

1 **(i) Title**

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3 MORPHOLOGICAL DESCRIPTION OF MALE GENITAL ORGANS OF MARCA'S MARMOSET (*Mico*
4 *marcai*)

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6 **(ii) Running head**

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8 MORPHOLOGICAL DESCRIPTION OF MALE GENITAL ORGANS OF *Mico marcai*

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10 **(iii) Authors**

11

12 Gustavo Henrique Lima de Siqueira¹

13 Felipe Ennes Silva²

14 Marcelo Ismar Silva Santana¹

15

16 **(iv) Author's affiliations**

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18 ¹ Wild Animal Anatomy Laboratory, School of Agricultural Sciences and Veterinary Medicine,
19 University of Brasília, Brasília, DF, Brazil; ² School of Environment & Life Sciences, University of
20 Salford, Salford, United Kingdom, Institute for Sustainable Development Mamirauá, Tefé, AM, Brazil.

21

22 **(v) Summary**

23

24 Morphological characterization of the genital organs of primates may bring significant contributions
25 to the understanding of different reproductive behaviours and support new conservation strategies.
26 However, relevant or detailed descriptions of genital morphology of several primate species are still
27 lacking. This study describes the gross and microscopic anatomy of the internal and external
28 genitalia of Marca's marmoset (*Mico marcai*). The same organs described in other primate species
29 were identified here, but some anatomical particularities were detected, such as absence of a dartos
30 tunic, presence of a vas deferens ampulla, absence of spongy erectile tissue in the pelvic urethra,
31 separation of prostate gland lobes by a longitudinal sulcus and lack of septation in the corpus
32 cavernosus and spongiosus at the level of the shaft and free portion of the penis. Keratinized type
33 1 spicules arising from epidermal or dermal projections were found in the free portion of the penis.

34 Microscopic analysis revealed a small bone (baculum) consisting of peripheral compact bone and a
35 central, non-ossified area filled with vascular tissue at the distal end of this portion of the penis.
36 Results of this study may support further comparative studies of primates reproductive ecology.

37

38 **Keywords:** Marmosets, Primates, Amazon Rainforest, Genital Organs, Morphology.

39

40 **(vi) Number of figures and tables**

41

42 Figures: 5 (five)

43

44 Tables: 4 (four)

45

46 **(vii) Main Text**

47

48 INTRODUCTION

49

50 The literature on the morphology of Neotropical Primates is well represented by a number of
51 taxonomic (e.g. Kobayashi, 1955; Hershkovitz, 1977; Lynch-Alfaro et al. 2012), ecological (e.g.
52 Sussman & Kinzey, 1984; Anapol & Lee, 1994, Garber & Rehg, 1999) and evolutionary studies (e.g.
53 Marroig & Cheverud, 2001, 2005). However, only few authors have contributed to understand the
54 importance of anatomical studies of genitals organs on the reproductive behavior and ecology of
55 primates (Dixon, 1989; Harcourt & Gardiner, 1994; Dixon 1998; Stockley 2002).

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

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

74

75 MATERIALS AND METHODS

76

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

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

88 Following gross characterization, tissue samples were collected from all genital organs.
89 Processing cassettes containing tissue fragments were immersed in 70% alcohol and washed in
90 Tissue-Tek® VIP® Jr. for dehydration in increasing (80% to 100%) ethanol concentrations and xylol
91 diaphanization.

92 Paraffin embedding and serial 5µm tissue slicing were performed using Leica EG1150 embedding
93 centre and Leica RM2125RT microtome respectively. Tissue sections were mounted on glass slides,
94 deparaffinized, stained with Hematoxylin-Eosin or Masson's trichrome and cover-slipped using
95 Entelan (Merck®). Slides were then analyzed under light microscopy (Olympus CX40 binocular
96 microscope) and photographed at different optical magnifications (40x, 100x, 200x and 400x) using
97 Leica DFC290 HD photomicroscope.

98 Anatomical descriptions in this study are in compliance with Nomina Anatomica Veterinaria
99 (2017).

100

101 **RESULTS**

102

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

104

105 Scrotum and Prepuce

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

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

121

122 Testes

123 The paired, levelled testes lied in different compartments within the scrotum and were separated
124 by a scrotal septum, externally visible as the scrotal raphe. This raphe ran from the perineal region
125 to the ventral segment of the prepuce and divided the scrotum in half (Fig. 1c). The oval-shaped
126 testes were similar in weight and size (Tables 1 and 2 respectively); testes were elongated in the
127 dorsoventral direction, with subtle laterolateral flattening and craniocaudal tilt (Fig. 1a).

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

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

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

140

141 Epididymis

142 The epididymis had an elongated "C" shape and was completely attached to the epididymal
143 border of the testes. Three distinct portions were identified: a large, flat head attached to the
144 extremitas capitata of the testis, a thin, elongated body running along the posterior testicular border
145 and a tail corresponding to a small, globose enlargement attached to the extremitas caudata of the

146 testis and continuous with the vas deferens. Of these, the epididymal head was the most prominent
147 (Table 2) (Fig. 1a).

148 The epididymal duct could be easily identified through the thin epididymal surface (Fig. 1a) as a
149 mesh of convoluted tubules lined with pseudostratified columnar epithelium containing stereocilia
150 and characterized by tall cells with slightly vacuolated, weakly stained cytoplasm and oval-shaped
151 or elongated nuclei located at the cell base or centrally. Tubules were also lined with a thin basal
152 lamina and surrounded by moderate amounts of fibrovascular tissue and smooth muscle cells (Fig.
153 3a-f).

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

158

159 Vas Deferens

160 The narrow vas deferens (Table 3) originated from the tail of the epididymis (Fig. 1a) and ran
161 along its body in a linear fashion. A small enlargement, the vas deferens ampulla (Table 3), formed
162 prior to the attachment to the urethral parenchyma (Fig. 1a) and extended to the ejaculatory
163 ostium.

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

171

172 Vesicular Gland

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

178 Each lobe was enveloped in large amounts of fibrovascular tissue consisting of dense connective
179 tissue with longitudinally or transversally oriented fibres. Moderate amounts of smooth muscle
180 fibres and small numbers of adipocytes were also noted; these encapsulated the organ and formed
181 the stroma, supporting and dividing the gland into lobes lined with pseudostratified epithelium.
182 Large amounts of amorphous material were observed in the glandular lumen (Fig. 4e,f).

183

184 Prostate Gland

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

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

191 Large amounts of fibrovascular tissue consisting of compact connective tissue, moderate
192 amounts of smooth muscle fibres and small numbers of adipocytes encapsulated the prostate and
193 formed the gland stroma. The stroma provided support and gave rise to several lobules containing
194 tubuloalveolar gland acini with digitiform projections supported by a delicate fibrovascular stroma,
195 which determined variable lumen width (Fig. 4a-c). Glandular lining consisting of a single layer of
196 polyhedral to columnar cells with finely stippled, weakly stained cytoplasm and round nuclei
197 predominantly located at the cell base. Small amounts of amorphous to granular material consistent
198 with serous content were found in the glandular lumen (Fig. 4d).

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

203

204 Bulbourethral Glands

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

207 Histologically, each gland was covered with small amounts of longitudinally and transversally
208 oriented collagen and skeletal muscle fibres intermingled with moderate amounts of fibrovascular
209 stroma and sparse smooth muscle cells (Fig. 4g). The stroma gave rise to a lobed pattern
210 characterized by thinly separated lobes formed by multiple tubules and acini comprising a single

211 layer of weakly stained columnar cells with round shaped to flattened nuclei located close to their
212 base. Small amounts of amorphous material were observed within some tubular units (Fig. 4g,h).
213 Bulbourethral duct systems were histologically similar to prostate gland duct systems (Fig. 4g).

214

215 Pelvic Urethra

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

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

228

229 Penis

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

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

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

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

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

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

260 The free portion of the penis contained a superficial layer of paved epithelium (Fig. 4d-i). Type 1
261 spicules arising from epidermal or dermal projections into the epidermis and containing multiple
262 layers of keratin, or presenting as corneal pearls, were found in multifocal areas of this epithelium
263 (Fig. 5d-h). The superficial dermis consisted of small amounts of loose connective tissue, while the
264 deep dermis contained dense connective tissue (Fig. 5g) with large numbers of collagen fibres and
265 small numbers of vessels and nerves. Large numbers of nerves and moderate numbers of venous
266 plexi were found at the transition to the tunica albuginea, particularly at the dorsal and ventrolateral
267 portions of the penis (Fig. 5d-f). In a deeper plane, the tunica albuginea surrounded the corpora
268 cavernosa and corpus spongiosus (Fig. 5d-f,i). The penile urethra remained within the corpus
269 spongiosus and was lined with transition or pseudostratified epithelium to the level of the external
270 ostium of the urethra, located caudoventral to the apical portion of the penis (Fig. 5d-f,h,i). Paved
271 epithelium lined the penile urethra from this point (Fig. 5h).

272 At the level of the free portion of the penis, the corpus cavernosus was gradually and largely
273 replaced by fibrous connective and adipose tissue; at its proximal end, small amounts of
274 fibrocartilaginous (Fig. 5d-f,h,i) tissue gave rise to a small penile bone dorsomedial to the penile
275 urethra (Fig. 5f,h,i). This microscopic, semiconical baculum was externally formed by mature bone

276 tissue consisting of bone matrix, osteocytes and osteoblasts and surrounded by thin layers of
277 collagen, fibroblasts and cartilaginous tissue and, more superficially, by compact connective tissue
278 containing moderate numbers of vessels and nerves. The central portion of the penile bone
279 consisted of well vascularized trabecular bone with dense ossification foci and adipose tissue (Fig.
280 5f,h,i).

281

282 **DISCUSSION**

283

284 *Mico marcai* had similar internal and external genital organs to other genera of primates such as
285 *Callimico goeldii*, *Simia entellus* (*Presbytis entellus entellus*), *Sapajus apella*, *Macaca radiata*,
286 *Chlorocebus aethiops*, and to monkeys in the genus *Hylobates* (Hill, 1959; Hill & Kanagasuntheram,
287 1959; David & Ramaswami, 1971; Teixeira, 2005; Lebelo, 2007; Prakash, Suresh, & Prithiviraj, 2009;
288 Dixson, 2012). However, proportions differed, as this anatomical feature is directly related to body
289 weight (Harcourt, Purvis & Liles, 1995).

290 *Mico marcai* testes were proportionally smaller compared to body weight, a feature consistent
291 with monogamous mating behaviour (Harcourt et al., 1981; Harcourt, Purvis & Liles, 1995). Similar
292 to other *Mico* species, *Mico marcai* social units observed in nature consisted of four individuals on
293 average (Ennes, Nunes & Bastos, 2013). However, lack of genetic evidence precludes conclusive
294 statements regarding the monogamous mating behavior of free-ranging marmosets at this stage
295 (Garber et al., 2015).

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

300 According to Anderson and Dixson (2009), vesicular and prostate gland size may be directly
301 related to relative testicular size in primates, i.e., animals with larger testicles are expected to have
302 larger glands. Well-developed glands are therefore consistent with multimale-multifemale mating
303 systems such as in *Saimiri*, which vesicular glands measure up to seven centimetres in length (Hill,
304 1960). Vesicular glands are comparatively less developed in *Mico marcai* (approximately 1 cm long)
305 and other monogamous genera such as *Callimico*, *Callithrix*, *Saguinus* and *Aotus*, and vestigial in
306 *Callicebus* and *Pithecia* (Hill, 1959; Dixson, 1998).

307 Such as in Neotropical and Old World Primates, *Mico marcai* vesicular glands corresponded to
308 lobed, pleated structures lined with pseudostratified columnar epithelium and arising directly from

309 the pelvic urethra (Hill, 1960; Prakash, Suresh, & Prithiviraj, 2009). In contrast with descriptions
310 given by Teixeira (2005) and Prakash, Suresh, & Prithiviraj (2009), the prostate gland lied dorsal to
311 the pelvic urethra and therefore did not envelop or penetrate the urethral wall (Hill &
312 Kawagasuntheram, 1959; David & Ramaswami, 1971; Oelrich, 1978; Ganzer et al., 2004; Mubiru et
313 al., 2007).

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

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

328 The small bulbourethral glands of *Mico marcai* were similar in shape to those of *Callimico goeldii*
329 and *Gorilla* and similar in size to those of *Callimico goeldii* (Hill, 1959; Oelrich, 1978). Prakash, Suresh,
330 & Prithiviraj (2009) were the only authors to associate the rudimentary size of these glands to the
331 polyandrous mating system described in *Macaca radiata*, suggesting a functional compensatory
332 effect - namely the production of larger volumes of fluid by the developed portion of the vesicular
333 glands for sperm cell transport and formation a solid cervicovaginal clot. Histological confirmation
334 of fully functional parenchyma in *Mico marcai* suggests this compensatory effect does not occur in
335 this species, despite small bulbourethral gland size.

336 Just as in *Callimico goeldii* and *Pan troglodytes*, the tail of the epididymis of *Mico marcai*, although
337 smaller, was more prominent than the head and round rather than triangular in shape, while the
338 epididymal body was narrow and thin (Hill, 1959; Martin & Gould, 1981). Histological findings in this
339 species were similar to descriptions given of genera *Macaca* and *Pan*, including the progressive
340 reduction in height of the pseudostratified epithelium overlying the head and tail of the epididymis,
341 the presence of stereocilia in all epididymal segments and the collection of sperm cells within the

342 epididymal tail (Ramos & Dym, 1977; Alsum & Hunter, 1978; Smithwick & Young, 1997; Lebelo,
343 2007).

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

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

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

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

369 The presence of type 1 spicules in the free portion of the penis of *Mico marcai* is thought to be a
370 feature common to most *Callitrichidae* (genera *Mico*, *Callibella*, *Callithrix*, *Callimico* and
371 *Leontopithecus*), which has not been described in genera *Cebuella* and *Saguinus* (Perkins, 1969;
372 Hershkovitz, 1977; Dixon, 2012; Weber et al., 2016).

373 The small-sized baculum is consistent with descriptions given of all other *Callitrichidae* and
374 primates in genera *Aotus* and *Pithecia*; this bone is lacking in monkeys in genera *Cacajao*, *Chiropotes*,

375 *Ateles*, *Lagothrix* and *Alouatta* (Hershkovitz, 1977; Dixson, 2012; Weber et al., 2016). Despite its
376 small size, *Mico marcai* baculum was histologically similar to that of *Sapajus apella* and other
377 *Callitrichidae* (Hershkovitz, 1977; Teixeira et al., 2015; Weber et al., 2016).

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

386 Different from *Macaca radiata* (Prakash, Suresh, & Prithiviraj; 2009), the dartos tunic could not
387 be identified in the scrotum of the specimens studied, supporting findings of Beattie (1927) and
388 Teixeira (2005) regarding *Callithrix jacchus* and *Sapajus apela* respectively. In contrast, similar to
389 *Callithrix argentata* (Perkins, 1969; Hershkovitz, 1977), *Callithrix jacchus* (Sutcliffe & Poole, 1978)
390 and *Saguinus fuscicollis* (Zeeler et al., 1988), large numbers of sebaceous glands were observed.

391 This is the first descriptive and comparative analyses of male genitalia of *Mico marcai*. Although
392 we identified similarities of the material analyzed here with those anatomical characteristics found
393 for other primates, there are some particularities of shape and size of the genitalia of this marmoset.
394 The testicles and accessory glands associated with the small pelvic urethra and the remarkable
395 presence of keratinized spines and its penile bone (crotch) are evidences that support a
396 monogamous reproductive behavioral system. Data presented are a baseline for further
397 morphological descriptions and for studies in primate reproductive biology.

398

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400

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405

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552

553 **(xi) Tables**

554

555 Table 1 – *Mico marcai* (Mm) body and testicular weight measurements (g) and percentage of the
556 testis weight in comparison with body weight (%).
557

	Testicular Weight (TW)		Body Weight (BW)	% TW x 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

558

559 Table 2 – *Mico marcai* (Mm) testicular and epididymal length (L), width (W) and thickness (T)
560 measurements (mm).
561

Organ	Testicles						Epididymis											
	Antimer	Right			Left			Right			Left							
Measure		L	W	T	L	W	T	Head			Tail			Head			Tail	
	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

562

563

564 Table 3 – *Mico marcai* (Mm) vas deferens, vas deferens ampullae, pelvic urethra and penis length
 565 (L) and diameter (D) measurements (mm).
 566

Organ	Vas Deferens				Ampullae				Pelvic Urethra		Penis					
	Antimer	Right		Left		Right		Left			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

567

568 Table 4 – *Mico marcai* (Mm) vesicular, prostate and bulbourethral gland length (L), width (W) and
 569 thickness (T) measurements (mm).
 570

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

571

572

573 **(xii) Figure legends**

574

575 **Fig. 1.** Photograph of *Mico marcai* male genitalia. (a) Complete set of genital organs - testes,
 576 epididymis, vas deferens, vas deferens ampulla, vesicular glands, prostate gland, pelvic urethra,
 577 bulbourethral glands and root, shaft and free portion of the penis (scale: 1cm); (b) Free portion of

578 the penis – note apex and spicules (scale: 0.5cm); (c): Scrotum – note the wrinkled skin, raphe and
579 close relationship with the prepuce (scale: 1cm). **Legend:** T: Testes; CapE: Head of the epididymis;
580 CauE: Tail of the epididymis; VD: Vas deferens; AVD: Vas deferens ampulla; GV: Vesicular gland; GP:
581 Prostate gland; GB: Bulbourethral glands; RP: Root of the penis; CP: Shaft of the penis; PLP: Free
582 portion of the penis; APL: Apex of the free portion of the penis; PS: Penile spicules; S: Scrotum; Pre:
583 Prepuce.

584
585 **Fig. 2.** Photomicrograph of *Mico marcai* scrotum, paratesticular tissues, prepuce, penis and testicle.
586 (a) Scrotal skin, sebaceous and sweat glands, paratesticular tissues and testicular parenchyma –
587 note the cremaster muscle surrounded by cremasteric fascia (blue circle) (TRI; 40x); (b) Prepuce,
588 preputial cavity, preputial diverticulum (black circle), free portion of the penis and penile urethra
589 (longitudinal section; HE, 100x); (c) Testicular parenchyma - note high density of seminiferous
590 tubules and scarce interstitial tissue with low cellularity (HE, 40x); (d) Testicular parenchyma - note
591 seminiferous tubules, male germ lineage, Sertoli (blue arrow) and Leydig (black arrow) cells (HE,
592 40x). **Legend:** SwG: Sweat gland; SbG: Sebaceous gland; TA: Tunica albuginea; T: Testicular
593 parenchyma; Pre: Prepuce; PC: Preputial cavity; PenU: Penile urethra; ST: Seminiferous tubules; I:
594 Interstitium; Black star: support tissue; HE: Hematoxylin-Eosin; TRI: Masson's Trichrome.

595
596 **Fig. 3.** Photomicrograph of *Mico marcai* epididymis and vas deferens. (a) Head of the epididymis -
597 note highly convoluted tubules (HE, 40x); (b) Head of the epididymis (HE, 400x); (c) Body of the
598 epididymis and adjacent testicular parenchyma (HE, 40x); (d) Body of the epididymis (HE, 400x); (e)
599 Tail of the epididymis, convoluted tubules and vas deferens (HE, 40x); (f) Tail of the epididymis (HE,
600 400x); (g) Vas deferens – note pleated epithelium (red arrow), inner (blue double-headed arrow)
601 and outer (yellow double-headed arrow) smooth muscle layers (TRI, 200x); (h) Vas deferens ampulla
602 – note circular and longitudinal smooth muscle layers of the vas deferens wall (blue and yellow
603 double arrows) (HE, 40x); (i) Vas deferens ampulla – note pleated epithelium (red arrow) and inner
604 smooth muscle layer (blue double-headed arrow) (HE, 200x). **Legend:** CapE: Head of the epididymis;
605 CorE: Body of the epididymis; CauE: Tail of the epididymis; PsE: Pseudostratified epithelium; L:
606 Lumen; Sptz: sperm cells; T: Testicular parenchyma; VD: Vas deferens; AVD: Vas deferens ampulla;
607 Black arrow: Stereocilia; Black star: Support tissue; HE: Hematoxylin-Eosin; TRI: Masson's Trichrome.

608
609 **Fig. 4.** Photomicrograph of *Mico marcai* pelvic urethra, prostate, vesicular and bulbourethral glands.
610 (a) Pelvic urethra, prostate and vesicular glands – note muscle layers of the pelvic urethra (black
611 double-headed arrow) (HE, 40x); (b) Prostate gland - relationship with the pelvic urethra; note
612 interlobar connection (double blue arrow), glandular ducts (black arrow) and muscle layers of the
613 pelvic urethra (black double-headed arrow) (HE, 40x); (c) Prostate gland - relationship with the pelvic
614 urethra; note prostate lobe (blue circle), interlobar septum (green double-headed arrow), glandular
615 ducts (black arrow) and muscle layers of the pelvic urethra (black double-headed arrow) (TRI, 40x);
616 (d) Prostate gland – note simple glandular epithelium (blue arrow) (HE, 400x); (e) Vesicular gland -
617 note vesicular gland lobe (red circle) and projection of the epithelium into the lumen (red star) (HE,
618 40x); (f) Vesicular gland - note pseudostratified glandular epithelium (red arrow) and projection into
619 the lumen (red star) (HE, 400x); (g) Bulbourethral gland - relationship with the pelvic urethra
620 (longitudinal section); note bulbourethral gland lobe (yellow circle) and glandular ducts (black
621 arrow) (HE, 40x); (h) Bulbourethral gland – note simple glandular epithelium (yellow arrow) (HE,
622 400x); (i): Pelvic urethra at prostate level (HE, 200x). **Legend:** GV: Vesicular gland; GP: Prostate
623 gland; GB: Bulbourethral gland; PelU: Pelvic urethra; L: Lumen; PsE: Pseudostratified epithelium of
624 the pelvic urethra; Black star: Support tissue; HE: Hematoxylin-Eosin; TRI: Masson's Trichrome.

625

626 **Fig. 5.** Photomicrograph of *Mico marcai* penile structures. (a) Root of the penis - note corpus
627 spongiosus, septated corpus cavernosus, tunica albuginea, septum and urethra (HE, 40x); (b) Root
628 of the penis - note corpus spongiosus, septated corpus cavernosus, tunica albuginea, septum,
629 urethra and muscle tissue (TRI, 40x); (c) Body of the penis - note single corpus cavernosus, tunica
630 albuginea and urethra (TRI, 40x); (d) Free portion of the penis - note single corpus cavernosus, tunica
631 albuginea, urethra, spicules and prepuce (HE, 40x); (e) Free portion of the penis showing the single
632 corpus cavernosus as it is replaced (HE, 40x); (f) Free portion of the penis and penile bone (HE, 40x);
633 (g) Skin overlying the free portion of the penis, with spicules (HE, 200x); (h) Free portion of the penis
634 (longitudinal section) - note external urethral ostium and keratinized squamous epithelium (black
635 circle) (HE, 40x); (i) Free portion of the penis (longitudinal section) (HE, 40x). **Legend:** PenU: penile
636 urethra; CCP: Corpus cavernosus of the penis; CSP: Corpus spongiosus of the penis; TA: Tunica
637 albuginea of the penis; Sep: Septum dividing the corpus cavernosus; M: Skeletal muscle; Black star:
638 Support tissue; KE: Keratinized squamous epithelium overlying the glans; PS: Penile spicules; Black
639 arrow: Nerves; Pre: Prepuce; OP: Penile bone; D: Dermis; APL: Apex of the free portion of the penis;
640 HE: Hematoxylin-Eosin; TRI: Masson's Trichrome.
641