ELEPHANTS · ANATOMY & EVOLUTION

Why Elephants Keep Their Testes Inside

Testicondy, the Afrotheria and the aquatic-ancestor idea — what is established, what is a hypothesis, and what is still a mystery.

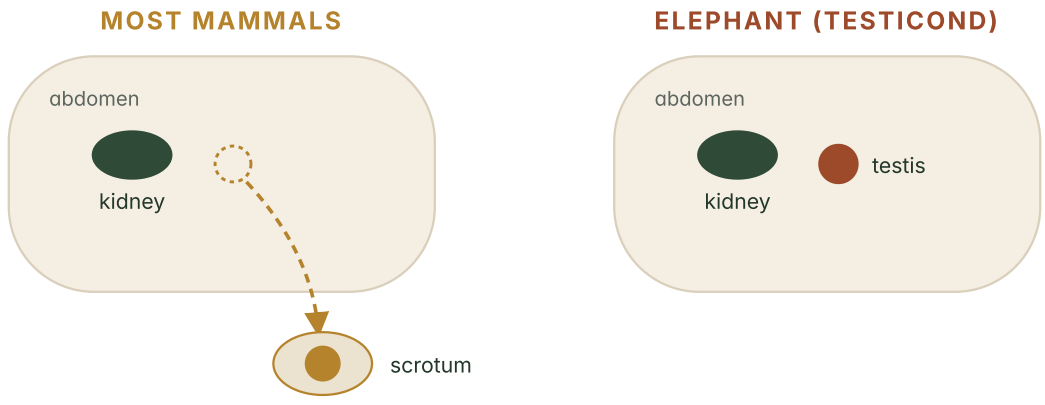
SERIES **SAFARI NOTES** FORMAT **FIELD & GUIDING NOTES** PUBLISHED BY **THE SAFARI SHOW**

> Guests often ask the question nobody else dares: where are a bull elephant's testes? The answer — inside his body, near his kidneys — opens up one of the more surprising stories in mammal evolution.

01 Testicondy: testes that stay inside

In most male mammals, the testes start developing high in the abdomen, near the kidneys, and then **descend** during development — through the **inguinal canal** and into a pouch of skin outside the body, the **scrotum**.

Elephants don't do this. A study of African elephant foetuses found the testes were **intra-abdominal** — they stay inside the body cavity for life. Mammals like this are called **testicond**, and the condition is **testicondy**.



Testis starts near the kidney, then descends through the inguinal canal to the scrotum.

Testis stays inside the abdomen, near the kidney. No descent, no scrotum.

Simplified, not to scale.

02 How descent normally works

Descent is guided by the **gubernaculum**, a cord of tissue linking the lower end of the developing testis to the groin. In mice, two genes are essential: **INSL3**, a hormone made by the testis, acts on its receptor **RXFP2** in the gubernaculum, making it grow and swell. Knock out either gene and the testes do not descend.

The elephant foetus study found **no gubernaculum** — and none of the other structures that go with descent (the pampiniform plexus of veins that cools the testes, the processus vaginalis, or a scrotum).

03 The Afrotheria: Africa's own family tree

DNA studies in the late 1990s revealed that a surprising mix of mammals form one ancient group that probably originated in Africa: the **Afrotheria**.

MEMBERS

An unlikely family

Elephants, sea cows (manatees and dugong), hyraxes, the aardvark, elephant shrews (sengis), golden moles and tenrecs.

TESTES

Mostly testicond

Elephants, manatees, hyraxes, elephant shrews, golden moles and tenrecs are testicond. The aardvark is the exception — its testes descend, but there is no scrotum.

04 Ancestral — or lost again?

Because so many afrotheres are testicond, it was long assumed this was the original mammal condition. A 2018 genetic study turned that around:

- In four testicond afrotheres (tenrec, golden mole, elephant shrew and manatee), the descent gene **RXFP2 is broken**, and **INSL3** is broken in three of them and altered in the fourth — "molecular vestiges" of genes that once worked.
- That means their ancestors **did** have descending testes. The researchers concluded that **testicular descent is the ancestral condition** in placental mammals.
- Each species broke the genes in a different way, at different times (RXFP2 losses tentatively dated to roughly 23–83 million years ago), so testicondy evolved **independently several times** within the Afrotheria.
- Here's the twist: in **elephants and hyraxes, both genes are still intact**. So why elephants don't descend their testes is **still unresolved**.

05 The temperature puzzle

Making and storing sperm needs temperatures **below 37 °C**, which is why most mammals keep their testes outside the body, slightly cooler than the core. Some testicond afrotheres, such as tenrecs and golden moles, have low body temperatures (below about 35 °C), which may remove the problem.

Elephants don't: their body temperature is about **36.8 °C** — similar to many scrotal mammals — and they have no countercurrent heat exchanger to cool the testes. **How elephants keep sperm healthy at body temperature is not known.**

Other mammals, such as dolphins, true seals and pangolins, also keep their testes inside the body, but they are not counted as true testicond species: their testes partly descend into the lower abdomen. Dolphins and seals cool them with special blood-flow arrangements; pangolins, with their low body temperature, may not need to.

06 The aquatic-ancestor idea

A popular explanation is that elephants descend from water-living ancestors, and internal testes are a leftover from that life — as in the sea cows, their closest living relatives. There is real evidence behind this, but it remains a hypothesis:

EVIDENCE	WHAT WAS FOUND	STRENGTH
Foetal kidneys	Elephant foetuses have **nephrostomes** in their developing kidneys, a feature of aquatic vertebrates not recorded in other live-bearing mammals (Gaeth et al. 1999).	SUGGESTIVE
Early trunk	The trunk is well developed in the earliest foetus examined. The lead author has suggested it may first have evolved as a snorkel.	SUGGESTIVE
Fossil teeth	Isotopes in tooth enamel of two early proboscideans, *Moeritherium* and *Barytherium* (late Eocene, about 37 million years ago), fit a **semi-aquatic** life in freshwater swamps or rivers (Liu et al. 2008). The authors note other explanations can't be ruled out.	SUPPORTS
Relatives	Elephants' closest living relatives are the fully aquatic sea cows, which are also testicond.	ESTABLISHED
Testes kept warm against cold water	No study tests this. And internal testes create a heat problem rather than solving a cold one.	NOT SUPPORTED

07 So what's the answer?

THE HONEST ANSWER

Elephants are testicond because their testes never descend — the foetus has no gubernaculum to guide them. Why evolution kept them that way is unresolved: the aquatic-ancestor idea is plausible but unproven, and elephants' descent genes are still intact.

Other suggestions you may hear — that internal testes protect the bull from thorns and branches, or that elephants make extra sperm to compensate — have not been tested in any study we could find.

ON THE GAME DRIVE — HOW TO SAY IT

"Bull elephants keep their testes inside, up near the kidneys. They share that with their closest living relatives — the manatees and dugongs — and with hyraxes, believe it or not. One idea is that elephants' ancestors lived partly in water, and there's some evidence for that in elephant embryos and fossil teeth. But the real puzzle is temperature: sperm normally need to be kept cooler than the body, and nobody yet knows how elephants manage it."

08 Key terms

Testicondy — Having testes that stay permanently inside the abdomen.

Gubernaculum	A cord of tissue that guides the testis down into the scrotum during development.
Inguinal canal	The passage in the groin through which descending testes pass.
INSL3 / RXFP2	A hormone and its receptor needed for the gubernaculum to develop and testes to descend.
Afrotheria	A group of mammals of African origin: elephants, sea cows, hyraxes, aardvark, elephant shrews, golden moles and tenrecs.
Nephrostome	A funnel-shaped opening in a developing kidney, typical of aquatic vertebrates.

In summary

- Elephants are **testicond**: their testes stay inside the abdomen, near the kidneys.
- Elephant foetuses have **no gubernaculum** or scrotum, so the testes never descend.
- Most of their afrothere relatives are testicond too, but genetics shows **descent was the ancestral state** — testicondy evolved again several times.
- Elephants' descent genes are still intact, and **how they keep sperm cool is unknown**.
- The **aquatic-ancestor** idea has supporting evidence but is a hypothesis, not a settled fact.

SOURCES

- Gaeth, A. P., Short, R. V. & Renfree, M. B. (1999). The developing renal, reproductive, and respiratory systems of the African elephant suggest an aquatic ancestry. *PNAS* 96(10): 5555–5558. doi:10.1073/pnas.96.10.5555
- Down To Earth. Jumbo went fishing (report on Gaeth et al.). https://www.downtoearth.org.in/environment/jumbo-went-fishing-17523
- Sharma, V., Lehmann, T., Stuckas, H., Funke, L. & Hiller, M. (2018). Loss of RXFP2 and INSL3 genes in Afrotheria shows that testicular descent is the ancestral condition in placental mammals. *PLOS Biology* 16(6): e2005293. https://publications.mpi-cbg.de/Sharma_2018_7155.pdf
- Smithsonian Magazine. Earliest mammals kept their cool with descended testicles (2018). https://www.smithsonianmag.com/science-nature/earliest-mammals-kept-their-cool-descended-testicles-180969476/
- Liu, A. G. S. C., Seiffert, E. R. & Simons, E. L. (2008). Stable isotope evidence for an amphibious phase in early proboscidean evolution. *PNAS* 105(15): 5786–5791. doi:10.1073/pnas.0800884105
- Stanhope, M. J. et al. (1998). Molecular evidence for multiple origins of Insectivora and for a new order of endemic African insectivore mammals. *PNAS* 95(17): 9967–9972. doi:10.1073/pnas.95.17.9967
- Murphy, W. J. & Eizirik, E. (2009). Placental mammals (Eutheria). In *The Timetree of Life*, Oxford University Press. https://timetree.org/public/data/pdf/Murphy2009Chap71.pdf

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