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Morphological description of male genital organs of Marca's marmoset (*Mico marcai*)

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Abstract

Morphological characterisation of the genital organs of primates may bring significant contributions to the understanding of different reproductive behaviours and support new conservation strategies. However, relevant or detailed descriptions of genital morphology of several primate species are still lacking. This study describes the gross and microscopic anatomy of the internal and external genitalia of Marca's marmoset (*Mico marcai*). The same organs described in other primate species were identified here, but some anatomical particularities were detected, such as absence of a dartos tunic, presence of a vas deferens ampulla, absence of spongious erectile tissue in the pelvic urethra, separation of prostate gland lobes by a longitudinal sulcus and lack of septation in the corpus cavernosus and spongiosus at the level of the shaft and free portion of the penis. Keratinised type 1 spicules arising from epidermal or dermal projections were found in the free portion of the penis. Microscopic analysis revealed a small bone (baculum) consisting of peripheral compact bone and a central, non-ossified area filled with vascular tissue at the distal end of this portion of the penis. Results of this study may support further comparative studies of primates' reproductive ecology.

KEYWORDS

amazon rainforest, genital organs, marmosets, morphology, primates

1 | INTRODUCTION

The literature on the morphology of Neotropical Primates is well represented by a number of taxonomic (e.g., Hershkovitz, 1977; Kobayashi, 1995; Lynch Alfaro, Silva-Júnior, & Rylands, 2012), ecological (e.g., Anapol & Lee, 1994; Garber & Rehg, 1999; Sussman & Kinzey, 1984) and evolutionary studies (e.g., Marroig & Cheverud, 2001, 2005). However, only few authors have contributed to understand the importance of anatomical studies of genitals organs on the reproductive behaviour and ecology of primates (Dixson, 1989; Dixson, 1998; Harcourt & Gardiner, 1994; Stockley, 2002).

In this regard, genital morphology—particularly male genital morphology—acquires great significance for comparative studies, extremely valuable for differentiation between closely related taxa (Eberhard, 1985, 2010; Fooden, 1976; Hershkovitz, 1977). Morphological descriptions of the male genitalia of Neotropical primates indicate interspecies differences, as pointed out by Hershkovitz (1977, 1993) in his brief descriptions of the gross anatomy of external organs of several genera. These differences are particularly related to morphological aspects of the penis, such as the presence or absence of a penile bone (baculum) and anatomical features of this bone and spicules, when present. Hershkovitz (1977)'s reports also include morphological descriptions of genitals of the "*Callithrix argentata* group," current genus *Mico* (Rylands, Coimbra-Filho, & Mittermeier, 2009; Rylands et al., 2000). Dixson (2012) also relied on comparative anatomy (predominantly gross anatomy) of the male external and internal genitalia to understand different mating systems of Neotropical and Old World primates. Microscopic morphological descriptions have been provided for few primates species such as *Callithrix jacchus* (Beattie, 1927), *Sapajus apella* (Teixeira, 2005), *Chlorocebus aethiops* (Lebelo, 2007) and *Macaca radiata* (Prakash, Suresh, & Prithiviraj, 2009).

Here, we presented the first anatomical and histological descriptions of male genital organs of *M. marcai* (Alperin, 1993) using an entirely new data set. Such descriptions are of great value in the establishment of comparative morphological parameters between primates and may support future studies on the reproductive behaviour and on the ecology of Amazonian marmosets.

2 | MATERIALS AND METHODS

Male genital organs of seven adult Marca's marmoset (*M. marcai*, Alperin, 1993) specimens weighing between 335 and 420 g (Table 1) and kept in individual jars containing 10% formaldehyde were used in this study. Specimens were obtained from the Mastozoology collection of Institute for Sustainable Development Mamirauá.

Genital organs were anatomically described, photographed and measured using a 0.01 mm resolution digital calliper (Starret®). The following measurements were made as follows: length, width and thickness of testes, epididymis, vesicular glands, prostate and bulbourethral glands; length and diameter of vas deferens and respective ampullae, pelvic urethra and penis (Tables 2–4). Given the need to preserve anatomical relationships between genital organs for histological analysis, only the testes were weighed; this was done prior to tissue fixation, using a 0.01 g sensitivity scale (Toledo Adventurer AR5120) (Table 1).

Following gross characterisation, tissue samples were collected from all genital organs. Processing cassettes containing tissue fragments were immersed in 70% alcohol and washed in Tissue-Tek® VIP® Jr. for dehydration in increasing (80%–100%) ethanol concentrations and xylol diaphanisation.

Paraffin embedding and serial 5 μm tissue slicing were performed using Leica EG1150 embedding centre and Leica RM2125RT microtome, respectively. Tissue sections were mounted on glass slides, deparaffinised, stained with haematoxylin–eosin or Masson's trichrome and cover-slipped using Entellan (Merck®). Slides were then analysed under light microscopy (Olympus CX40 binocular microscope) and photographed at different optical magnifications (40×, 100×, 200× and 400×) using Leica DFC290 HD photomicroscope.

Anatomical descriptions in this study are in compliance with Nomina Anatomica Veterinaria (2017).

3 | RESULTS

Morphological descriptions of *M. marcai* male genital organs are given below.

3.1 | Scrotum and prepuce

The short prepuce consisted of a thick layer of wrinkled, light-coloured skin, which completely enveloped the free portion of the penis. The preputial ostium was large, and the internal lamina began at the level of this opening to end at the junction between the shaft and the free portion of the penis, where it formed a small diverticulum demarcating the caudal limit of the preputial cavity (Figures 1b–c and 2b). The symmetrical, globose scrotum was continuous with the prepuce and not very pendulous; the scrotal skin was also wrinkled and light coloured. Sparsely distributed brownish hairs were observed on the prepuce and dorsal segment of the scrotum (Figure 1c).

Microscopically, the prepuce consisted of paved epithelium and a submucosal layer of loose, well-vascularised connective tissue (Figure 2b). The scrotum was lined with similar, low thickness epithelium, with few melanocytes distributed in the basal layer. The papillary and reticular dermis consisted of loose and dense connective tissue, respectively; large numbers of collagen fibres and fibroblasts were seen in the reticular dermis, together with small numbers of hair follicles, large numbers of sebaceous glands and moderate numbers of sweat glands. The dartos tunic was lacking, and only the combined cremasteric fascia, cremaster muscle and tunica albuginea could be identified (Figure 2a).

3.2 | Testes

The paired, levelled testes lied in different compartments within the scrotum and were separated by a scrotal septum, externally visible as the scrotal raphe. This raphe ran from the perineal region

TABLE 1 *Mico marcai* (Mm) body and testicular weight measurements (g) and percentage of the testis weight in comparison with body weight (%)

	Testicular weight (TW)		Body weight (BW)	% TW × BW		
	Right	Left		Right	Left	Mean
Mm1	0.57	0.52	390.0	0.146	0.133	0.140
Mm2	0.63	0.67	420.0	0.150	0.160	0.155
Mm3	0.56	0.60	395.0	0.142	0.152	0.147
Mm4	0.42	0.42	335.0	0.125	0.125	0.125
Mm5	0.44	0.47	350.0	0.126	0.134	0.130
Mm6	0.54	0.52	377.5	0.143	0.138	0.141
Mm7	0.65	0.58	410.0	0.159	0.141	0.150
Mean	0.54	0.54	382.5	0.142	0.140	0.141

TABLE 2 *Mico marcai* (Mm) testicular and epididymal length (L), width (W) and thickness (T) measurements (mm)

Organ	Testicles						Epididymis											
							Right						Left					
Antimer	Right			Left			Head			Tail			Head			Tail		
Measure	L	W	T	L	W	T	L	W	T	L	W	T	L	W	T	L	W	T
Mm1	12.92	7.16	5.67	12.75	6.17	6.58	1.96	4.84	3.71	3.52	2.53	2.29	1.93	4.17	4.30	3.48	2.18	2.66
Mm2	15.53	9.15	6.38	15.85	9.42	6.43	2.35	6.19	4.17	4.24	3.23	2.58	2.40	6.37	4.20	4.32	3.32	2.59
Mm3	14.42	8.40	6.02	16.51	8.71	7.80	2.18	5.68	3.94	3.93	2.69	2.43	2.50	5.89	5.10	4.50	3.07	3.15
Mm4	12.20	7.25	4.95	12.08	7.18	4.90	1.85	4.90	3.24	3.33	2.56	2.00	1.83	4.86	3.20	3.30	2.53	1.98
Mm5	12.39	8.67	4.68	12.45	8.54	4.75	1.88	5.87	3.06	3.38	3.06	1.89	1.89	5.78	3.11	3.40	3.01	1.92
Mm6	12.74	8.06	7.64	12.93	8.18	7.47	1.93	5.45	4.99	3.47	2.84	3.09	1.96	5.53	4.88	3.53	2.89	3.02
Mm7	15.14	7.50	3.72	14.65	7.18	3.91	2.29	5.07	2.43	4.13	2.65	1.50	2.22	4.86	2.56	3.99	2.53	1.58
Mean	13.62	8.03	5.58	13.89	7.91	5.98	2.06	5.43	3.65	3.71	2.79	2.25	2.10	5.35	3.90	3.79	2.79	2.41

TABLE 3 *Mico marcai* (Mm) vas deferens, vas deferens ampullae, pelvic urethra and penis length (L) and diameter (D) measurements (mm)

Organ	Vas deferens				Ampullae						Penis					
Antimer	Right		Left		Right		Left		Pelvic urethra		Root		Shaft		Free portion	
Measure	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D
Mm1	28.69	0.75	28.54	0.76	5.32	1.17	5.39	1.22	13.50	1.72	7.98	5.54	9.25	3.30	6.65	2.81
Mm2	28.43	0.72	28.32	0.75	6.55	1.31	6.66	1.38	13.50	1.72	9.85	5.46	10.15	3.50	6.42	3.02
Mm3	27.98	0.81	28.02	0.77	6.4	1.24	6.44	1.26	13.67	1.79	7.12	3.76	9.44	3.07	7.02	2.82
Mm4	28.74	0.77	28.82	0.74	5.66	1.18	5.71	1.20	15.66	1.89	9.26	5.92	9.76	3.97	7.95	3.30
Mm5	27.87	0.84	27.96	0.80	5.43	1.34	5.38	1.36	14.68	1.81	6.38	5.12	9.10	3.47	8.73	3.62
Mm6	29.01	0.79	28.92	0.81	5.37	1.45	5.25	1.37	14.99	1.83	9.01	5.89	9.60	4.16	8.18	3.7
Mm7	27.77	0.76	28.80	0.79	6.21	1.23	6.12	1.18	15.51	1.74	6.89	5.94	7.33	3.01	6.99	2.86
Mean	28.36	0.78	28.48	0.77	5.85	1.27	5.85	1.28	14.50	1.79	8.07	5.38	9.23	3.50	7.42	3.16

TABLE 4 *Mico marcai* (Mm) vesicular, prostate and bulbourethral gland length (L), width (W) and thickness (T) measurements (mm)

Organ	Vesicular glands						Prostate						Bulbourethral glands					
Antimer	Right			Left			Right			Left			Right			Left		
Measure	L	W	T	L	W	T	L	W	T	L	W	T	L	W	T	L	W	T
Mm1	10.36	6.87	2.80	10.47	6.95	2.87	6.35	7.11	3.86	6.16	6.95	3.58	3.82	3.35	2.87	3.81	3.33	2.85
Mm2	10.26	6.79	2.69	10.24	6.78	2.74	5.01	6.01	3.69	5.31	6.27	3.74	3.83	3.34	2.85	3.82	3.33	2.84
Mm3	10.36	6.85	2.83	10.31	6.81	2.81	5.11	6.44	3.02	5.08	6.77	3.02	3.80	3.31	2.88	3.84	3.32	2.85
Mm4	10.02	5.83	2.67	9.98	5.78	2.65	6.27	7.61	3.31	6.16	7.55	3.81	3.81	3.33	2.86	3.83	3.31	2.86
Mm5	10.10	6.02	2.71	10.05	5.99	2.69	5.09	6.38	3.78	6.14	6.37	3.45	3.84	3.36	2.88	3.85	3.32	2.85
Mm6	10.40	6.72	2.72	10.2	6.67	2.64	4.98	6.11	3.72	5.22	6.13	3.63	3.81	3.34	2.85	3.82	3.34	2.83
Mm7	10.18	6.60	2.68	10.14	6.54	2.68	6.13	6.99	3.06	6.15	7.34	3.77	3.83	3.33	2.89	3.81	3.31	2.84
Mean	10.24	6.53	2.73	10.20	6.50	2.73	5.56	6.66	3.49	5.75	6.77	3.57	3.82	3.34	2.87	3.82	3.32	2.85

to the ventral segment of the prepuce and divided the scrotum in half (Figure 1c). The oval-shaped testes were similar in weight and size (Tables 1 and 2, respectively); testes were elongated in the dorsoventral direction, with subtle laterolateral flattening and craniocaudal tilt (Figure 1a).

Microscopic examination revealed mild immersion of connective fibres from the tunica albuginea into the testicular parenchyma; trabecular projections arising from these fibres divided the testes into multiple intercommunicating, poorly demarcated lobes, each comprising variable numbers of convoluted seminiferous tubules and supported by loose connective tissue containing vessels, nerves, small to moderate numbers of Leydig cells and a thin layer of myoid cells (Figure 2c,d).

Sertoli cells extending from the basal lamina towards the tubular lumen and spermatogenic cells occupying the existing spaces among support cells were observed within the seminiferous tubules. Not all seminiferous tubules contained sperms in their lumen (Figure 2d).

Seminiferous tubules ran towards the rete testis via straight tubules lined with cuboid cells or simple squamous epithelium supported by connective tissue fibres and smooth muscle cells. The rete testis was directly connected to the vas deferens, which penetrated the tunica albuginea at the level of the extremitas capitata of the testes to form the epididymal duct.

3.3 | Epididymis

The epididymis had an elongated "C" shape and was completely attached to the epididymal border of the testes. Three distinct portions were identified as follows: a large, flat head attached to the extremitas capitata of the testis, a thin, elongated body running along the posterior testicular border and a tail corresponding to a small, globose enlargement attached to the extremitas caudata of the testis and continuous with the vas deferens. Of these, the epididymal head was the most prominent (Table 2) (Figure 1a).

The epididymal duct could be easily identified through the thin epididymal surface (Figure 1a) as a mesh of convoluted tubules lined with pseudostratified columnar epithelium containing stereocilia and characterised by tall cells with slightly vacuolated, weakly stained cytoplasm and oval-shaped or elongated nuclei located at the cell base or centrally. Tubules were also lined with a thin basal lamina and surrounded by moderate amounts of fibrovascular tissue and smooth muscle cells (Figure 3a–f).

Differences in epithelium height and amounts of peritubular fibromuscular tissue were also noted. The epithelium was taller and supports tissue more abundant at the head of the epididymis compared to the body and tail. Small collections of sperm cells, cellular remnants and amorphous material were also found in the lumen of several tubules, particularly in the tail (Figure 3a–f).

3.4 | Vas deferens

The narrow vas deferens (Table 3) originated from the tail of the epididymis (Figure 1a) and ran along its body in a linear fashion. A

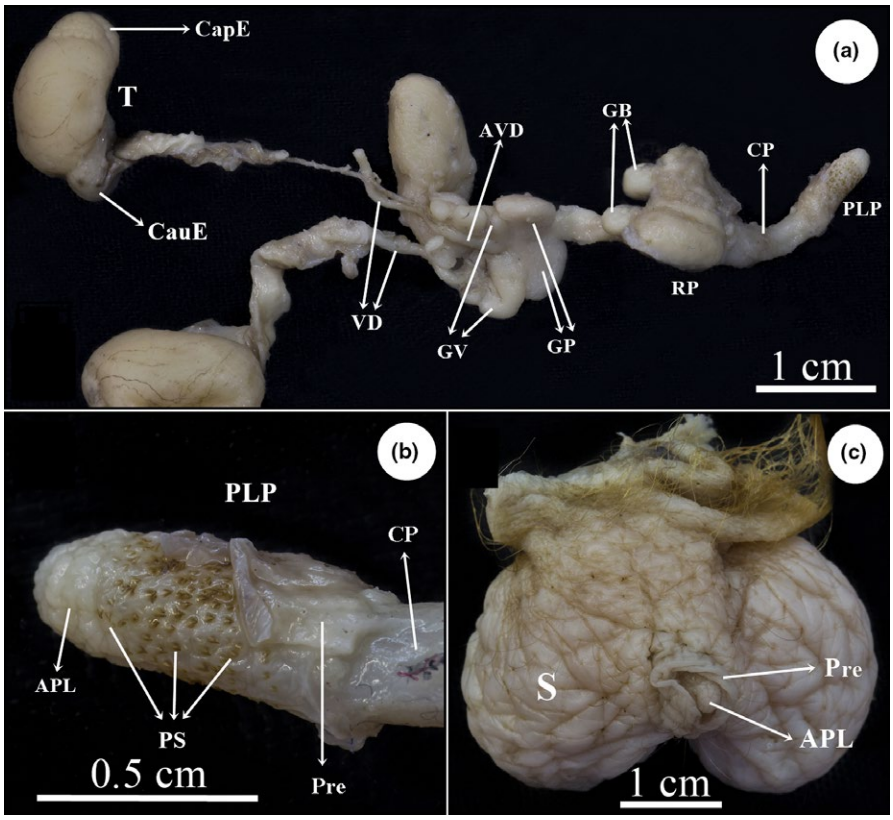

FIGURE 1 Photograph of *Mico marcai* male genitalia. (a) Complete set of genital organs—testes, epididymis, vas deferens, vas deferens ampulla, vesicular glands, prostate gland, pelvic urethra, bulbourethral glands and root, shaft and free portion of the penis (scale: 1 cm); (b) free portion of the penis—note apex and spicules (scale: 0.5 cm); (c): scrotum—note the wrinkled skin, raphe and close relationship with the prepuce (scale: 1 cm). T: testes; CapE: head of the epididymis; CauE: tail of the epididymis; VD: vas deferens; AVD: vas deferens ampulla; GV: vesicular gland; GP: prostate gland; GB: bulbourethral glands; RP: root of the penis; CP: shaft of the penis; PLP: free portion of the penis; APL: apex of the free portion of the penis; PS: penile spicules; S: scrotum; Pre: prepuce

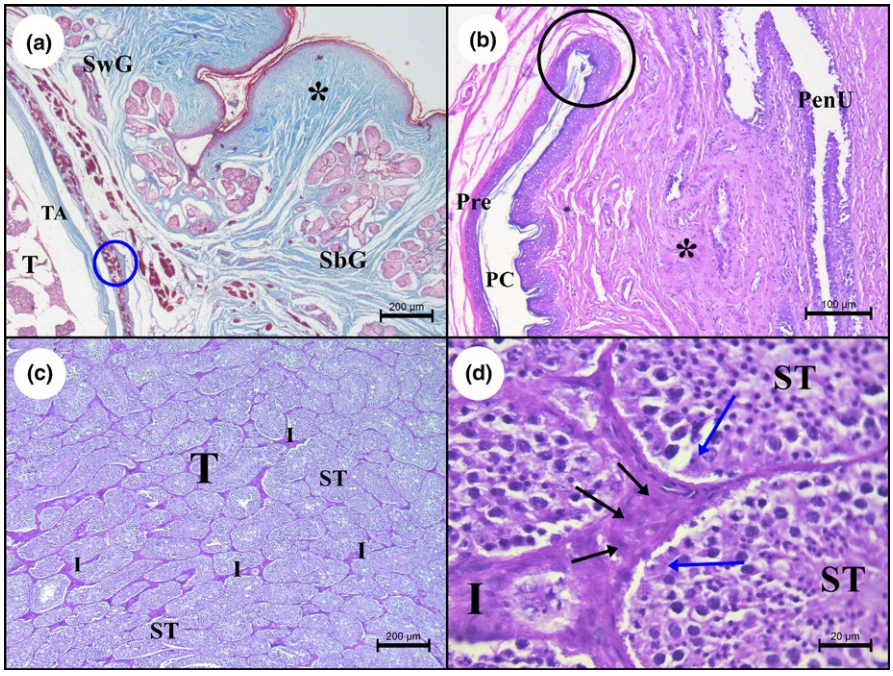

FIGURE 2 Photomicrograph of *Mico marcai* scrotum, paratesticular tissues, prepuce, penis and testicle. (a) Scrotal skin, sebaceous and sweat glands, paratesticular tissues and testicular parenchyma—note the cremaster muscle surrounded by cremasteric fascia (blue circle) (TRI; 40×); (b) prepuce, preputial cavity, preputial diverticulum (black circle), free portion of the penis and penile urethra (longitudinal section; HE, 100×); (c) testicular parenchyma—note high density of seminiferous tubules and scarce interstitial tissue with low cellularity (HE, 40×); (d) testicular parenchyma—note seminiferous tubules, male germ lineage, Sertoli (blue arrow) and Leydig (black arrow) cells (HE, 40×). SwG: sweat gland; SbG: sebaceous gland; TA: tunica albuginea; T: testicular parenchyma; Pre: prepuce; PC: preputial cavity; PenU: penile urethra; ST: seminiferous tubules; I: interstitium; Black star: support tissue; HE: haematoxylin–eosin; TRI: Masson's trichrome

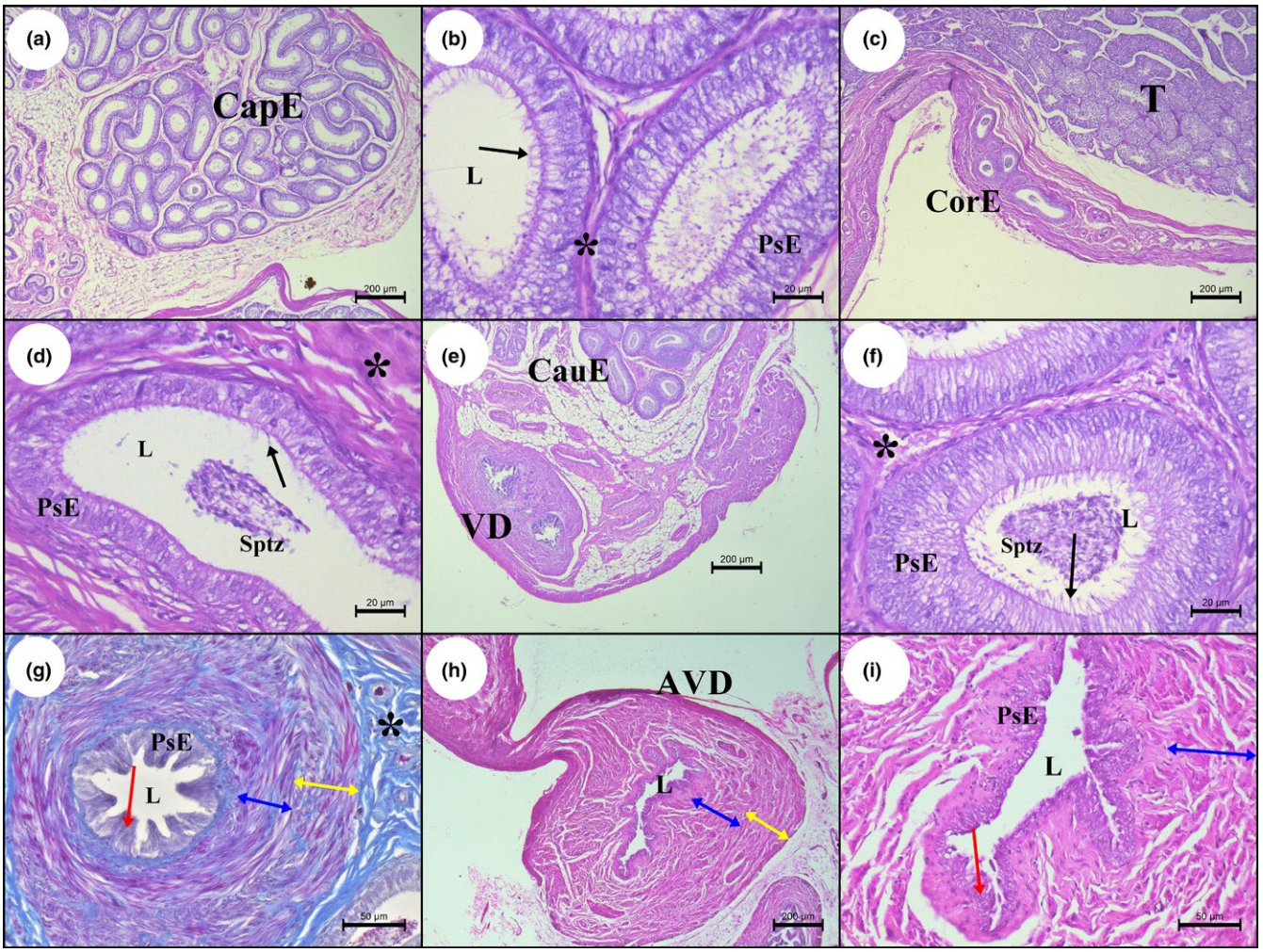

FIGURE 3 Photomicrograph of *Mico marcai* epididymis and vas deferens. (a) Head of the epididymis—note highly convoluted tubules (HE, 40×); (b) head of the epididymis (HE, 400×); (c) body of the epididymis and adjacent testicular parenchyma (HE, 40×); (d) body of the epididymis (HE, 400×); (e) tail of the epididymis, convoluted tubules and vas deferens (HE, 40×); (f) tail of the epididymis (HE, 400×); (g) Vas deferens—note pleated epithelium (red arrow), inner (blue double-headed arrow) and outer (yellow double-headed arrow) smooth muscle layers (TRI, 200×); (h) Vas deferens ampulla—note circular and longitudinal smooth muscle layers of the vas deferens wall (blue and yellow double arrows) (HE, 40×); (i) Vas deferens ampulla—note pleated epithelium (red arrow) and inner smooth muscle layer (blue double-headed arrow) (HE, 200×). CapE: head of the epididymis; CorE: body of the epididymis; CauE: tail of the epididymis; PsE: pseudostratified epithelium; L: lumen; Sptz: sperm cells; T: testicular parenchyma; VD: Vas deferens; AVD: Vas deferens ampulla; Black arrow: stereocilia; Black star: support tissue; HE: haematoxylin–eosin; TRI: Masson's trichrome

small enlargement, the vas deferens ampulla (Table 3), formed prior to the attachment to the urethral parenchyma (Figure 1a) and extended to the ejaculatory ostium.

Histologically, the vas deferens and ampulla had a pleated lumen lined with pseudostratified columnar epithelium containing small numbers of short stereocilia, slightly vacuolated, weakly stained cytoplasm and round-shaped nuclei. The thin tunica submucosa consisted of a thin basal lamina surrounded by moderate amounts of fibrovascular tissue and smooth muscle cells. The muscle layer comprised two smooth muscle strata with fibres arranged in a circular or longitudinal orientation—the inner and outer stratum, respectively (Figure 3e,g). The lumen was wider and muscle layers clearly thicker at the ampulla compared to the vas deferens (Figure 3h,i).

3.5 | Vesicular gland

Vesicular gland lobes were similar in size (Table 4) and projected dorsolaterally to the neck of the urinary bladder. Each lobe had a craniodorsally directed free extremity and a caudoventral extremity in close relationship with prostate gland lobes, along with dorsal and ventral convex lobed surfaces and two borders—a convex lateral border and a medial, slightly concave border in contact with the vas deferens ampulla (Figure 1a).

Each lobe was enveloped in large amounts of fibrovascular tissue consisting of dense connective tissue with longitudinally or transversally oriented fibres. Moderate amounts of smooth muscle fibres and small numbers of adipocytes were also noted; these encapsulated the organ and formed the stroma, supporting and dividing

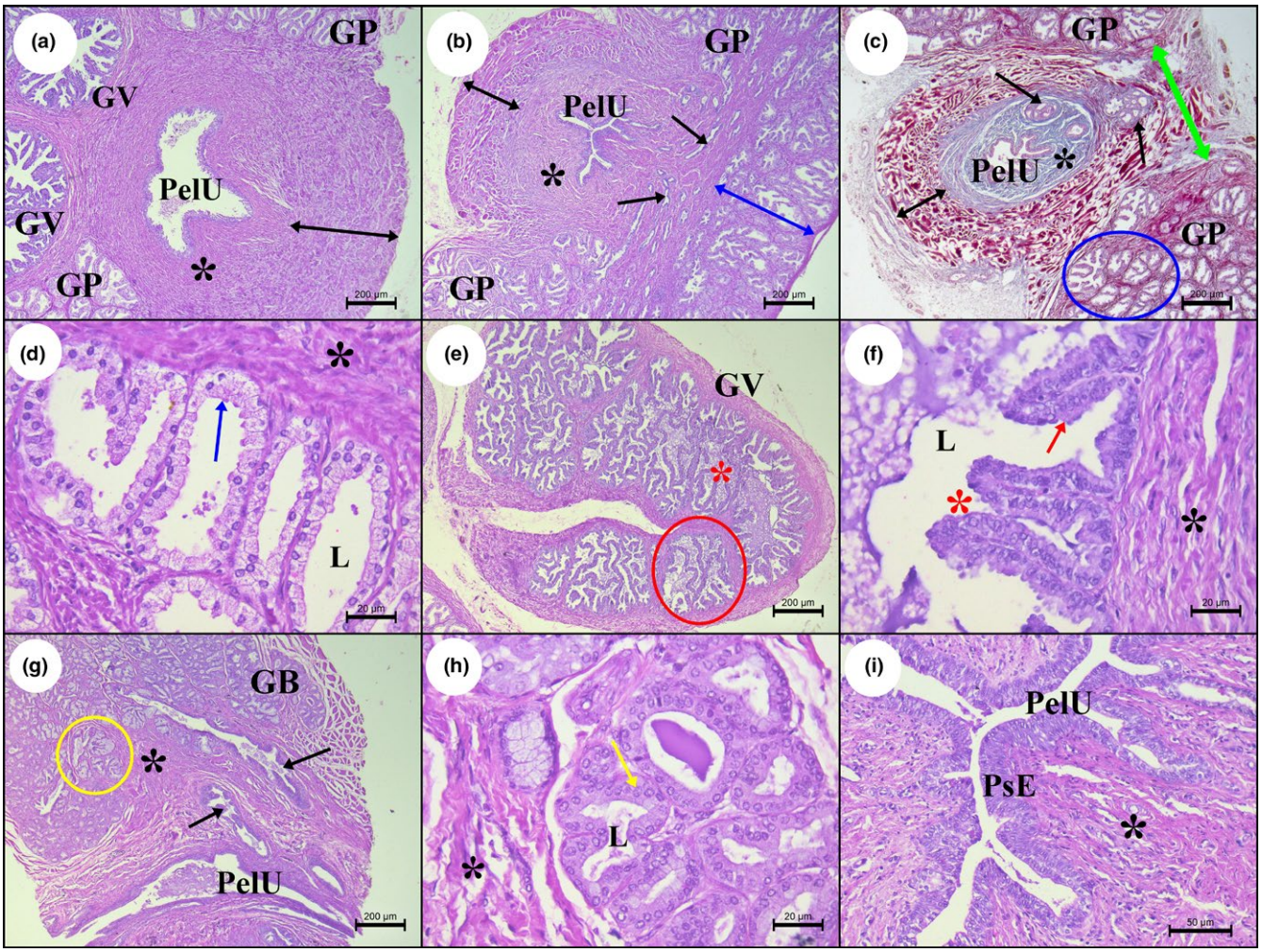

FIGURE 4 Photomicrograph of *Mico marcai* pelvic urethra, prostate, vesicular and bulbourethral glands. (a) Pelvic urethra, prostate and vesicular glands—note muscle layers of the pelvic urethra (black double-headed arrow) (HE, 40×); (b) prostate gland—relationship with the pelvic urethra; note interlobar connection (double blue arrow), glandular ducts (black arrow) and muscle layers of the pelvic urethra (black double-headed arrow) (HE, 40×); (c) prostate gland—relationship with the pelvic urethra; note prostate lobe (blue circle), interlobar septum (green double-headed arrow), glandular ducts (black arrow) and muscle layers of the pelvic urethra (black double-headed arrow) (TRI, 40×); (d) prostate gland—note simple glandular epithelium (blue arrow) (HE, 400×); (e) vesicular gland—note vesicular gland lobe (red circle) and projection of the epithelium into the lumen (red star) (HE, 40×); (f) vesicular gland—note pseudostratified glandular epithelium (red arrow) and projection into the lumen (red star) (HE, 400×); (g) bulbourethral gland—relationship with the pelvic urethra (longitudinal section); note bulbourethral gland lobe (yellow circle) and glandular ducts (black arrow) (HE, 40×); (h) bulbourethral gland—note simple glandular epithelium (yellow arrow) (HE, 400×); (i): pelvic urethra at prostate level (HE, 200×). GV: vesicular gland; GP: prostate gland; GB: bulbourethral gland; PelU: pelvic urethra; L: lumen; PsE: pseudostratified epithelium of the pelvic urethra; Black star: support tissue; HE: haematoxylin–eosin; TRI: Masson's trichrome

the gland into lobes lined with pseudostratified epithelium. Large amounts of amorphous material were observed in the glandular lumen (Figure 4e,f).

3.6 | Prostate gland

The prostate corresponded to a small (Table 4), compact, smooth and dorsoventrally flattened gland located caudal to vesicular gland lobes and dorsal to the pelvic urethra. Right and left prostate lobes were separated by a discrete midline sulcus and did not envelop the urethra (Figure 1a).

The organ had a free dorsal surface, a ventral surface in direct contact with the pelvic urethra and two free lateral borders—a cranial border in close contact with vesicular gland lobes and one slightly convex caudal border (Figure 1a).

Large amounts of fibrovascular tissue consisting of compact connective tissue, moderate amounts of smooth muscle fibres and small numbers of adipocytes encapsulated the prostate and formed the gland stroma. The stroma provided support and gave rise to several lobules containing tubuloalveolar gland acini with digitiform projections supported by a delicate fibrovascular stroma, which determined variable lumen

width (Figure 4a–c). Glandular lining consisting of a single layer of polyhedral to columnar cells with finely stippled, weakly stained cytoplasm and round nuclei predominantly located at the cell base. Small amounts of amorphous to granular material consistent with serous content were found in the glandular lumen (Figure 4d).

In four specimens, a thick septum of dense connective tissue completely separated prostate lobes (Figure 4c) while, in the three remaining specimens, prostate lobes were connected by glandular tissue (Figure 4b). Prostate gland duct systems were surrounded by stroma and lined with polyhedral cells forming a pseudostratified or transitional epithelium (Figure 4b,c).

3.7 | Bulbourethral glands

The small (Table 4), round-shaped, smooth bulbourethral glands lied dorsoventrally to the terminal portion of the pelvic urethra and attached caudally to the root of the penis (Figure 1a).

Histologically, each gland was covered with small amounts of longitudinally and transversally oriented collagen and skeletal muscle fibres intermingled with moderate amounts of fibrovascular stroma and sparse smooth muscle cells (Figure 4g). The stroma gave rise to a lobed pattern characterised by thinly separated lobes formed by multiple tubules and acini comprising a single layer of weakly stained columnar cells with round-shaped to flattened nuclei located close to their base. Small amounts of amorphous material were observed within some tubular units (Figure 4g,h). Bulbourethral duct systems were histologically similar to prostate gland duct systems (Figure 4g).

3.8 | Pelvic urethra

The long, tubular pelvic urethra (Table 3) was divided into three well-defined portions, a very short pre-prostatic portion extending from the inner urethral ostium to the caudal border of the prostate, a prostatic portion in close contact with the prostate gland and extending to its caudal border and a membranous portion limited by the penile root (Figures 1a and 4a–c,g). From this point, the so-called penile urethra travelled along the penile shaft to end at the level of the external urethral orifice (Figure 5h).

All three portions of the pelvic urethra were lined with transition or pseudostratified epithelium. The lamina propria contained large amounts of fibrovascular tissue composed of dense connective tissue, moderate numbers of vessels and smooth muscle fibres and small numbers of adipocytes. Skeletal muscle fibres arranged in a circular (deep) or longitudinal fashion (superficial) were noted superficial to the connective tissue; these were covered with an adventitious tunic consisting of modest amounts of loose connective tissue and multiple blood vessels (Figure 4a–c,g,i).

3.9 | Penis

The penis was elongated and cylindrical in shape and comprised a broad root, a shaft and a free portion. The shaft was slightly wider than the free portion, which was covered by the prepuce so that only the apical extremity could be visualised through the preputial ostium (Table 3) (Figure 1a–c).

The most prominent portion of the penis corresponded to the voluminous, cranioventrally elongated root formed by the bulbus penis. This structure lied between both well-developed ischiocavernosus muscles and was covered by bulbospongiosus muscle fibres (Figure 1a).

The penile shaft was cylindrical, uniform in girth and somewhat flattened in a laterolateral direction. Cross section revealed a single corpus cavernosus and a corpus spongiosus enclosing the penile urethra. The inner preputial lamina marked the limit between the shaft and the free portion of the penis (Figure 1a,b).

The scarcely pigmented free portion of the penis was characterised by large numbers of papillae giving rise to one or two rigid, brownish and caudally directed spicules consistent with type 1 spicules described by Dixson (2012). The apex of the penis lacked a distinct glans (Figure 1a,b).

Histologically, the corpus spongiosus of the ventrally located bulbus penis consisted of a venous plexus supported by moderate amounts of loose connective tissue and smooth muscle fibres. Other structures recognised were the penile urethra enclosed by the corpus spongiosus and lined with transition or pseudostratified epithelium, and two corpora cavernosa located dorsal to the penile urethra; these had similar structure to the corpus spongiosus and were separated by a thick septum of dense connective tissue. A thick penile tunica albuginea containing large amounts of dense connective tissue consisting of longitudinally and transversally arranged collagen fibres surrounded the corpora cavernosa and corpus spongiosus of the penis. This tunic was covered with thick layers of longitudinally and transversally arranged skeletal muscle fibres intermingled with and surrounded by small amounts of fibrovascular tissue (Figure 5a,b).

Cross section of the penile shaft revealed a single, non-septated corpus cavernosus and a corpus spongiosus. Both structures were well-developed and contained numerous vessels demarcated by stroma consisting of fibrovascular and loose connective tissue surrounded by a penile tunica albuginea similar to the one found at the root. Moderate amounts of connective tissue containing veins, arteries and nerves completely surrounded the penis external to this tunic (Figure 5c). The ventrally positioned penile urethra was enclosed by the corpus spongiosus and lined with transition or pseudostratified epithelium (Figure 5c).

The free portion of the penis contained a superficial layer of paved epithelium (Figure 4d–i). Type 1 spicules arising from epidermal or dermal projections into the epidermis and containing multiple layers of keratin, or presenting as corneal pearls, were found in multifocal areas of this epithelium (Figure 5d–h). The superficial dermis consisted of small amounts of loose connective tissue, while the deep dermis contained dense connective tissue (Figure 5g) with large numbers of collagen fibres and small numbers of vessels and nerves. Large numbers of nerves and moderate numbers of venous plexi were found at the transition to the tunica albuginea, particularly at the dorsal and ventrolateral portions of the penis (Figure 5d–f). In a deeper plane, the tunica albuginea surrounded

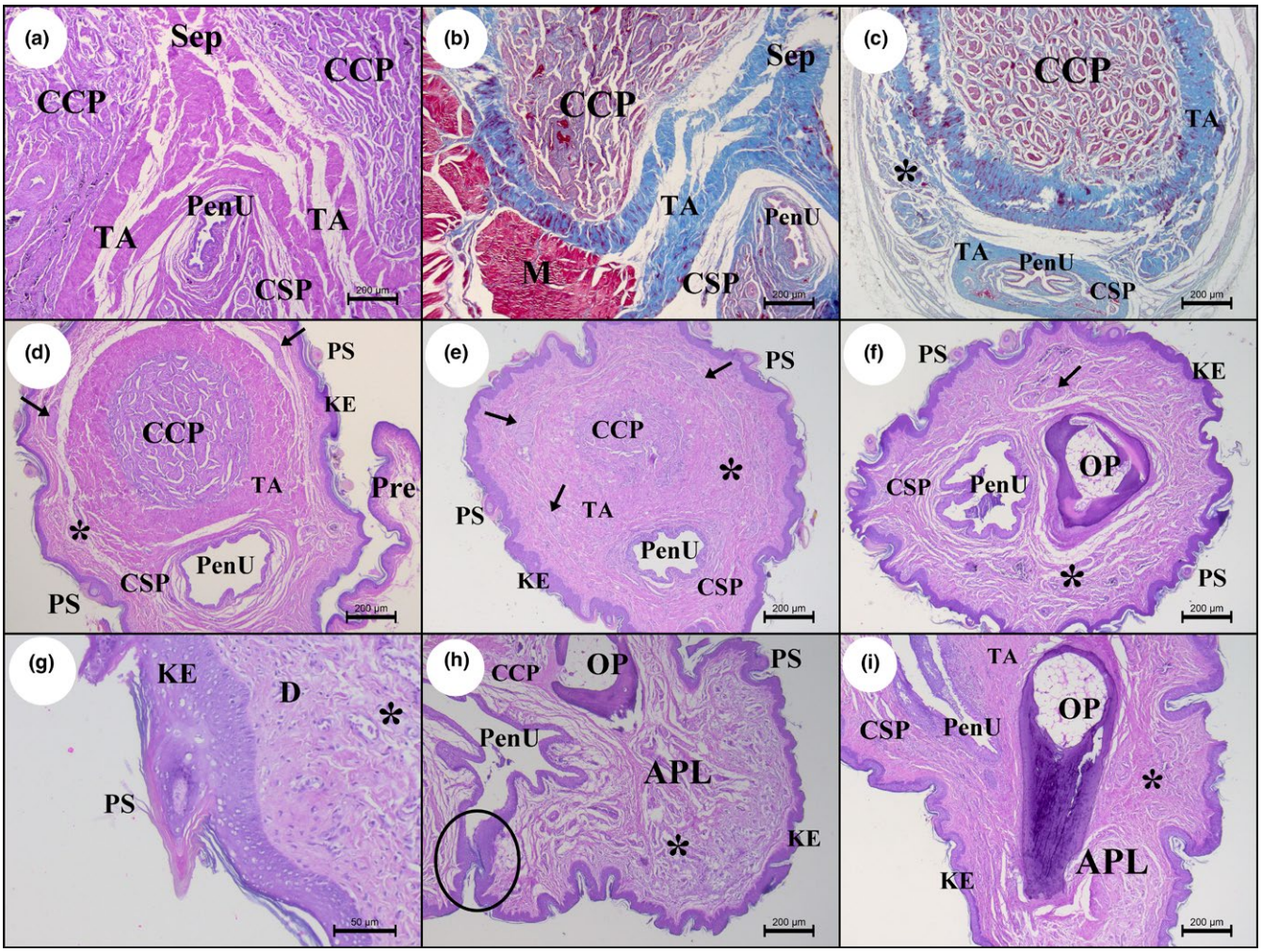

FIGURE 5 Photomicrograph of *Mico marcai* penile structures. (a) Root of the penis—note corpus spongiosus, septated corpus cavernosus, tunica albuginea, septum and urethra (HE, 40×); (b) root of the penis—note corpus spongiosus, septated corpus cavernosus, tunica albuginea, septum, urethra and muscle tissue (TRI, 40×); (c) body of the penis—note single corpus cavernosus, tunica albuginea and urethra (TRI, 40×); (d) free portion of the penis—note single corpus cavernosus, tunica albuginea, urethra, spicules and prepuce (HE, 40×); (e) free portion of the penis showing the single corpus cavernosus as it is replaced (HE, 40×); (f) free portion of the penis and penile bone (HE, 40×); (g) skin overlying the free portion of the penis, with spicules (HE, 200×); (h) free portion of the penis (longitudinal section)—note external urethral ostium and keratinised squamous epithelium (black circle) (HE, 40×); (i) free portion of the penis (longitudinal section) (HE, 40×). PenU: penile urethra; CCP: corpus cavernosus of the penis; CSP: corpus spongiosus of the penis; TA: tunica albuginea of the penis: Sep: septum dividing the corpus cavernosus; M: skeletal muscle; Black star: support tissue; KE: keratinised squamous epithelium overlying the glans; PS: penile spicules; Black arrow: nerves; Pre: prepuce; OP: penile bone; D: dermis; APL: apex of the free portion of the penis; HE: haematoxylin–eosin; TRI: Masson's trichrome

the corpora cavernosa and corpus spongiosus (Figure 5d–f,i). The penile urethra remained within the corpus spongiosus and was lined with transition or pseudostratified epithelium to the level of the external ostium of the urethra, located caudoventral to the apical portion of the penis (Figure 5d–f,h,i). Paved epithelium lined the penile urethra from this point (Figure 5h).

At the level of the free portion of the penis, the corpus cavernosus was gradually and largely replaced by fibrous connective and adipose tissue; at its proximal end, small amounts of fibrocartilaginous (Figure 5d–f,h,i) tissue gave rise to a small penile bone dorsomedial to the penile urethra (Figure 5f,h,i). This microscopic, semiconical baculum was externally formed by mature bone tissue consisting of bone matrix, osteocytes and osteoblasts and surrounded by thin layers of collagen, fibroblasts and cartilaginous tissue and, more superficially, by compact connective tissue containing moderate numbers of vessels and nerves. The central portion of the penile bone consisted of well-vascularised trabecular bone with dense ossification foci and adipose tissue (Figure 5f,h,i).

4 | DISCUSSION

Mico marcai had similar internal and external genital organs to other genera of primates such as *Callimico goeldii*, *Simia entellus* (*Presbytis*

entellus entellus), *S. apella*, *M. radiata*, *C. aethiops* and to monkeys in the genus Hylobates (David & Ramaswami, 1971; Dixson, 2012; Hill, 1959; Hill & Kanagasuntheram, 1959; Lebelo, 2007; Prakash et al., 2009; Teixeira, 2005). However, proportions differed, as this anatomical feature is directly related to body weight (Harcourt, Purvis, & Liles, 1995).

Mico marcai testes were proportionally smaller compared with body weight, a feature consistent with monogamous mating behaviour (Harcourt, Harvey, Larson, & Gshort, 1981; Harcourt et al., 1995). Similar to other *Mico* species, *M. marcai* social units observed in nature consisted of four individuals on average (Ennes, Nunes, & Bastos, 2013). However, lack of genetic evidence precludes conclusive statements regarding the monogamous mating behaviour of free-ranging marmosets at this stage (Garber, Porter, Spross, & Di Fiore, 2015).

Lower Leydig cell density is thought reflect seasonal reproductive behaviour (Bansode, Chowdhury, & Dhar, 2003). Low numbers of Leydig cells in the testes studied may, therefore, suggest seasonal reproductive behaviour of *M. marcai*. The fact that not all seminiferous tubules in the sample studied contained sperm cells supports this hypothesis.

According to Anderson and Dixson (2009), vesicular and prostate gland size may be directly related to relative testicular size in primates, that is, animals with larger testicles are expected to have larger glands. Well-developed glands are therefore consistent with multimale–multifemale mating systems such as in *Saimiri*, which vesicular glands measure up to seven centimetres in length (Hill, 1960). Vesicular glands are comparatively less developed in *M. marcai* (approximately 1 cm long) and other monogamous genera such as *Callimico*, *Callithrix*, *Saguinus* and *Aotus*, and vestigial in *Callicebus* and *Pithecia* (Dixson, 1998; Hill, 1959).

Such as in Neotropical and Old World Primates, *M. marcai* vesicular glands corresponded to lobed, pleated structures lined with pseudostratified columnar epithelium and arising directly from the pelvic urethra (Hill, 1960; Prakash et al., 2009). In contrast with descriptions given by Teixeira (2005) and Prakash et al. (2009), the prostate gland lied dorsal to the pelvic urethra and therefore did not envelop or penetrate the urethral wall (David & Ramaswami, 1971; Ganzer, Köhler, Neuhaus, Dorschner, & Stolzenburg, 2004; Hill & Kanagasuntheram, 1959; Mubiru et al., 2007; Oelrich, 1978).

Mico marcai prostate had two lobes positioned on either side of a shallow longitudinal groove, different from other primates (e.g., *Ateles*, *Callicebus*, *Cercocebus*, *Erythrocebus*, *Hylobates*, *Macaca*, *Pan*, *Papio* and *Saimiri*), in which prostate lobes lie craniocaudal to the pelvic urethra and are macroscopically separated by a transverse groove (Lewis, Kim, Irani, & Roberts, 1981; Mubiru et al., 2007). In four specimens in this study, this groove was continuous with a thick median septum of compact connective tissue, which completely divided the gland. No mention of this feature has been found in the literature. In the three remaining specimens, this separation was absent, and the glandular tissue distributed between both gland lobes in a continuous fashion.

The presence of a physical barrier between gland lobes in *M. marcai* is not reflected in histology: Tubuloalveolar acini were similar between lobes, a typical feature of this species. David and Ramaswami (1971), Lewis et al. (1981) and Mubiru et al. (2007) reported larger irregular acini in the cranial prostate lobe in Neotropical and Old World monkeys, compared to a more uniform pattern in the caudal lobe. However, in spite of morphological differences between species, the prostate function is thought to be similar.

The small bulbourethral glands of *M. marcai* were similar in shape to those of *C. goeldii* and *Gorilla* and similar in size to those of *C. goeldii* (Hill, 1959; Oelrich, 1978). Prakash et al. (2009) were the only authors to associate the rudimentary size of these glands to the polyandrous mating system described in *M. radiata*, suggesting a functional compensatory effect—namely the production of larger volumes of fluid by the developed portion of the vesicular glands for sperm cell transport and formation a solid cervicovaginal clot. Histological confirmation of fully functional parenchyma in *M. marcai* suggests this compensatory effect does not occur in this species, despite small bulbourethral gland size.

Just as in *C. goeldii* and *Pan troglodytes*, the tail of the epididymis of *M. marcai*, although smaller, was more prominent than the head and round rather than triangular in shape, while the epididymal body was narrow and thin (Hill, 1959; Martin & Gould, 1981). Histological findings in this species were similar to descriptions given of genera *Macaca* and *Pan*, including the progressive reduction in height of the pseudostratified epithelium overlying the head and tail of the epididymis, the presence of stereocilia in all epididymal segments and the collection of sperm cells within the epididymal tail (Alsum & Hunter, 1978; Lebelo, 2007; Ramos & Dym, 1977; Smithwick & Young, 1997).

In the specimens studied, total vas deferens length was similar to *C. goeldii* (Hill, 1959), but differed from these and other primates due to the presence of a discrete enlargement of its final portion (the ampulla), where the muscle layer was notably thicker (Alsum & Hunter, 1978; Ramos, 1979; Ramos & Dym, 1977; Smithwick & Young, 1997). However, as in genus *Macaca*, the vas deferens and ampulla were lined with pseudostratified columnar epithelium of homogeneous height (Ramos, 1979) in spite of differences in wall thickness and lumen width, suggesting differences are limited to macroscopic features.

Stereocilia are thought to greatly increase vas deferens surface area and sperm cell storage capacity (Schimming, 2001). Small numbers of short stereocilia observed in *M. marcai* may, therefore, suggest sperm cell storage to be a function of the highly pleated mucosa, particularly at the level of the ampulla. Similar features have been described at the terminal portion of the vas deferens (Schimming, 2001).

Gross examination of the pelvic urethra of specimens dissected in this study revealed a different pattern from descriptions given of *C. goeldii*, with total length corresponding to approximately 30% of the length described for that species; also, as in Hylobates, the organ was straight rather than s-shaped (Hill, 1959; Hill & Kanagasuntheram, 1959). Similar to *Sapajus apela* (Teixeira, 2005), no spongious erectile tissue was found in the wall of the pelvic urethra in *M. marcai*.

Morphological and histological features of the penis also vary widely between primates. Great morphological diversity clearly demonstrates that, different from monogamous species such as *Callitrichidae* (*Callithrix*, *Saguinus*, *Cebuella*) and monkeys in the genera *Aotus* and *Callicebus* (Dixson, 1987), non-gregarious species or multimale–multifemale groups tend to present a larger glans, a baculum and numerous large, well-developed, keratinised spicules. *M. marcai* may, therefore, be included in the first group, given the presence of small penile spicules, microscopic baculum and proportionally smaller testes and accessory genital glands (Harcourt et al., 1981).

The presence of type 1 spicules in the free portion of the penis of *M. marcai* is thought to be a feature common to most *Callitrichidae* (genera *Mico*, *Callibella*, *Callithrix*, *Callimico* and *Leontopithecus*), which has not been described in genera *Cebuella* and *Saguinus* (Dixson, 2012; Hershkovitz, 1977; Perkins, 1969; Weber, Santana, Ennes, & Araújo, 2016).

The small-sized baculum is consistent with descriptions given of all other *Callitrichidae* and primates in genera *Aotus* and *Pithecia*; this bone is lacking in monkeys in genera *Cacajao*, *Chiropotes*, *Ateles*, *Lagothrix* and *Alouatta* (Dixson, 2012; Hershkovitz, 1977; Weber et al., 2016). Despite its small size, *M. marcai* baculum was histologically similar to that of *S. apella* and other *Callitrichidae* (Hershkovitz, 1977; Teixeira et al., 2015; Weber et al., 2016).

As in genera *Pan* and *Sapajus* (*S. apella*) (Cold & McGrath, 1999; Teixeira et al., 2015), the corpus cavernosus of the penis of *M. marcai* consisted of a single structure, in contrast with the paired structure described in genera *Macaca*, *Papio*, *Chlorocebus*, *Brachyteles* and *Callibella* (Cold & McGrath, 1999; Dixson, Pissinatti, & Anderson, 2004; Lebelo, 2007; Weber et al., 2016). However, the corpus cavernosus of the penis did not differ histologically between *M. marcai* and *Callibella humilis*, except for the for the fact that the connective tissue septum arising from the tunica albuginea split the corpus cavernosus into two portions all along the penis in the latter species (Weber et al., 2016).

Different from *M. radiata* (Prakash et al., 2009), the dartos tunic could not be identified in the scrotum of the specimens studied, supporting findings of Beattie (1927) and Teixeira (2005) regarding *C. jacchus* and *Sapajus apela* respectively. In contrast, similar to *Callithrix argentata* (Hershkovitz, 1977; Perkins, 1969), *C. jacchus* (Sutcliffe & Poole, 1978) and *Saguinus fuscicolis* (Zeller, Epple, Kuderling, & Kuhn, 1988), large numbers of sebaceous glands were observed.

This is the first descriptive and comparative analyses of male genitalia of *M. marcai*. Although we identified similarities of the material analysed here with those anatomical characteristics found for other primates, there are some particularities of shape and size of the genitalia of this marmoset. The testicles and accessory glands associated with the small pelvic urethra and the remarkable presence of keratinised spines and its baculum are evidences that support a monogamous reproductive behavioural system. Data presented are a baseline for further morphological descriptions and for studies in primate reproductive biology.

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