

The erection mechanism of the ratite penis

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Abstract

The erection mechanism of the penis in most vertebrates is blood vascular. A major evolutionary transition occurred in birds, where the erection mechanism changed from blood vascular to lymphatic. Within birds, however, the erection mechanism of the ratite penis has remained unknown. Early work suggested that the erection mechanism in ostrich *Struthio camelus* was blood vascular while no description existed for the emu *Dromaius novaehollandiae* or the rhea *Rhea americana*. Because the penis in all other described birds has a lymphatic erection mechanism, clarifying that the erection mechanism of ratites is of great importance to understanding one of the major evolutionary transitions of penis morphology within amniotes. Here, we show that the erection mechanism of ratites is lymphatic, confirming that the evolutionary transition to lymphatic erection occurred in the last common ancestor of Aves.

Introduction

Most birds lack a penis, but both the Paleognathes and the Galloanseridae are among the few avian groups that retain it (Montgomerie & Briskie, 2007).

The avian penis is likely homologous with the reptile penis (Jones, 1915; King, 1981); however, several characters of the penis have changed between the two groups. One important difference is the erection mechanism, which in reptiles is generally described as blood vascular (Jones, 1915; Gerhardt, 1933), whereas in birds is generally considered lymphatic (King, 1981). The lymph needed for lymphatic erection to take place in birds is produced in the paralympathic bodies [also referred to as the *lymphobulbus phalli* (King, 1993) and the vascular body of the phallus (Oliveira & Mahecha, 2000)], which are ellipsoid spongy organs located alongside the urodeum (or middle compartment of the cloaca).

Within birds, the erection mechanism of the Galloanseridae has been shown to be lymphatic, whereas the erection mechanism of the ratites has remained contentious (King, 1981; Montgomerie & Briskie, 2007). Early reports suggested that the erection mechanism of the ostrich could be blood vascular (Müller, 1836; Boas, 1891), whereas others have suggested that the erection mechanism is lymphatic (Grimpe, 1923; cited by Gerhardt, 1933). The presence of a 'spongy cushion' lying ventrally between the urodeum and the base of the phallus in the ostrich was reported by Grimpe (1923; cited by Gerhardt, 1933), which Gerhardt considered to be the paralympathic bodies. However, the original reference has been lost, and no further work on establishing the presence or absence of paralympathic bodies has been carried out. King (1981, p. 137)

declared that 'the lack of reliable information about the presence or absence of a vascular body in the ratites remains one of the most striking defects in our knowledge of morphology in birds'.

The erection mechanism of all large-bodied ratites has remained unknown despite recent work on cloacal morphology in the ostrich. A recent examination of the ostrich cloaca did not comment on the function or components of the phallus (Warui, Erlwanger & Skadhauge, 2009). Detailed work on the ostrich's blood supply reported that thin branches of the pudendal artery are found near the base of the phallus where they form an arterial plexus or network (Elias, Aire & Soley, 2007, 2008).

Recently, two studies showed a clear presence of paralympathic bodies in the tinamous (family tinamidae), the closest relatives of the ratites: in the intromittent penis of the spotted tinamou *Nothura maculosa* (Oliveira & Mahecha, 2000) and in the non-intromittent penis of the genus *Crypturellus* (family tinamidae) (Brennan *et al.*, 2008). Although tinamous were recently placed within the order ratites (Harshman *et al.*, 2008), this hypothesis is not universally supported.

The phallus of large-bodied ratites has a fixed portion that attaches to the floor of the proctodeum (the cloacal compartment nearest the vent), and a free portion that constitutes the body of the penis. The body of the penis in ratites has three major components: a pair of fibrous bodies that begin in the fixed portion of the penis (the left one being larger than the right), a core of elastic tissue known as the elastic vascular body, and an external channel through which sperm travels (*sulcus spermaticus*) (King, 1981).

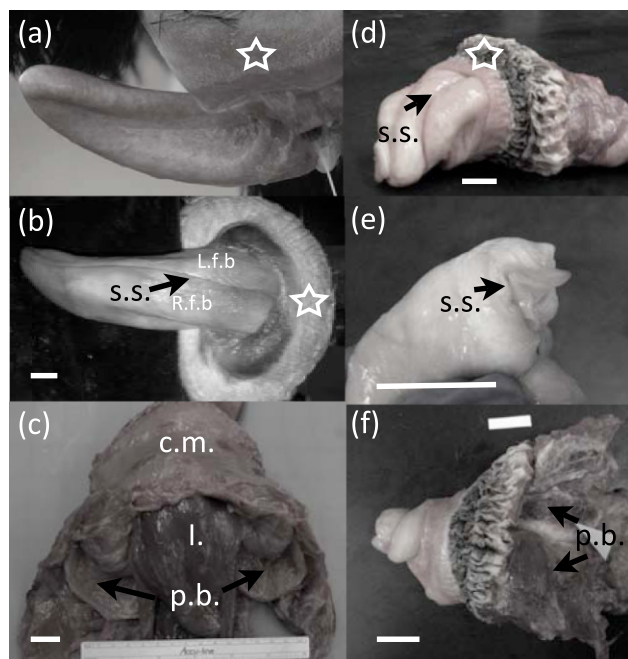


Figure 1 The penis of ostrich (a–c) and emu (d–f). The ostrich penis protrudes from the cloaca during micturition and defecation (a). Its conical structure bends towards the left; the left fibrolymphatic body (*l.f.b.*) is larger than the right (*r.f.b.*) (b). The paralympathic bodies (*p.b.*) are paired and located under the urodeum, here shown from the ventral aspect (c). The emu penis has a typical spiral shape (d), and the tip of the penis is eversible, with a single spiral (e). The paralympathic bodies are located under the urodeum (f). * Dorsal aspect of the cloaca. *S.s.*, *Sulcus spermaticus*. Scale bar: 2 cm. *l.*, intestine; *c.m.*, cloacal muscles.

The penis of the ostrich is a single shaft that bends to the left because of the asymmetry in size of the fibrous bodies. The fibrous bodies have been reported to lack any erectile spaces (Müller, 1836), although King (1981) doubts this conclusion. During copulation and defecation, the penis protrudes from the floor of proctodeum where it usually rests (Gerhardt, 1933; Fig. 1a and b). Movement of the penis is achieved through the action of the muscles that lift and retract the phallus (*musculus levator phalli* and *musculus retractor phalli*). The ostrich penis lacks an invaginated portion of the penis, and therefore, it is classified as a type A phallus (lacking a blind tubular cavity; King, 1981).

The penis of the emu (Fig. 1d) was described in some detail by Müller (1836), Boas (1891) and Gerhardt (1933), again without noting the erection mechanism. The emu penis has asymmetric fibrous bodies and an eversible region at the tip (Fig. 1e). The tip is invaginated at rest, and it is therefore classified as a type B phallus (possessing a blind tubular cavity; King, 1981).

The rhea penis was described in detailed by Müller (1836), without mention of the erection mechanism, while Gerhardt (1933) suggested that it could be lymphatic, but without any evidence to support his assertion. The penis in rhea has asym-

metric fibrous bodies and a blind tubular cavity (type B phallus; King, 1981). Some males have a fully inflatable and eversible corkscrew-shaped phallus that can vary greatly in length, while other males lack the corkscrew shape altogether (Góes, 2004; Góes *et al.*, 2010).

We examined the penis of one adult fully reproductive male ostrich and three adult fully reproductive male emu, and we report the unequivocal presence of paralympathic bodies. We also analyzed published pictures of everting rhea penises from Góes (2004) that show lymph flow into the penis, and we find support for the hypothesis that lymphatic penis erection is a synapomorphy of Aves. We also use histology and direct manipulation of fresh penises to suggest how the lymphatic erection mechanism works in these large ratites.

Methods

Dissection of the penis structures was done on a fresh emu cloaca (from a private farm in Connecticut, US) and on a frozen ostrich cloaca (from a private farm in New Mexico, US). The males were adults in reproductive condition. The fresh emu specimen (3-year-old male Yale Peabody Museum 139717) had just begun to sit on eggs when the organs were collected. Two other emu specimens (2-year-old males) were collected from a private farm in Tennessee, US, and their cloacas were preserved in formalin 10% prior to shipment. The ostrich male was an adult (6 years old), in full reproductive condition as determined by its red legs and red-bill coloration. The cloacal tissue was frozen and shipped overnight for dissection. All the specimens were sacrificed by the farmers, and their organs were donated to our research. After removing all the connective tissue, we removed muscle bundles to search for the paralympathic bodies.

We examined cross-sectional histological slides of the tissue at the base, middle and tip of the body of the penis of one emu male and the ostrich specimen, that were preserved in buffered formalin 10% and stained both hematoxylin and eosin and Mason's trichrome (following Gray, 1954), primarily to distinguish connective tissue, blood vessels and smooth muscle.

Results

In both emu and ostrich, we found paralympathic bodies located on either side of the urodeum, underneath the cloacal muscles (Fig. 1c and f). In ostrich, they are large ellipsoids of a spongy consistency measuring 8 cm × 4 cm (Fig. 1c), while in emu, they measure 4.0 cm × 2.5 cm (Fig. 1f).

In cross-section, the ostrich penis has a clear concentric layer of collagen fibers running parallel to one another directly under the epidermis (Fig. 2a). The area just below this organized collagen presents heavy vascularization (Fig. 2b). The ostrich penis is always stiff even in the absence of inflation, except at the tip where the tissue is more flexible. This stiffness results from the fibrous bodies, which are composed of a dense collagen matrix that is largely disorganized, except in the areas surrounding the many narrow lymphatic spaces, where the fibers are arranged running in parallel to one another. The more flexible tissue toward the tip of the penis is composed

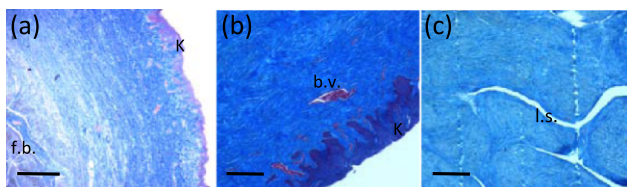


Figure 2 Histological cross-section of ostrich penis. Trichrome stain. Collagen shown in blue (a). Transition between the outer layer of circumferential collagen and the fibrous body (*f.b.*). Keratin (*k*) in the epidermis is shown pink (4 \times), scale bar 1 mm. (b) Epidermis and some disorganized collagen immediately below (10 \times) with some blood vessels (*b. v.*) (c) A lymphatic space (*l.s.*) within the fibrous body (10 \times). Scale bar (b, c) 200 μ m.

primarily of the elastic vascular body. The boundary between the tissue of the fibrous bodies and the elastic vascular body is not discrete, but rather a gradual change in the collagen density and fiber packing. In the elastic body, the fibers are less dense, and the lymphatic spaces are smaller than those found within the fibrous bodies (Fig. 2c). Few blood vessels are seen within the fibrous bodies or the elastic vascular body. The collagenous connective tissue in the elastic body is irregular, and fibers run in all directions (Fig. 2c).

In all three emu specimens observed, the eversible portion of the penis was small, with a single full turn of the *sulcus spermaticus* at the tip (Fig. 1e). In cross-section, the collagen matrix in the emu penis is dense and disorganized just as in ostrich, but the separation between the fibrous bodies and the elastic vascular body is well demarcated. In addition, the emu has a tubular cavity lined with secretory cells (the blind tubular cavity of a type B penis), surrounded by dense elastic tissue. In both ostrich and emu, there are abundant fibroblasts embedded in the connective tissue.

Photographs of everting rhea penises from Goes (2004) show that in some males, the eversible portion of the penis can be very long (at least 30–40 cm), and it has a corkscrew shape. Clear lymphatic fluid can be seen flowing into the penis.

Discussion

The erection mechanism of the ratite penis is lymphatic, not blood vascular as has been suggested. It is likely that Grimpe (1923) indeed found the paralympathic bodies when he described the ‘spongy cushions’ in the cloaca. The location and description of the arterial plexus or network found at the root of the phallus (Elias *et al.*, 2007, 2008) make it likely that these are surrounding the paralympathic bodies to provide the lymph needed for erection. All vertebrates reportedly have a blood vascular penis-erection mechanism, and the novel lymphatic erection in birds is notable (King, 1981). Whether all reptiles do in fact lack a lymphatic erection mechanism is unknown, and modern anatomical studies in this group would shed light on whether the transition from blood to lymph occurred only in the last common ancestor of Aves.

The lymphatic system is a low-pressure circulatory system and therefore not ideal where maintenance of an erection is

required. A lymphatic penile-erection mechanism has to be fundamentally different from blood vascular erection. In waterfowl, lymph can be seen accumulating at the base of the cloaca as the male threads on top of the female prior to copulation. When the male lowers his cloaca to meet the female’s cloaca, release of the sphincter muscles allows the lymph to flow freely into the large lumen of the penis causing explosive eversion (Brennan, Clark & Prum, 2010). Because ejaculation happens at the moment of maximum eversion, the lymph is also pushing the seminal fluid from the base of the ejaculatory groove, along the length of the *sulcus spermaticus* to the tip of the penis (Brennan *et al.*, 2010). Immediately after ejaculation, the penis is flaccid, and it is slowly returned to the cloaca (Brennan *et al.*, 2010). Natural eversion in the corkscrew-shape penis of rhea may work in a similar manner given the large continuous lumen space that fills out with lymph as evidenced in the photographs we examined. However, the high density of collagen fibers found throughout the penis of ostrich and emu, and the absence of a large continuous lumen space, suggests that lymph does not flood inside the penis of these species to evert it or elongate to the extent that this is seen in rhea and waterfowl. We hypothesize that in ostrich and emu, lymph is acting primarily to engorge the penis and to transport semen that has been ejaculated from the seminal papillae along the *sulcus spermaticus*, to aid in ejaculation. This would be the same function as that of lymph flowing into the non-intromittent penis of tinamous and galliformes, where the presence of paralympathic bodies has been well established (Nishiyama, 1955; Brennan *et al.*, 2008). However, a functional study of the role of lymph flow in the ratite penis is needed to fully understand how the erection mechanism works in this group of birds.

The body of the ostrich penis occupies most of the proctodeum, and it must be extruded from the vent to allow defecation and urination (Fig. 1a; Fowler, 1991). This penis extrusion is carried out by muscular action of a pair of muscles, the *m. levator phalli*. It is likely that in both ostrich and emu, the penis is similarly protracted by muscular action when copulation takes place, and that lymph then flows in to aid in engorgement and ejaculation. Reports that the ostrich penis changes from 20 cm when flaccid to 40 cm when erect (Gerhardt, 1933) are likely the result of the full protrusion of the phallus showing its entire shaft, rather than a significant change in length. Our attempts to fill the ostrich penis shaft with fluid resulted only in changes in the diameter of the shaft, but not elongation of the penis itself. It is clear, however, that contrary to the report by Müller (1836), the fibrous bodies have erectile spaces within them, and these likely fill up with lymph to add to the stiffness of the penis during copulation. The dense regular arrangement of collagen fibers in the layer immediately under the skin and within the fibrous bodies suggests that these areas have higher tensile strength and stretch resistance.

The age of the males and the time of the year when specimens are collected have important consequences for the description of genital morphology. For example, waterfowl penis undergoes dramatic seasonal changes (Hohn, 1960 and P. L. R. Brennan *et al.*, unpublished data), and it continues to grow

during the lifetime of an individual (P. L. R. Brennan *et al.*, unpublished data). Although we know that the phallus of juvenile ostrich is shorter than in adults (Fowler, 1991), no studies have been conducted in ratites to determine whether their penis changes seasonally, or with age as it is the case in waterfowl. Failure to account for these variables may be the reason for some of the contradictions in the early literature describing the penises of ratites. Rhea males differ greatly in penis morphology; some males are classified as having a small phallus (<3 cm), whereas others have large penises (>3 cm) (Góes *et al.*, 2010). Some males with large penises have a corkscrew spiral while others do not (Góes, 2004; Góes *et al.*, 2010). Góes *et al.* (2010) report that all the males they examined were 3–4 years old, but it is unclear which males were examined during the breeding season. The penis of all males reportedly remained small during the nonbreeding season (Góes *et al.*, 2010). It is likely that the older males during the reproductive season are the ones that develop a full corkscrew-shape penis with an elongated eversible portion. Studies of seasonality and ontogeny of penis development are needed in all ratites.

In conclusion, we report the presence of paralympathic bodies in the ratite penis, which combined with the absence of blood sinuses suggest that the erection mechanism is lymphatic. In rhea, the lymph likely acts in everting and inflating the penis as well as in transporting semen. However, lymph is unlikely to flow in large quantities in the penis of ostrich or emu to change their length dramatically as both of these species have dense penises lacking large lumen spaces. We propose that in these two species, lymph aids primarily in engorging the phallus and pushing the semen during ejaculation.

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