The Gubernaculum and the Evolution of Testicular Descent

David M. Darda*

*Corresponding Author: dardad@cwu.edu

HAPS Educator. Vol 21, No. 3, pp. 12-19. Published December 2017.

doi: 10.21692/haps.2017.048

Darda D.M. (2017). The Gubernaculum and the Evolution of Testicular Descent. *HAPS Educator* 21 (3): 12-19. doi: 10.21692/haps.2017.048

The Gubernaculum and the Evolution of Testicular Descent

David M. Darda, PhD
Department of Biological Sciences, 400 East University Way, Central Washington University
Ellensburg, WA 98926
dardad@cwu.edu

Abstract
Adding an evolutionary perspective to anatomy teaching can enrich student learning. One way of introducing evolutionary concepts into a course is by "sneaking it in" by presenting interesting and sometimes entertaining "stories" that add anatomical detail, encourage critical thinking, and illustrate underlying evolutionary history and concepts. The gubernaculum tells one such story; a story that involves the movement of the testes through the fetal abdominal cavity and finally into the scrotum. While it is well understood that the proximate importance of this migration is to guarantee an appropriate thermal environment for sperm production, our understanding of the role of the gubernaculum in anchoring, pulling, and clearing the way for the testes as they descend is only now coming to light. Even less clear is our understanding of the evolutionary forces that ultimately led to such a seemingly vulnerable positioning of the testes. Multiple hypotheses have been proposed, and whether one or more can ultimately explain the seemingly complicated process and curious anatomy, the essential evolutionary test has obviously been met– it works. doi: 10.21692/haps.2017.048

Key words: anatomy, evolution, teaching, gubernaculum, testis descent

The information contained in this article will enhance student comprehension of the gubernaculum and their appreciation for the evolutionary history of testicular descent and related concepts associated with the pedagogy of courses in Human Anatomy and Human Anatomy and Physiology.

Introduction

Learning (and teaching) anatomy can be dry. We ask our students to learn (memorize, retrieve) an extensive catalog of body parts whose names are mostly derived from languages with which they have had little formal experience. What brings anatomy alive and relevant to both teacher and student is the context within which it is placed. In medical and other professional health care programs, that context is strongly clinical. Knowledge of anatomy and its development (embryology) is critical in developing an understanding of how the body functions, and therefore how it fails to function.

At the undergraduate (bachelors) level, Human Anatomy courses, often taught as combined courses in both Human Anatomy and Physiology, are understandably less about clinical understanding, and primarily cover normal body structures and functions. Clinical considerations are often covered briefly only as time allows, and embryological context, if included, is limited to brief highlights of a few organ systems (e.g. bones, brain, reproductive organs). So, while the contexts are similar to the professional program course, they might be better referred to as "clinical lite" and "developmental lite".

Another contextual theme for anatomical study, which is of great historical and practical value, is evolution. Teaching anatomy with an evolutionary context has traditionally been the role of comparative anatomy courses taught at the undergraduate level. Unfortunately, these courses are less common than in the past and are often not the first choice for pre-health professional students, who more often than not opt for Human Anatomy and Physiology courses (Darda 2010).

Introduction of evolutionary topics into professional school anatomy courses and undergraduate anatomy or Anatomy and Physiology courses can be challenging. Instructors are faced with covering a tremendous amount of material in a very limited time. There is little time to approach topics that are not directly relevant to the outcomes of a curriculum. Additionally, students may not be receptive. After all, they are already overextended and are not easily persuaded to spend time and thought on topics they might see as peripheral at best.

As a comparative anatomist, I believe strongly that putting human anatomy in an evolutionary context is important, and the fact that the most recent annual meeting of the Human Anatomy and Physiology Society (HAPS 2017) was centered on the theme of bringing more evolution into Human Anatomy and Anatomy and Physiology courses indicates that I am not alone. But how to do it…

One thing I have done in my Human Anatomy and Physiology classes is to essentially "sneak it in" by focusing in on a few structures that can be used to illustrate interesting evolutionary concepts and have compelling, and sometimes even entertaining, stories (Darda 2016). Sometimes I simply fold these stories into my lectures using PowerPoint slides to augment the story. For some of these structures, I have prepared written essays that can be assigned as outside

continued on next page

reading. In either case, I have found that the resulting discussions can be lively, and that students seem more likely to ask "big picture" questions about human form throughout the course.

Here I present an example essay on one such structure – the gubernaculum. This often-overlooked embryonic structure has long been thought to be key in mammalian testicular descent, a topic usually covered at least briefly in Anatomy and Physiology during study of the reproductive system. Not only is this process important to the proper production of sperm and therefore to reproduction, a topic that I have found my students are innately interested in, but as it turns out, it has a fascinating evolutionary story. In this version, I include literature citations, thus making it a kind of review paper, but it is written in an informal style intended to engage students on a more personal level.

Governor of the Testes– an essay

Among the thousands of names of anatomical structures, one that has always struck me as one of the funniest sounding is associated with the human reproductive system – the gubernaculum. Gubernaculum. It's pronounced pretty much just like it looks. Guber-nac-u-lum. Just say it a couple of times and see if it brings a smile.

Maybe the root of the word, *guber*, is just one of those words that sounds funny to our ears. Maybe it brings to mind boxes of chocolate covered peanuts – *Goobers*. And, where there are *Goobers*, their movie candy cousin, *Raisinettes*, and the advertising jingle can't be far (YouTube 2013). Or perhaps it brings forth images of Goober Pyle, from *The Andy Griffith Show* of the 1960's who took over running the Mayberry gas station after his cousin Gomer left. Goober was an unsophisticated but kindhearted yokel who was oblivious to any complexity in the world around him, and he's probably why we still refer to someone who's a bit of a goofball as a goober. *Goobers* and *Raisinettes*, Goober and Gomer - definitely not the most serious or somber of images!

I guarantee none of this was on John Hunter's mind when he coined the term in 1762. Hunter was a famous 18th century Scottish anatomist, and what was on his mind was the interesting phenomenon of testicular descent during fetal development. It was in his first scientific paper, "The State of the Testis in the Foetus and on the Hernia Congenita", where he named the *gubernaculum testis* "because it connects the testis with the scrotum, and directs its course in its descent" (Heyns and Hutson 1995, Hunter 1762, Tremblay 2010). It turns out that the term gubernaculum is derived from both Latin (*gubernator*) and Greek (*kubernon*) words meaning "to steer", and has been used to refer to a ship's rudder or to "other guiding structures". It is also where we get the term gubernatorial, which refers to a state's governor or his/her office.

So, although odd sounding to us, the term is perfectly descriptive. In human biology, the gubernaculum is a cordlike length of soft tissue that is associated with guiding the movement of ovaries and testes during embryonic development (Costa *et al*. 2002). And, it turns out that the term has at least one other use in biology. In nematode worms, the gubernaculum is a structure found in males that is instrumental in guiding the protrusion of a spicule associated with copulation and transfer of sperm into the female (Bird 1971).

Moving Gonads

The human reproductive system stands apart from other organ systems in a couple of fundamental ways. First, it's all about the future. All the other organ systems function as if they've taken the advice of those lifestyle gurus who urge us to "live in the moment" or "be here now". They carry out all those functions necessary to keep us alive and kicking in the present – moving around, obtaining and processing energy, perceiving our environment, controlling our internal environment, and getting rid of waste products. The reproductive system exists so we can have kids, kids who have a bunch of our genes. Those genes represent evolutionary success. If our genes are moved along to the next generation, there is the chance that our genes will continue into the future of humankind. If we don't have kids, we really don't need to have a reproductive system. Unlike the other organ systems, we can lead a full life without ever using it, at least for its ultimate purpose.

The second thing that sets the reproductive system apart from the other organ systems is that it is so different in males and females. No equality here. To learn about the human reproductive system is to learn about two systems. This is not news, but what might be is that there is a time when no matter how close you examine males and females, you can't tell them apart. What embryologists call the indeterminate period lasts for about the first six weeks of our development. During this time, testes and ovaries develop from the same tissue, the ducts that will come to form the vas deferens and the uterus are present in all embryos, and the external genitalia are indistinguishable. In fact, if not for the production of testosterone beginning about week seven, an embryo will develop in many ways as a female, regardless of its genetic sex.

Once testosterone arrives on the scene, the male embryo heads down a distinctively different route. One major difference is what happens to the position of the testes. In both sexes, the gonads develop inside the body adjacent to the kidneys. In females, the ovaries remain in this same general area of the body into adulthood. The testes however undertake a seven-month journey to eventually take up residency in the scrotal sac, well outside the body cavity. Two questions jump to mind. How and why? Neither is easily answered, but let's take them in order.

continued on next page

How? The Gubernaculum as an Anchor, a Tractor, and a Snowplow

It's not like the testes have a mind of their own and a GPS navigation system, but somehow they travel all the way from the embryonic lower back region, down and forward toward the abdominal wall, through an opening in that wall, and eventually sliding into home, the scrotum. Most of what we know about the mechanism of this descent is based on descriptive anatomy. Our understanding of the hormonal and genetic control of this changing anatomy is growing but still far from complete.

Since we cannot directly observe the testicular journey, anatomists have had to piece together the details of the process based on detailed dissections of human embryos and fetuses (Heyns and Hutson 1995). Such specimens are not numerous and often not available for examination, so our knowledge of the human condition has been augmented by studying other mammals that have scrotal testes (Hutson *et al*. 2016). A good general picture has emerged, and while some workers have described up to eight distinguishable phases from beginning to finish, most researchers now refer to two phases – the *transabdominal* phase and the *inguinoscrotal* or *passage* phase (Barteczko and Jacob 2000, Heyns and Hutson 1995, Hutson *et al*. 2004, Hutson *et al*. 2016).

To some extent, this early change in position is not due to actual movement, but *relative* movement. That is, the testes stay basically where they are and other structures grow and move around them. This hypothesis involves the gubernaculum in the role of an anchor - one structure holding another in place. In this case, the gubernaculum holding the testis steady while the abdominal cavity and organs expand greatly upward (Hutson *et al*. 2004, Mamoulakis *et al*. 2015).

Detailed analysis has supported this hypothesis, but only as a partial (though maybe a major) explanation of transabdominal "movement". By comparing the position of the testes with other abdominal structures, it is apparent that the testes do actually move (Barteczko and Jacob 2000, Costa *et al*. 2002). This movement is not easily explained, but the gubernaculum is a suspect, this time not as an anchor, but as a tractor. Depending on your preference, you can think of a farm tractor or a Star Trek tractor beam. They both pull, and that may be what the gubernaculum does.

The gubernaculum forms as an elongate, cordlike structure extending from the testes to the subdermal area where the scotum will form. It is made up of cells that produce a jelly-like material and various kinds of microscopic fibers. Some

The *transabdominal phase* describes the movement of the testis from its initial position adjacent to the developing kidneys in the back of the abdominal cavity to the anterior wall of the abdomen in the area of the groin (Figure 1). It begins shortly after testosterone has put an end to the indeterminate phase (7-8 weeks) and lasts until about week 15 (Hutson *et al*. 2016). The exact path is well established, the forces involved less so.

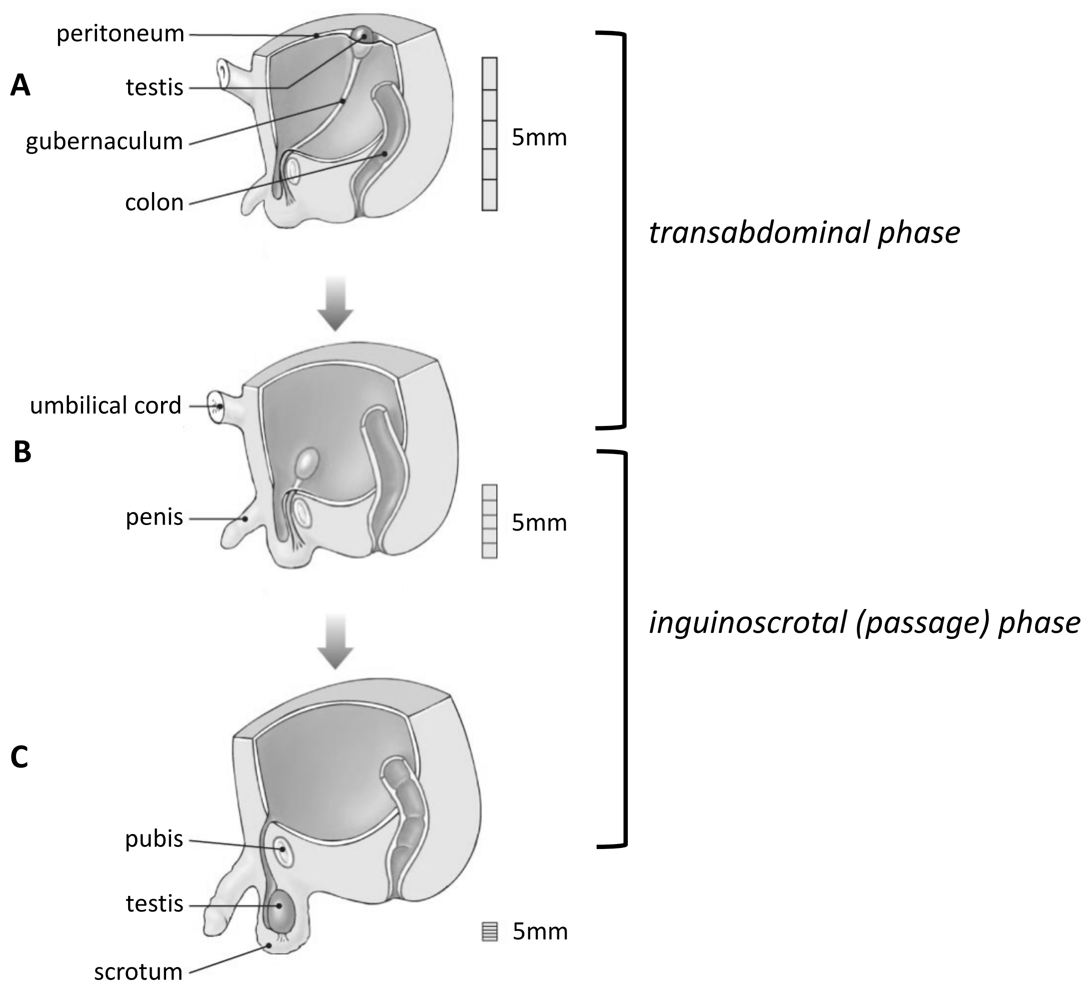

Figure 1. Phases of testicular descent. The transabdominal phase **(A-B)** occurs approximately between weeks 7 and 15. The inguinoscrotal (passage) phase **(B-C)** occurs approximately between weeks 25 and 35. With permission after Martini and Nath, 2010, p. 899.

continued on next page

are strong collagenous fibers; similar to the collagen that makes our skin flexible yet tough. Some are elastic fibers, capable of stretching and returning to shape (Barteczko and Jacob 2000, Costa *et al*. 2002, Mamoulakis *et al*. 2015). The presence and importance of muscle fibers in the gubernaculum is a little more controversial.

While both smooth and skeletal muscle fibers have been reported in the gubernaculum, their role in traction is debated. Tanyel *et al*. (2005) argue that smooth muscle develops from the mesothelial layer of the gubernaculum and is a primary force in testis descent. Barteczko and Jacob (2000) agree that smooth and striated muscle fibers are present in the gubernaculum, but suggest that because they are sparse and not oriented longitudinally, they cannot generate significant traction force.

An alternative mechanism for generating gubernaculum traction is the remodeling of its tissue make-up. Costa *et al*. (2002) reported a gradual replacement of the jelly-like extracellular matrix found in an early gubernaculum with more collagenous and elastic fibers. They suggest that this should lead to a decrease the size of the gubernaculum, and might therefore explain its shortening and a resulting pulling on the testes.

The second phase of testis descent, the *inguinoscrotal* or *passage* phase, results in the testes passing through preformed openings in the abdominal wall between weeks 25-35 of development (Figure 1) (Hutson *et al*. 2016). These openings are called inguinal canals, a term derived from the Latin word *inguinalis*, which means groin. The testes therefore bid farewell to the intestines and liver, move out of the abdominal cavity, and end up in the connective tissues just underneath the skin.

Inguinal canals begin as very small openings, and they form in embryos of both sexes. In females they are short-lived, never grow in size, and quickly seal shut, never to open again. In males however, the gubernacula extend into each of the inguinal canals, and under the influence of testosterone, they swell in size, increase substantially in diameter, and as a result cause the inguinal canals to increase in size as well (Figure 2) (Barteczko and Jacob 2000, Heyns and Hutson 1995, Hutson *et al*. 2016, Mamoulakis *et al*. 2015). The gubernacula seem to be clearing a path for the testes to pass through the abdominal wall much like a snowplow clears the way for cars to pass through a wall of snow.

Even with an opening prepared, getting the testis through such a tight space would appear to require some kind of force. Recent evidence suggests two potential forces at work - one a push, the other a pull. Increasing pressure within the abdominal cavity due to the growing intestines, liver, and stomach generates the pushing force. The pulling force may be added by the gubernaculum, which at this point migrates into the scrotum, essentially dragging the testis along with it (Figure 2). Whether muscle tissue plays a role is unclear, but once the snowplow gubernaculum has opened up the tunnel, it then appears to pull like a tractor, and with a little pressure from the other side, the testis "pops" into the subdermal space. This "pop" actually takes two to three days and usually occurs around the 26th week of development (Barteczko and Jacob 2000, Heyns and Hutson 1995, Hutson *et al*. 2016, Mamoulakis *et al*. 2015).

By week 35, the testes have made their final descent into the scrotal sac, which has developed as an outpocketing of the skin, lined with muscle and connective tissue. In adult males, all that remains of the gubernaculum is a very reduced piece of tissue, the scrotal ligament (ligamentum scrotale testis), which continues to anchor the testes to the floor of the scrotum (Figure 2) (Barteczko and Jacob 2000).

Once the testes are through, the inguinal canals begin the process of sealing over. Usually by birth the muscles and connective tissues have obliterated any opening, and

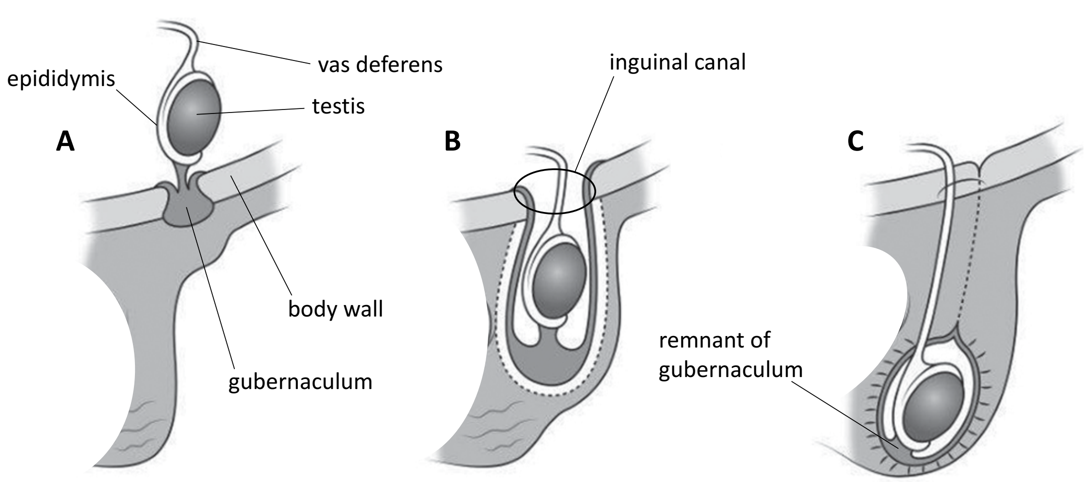

Figure 2. Passage of testis through the abdominal wall into the scrotum. **(A)** Testis and swollen gubernaculum at the beginning of the inguinoscrotal phase (25-28 weeks). **(B)** Gubernaculum migrating and pulling testis into the scrotal sac (approximately 35 weeks). **(C)** Final positioning of the testis and closure of inguinal canal (35-40 weeks). With permission after Hutson *et al*., 2016.

continued on next page

only the spermatic cords, with their blood vessels, nerves, and vas deferens penetrate the abdominal wall and mark the position where the canals had been. If this sealing process falls short, an inguinal hernia can result and may be surgically repaired to prevent possible complications. Even when proper developmental closure occurs, the inguinal canal area remains a weak point and explains why inguinal hernias are primarily a problem for men (Jenkins and O'Dwyer 2008).

Ninety-five to ninety-eight percent of full-term newborn males and about 70% of premature males have fully descended testes, and of those who don't, most finish the process within the first three to four months of life outside the womb (Goel *et al*. 2015, Niedzielski *et al*. 2016). When testes do not descend, the condition is called *cryptorchidism*; a term that makes sense when you know that *orkhid* is a Greek word for testicle and *crypto* means hidden – hidden testicle. Cryptorchidism can affect one or both testicles, and while a testis might get hung up anywhere along the path of descent, the most common location of undescended testes is in the inguinal canal. More rarely, a testis will make it through the canal, but follow the pathway of a gubernaculum that somehow misses its proper destination in the scrotum. Such ectopic testes end up as subdermal structures in the lower abdomen or the inner thigh, and sometimes even cross over to the other side of the body (Niedzielski *et al*. 2016).

If a testis does not eventually descend on its own, surgical correction is called for, as it will not mature properly, sperm counts and sperm quality are reduced, and there is an increased risk of developing testicular cancer (Docimo *et al*. 2000, Tremblay 2010). If both testes do not descend, sterility is a common result. This is why one of the routine tests done on newborn baby boys is to see if both testes have descended. Knowing this, when my first son was born, instead of asking the more typical new-father questions such as, "Are there ten fingers? Ten toes?", my first question to the doctor was, "Are his testicles descended?" A little knowledge can sometimes make you sound pretty silly!

Why? Multiple Hypotheses and Alternative Solutions

"Why" questions about biological systems are almost always more difficult to answer than "how" questions, and in the case of testis descent, I have always thought more along the lines of "why in the hell"! Come on, doesn't it just seem insane to have these organs, the ones without which we could not reproduce and upon which the future of the human species exists, dragging around the abdominal cavity, being pushed and pulled through the body wall, and eventually coming to hang precariously outside the main body in a flimsy sack exposed to all manner of abuse? I suspect that most all boys and men have experienced some incident, perhaps on the playground or playing sports, involving a blow to the groin and the resulting excruciating pain and more agonizing fear of long-term damage. What a seemingly stupid design!

Stupid or not, there must be some explanation for this apparent anatomical joke, and while we do seem to pretty much understand the most immediate functional reason for scrotal testes, we are less sure of why this particular evolutionary pathway came about. In biology, we would say that we feel we have a good understanding the *proximate* forces at work but are more unclear about the *ultimate* (evolutionary) causes.

Several hypotheses have been proposed as the reason many mammalian species, including humans, have scrotal testes (Kleisner *et al.* 2010, Mamoulakis *et al*. 2015, Werdelin and Nilsonne 1999). Three of these have received less attention, but are nevertheless worthy of consideration. The *display hypothesis* (Portman 1952) suggests that the scrotum evolved as a signaling device in social competition. This derives from the fact that the scrotum is brightly or distinctively colored in some species, especially some primates (Figure 3). The *training hypothesis* (Freeman 1990) is based on the idea that due to the long, convoluted testicular arteries and low blood pressure, the testes are subject to a decreased blood supply. This oxygen stress leads to increased mitochondrial numbers with enhanced metabolic efficiency. Fewer sperm are produced, but those

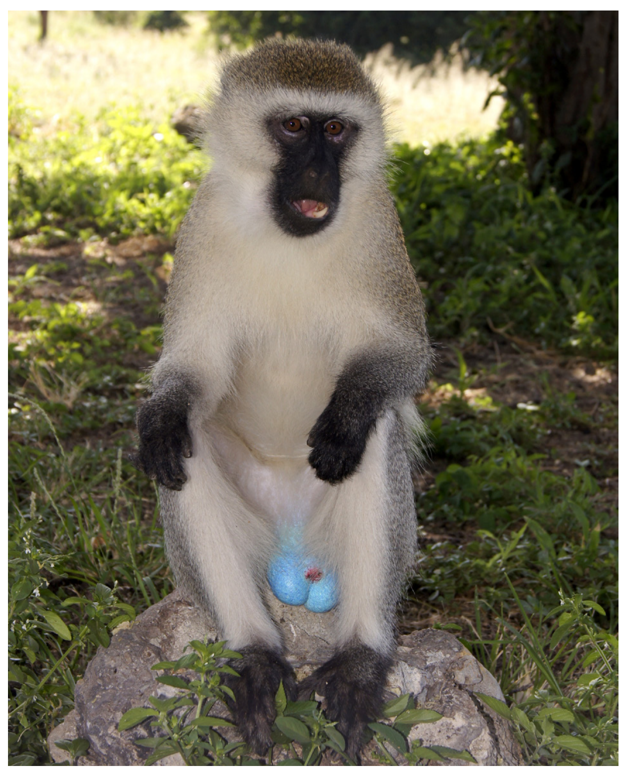

Figure 3. A vervet monkey (*Chlorocebus pygerythrus*) from Tarangire National Park in Tanzanea illustrating vivid blue coloration of the scrotum. Photo courtesy of Konrad Mebert.

continued on next page

that are produced are of higher quality. The *galloping hypothesis* (Frey 1991) proposes that scrotal testes evolved to avoid the strong intra-abdominal pressure fluctuations associated with galloping or running that might negatively affect spermatogenesis.

These hypotheses vary in their level of support. The *display hypothesis* and the *training hypothesis* seem to primarily offer proximate explanations for the presence of scrotal testes but are perhaps less likely to explain the ultimate reason such an anatomy might originally have come about. Phylogenetic analysis gives some support to the galloping hypothesis (Kleisner *et al*. 2010), and it has recently been examined in the context of the evolution of endothermy (Lovegrove 2014).

The explanation most often offered for scrotal testes has to do with temperature, and is summarized nicely by Marieb and Hoehn (2017 p. 889): "…because viable sperm cannot be produced in abundance at core body temperature (37°C), the superficial location of the scrotum, which provides a temperature about 3°C lower, is an essential adaptation." In cases of human cryptorchidism, where the testes are subjected to core body temperature, fertility rates are greatly reduced and the risk of testicular tumors is increased. The scrotum therefore provides the cooler environment necessary for the proper production of sperm, what I will refer to here as the *cool spermatogenesis hypothesis*.

Temperature also plays a role in three other hypotheses that attempt to explain why scrotal testes evolved. The *cold storage hypothesis* (Bedford 1978) has been proposed based on the fact that although the testes produce sperm, it is stored in the epididymis, a small tubular organ closely associated with the testis and also located in the scrotum. While the temperature is hardly cold, it is lower than internal body temperature, and perhaps better for sperm vitality while they wait to be moved on through the system. The *mutation hypothesis* (Short 1997) suggests that the evolutionary advantage of lower temperature is to keep the rate of mutation at acceptable levels. In fact, in humans, mutation rates are lower among males than females (Mamoulakis *et al*. 2015). Finally, the *activation hypothesis* (Gallup *et al*. 2009) suggests that the storage of sperm at a lower temperature might result in a type of "thermal shock" when introduced into the female reproductive tract, resulting in increased motility and more likely fertilization.

The *cool spermatogenesis*, *cold storage*, and *activation hypotheses* not only offer strong proximate reasons for scrotal testes, but also implicate the importance of testicular temperature in reproductive, and therefore evolutionary success. Further evidence supporting temperature-related hypotheses is seen by looking more broadly at other mammals. While most mammals have scrotal testes like us, others fall into two alternative broad categories – *descended ascrotal* and *abdominal*. The first category contains a broad representation of mammals such as whales, seals, hedgehogs, sloths, moles, and the rhinoceros. In these animals, the testes descend through the abdominal wall, but do not move into a scrotum. Instead, they remain just under the skin, close to the body. More interesting are the mammals whose testes do not descend out of the abdominal cavity at all, a condition also referred to as testicondy. This is a more restricted group and contains the primitive duck-billed platypus, the small mostly African hyraxes, the aquatic dugongs and manatees, and elephants (Freeman 1990, Kleisner *et al*. 2010, Lovegrove 2014, Werdelin and Nilsonne 1999).

If the temperature-related hypotheses explaining scrotal testes are correct, we would predict that either the testicular and/or epididymal temperatures in all three anatomical arrangements would be lower than core body temperature, or that overall body temperature would be lower in those mammals with abdominal testes and those whose testes are descended but ascrotal. To test the hypothesis, we would then need to have data on both core and testis/epididymis temperatures in mammals representing all three testis positions. Unfortunately, little such data exists. But, where it does, it is mostly supportive. Hedgehogs, monotremes, and hyraxes for example have natural core body temperatures lower than most other mammals and below the temperature where spermatogenesis begins to be disrupted. Others have anatomical or behavioral mechanisms to keep the testes cool in spite of their location. Seals for example have a plexus of veins associated with their testes that help to remove heat and keep them cool (Lovegrove 2014, Werdelin and Nilsonne 1999).

There are exceptions however. Data for Asian elephants, which have abdominal testes, indicate a core body temperature of approximately 36°C (96.8 °F), and although this is where sperm production would be expected to be negatively affected, they seem to exhibit no reproductive problems (Werdelin and Nilsonne 1999). Then… there are birds. Birds, like mammals, are homeotherms and thus regulate their internal body temperature at a constant level, usually well above the environment around them. In fact, their body temperatures are higher, sometimes much higher, (38.5 - 43.8 °C; 101.3 - 110.8 °F) than those of mammals (Prinzinger *et al*. 1991). All birds have abdominal testes, and while this condition is likely an adaptation for flight, the point here is that even though the testes are subjected to high temperatures, there is surely no problem with sperm production. Just look out your window and check out the house sparrows, starlings, and crows!

So, birds (and elephants) show us that there is at least one other solution to the temperature problem other than relying on the gubernaculum to guide the testes out of the abdominal furnace and into the air-conditioned coolness

continued on next page

of the scrotum. Current evidence indicates that birds and mammals evolved from separate reptile-like, ectothemic ancestors whose body temperature depended on the environment. Why were bird testes able to physiologically adapt to increased temperatures during evolution while mammal testes did not? We may never know that answer, but these two very different evolutionary solutions to solving the temperature problem show us a couple of interesting things about evolution in general.

First, there is not always a single evolutionary solution to an adaptive problem, and second, not all solutions are elegant. Beauty is of course in the eye of the beholder, but I would contend that the bird solution is the way to go. No complex migration to screw up. No unnecessary exposure and increased risk of damage (and pain!) to very important organs. But both systems work, and judging from the success of both birds and mammals, they work just fine. Evolution doesn't care about our ideas of beauty or good engineering. All that matters is results. All that matters is reproduction. If it takes seven months and a governor acting as an anchor, a tractor, and snowplow to keep the sperm flowing, that is just fine.

Perspective

It is my hope and belief that anatomical evolutionary stories such as this one accomplish several things as we attempt to stimulate our students' curiosity and learning:

1. The addition of anatomical and developmental detail not easily covered within the usual bounds of a course. For instance, while testicular descent might be covered in a Human Anatomy and Physiology course, the structural make-up of the gubernacum, its role, and the details of each phase, is likely not.
2. The introduction of evolutionary concepts to students, some of whom may not have had such exposure. The essay above introduces or reviews the biological meaning of proximate and ultimate forces, emphasizes that there can be multiple evolutionary solutions to a similar problem, and that the true selective test for a structure is whether it works.
3. An increased student appreciation "that humans are not "creatures" set apart from nature but are clearly animals and, therefore, both part of nature and a product of natural (biological) processes… profound ideas of the last two centuries" (Nickels, *et al*. 1996). As for scrotal testes, comparison with other mammals easily illustrates this idea.
4. The development of critical thinking by examining historical and current hypotheses concerning human form and function through the filter of the scientific process. It is probably surprising to a student that there are so many hypothesis that attempt to explain testicular descent, and one can hardly read about them without critically examining them and deciding the strengths and weaknesses of each.
5. Increased student engagement and participation by developing their desire and ability to ask deeper questions about the human organism many of them will spend their careers trying to understand. As Milton Hildebrand stated in the introduction to his classic comparative anatomy text, "Through interpretation one becomes less of a practitioner and more of a professional, less a technician and more a scholar, less a cataloger of facts and more an expert. This benefit is difficult to measure, yet can be one of great value to the individual." (Hildebrand 1988 p. 4).

Acknowledgments

Comments and suggestions from two anonymous reviewers were greatly appreciated.
The photograph in Figure 3 was kindly provided by Konrad Mebert.

About the Author

Dave Darda, PhD. is a professor of Biological Sciences at Central Washington University in Ellensburg, Washington (dardad@cwu.edu). His areas of interest are the evolution of vertebrate form, the influences of development on evolution, and herpetology. He has been teaching anatomical science courses for more than 30 years.

Literature Cited

Barteczko KJ, Jacob MI (2000) The testicular descent in human: origin, development and fate of the gubernaculum hunteri, processus vaginalis peritonei, and gonadal ligaments. *Adv Anat Embryol Cell Biol* 156: 1-95.

Bedford JM (1978) Anatomical evidence for the epididymis as the prime mover in the evolution of the scrotum. *Am J Anat* 152: 483-507.

Bird AF (1971) The Structure of Nematodes. New York, NY: Academic Press.

Costa WS, Sampaio FJB, Favorito LA, Cardoso, LEM (2002) Testicular migration: Remodeling of connective tissue and muscle cells in human gubernaculum testis. *J Urol* 167: 2171-2176.

Darda DM (2010) Observations by a university anatomy teacher and a suggestion for curricular change: integrative anatomy for undergraduates. *Anat Sci Educ* 3: 73–76.

Darda DM (2016) Bringing evolution into anatomy and physiology: the uvula and the story it tells. *HAPS Educator* 20: 71-75.

Docimo SG, Silver RI, Cromie W (2000) The undescended testicle: diagnosis and management. *Am Fam Physician* 62: 2037-2044.

Freeman S (1990) The evolution of the scrotum: a new hypothesis. *J Theor Biol* 145: 429-445.

continued on next page

Frey, R (1991) On the cause of the mammalian descent of the testes (descensus-testiculorum). *Z Zool Sys Evolut-Forsch* 29: 40-65.

Gallup GG, Finn MM, Sammis B (2009) On the origin of descended scrotal testicles: the activation hypothesis. *Evol Psychol* 7: 517-526.

Goel P, Rawat JD, Wakhlu A, Kureel SN (2015) Undescended testicle: an update on fertility in cryptorchid men. *Indian J Med Res* 141: 163-171.

HAPS (Human Anatomy and Physiology Society) (2017) HAPS 2017 31st Annual Conference. Retrieved from http://www.hapsweb.org/?page=HAPS201731st 8/24/17.

Heyns CF, Hutson JM (1995) Historical review of theories on testicular descent. *J Urol* 153: 754-767.

Hildebrand M (1988) Analysis of Vertebrate Structure (Third Edition). New York, NY: Wiley.

Hunter J (1762) Observations on the state of the testis in the foetus, and on the hernia congenita. In: W. Hunter (Ed.) Medical Commentaries (pp. 75-90). London: by A. Hamilton for A. Miller.

Hutson JM, Li R, Vikraman J, Loebenstein M (2016) What animal models of testicular descent and germ cell maturation tell us about the mechanism in humans. *Eur J Pediatr Surg* 26: 390-398.

Hutson JM, Sasaki Y, Huynh J, Yong E, Ting A (2004) The gubernaculum in testicular descent and cryptorchidism. *Turk J Pediatr* 46: 3-6.

Jenkins JT, O'Dwyer PJ (2008) Inguinal hernias. *BMJ* 336: 269-272.

Kleisner K, Ivell R, Flegr J (2010) The evolutionary history of testicular externalization and the origin of the scrotum. *J Biosci* 35: 27-37.

Lovegrove BG (2014) Cool sperm: why some placental mammals have a scrotum. *J Evol Biol* 27: 801-814.

Mamoulakis C, Antypas S, Sofras F, Takenaka A, Sofikitis N (2015) Testicular descent. *Hormones* 14: 515-530.

Marieb EN, Hoehn K (2017) Anatomy and Physiology (Sixth Edition). San Francisco, CA: Pearson.

Martini FH, Nath JL (2010) Anatomy and Physiology (Second Edition). San Francisco, CA: Pearson Benjamin Cummings.

Nickels MK, Nelson CE, Beard J (1996) Better biology teaching by emphasizing evolution and the nature of science. *Am Biol Teach* 58: 332-336.

Niedzielski JK, Oszukowska E, Stowikowska-Hilczer J (2016) Undescended testis – current trends and guidelines: a review of the literature. *Arch Med Sci* 12: 667-677.

Portman A (1952) Animal Forms and Patterns. New York, NY: Schocken.

Prinzinger R, Prebmar A, Schleucher (1991) Body temperature in birds. *Comp Biochem Physiol* 99A: 499-506.

Short RV (1997) The testis: the witness of the mating system, the site of mutation and the engine of desire. *Acta Paediatr Suppl* 422: 3-7.

Tanyel FC, Talim B, Atilla P, Muftuoglu S, Kale G (2005) Myogenesis within the human gubernaculum: histological and immunohistochemical evaluation. *Eur J Pediatr Surg* 15: 175-179.

Tremblay JJ (2010) What signals testis descent? *Biol Reprod* 83: 687-689.

Werdelin L, Nilsonne A (1999) The evolution of the scrotum and testicular descent in mammals: a phylogenetic view. *J Theor Biol* 196: 61-72.

YouTube (2013) Goobers and Raisinets 1971 Jingle. IMNURAUMAN. Retrieved from https://www.youtube.com/watch?v=GiVt1FIpgEE 8/24/17.

■