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The gross reproductive morphology of the male Temminck's pangolin *Smutsia temminckii* (Smuts, 1832)

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Abstract

The Temminck's pangolin (*Smutsia temminckii*) is one of eight pangolin species worldwide and the only pangolin present in southern Africa. Historically, pangolins have not been able to reproduce successfully in captivity and this may be in part due to the lack of knowledge and understanding with regards to the pangolin reproductive system (anatomy, physiology, biology) in all eight species. This original study describes the gross anatomy of the male Temminck's pangolin from three adult individuals investigated. The male Temminck's pangolin presented a short, conical penis with ascrotal (internal) testes, similar to many other myrmecophagous mammals such as the aardvark (*Orycteropus* sp.) and anteaters (suborder: Vermilingua). However, the orientation of the penis of the Temminck's pangolin differed in that it was oriented cranioventrally, in contrast to the caudal orientation of the giant anteater. The testes were found to be bilaterally flattened with an elongate oval shape, similar to the aardvark. The specific characteristics of the reproductive tract of the male Temminck's pangolins are thought to be adaptations to their peculiar lifestyle as the male portrays characteristics that indicate adaptation to a lower basal metabolic rate and body temperature as well as to their defensive mechanism of rolling up into a ball. Our study suggests the male Temminck's pangolin reproductive anatomy is most similar and comparable to the Xenarthrans and the aardvark that display the same fossorial activities as pangolins, and the male morphology is not comparable to the phylogenetically closely-related Carnivora.

KEYWORDS
ascrotal testes, crura, pangolin, penis, Pholidota, reproduction

1 | INTRODUCTION

There are eight pangolin species worldwide that belong to the unique order Pholidota (Gaudin et al., 2020). These myrmecophagous mammals face increased pressure in the wild due to extensive illegal poaching (Challender et al., 2020) and with their numbers in decline (IUCN, 2022), all eight species have been listed on Appendix I by CITES (Cites, 2022). There is still very little literature available on the reproductive morphology of the male pangolin across the eight species. There are some basic descriptions of the reproductive organs and their relative positions, but no specific focus on the reproductive system as a whole. The general reproductive morphology descriptions available for male pangolins include a small but well-developed penis with anteriorly fused *Corpora cavernosa* (Gaudin et al., 2020; Wu et al., 2020) positioned anterior to the anus (Chong et al., 2020; Wicker, Lourens, & Hai, 2020) with a short perineum present (Jansen et al., 2020). The testes are housed within a fold of skin located in the inguinal area, therefore termed ascrotal (Gaudin et al., 2020; Gudehus et al., 2020; Jansen et al., 2020; Pietersen et al., 2020; Wu et al., 2020).

Of all eight species, most of the male reproductive research has focused on the Javan or Sunda pangolin (*Manis javanica*) by Akmal et al. (2014, 2015) who investigated the male reproductive organs and the associated accessory genital glands (*Glandulae genitales accessoriae*). *M. javanica* possess ascrotal testes, equal in size and ovoid in shape, and located subcutaneously in the inguinal area. The epididymis of this species is described as having a typical morphology (*Caput epididymidis*, *Corpus epididymidis and Cauda epididymidis*). The penis is small and tapering with the crura attaching to the pubic bone and has a cranioventral orientation and is located within the preputial cavity. Akmal et al. (2014, 2015) also reported the presence of paired vesicular glands (*Glandula vesicularis*), a prostate gland (*Prostata*) and bulbourethral glands (*Glandula bulbourethralis*), although the latter were not visible macroscopically for the Sunda pangolin.

The studies undertaken by Akmal et al. (2014, 2015) are significant in that they describe the reproductive morphology of this Asian male pangolin species; however, it is possible that reproductive parameters may vary between the eight species of pangolin. Temminck's pangolin (*Smutsia temminckii*) is the only pangolin present in southern Africa (Pietersen et al., 2014, 2020) and is listed as Vulnerable by the International Union for the Conservation of Nature (IUCN, 2022). It possesses a bipedal gait with the pelvis more vertically orientated than other pangolins species (Kingdon, 1971) and this may have an influence on the reproductive morphology. The only information known on the male reproductive morphology of Temminck's pangolin refers to the ascrotal nature of the inguinal testes (Pietersen et al., 2020), otherwise it is ultimately undescribed. The need for a comprehensive description of the morphology of Temminck's pangolins' male reproductive tract is therefore clear and is the motivation to describe the reproductive anatomy of the male of this species and develop a methodology for assessing and describing reproductive anatomy of pangolins.

2 | MATERIALS AND METHODS

Three male Temminck's pangolin of varying size and weight (10.1, 10.6 and 11.46 kg) were obtained in a frozen state from the African Pangolin Working Group (APWG), a registered Non-Profit Organization (NPO 123–147) (Pretoria, South Africa), the Johannesburg Wildlife Veterinary Hospital (FH 17/15890), as well as from the SANBI Biobank (SANBI/RES/P2021/28). These specimens had been recovered out of the illegal wildlife trade, and sadly succumbed to either aliments or injuries inflicted from said trade. The frozen specimens were processed at the Arcadia campus of Tshwane University of Technology in Pretoria where they were placed in 150-litre containers and allowed to thaw and immersion-fix in 10% neutral-buffered formalin solution. Once completely thawed, a medial incision was made on the ventral surface from the base of the throat down to the pubis to ensure proper fixation and preservation of the internal organs. The specimens were then left for a minimum of 2 weeks in the fixation solution. Once completely preserved, one specimen was then removed at a time from the formalin solution and rinsed with municipal water in a basin continuously for 48 h before the dissection commenced. Prior to dissection, each specimen was weighed using a Rapala 25-kg mini digital scale. All specimens were that of adult individuals (>8 kg) as those that are below 6 kg are classified as sexually immature or juvenile (Johannesburg Wildlife Veterinary Hospital, Pers. Com. 2020).

The musculature of the specimens was quite stiffened, potentially due to the stage of decay or rigour mortis when originally frozen, and a basic retractor was used to assist in holding the hind legs apart. The skin and musculature in the groin region were incised and the reproductive tract together with the bladder was cut loose from the pelvis and removed leaving the pelvic bones intact. Most of the male reproductive anatomy is extra-abdominal therefore there was no need to remove the pubis. The reproductive tract was observed and photographed in situ before being removed in its entirety and placed in 10% neutral-buffered formalin. Prior to further analysis the reproductive tract was rinsed for 48 h and then further dissected. Muscle and skin layers surrounding the penis were reflected to expose the penis and cross sections were made through the penis at the *Radix penis*, *Corpus penis and Glans penis* to assess the internal structures. Ex situ observations, photographs and measurements using a digital vernier calliper (Dexter 0–150 mm) were taken. Each measurement in the study was taken three times and an average calculated for the final measurement.

Both the left and right testis were measured from the cranial pole (*Extremitas capitata*) to the caudal pole (*Extremitas caudat*) to determine length, and from epididymal margin (*Margo epididymalis*) to the free margin (*Margo liber*) to determine width at the widest point. The penis was measured from the most distal point (*Glans*) to the point at which the two crura meet at the root of the penis (*Radix penis*).

3 | RESULTS

3.1 | Penis

The external anatomy consisted of a small, conical penis (Figures 1 and 2) orientated cranioventrally within a prepuce and positioned anterior to the anus.

The root of the penis (*Radix penis*) comprised both the crus of the penis as well as the bulb of the penis (*Bulbus penis*) (Figure 3). The two crura, which are comprised of *Corpus cavernosum penis* erectile tissue, originated from the left and right ischium of the pelvis and were each surrounded by a *M. ischiocavernosus*. The crura extended ventromedially and fused in the midline to flank the bulb (Figure 3).

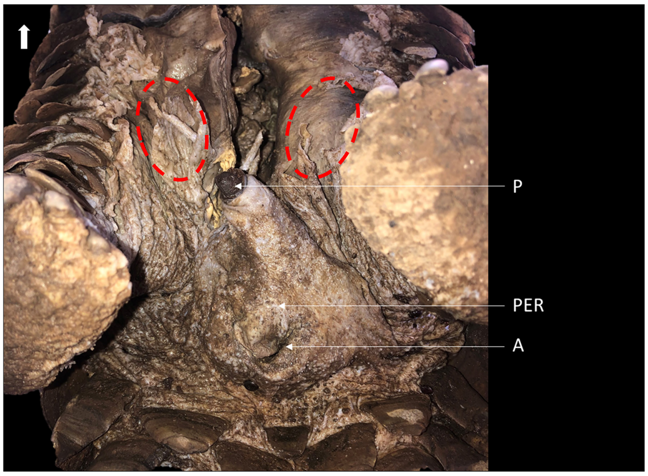

FIGURE 1 Ventral view of external reproductive organs of an 11.46 kg male Temminck's pangolin. Penis (P); Perineum (PER); Anus (A). Dotted red circles indicate the approximate location and orientation of the testes.

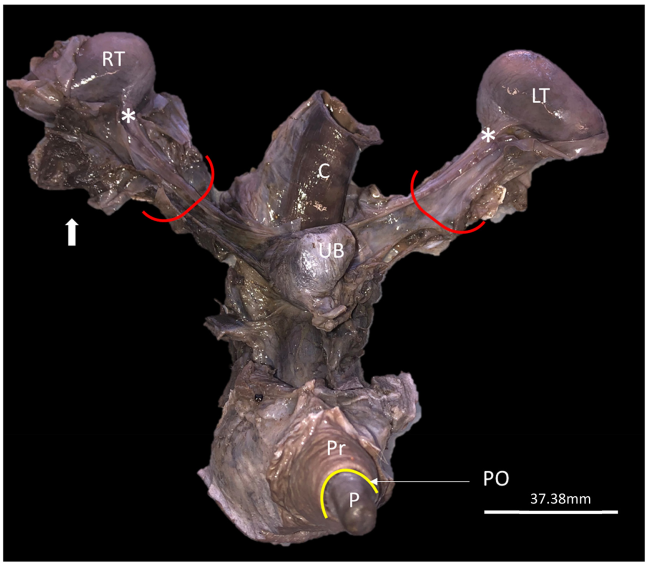

FIGURE 2 Ventral view of dissected reproductive organs of a 11.46 kg male *Smutsia temminckii* ex situ. Right testis (RT); Left testis (LT); Vas deferens (*Ductus deferens*) indicated by *, Spermatic cord indicated by red circle; Colon (C); Urinary Bladder (UB); Prepuce (Pr); Penis (P); Preputial opening (PO).

The bulb of the penis was quite pronounced and covered by the *M. bulbospongiosus*. The length of the penis ranged from 45.91–63.97 mm (Table 1).

From the bulb of the penis, the body of the penis (*Corpus penis*) and the glans of the penis (*Glans penis*) have a straight configuration and is directed cranioventrally. The craniodorsal part of the penile body consisted of *Corpus cavernosa* erectile tissue (Figure 4b). The surface of the cavernous tissue forms a concavity for the *Corpus spongiosum penis* erectile tissue (Figure 4b). The *Corpus spongiosum penis*, which originated from the pelvis, surrounded the penile urethra and continued distally with the *Corpus cavernosa penis*. The

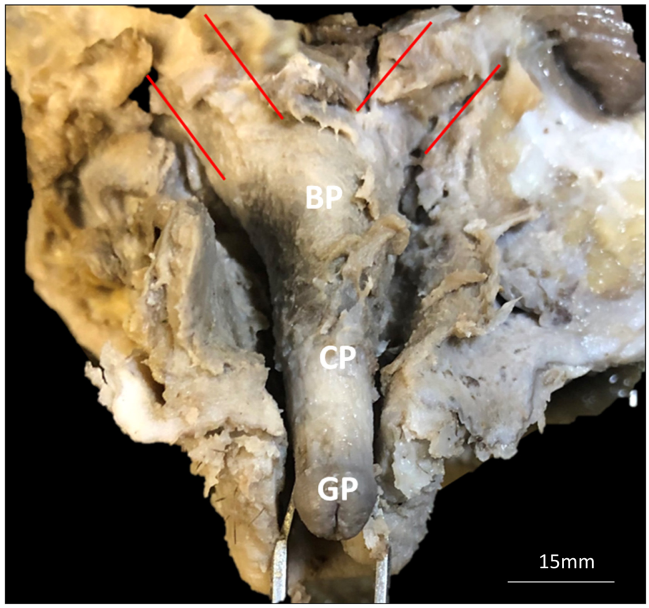

FIGURE 3 Dorso-caudal view of the penis of a 10.10 kg S. temminckii. The prepuce and muscles are reflected to expose the entire penis. Red lines indicate the converging crura at the bulb of the penis (Bulbus penis) (BP); Corpus penis (CP); Glans penis (GP).

TABLE 1 Measurements (mm) of reproductive organs for three male Temminck's pangolins.

Left testis		Right testis		Penis length	Total body weight (kg)
Length	Width	Length	Width		
42.38	20.69	43.80	20.75	56.38	10.60
26.11	14.41	32.27	12.61	63.97	10.10
37.38	19.11	28.34	10.77	45.91	11.46

Corpus cavernosum ultimately terminated at the start of the *Glans penis* (Figure 4). There was no *Os penis* present macroscopically.

The glans of the penis consisted of *Corpus spongiosum penis* which surrounded the penile urethra, as well as *Corpus spongiosum glandis* which made up the craniodorsal half of the *glans* of the penis (Figure 4c).

The prepuce is the fold of skin that covered the glans of the penis. In all specimens, the penis was, at least partly, extruded. The prepuce consisted of an external and internal lamina where the external lamina was visible externally and met the internal lamina at the preputial opening (Figure 2).

3.2 | Testes

The testes were an elongated oval shape (Figure 2), slightly bilaterally flattened and encapsulated within a fibrous layer (*Tunica albuginea*) and located in the inguinal region. The testes were 26.11–43.80 mm in length and 10.77–20.75 mm in width (Table 1) and positioned parallel with the midline of the body, with the

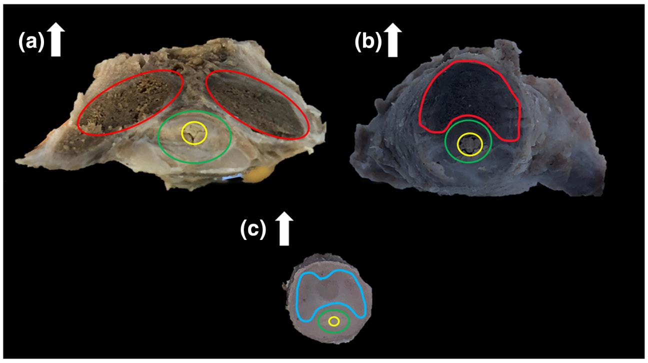

FIGURE 4 Cross section through the penis at Radix penis (a), Corpus penis (b), and Glans penis (c). Corpus cavernosa tissue indicated by red in the crura of the root of the penis (a) and in the cavernous body (b). Corpus spongiosum penis indicated by green, Corpus spongiosum glandis indicated by blue, and urethra indicated by yellow. Arrows indicate cranial direction.

cranial pole of the testis (*Extremitas capitata*) oriented cranially and the caudal pole (*Extremitas caudata*) oriented caudally. The epididymis was elongated and positioned lateral to each testis and conformed to general epididymal morphology (*Caput*, *Corpus* and *Cauda epididymidis*) (Figure 5). The *Cauda epididymidis* was quite large and covered the entirety of the *Extremitas caudata* (caudal pole of testis) (Figure 5). A small ligament (*Ligamentum testis proprium*) attaching the caudal pole of the testis to the tail of the epididymis was observed. The testicular bursa (*Bursa testicularis*), formed between the *Corpus epididymidis* and the testis, was present on the lateral surface of the testis (*Facies lateralis*). The *Ductus deferens* or *vas deferens*, the continuation of the epididymal duct, extended from the tail of the epididymis of each testis (Figure 6) and continued caudomedially in the spermatic cord (*Funiculus spermaticus*) to enter the abdomen through the inguinal canal and terminated at the neck of the urinary bladder (Figure 2). In addition to the deferent duct, the spermatic cord also contained the *Arteria testicularis* and *Plexus pampiniformis* (Figure 6). These structures were enclosed by the *Mesorchium* (Figure 6).

The accessory genital glands were not immediately obvious macroscopically. Upon palpation there was thickened tissue identified around the pelvic urethra immediately caudal to the neck of the urinary bladder presumed to be the prostate gland based on common mammalian reproductive anatomy. In this study there were no bulbourethral glands, vesicular glands or ampullae of the deferent duct identified.

4 | DISCUSSION

There is little anatomical literature available on pangolins, and therefore, the reproductive morphology of other species that were considered similar based on different criteria such as convergent evolution (*Xenarthra*-shared derived characteristics) (Gaubert et al., 2018; Rose & Gaudin, 2010), genetics (*Carnivora*) (Wells, 1968)

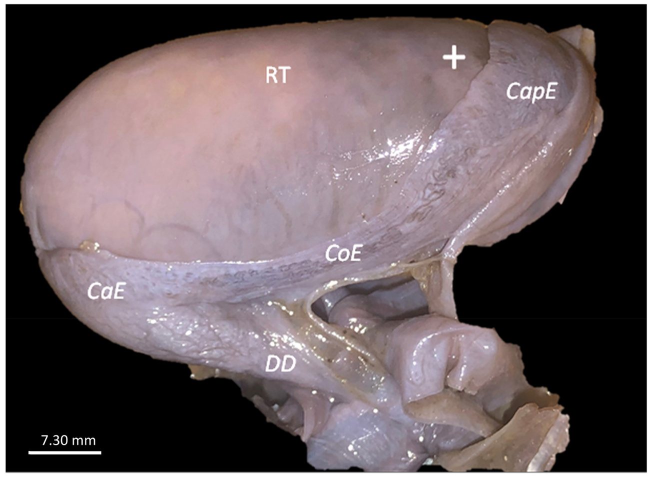

FIGURE 5 Structure of the epididymis on the lateral surface (*Facies lateralis*) of the right testis (RT). *Cauda epididymis* (CaE) Tail; *Corpus epididymis* (CoE) Body; *Caput epididymis* (CapE) Head. Cranial pole of testis (*Extremitas capitata*) indicated by +; Vas deferens (*Ductus deferens*) (DD).

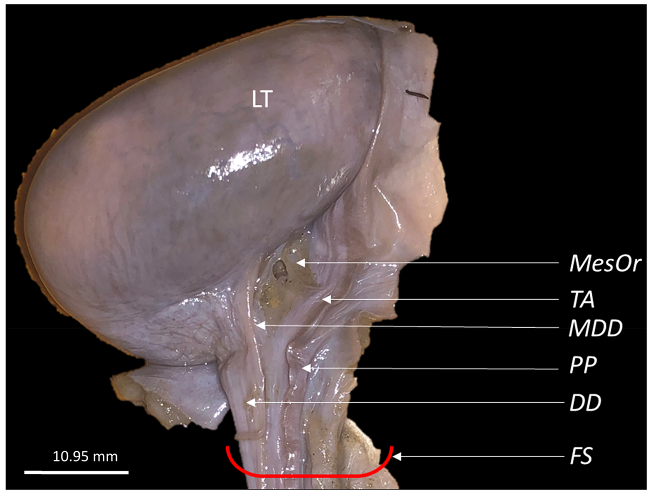

FIGURE 6 Vas deferens (*Ductus deferens*) (DD) and spermatic cord (*Funiculus spermaticus*) (FS) and associated connective (*Mesoductus deferens*) (MDD) and Mesorchium (MesOr), and blood vessels Testicular artery (*Arteria testicularis*) (TA) and Pampiniform plexus (PP) of the left testis (LT).

and geography (Aardvark, *Orycteropus afer*) (Wojick et al., 2018) were investigated comparatively to assist in describing the male reproductive morphology of the Temminck's pangolin.

Pangolins in general have morphological characteristics that make them unique relative to other mammals. The typical male mammalian reproductive form is scrotal testes (Kleisner et al., 2010; Lovegrove, 2014); however, Temminck's pangolin is ascrotal, specifically oval testes with an inguinal position (Pietersen et al., 2020). The ascrotal morphology and location of the testes is also seen in the aardvark (*O. afer*) (Wojick et al., 2018) (geographically similar species) and is consistent with the morphology described for *Manis javanica* as reported by Akmal et al. (2014).

The evolutionary phenomenon of ascrotal mammals has been hypothesized to be a result of secondary internalization of the testes (Lovegrove, 2014). With regards to pangolins, a possible explanation for the ascrotal testes is linked to the defensive rolling behaviour of pangolins not being physically hindered by the presence of an external feature. This is potentially supported by the fact that ascrotal testes are seen in other mammals that defensively roll up into a protective, armoured ball such as armadillos and tenrecs (testicond) or hedgehogs (inguinal) (Bedford et al., 2000; Lovegrove, 2014; Talmage & Buchanan, 1954).

A second consideration is the metabolic rate of pangolins and their fossorial behaviour. Pangolins are primarily nocturnal, reside in burrows and are reported to have a low metabolic rate (Lin et al., 2015; Mahmood et al., 2020; Pietersen et al., 2020; Wu et al., 2020) where Temminck's pangolin has been reported to have a resting metabolic rate half that of other eutherian mammals (Pietersen et al., 2020). The primary function of the scrotum is to maintain the testes at a lower temperature than the core body temperature (Lovegrove, 2014). Therefore, a lower metabolic rate and body temperature would suggest that there is no functional need for a scrotum as spermatogenesis is theoretically not impacted or influenced as in scrotal mammals with a higher metabolic rate (Akmal et al., 2014).

Other examples of mammals with ascrotal or undescended testes include marine mammals such as dolphins (cetacea), manatees (sirenia) and phocid or earless seals (pinnipedia). These diving mammal species, however, have a relatively high core temperature which could inhibit spermatogenesis. Hyperthermic conditions of the testes in these marine mammals are prevented by means of an extensive counter current heat exchange system of blood vessels which results in the local cooling of the reproductive tissue (i.e. testes and epididymides) (Atkinson, 1997; Rommel et al., 2001, 2007).

The small conical penis is well developed and located ventral to the anus with a cranioventral orientation. Akmal et al. (2014, 2015) reported findings in the Sunda pangolin (*Manis javanica*) that are consistent with our study. A small conical penis is also found in the giant anteater (*Myrmecophaga tridactyla*) (Rossi et al., 2012), a species considered similar based on shared derived characteristics such as diet-convergence, however, here the orientation of the penis is caudal (Fromme et al., 2021; Takami et al., 1998).

There are few reported sightings of copulation in pangolins. However, there have been observations of male Chinese pangolin (*Manis pentadactyla*), Indian pangolin (*Manis crassicaudata*), white-bellied pangolin (*Phataginus tricuspis*) and black-bellied pangolin (*Phataginus tetradactyla*) mounting females either from the side or rear while entwining their tails to ensure the genitals meet (Gudehus et al., 2020; Jansen et al., 2020; Mahmood et al., 2020; Wu et al., 2020). This atypical posture of pangolins when mounting is most likely to accommodate the species' broad tail which can only curl ventrally and could therefore inhibit copulation during a more typical posture (Zhang et al., 2019). In this atypical position, external genitalia of the male animal may be more prone to trauma. The short, conical shape and ventro-cranial position of the penis, as well as the inguinal position of the testes, may therefore be an adaptation to the peculiar copulatory behaviour of pangolins.

The thickened tissue palpated in the area immediately caudal to the neck of the urinary bladder was assumed to be the prostate gland. The presence of a similar structure described as the prostate gland in species such as the sloth and aardvark has been noted (Wislocki, 1928; Wojick et al., 2018). These species often portray similar physical characteristics to the pangolin due to convergent evolution (Hayssen, 2009, 2010, 2011; Wislocki, 1928). No vesicular glands (*Vesiculae seminales*) were observed macroscopically, however the thickened tissue caudal to the urinary bladder could potentially contain both the prostate and vesicular glands. There was no ampulla of the deferent ducts visible. The ampullae are typically found in carnivores (Dyce et al., 1996), and the absence of this at macroscopic level in the Temminck's pangolin substantiates the dissimilarity to carnivores. The bulbourethral glands were not visible macroscopically. However, Akmal et al. (2014, 2015) reported the presence of the bulbourethral gland in the Sunda pangolin at microscopic level. Therefore, further light microscopic investigations of the morphology of the reproductive system and associated accessory genital glands by dissecting the reproductive organ from the level of the urinary bladder to the penis to establish the existence of these glands for this species of pangolin are recommended.

Understanding the morphology of a species provides the basis for further understanding function, which is an important aspect in formulating successful conservation management plans such as captive breeding programs. These programs have the potential to help increase the severely declining pangolin population numbers, but with minimal to no published research on the reproductive biology of pangolins this is very difficult to institute as we know that pangolins are extremely sensitive to their environment and to stress (Wicker, Cabana, et al., 2020). This is indeed also true for investigations published on the ex-situ husbandry and gestation in captive pangolins. Those few studies published all conclude that pangolins are difficult to maintain in captivity and high rates of mortality occur due to stress suppressing immune responses rendering pangolins vulnerable to infections or diseases (Choo et al., 2016; Mohapatra & Panda, 2014; Wicker, Cabana, et al., 2020). Our study provides a starting point with the description of the reproductive morphology for the male Temminck's pangolin, further functional morphological studies could provide crucial insight needed into the functional reproductive biology of the species and how this is impacted or impeded by anthropogenically controlled environments.

5 | CONCLUSION

It is apparent from the literature and the findings of our study that the reproductive morphology of the male Temminck's pangolin is most similar and comparable to the Xenarthrans and the Aardvark that display the same fossorial activities as pangolins, and the male morphology is not comparable to the genetically similar Carnivora.

The importance of understanding the reproductive morphology of the male pangolin relates directly to further understanding how to assist these animals in potential initiate captive breeding programs. Further insights are required into the presence or absence of certain accessory genital glands in understanding the physical workings of the male reproductive system to ensure the species can continue surviving in the wild. Sadly, if poaching pressure persists at the current level, it is perceivable that pangolins may only occur in captive scenarios.

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FUNDING INFORMATION

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CONFLICT OF INTEREST STATEMENT

There was no conflict of interest to report.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ETHICS STATEMENT

Ethical clearance for this project was submitted to and approved by the Tshwane University of Technology's Animal Ethics Committee through the Faculty Research and Innovation Committee (Ref #: AREC2020/06/002). Government research approval from the Department of Agriculture, Land Reform and Rural Development in terms of Section 20 of the Animal Diseases Act (35 of 1984) was approved and granted valid from 15 February 2022 to 20 August 2024. A SANBI National Zoological Gardens Animal Research Ethics and Scientific Committee (ARESC) approval was granted (SANBI/RES/P2021/28). Furthermore, all legal documentation to receive, possess, transport, and dissect dead pangolins was applied for and obtained from the National Department of Forestry Fisheries and Environment (Original Permit number 278/64, first renewal permit number 27875, second renewal permit number 52917).

PATIENT CONSENT

No live animals were used in this study, or any trials carried out on humans.

PERMISSION TO REPRODUCE MATERIAL FROM OTHER SOURCES

No material from other sources other than those mentioned above were requested.

CLINICAL TRIAL REGISTRATION

No clinical trials were undertaken as part of this study.

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