliac artery](#)).<sup>[13][14]</sup>

- The testis has collateral blood supply from the cremasteric artery (a branch of the [inferior epigastric artery](#), which is a branch of the [external iliac artery](#)), and the artery to the ductus deferens (a branch of the [inferior vesical artery](#), which is a branch of the internal iliac artery).<sup>[15][16]</sup> Therefore, if the testicular artery is ligated, e.g., during a Fowler-Stevens [orchiopexy](#) for a high undescended testis, the testis will usually survive on these other blood supplies.<sup>[17]</sup>
- Lymphatic drainage of the testes follows the testicular arteries back to the [paraaortic lymph nodes](#), while lymph from the scrotum drains to the [inguinal lymph nodes](#).<sup>[13][16]</sup>

## Layers

3D anatomy of the layers surrounding the testis

Many anatomical features of the adult testis reflect its developmental origin in the [abdomen](#). The layers of tissue enclosing each testicle are derived from the layers of the anterior [abdominal wall](#).<sup>[1]</sup> The [cremasteric muscle](#) arises from the [internal oblique muscle](#).<sup>[1][18]</sup>

## The blood–testis barrier

*Main article: [Blood–testis barrier](#)*

Large molecules cannot pass from the blood into the lumen of a seminiferous tubule due to the presence of [tight junctions](#) between adjacent Sertoli cells.<sup>[13]</sup> The spermatogonia occupy the basal compartment (deep to the level of the tight junctions) and the more mature forms, such as primary and secondary spermatocytes and spermatids, occupy the adluminal compartment.<sup>[13]</sup>

The function of the blood–testis barrier may be to prevent an [auto-immune](#) reaction.<sup>[13]</sup> Mature sperm (and their [antigens](#)) emerge significantly after immune tolerance is set in infancy.<sup>[13]</sup> Since sperm are antigenically different from self-tissue, a male animal can react immunologically to his own sperm. The male can make antibodies against them.<sup>[13]</sup>

Injection of sperm antigens causes inflammation of the testis (auto-immune orchitis) and reduced fertility.<sup>[13]</sup> The blood–testis barrier may reduce the likelihood that sperm proteins will induce an immune response.<sup>[19]</sup>

## Temperature regulation and responses

Carl Richard Moore in 1926<sup>[20]</sup> proposed that testicles were external due to [spermatogenesis](#) being enhanced at temperatures slightly less than core body temperature outside the body. The spermatogenesis is less efficient at lower and higher temperatures than 33 °C. Because the testes are located outside the body, the smooth tissue of the scrotum can move them closer or further away from the body.<sup>[5]</sup> The temperature of the testes is maintained at 34.4 °C, a little below body temperature, as temperatures above 36.7 °C impede spermatogenesis.<sup>[1][5]</sup> There are a number of mechanisms to maintain the testes at the optimum temperature.<sup>[21]</sup>

The cremasteric muscle covers the testicles and the [spermatic cord](#).<sup>[22]</sup> When this muscle contracts, the cord shortens and the testicles move closer up toward the body, which provides slightly more warmth to maintain optimal testicular temperature.<sup>[22]</sup> When cooling is required, the cremasteric muscle relaxes and the testicles lower away from the warm body and are able to cool.<sup>[22]</sup> Contraction also occurs in response to [physical stress](#), such as blunt trauma; the testicles withdraw and the scrotum shrinks very close to the body in an effort to protect them.<sup>[23]</sup>

The [cremasteric reflex](#) will reflexively raise the testicles. The testicles can also be lifted voluntarily using the [pubococcygeus](#) muscle, which partially activates related muscles.

## Gene and protein expression

*Further information: [Bioinformatics § Gene and protein expression](#)*

The [human genome](#) includes approximately 20,000 protein coding genes: 80% of these [genes are expressed](#) in adult testes.<sup>[24]</sup> The testes have the highest fraction of tissue type-specific genes compared to other organs and tissues.<sup>[25]</sup> About 1000 of them are highly specific for the testes,<sup>[24]</sup> and about 2,200 show an elevated pattern of expression. A majority of these genes encode for proteins that are expressed in the seminiferous tubules and have functions related to spermatogenesis.<sup>[25]</sup> Sperm cells express proteins that result in the development of [flagella](#); these same proteins are expressed in the female in cells lining the [fallopian tube](#) and cause the development of [cilia](#). Sperm cell flagella and fallopian tube cilia are [homologous](#) structures. The testis-specific proteins that show the highest level of expression are [protamines](#).<sup>[26]</sup>

## Development

*Main article: [Development of the gonads § Testis](#)*

There are two phases in which the testes grow substantially. These are the embryonic and pubertal phases. During mammalian development, the gonads are at first capable of becoming either [ovaries](#) or testes.<sup>[27]</sup> In humans, starting at about week 4, the gonadal rudiments are present within the [intermediate mesoderm](#) adjacent to the developing kidneys. At about week 6, [sex cords](#) develop within the forming testes.<sup>[1][28]</sup> These are made up of early Sertoli cells that surround and nurture the germ cells that migrate into the gonads shortly before sex determination begins.<sup>[1]</sup> In males, the sex-specific gene [SRY](#) that is found on the [Y chromosome](#) initiates sex determination by downstream regulation of sex-determining factors (such as [GATA4](#), [SOX9](#) and [AMH](#)), which lead to development of the male phenotype, including directing development of the early bipotential gonad toward the male path of development.<sup>[1]</sup>

Testes follow the path of descent, from high in the posterior fetal abdomen to the inguinal ring and beyond to the [inguinal canal](#) and into the [scrotum](#).<sup>[29]</sup> In most cases (97% full-term, 70% [preterm](#)), both testes have descended by birth.<sup>[29][30]</sup> In most other cases, only one testis fails to descend. This is called [cryptorchidism](#). In most cases of cryptorchidism, the issue will mostly resolve itself within the first half year of life. However, if the testes do not descend far enough into the scrotum, surgical anchoring in the scrotum is required due to risks of infertility and [testicular cancer](#).<sup>[30]</sup>

The testes grow in response to the start of spermatogenesis. Size depends on lytic function, sperm production (amount of spermatogenesis present in testis), [interstitial fluid](#), and Sertoli cell fluid production. The testicles are fully descended before the male reaches puberty.

## Clinical significance

### Protection and injury

*Further information: [Testicular pain](#)*

- The testicles are very sensitive to impact and injury. The pain involved travels up from each testicle into the abdominal cavity, via the [spermatic plexus](#), which is the primary nerve of each testicle.<sup>[31]</sup> This will cause pain in the hip and the back. The pain usually fades within a few minutes.
- [Testicular torsion](#) is a medical emergency. This is because the longer it takes to access medical intervention with respect to extending ischemia, the higher

the chance that the testicle will be lost. There is a 90% chance to save the testicle if de-torsion surgery is performed within six hours of testicular torsion onset.<sup>[32]</sup>

- **Testicular rupture** is severe trauma affecting the tunica albuginea.<sup>[33]</sup>
- Penetrating injuries to the scrotum may cause **castration**, or physical separation or destruction of the testes, possibly along with part or all of the penis, which results in total sterility if the testicles are not reattached quickly. In an effort to avoid severe infection, ample application of **saline** and **bacitracin** help remove debris and foreign objects from the wound.<sup>[34]</sup>
- **Jockstraps** support and protect the testicles.

## Diseases and conditions

### Testicular disease

**Specialty**      Urology, Reproductive medicine

- To improve the chances of catching cases of **testicular cancer**, other **neoplasms**, or other health issues early, regular **testicular self-examination** is recommended.
- **Varicocele**, swollen vein(s) from the testes, usually affecting the left side, the testis usually being normal.<sup>[35][36]</sup>
- **Hydrocele testis** is swelling around testes caused by accumulation of clear liquid within a membranous sac, the testis usually being normal. It is the most common cause of scrotal swelling.<sup>[37]</sup>
- **Spermatocele** is a retention cyst of a tubule of the **rete testis** or the head of the **epididymis** distended with barely watery fluid that contains spermatozoa.<sup>[36]</sup>
- **Endocrine disorders** can also affect the size and function of the testis.
- Certain inherited conditions involving mutations in key developmental genes also impair testicular descent, resulting in abdominal or inguinal testes, which remain nonfunctional and may become cancerous.<sup>[38]</sup> Other genetic conditions can result in the loss of the **Wolffian ducts** and allow for the persistence of **Müllerian ducts**. Both excess and deficient levels of **estrogens** can disrupt **spermatogenesis** and cause **infertility**.<sup>[39]</sup>

- [Bell-clapper deformity](#) is a deformity in which the testicle is not attached to the scrotal walls, and can rotate freely on the spermatic cord within the tunica vaginalis. Those with Bell-clapper are at a higher risk of testicular torsion.<sup>[40][41]</sup>
- [Orchitis](#) is inflammation of the testicles
- [Epididymitis](#) is a painful inflammation of the epididymis or epididymides, frequently caused by bacterial infection but sometimes of unknown origin.
- [Anorchia](#) is the absence of one or both testicles.
- [Cryptorchidism](#), or "undescended testicles", is when the testicle does not descend into the scrotum of an infant boy.<sup>[30]</sup>
- Testicular enlargement is an [unspecific](#) sign of various testicular diseases, and can be defined as a testicular size of more than 5 cm ([long axis](#)) × 3 cm (short axis).<sup>[42]</sup>
- [Blue balls](#) is a condition concerning temporary fluid congestion in the testicles and [prostate](#) region, caused by prolonged [sexual arousal](#).

[Testicular prostheses](#) are available to mimic the appearance and feel of one or both testicles, when absent as from injury or as treatment in association to [gender dysphoria](#). There have also been some instances of their implantation in dogs.

Scientists are working on developing lab-grown testicles that might help infertile men in the future.<sup>[43]</sup>

## Effects of exogenous hormones

To some extent, it is possible to change testicular size. Short of direct injury or subjecting them to adverse conditions, e.g., higher temperature than they are normally accustomed to, they can be shrunk by competing against their intrinsic hormonal function through the use of externally administered [steroidal](#) hormones. Steroids taken for muscle enhancement (especially [anabolic steroids](#)) often have the undesired side effect of testicular shrinkage.

Stimulation of testicular functions via [gonadotropic-like hormones](#) may enlarge their size. Testes may shrink or atrophy during [hormone replacement therapy](#) or through [chemical castration](#).

In all cases, the loss in testes volume corresponds with a loss of spermatogenesis.

## Society and culture



Further information: [Testicles as food](#) and [Sex selection](#)



Depiction of [bake-danuki](#) with oversized testicles

The testicles of [calves](#), [lambs](#), [roosters](#), [turkeys](#), and other animals are eaten in many parts of the world, often under [euphemistic culinary names](#). Testicles are a by-product of the castration of young animals raised for meat, so they might have been a late-spring seasonal specialty.<sup>[44]</sup> In modern times, they are generally frozen and available year-round.

In the [Middle Ages](#), men who wanted a boy sometimes had their left testicle removed. This was because people believed that the right testicle made "boy" sperm and the left made "girl" sperm.<sup>[45]</sup> As early as 330 BC, [Aristotle](#) prescribed the ligation (tying off) of the left testicle in men wishing to have boys.<sup>[46]</sup>

## Etymology and slang

One theory about the etymology of the word *testis* is based on [Roman law](#). The original [Latin](#) word *testis*, "witness", was used in the firmly established legal principle "*Testis unus, testis nullus*" (one witness [equals] no witness), meaning that testimony by any one person in court was to be disregarded unless corroborated by the testimony of at least another. This led to the common practice of producing two witnesses, bribed to testify the same way in cases of lawsuits with ulterior motives. Since such witnesses always came in pairs, the meaning was accordingly extended, often in the diminutive (*testiculus*, *testiculi*).<sup>[citation needed]</sup>

Another theory says that *testis* is influenced by a loan translation, from Greek *parastatēs* "defender (in law), supporter" that is "two glands side by side".<sup>[47]</sup>

There are multiple slang terms for the testes. They may be referred to as "balls". Frequently, "[nuts](#)" (sometimes intentionally misspelled as "nutz") are also a slang term for the testes due to the geometric resemblance. One variant of the term includes "Deez Nuts", which was used for a [satirical political candidate in 2016](#).

In [Spanish](#), the term *huevos* is used, which is Spanish for [eggs](#).

## Other animals



Testicles of a [rooster](#)

### External appearance

In [seasonal breeders](#), the weight of the testes often increases during the breeding season.<sup>[48]</sup> The [testicles of a dromedary camel](#) are 7–10 cm (2.8–3.9 in) long, 4.5 cm (1.8 in) deep and 5 cm (2.0 in) in width. The right testicle is often smaller than the left.<sup>[49]</sup>

In [sharks](#), the testicle on the right side is usually larger. In many bird and mammal species, the left may be larger. [Fish usually have two testes](#) of a similar size. The primitive [jawless fish](#) have only a single testis, located in the midline of the body, although this forms from the fusion of paired structures in the embryo.<sup>[50]</sup>

### Location

#### Internal

The basal condition for mammals is to have internal testes.<sup>[51]</sup> The testes of [monotremes](#),<sup>[52][53]</sup> [xenarthrans](#),<sup>[53]</sup> and [afrotherians](#)<sup>[54]</sup> remain within the abdomen ([testicondy](#)). There are also some [marsupials](#) with external testes<sup>[55][56][57]</sup> and

boreoeutherian mammals with internal testes, such as the rhinoceros.<sup>[58]</sup> Cetaceans such as whales and dolphins also have internal testes.<sup>[59][60]</sup> As external testes would increase drag in the water, they have internal testes, which are kept cool by special circulatory systems that cool the arterial blood going to the testes by placing the arteries near veins bringing cooled venous blood from the skin.<sup>[61][62]</sup> In odobenids and phocids, the location of the testes is para-abdominal, though otariids have scrotal testes.<sup>[63]</sup>

## External

Boreoeutherian land mammals, the large group of mammals that includes humans, have externalized testes.<sup>[64]</sup> Their testes function best at temperatures lower than their core body temperature. Their testes are located outside of the body and are suspended by the spermatic cord within the scrotum.

There are several hypotheses as to why most boreotherian mammals have external testes that operate best at a temperature that is slightly less than the core body temperature. One view is that it is stuck with enzymes evolved in a colder temperature due to external testes evolving for different reasons. Another view is that the lower temperature of the testes simply is more efficient for sperm production.

The classic hypothesis is that cooler temperature of the testes allows for more efficient fertile spermatogenesis. There are no possible enzymes operating at normal core body temperature that are as efficient as the ones evolved.

Early mammals had lower body temperatures and thus their testes worked efficiently within their body. However, boreotherian mammals may have higher body temperatures than the other mammals and had to develop external testes to keep them cool. One argument is that mammals with internal testes, such as the monotremes, armadillos, sloths, elephants, and rhinoceroses, have a lower core body temperatures than those mammals with external testes.<sup>[citation needed]</sup>

Researchers have wondered why birds, despite having very high core body temperatures, have internal testes and did not evolve external testes.<sup>[65]</sup> It was once theorized that birds used their air sacs to cool the testes internally, but later studies revealed that birds' testes are able to function at core body temperature.<sup>[65]</sup>

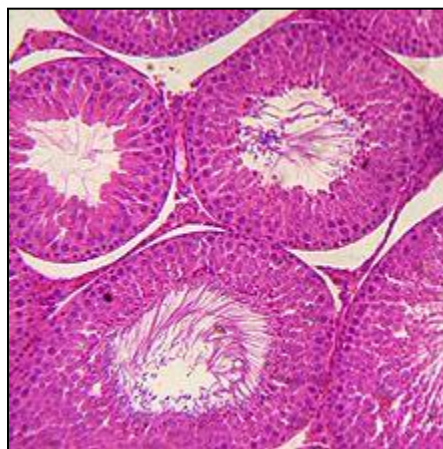
Some mammals with seasonal breeding cycles keep their testes internal until the breeding season. After that, their testes descend and increase in size and become external.<sup>[66]</sup>

The ancestor of the boreoeutherian mammals may have been a small mammal that required very large testes for [sperm competition](#) and thus had to place its testes outside the body.<sup>[67]</sup> This might have led to enzymes involved in spermatogenesis, spermatogenic [DNA polymerase beta](#) and [recombinase](#) activities evolving a unique temperature optimum that is slightly less than core body temperature. When the boreoeutherian mammals diversified into forms that were larger or did not require intense sperm competition, they still produced enzymes that operated best at cooler temperatures and had to keep their testes outside the body. This position is made less parsimonious because the [kangaroo](#), a non-boreoeutherian mammal, has external testicles. Separately from boreoeutherian mammals, the ancestors of kangaroos might have also been subject to heavy sperm competition and thus developed external testes; however, kangaroo external testes are suggestive of a possible adaptive function for external testes in large animals.

One argument for the [evolution of external testes](#) is that it protects the testes from abdominal cavity pressure changes caused by jumping and galloping.<sup>[68]</sup>

Mild, transient scrotal heat stress causes DNA damage, [reduced fertility](#) and abnormal embryonic development in mice.<sup>[69]</sup> DNA strand breaks were found in spermatocytes recovered from testicles subjected to 40 °C or 42 °C for 30 minutes.<sup>[69]</sup> These findings suggest that the external location of the testicles provides the adaptive benefit of protecting spermatogenic cells from heat-induced DNA damage that could otherwise lead to infertility and [germline mutation](#).

## Size



Cross section of rabbit testis, photographed in [bright-field microscopy](#) at 40× magnification

The [relative size of the testes](#) is often influenced by [mating systems](#).<sup>[70]</sup> Testicular size as a proportion of body weight varies widely. In the mammalian kingdom, there is a tendency for testicular size to correspond with multiple mates (e.g., harems, [polygamy](#)). Production of testicular output sperm and spermatid fluid is also larger in polygamous animals, possibly a [spermatogenic competition](#) for survival. The testes of the [right whale](#) are likely to be the largest of any animal, each weighing around 500 kg (1,100 lb).<sup>[71]</sup>

Among the [Hominidae](#), [gorillas](#) have little [female promiscuity](#) and sperm competition and the testes are small compared to body weight (0.03%). [Chimpanzees](#) have high promiscuity and large testes compared to body weight (0.3%). Human testicular size falls between these extremes (0.08%).<sup>[72]</sup>

Testis weight also varies in seasonal breeders like [red foxes](#),<sup>[73]</sup> [golden jackals](#),<sup>[74]</sup> and [coyotes](#).<sup>[48]</sup>

## Internal structure

[Amphibians](#) and most fish do not possess seminiferous tubules. Instead, the sperm are produced in spherical structures called *sperm ampullae*. These are seasonal structures, releasing their contents during the breeding season, and then being reabsorbed by the body. Before the next breeding season, new sperm ampullae begin to form and ripen. The ampullae are otherwise essentially identical to the seminiferous tubules in [higher vertebrates](#), including the same range of cell types.<sup>[50]</sup>