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1 **TITLE**

2 Sexual selection and sperm diversity in primates

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15 **KEYWORDS:** sexual selection; sperm competition; semen evaluation; testes; sperm
16 allocation; trade-off

17

18 **ABSTRACT:** 150 words maximum

19 Many aspects of primate sperm physiology and reproductive behavior have been
20 influenced by sexual selection, especially in taxa exposed to sperm competition where
21 females mate with multiple partners. Primate sperm diversity reflects therefore the
22 evolutionary divergences of the different primate species and the impact of a
23 combination of variables exerting selection pressures on sperm form, function, and
24 competition. Thereby, mating systems, life cycle or ecological variables are some of the
25 important factors driving sperm diversity and explaining variation in terms of sperm
26 morphology, parameters or male sexual characters. Here, we address primate sperm
27 diversity through a compilation of all data available in the literature concerning primate
28 sperm parameters and relationships between them. We then review the most important
29 variables, e.g. seasonality, social constraints or trade-off between investments in
30 precopulatory and postcopulatory sexual traits, which can influence primate sperm
31 diversity and discuss also their relevance to our understanding of human reproduction.

32

33 INTRODUCTION

34 Mammalian spermatozoa are motile, highly differentiated and oriented haploid cells
35 with a specific size, shape and axes of symmetry. They are composed of a head and a
36 flagellum and of various subcellular structures adapted to the physiological processes
37 that are essential for the reproduction of the species (capacitation, acrosomal reaction,
38 gametic fusion). Basic head structure is a haploid nucleus containing a highly
39 compacted chromatin, with very little cytoplasm and covered at the apical pole by the
40 acrosome, a large secretion vesicle derived from the Golgi apparatus. The flagellum
41 ensures cell mobility and is divided into three parts: an intermediate piece surrounded
42 by a mitochondria sheath, a large main piece and a short terminal piece. This base
43 structure is preserved in all mammals with specificities for some taxa such as the head
44 sickle shape in rodents.

45 Primates are an order within placental mammals that includes more than 500 species.
46 While primate sperm displays a considerable uniformity, there are still some variations
47 between species in terms of sperm morphology and overall sperm parameters. This
48 primate sperm diversity reflects the evolutionary divergences of the different taxa and is
49 the result of a combination of variables exerting selection pressures on them, such as
50 mating system variables, life cycle characteristics or ecological variables.

51 The first part of this review will describe primate sperm diversity through a compilation
52 of all data available in the literature. The second part will be devoted to the most
53 important mechanisms and factors influencing sperm form, function, and competition
54 across primates.

55 1. About primate form and shape

56 1.1. Sperm morphometry

57 The action of centripetal forces on spermatozoa evolution has considerably reduced
58 morphological variations between the different species and created an overall
59 mammalian morphometric uniformity (1980 Gould). Sperm global shape is well
60 preserved among primates, but some interspecies variations are still observed, mainly
61 regarding spermatozoa length. We compiled species-specific primate sperm
62 morphometric data of 76 primates (table 1). Across all species analyzed, mean±SE total
63 sperm length is 70.69 ± 10 μM with a ratio of 2.4 between the shortest and longest
64 representatives *Lepilemur mustelinus* (52 μM) and *Ateles paniscus* (124.61 μM). With a
65 56.15 μM total length, *Homo sapiens* is below average and also the shortest
66 representative of Hominidae family, more than 15% less than *Pongo pygmaeus*. Head
67 length ranged from 2.8 to 9.0 μM with a mean of 5.83 ± 0.84 μM , accounting for 8.2 %
68 of total sperm length. Midpiece length ranged from 3.56 to 20.7 μM with a mean of
69 10.07 ± 2.13 μM , accounting for 14.3 % of total sperm length. Tail length ranged from
70 17.3 to 83.5 μM with a mean of 55.14 ± 10.10 μM , accounting for 77.9 % of total sperm
71 length. Human sperm are again under average among primates, especially regarding the
72 midpiece length.

73 Sperm length is the result of a complex set of evolutionary pressures such as the female
74 reproductive tract (2012 Higginson), metabolic requirements of sperm (2011
75 Gomendio) or sperm competition which can exert a positive (2009 Fitzpatrick) or
76 negative (1997 Stockley) influence (see below in 2.1). In human, having long
77 spermatozoa appears to be an advantage as the overall lengths of sperm components and
78 their degree of variability within an ejaculate have been positively associated with
79 sperm concentration and motility (2013 Mossman), which are significant fertility
80 determinants.

81 Regarding the head, human sperm is similar to the chimpanzee shape (ellipticity=1.61
82 and elongation=0.23). However, the pleiomorphic nature of human ejaculate allows us
83 to identify two populations similar to those observed in other great apes, albeit with
84 smaller volumes. The first is similar to orangutans sperm with a large paddle-shaped
85 head and thinner in the vertical dimension (ellipticity=1.40 and elongation=0.17). The
86 second is similar to gorilla, with a shape intermediate to the previous two
87 (ellipticity=1.38 and elongation=0.16).

88 **1.2. Sperm parameters**

89 We compiled literature data on sperm parameters from 43 primate species. Summarized
90 in [table 2](#), these data support the known high heterogeneity of primate ejaculates, both
91 at the inter- and intra-species levels.

92 **1.2.1. Collection method**

93 1.2.1.1. Masturbation

94 Masturbation is the natural and best collection method to obtain ejaculates truly
95 representative of testicular function. In human, semen analyses are therefore carried out
96 on samples obtained by masturbation under specific disinfection and abstinence
97 protocols. While the aseptic conditions of the human clinic are clearly not reproducible
98 for other primates, it is still possible to obtain great ape masturbation samples from
99 Gorilla (1997 Pope, 2005 O'brien, 2008 Nascimento), Pan (1988 Marson, 1993 Gould,
100 1995 Young, 1998 Younis, 2004 Kuehl, 2005 Agca, 2008 Nascimento, 2018 Yu) and
101 Pongo (1995 Joslin), with higher total sperm counts and fewer abnormal forms than
102 samples obtained via electrostimulation methods (1989 Schaffer, 1995 Gould, 1995
103 Young, 1996 Gould). Semen collection can be manual as part of specific training or
104 assisted via artificial vaginas.

105 As male masturbation is the most frequent sexual behavior observed after copulation
106 (2003 Thomsen, 2005 Frearson, 2012 Dixson) for primate species, another method
107 consists in collecting the products of punctual masturbation on the ground (in *Macaca*
108 (2014 Thomsen), *Papio* (1969 Kraemer) and *Chlorocebus* (1999 Hiyaka)). This non-
109 invasive collection method allows some precious semen analysis (2004 Dejuq-
110 Rainsford, 2006 Thomsen, 2012 Inoue), but soil contamination prevents us from
111 accurately assessing the quality and fertilizing potential of the male. Another pitfall
112 associated with these samplings is the potential difficulty of quickly collecting the
113 material prior its consumption by the male (personal observations).

114 1.2.1.2. Epididymal extraction

115 Samples obtained by epididymal extraction are numerous and are mainly collected
116 opportunistically following castrations (2000 Gupta) or in post-mortem contexts (2001
117 Kusunoki, 2005 Anderson, 2008 Dong). Analysis of sperm from the tail of the
118 epididymis allows to acquire some data on sperm morphometry or production but is not
119 representative of an individual's ejaculate and fertility potential.

120 1.2.1.3. Electro-stimulation

121 Electro-stimulation (ES) is the most widely used method for primate semen collection
122 (1968 Ackerman, 1978 Gould, 1980 Platz, 1983 Bader, 2002 Aslam, 2003 Amboka,
123 2007 Vidal, 2009 Da Silva, 2016 Oliveira, 2016 Swanson, 2017 Sampaio, 2018
124 Devilliers, 2019 Arakaki) including Human (1996 Nehra). Using rectal probe or penis
125 electrodes, ES has many practical and logistical advantages (no training required,
126 programmable in time, sleeping individuals), but this approach has also several
127 drawbacks.

128 Indeed, ES is restricted to facilities with a laboratory because of the devices needed for

129 basic (incubator, centrifuge) or advanced sperm analysis (CASA device) and the
130 monitoring period required at the end of the experiment due to the invasive nature of the
131 method. Beyond the dangers associated with the capture and immobilization of an adult
132 male in the wild, this induces a high level of stress to the subject but also to the group as
133 a whole (2014 Thomsen), with possible negative repercussions at reintroduction time. In
134 order to obtain consistency in physiological response, specific protocols have to be
135 establish for each species regarding both anesthetic and stimulation phase (1990
136 Durrant, 1996 Morrell). Anesthesia presents significant health risks for the animals and
137 limits the sampling frequency, whereas the stimulation phase requires trained
138 technicians, with rectal probe placement being essential to obtain ejaculation and avoid
139 burns. Even with robust protocols, some studies indicate that ejaculates obtained by ES
140 tend to contain more immature sperm (1992 Matsubayashi, 1996 Morrell, 2014
141 Thomsen) and more coagulum formation (1986 Wildt, 1989 Schaffer) than those
142 obtained by masturbation.

143 It should be noted that urethral massage is a good complement to electro-ejaculation
144 techniques to recover residual semen and increase the volume of the sample.

145 Finally, ES appears to be best suited for larger primates and safer alternative methods
146 (vaginal washing and penile vibrostimulation; see below for further details) have been
147 developed for smaller species for which ES may be unsuitable or unsuccessful (1996
148 Morrell, 2000 Kuederling, 2004 Schneiders).

149 1.2.1.4. Vaginal washing

150 Vaginal washing (VW) consists of retrieving a male's ejaculate by washing a female's
151 vagina quickly after a successful coitus. This method has been developed in small
152 primates, such as marmosets (1996 Kuederling, 1996 Morrell, 1997 Morrell, 1998

153 Morrell, 2004 Schneiders) and macaques (1973 Cho), for which sedation is not required
154 to obtain the sample. Although VW allows the collection of natural ejaculates for
155 assisted reproduction techniques (1996 Kuderling, 1996 Morrell, 1997 Morrell, 1998
156 Morrell), it is less efficient for sperm parameters analysis as the sample is contaminated
157 by secretions and some of it is lost in the female genital tract (1996 Kuderling, 1996
158 Morrell). VW protocols are time-consuming to set up and carry out, and have to be
159 species-specific (2004 Schneiders). The VW is therefore effective but limited to specific
160 applications in small species at this time.

161 1.2.1.4. Penile vibrostimulation

162 This procedure provides ejaculate through normal ejaculation via application of
163 vibration to the penis of a restrained individual. Although there is no need to sedate the
164 animal, it must be trained to the restriction chair. This method proved its worth in
165 marmosets (2000 Kuederling, 2005 Hernandez-Lopez, 2005 Valtonen, 2012 Valle, 2016
166 Swanson, 2018 Arakaki), macaques (2000 Kholkute) and saïmiris (1997 Yeoman, 1998
167 Yeoman).

168 The main benefit of this procedure is, as with masturbation, the production of a natural
169 ejaculate that displays a higher number of motile and total sperm versus
170 electrostimulation (1995 Young, 1997 Yeoman, 1998 Yeoman). The main concern is that
171 this protocol is obviously challenging to implement for great apes, but recent studies
172 (2018 Arakaki) pointed out that, with species-specific adaptations, this technique could
173 be very promising.

174 In conclusion, from a practical point of view, inter-species constraints do not allow to
175 propose an optimal method consensus and each collection must be considered on a case-
176 by-case basis according to the species and to the context. From a biological point of

177 view, ejaculates obtained through natural ejaculation (masturbation and
178 vibrostimulation) proved their superiority and should be favored when possible.

179 **1.2.2. Sperm motility**

180 The average primate has about two-thirds motile sperm in an ejaculate, a proportion that
181 logically correlates with vitality (measured as the percentage of intact membrane
182 sperm). It is challenging to interpret motility data because of the very high variability in
183 the percentage of motile sperm with ejaculates ranging from almost fully motile to fully
184 immobile present in all families.

185 The heterogeneity of motility data comes in part from the inherent limitations of data
186 collection protocols (discussed in section 1.3), but mostly from the existence of sperm
187 subpopulations in mammalian ejaculates (2004 Holt). Many studies concluded that
188 variations among these sub-populations have functional relevance with identified
189 associations to fertility or post-freezing survival outcomes (2001 Thurston, 2006
190 Martinez, 2008 Muino, 2009 Ortega-Ferrusola, 2010 Dorado, 2013 Ramon, 2014
191 Beracochea, 2015 Yaniz, 2016 Santaloria).

192 Although the development of computer-assisted sperm analysis (CASA) systems has
193 made it possible to bring more accuracy and depth to mobility studies, the majority of
194 the observations compiled here have been carried out manually by technicians, as these
195 systems are rarely used outside of human medicine. Among CASA parameters, average
196 straight-line velocity is recognized as a main factor in fertility (1999 Birkhead, 2005
197 Malo) and have previously been correlated with total sperm length (2009 Lupold, 2009
198 Gomez Montoto, 2011 Tourmente) and relative testes mass in mammals (2011
199 Tourmente). However, in light of the limited data available for mobility parameters in
200 the literature ([table 3](#)), it is not yet established whether these results can be reproducible

201 for primates alone.
202 Nevertheless, we can observe that human has a curvilinear velocity, a proxy for the
203 effective sperm velocity, lower than that of other primates. This confirms conclusions of
204 previous studies (2011 Maree) showing that sperm from polygynandrous primate
205 species swims faster than human one. Motility percentages for *Homo* and *Gorilla* taxa
206 are lower than those of *Pan* and *Pongo*, which suggests that sperm from
207 polygynandrous primates swim faster than sperm from species less exposed to sperm
208 competition in general. It is also plausible that the mobility alterations in *Homo* and
209 *Gorilla* are only the result of the pleiotropism present in the ejaculate of these taxa,
210 abnormal forms sperm producing lower velocities than normal form sperm. Again, the
211 limited number of studies using CASA does not allow us to reach a robust conclusion.
212 Other issues would also benefit from more CASA studies, for example, we still do not
213 know if larger sperm swim faster when there is a higher risk of sperm competition in
214 some primate species like demonstrated in rodents (2011 Montoto).

215 **1.2.3. Sperm morphology**

216 In human reproductive medicine, the criteria for defining normal-form sperm (NFS)
217 have been established by averaging the observed characteristics of the sperm population
218 that reach the oocyte (2010 Cooper). Morphological analyses of assisted reproduction
219 centers are mostly based on the World Health Organization guidelines on semen
220 analysis, which use very strict analysis criteria and a pathological cutoff established at
221 4% NFS. Based on these criteria, the species presenting the lowest and highest rates of
222 NFS are from the Hominidae family with 23.75% and 98.5% NFS for *Gorilla gorilla*
223 and *Pongo pygmaeus* respectively.

224 Of all 43 primate species studied, the spermatozoa from the ejaculate of Human and

225 Gorilla spp. are the only ones characterized by an extreme pleiomorphism with 23.75%
226 and 32.22% NFS respectively. These two species also exhibit more variation in size and
227 shape within a single ejaculate than some species between them. The pleiomorphic
228 nature of sperm found in both species does not seem to affect their fertility, whereas
229 when abnormal forms are found in other species, they are associated with infertility or
230 occur outside the reproduction period (1983 Gould, 1993 Seier, 2002 Hernandez-Lopez,
231 2016 Pina-Aguilar). Again, these sub-populations could present functional relevance
232 and play a key role in fertility. However, the relationship between sperm morphology
233 and fertility is still debated and results are controversial (for review, see 2016 Garcia-
234 Vasquez). These very low NFS rates could be explained by the lack of pressure from
235 sperm competition. Indeed, it has been shown in other taxa that an absence of sperm
236 competition leads to increases of abnormal sperm form in the naked mole-rat (2011 van
237 der Horst) and of morphological variability in insects (2011 Fitzpatrick). Since gorillas
238 and humans are considered polygynous or mildly polygynous species (2005 Marlowe),
239 they are not supposed to be exposed to high sperm competition pressure and they may
240 therefore allocate their resources to other parameters (see below for further details).

241 It is to note that the New World monkey *Callithrix penicillata* is also described with a
242 low NFS (30,17%) but this species should not be considered as pleiomorphic, as this
243 affirmation is based on a single study (2018 Arakaki) of four animals collected during
244 the rainy season and the *Callithrix* genus is known for its large range of NFS (range
245 25% to 91.9% NFS in *Callithrix jacchus* according to data from 127 individuals among
246 9 studies: 1991 Cui, 1996 Cui, 1996 Morrell, 1997 Morrell, 2004 Schneiders, 2009 Da
247 silva, 2014 Valle, 2016 Swanson, 2018 Arakaki).

248 **1.3. Testes mass**

249 Total testes mass of 71 primate species are compiled in [table 4](#) and illustrate primate
250 diversity, with a ratio of 400 between the lightest and heaviest representatives *Cebuella*
251 *pygmaea* (0.16 g per testis) and *Pan paniscus* (67.6 g per testis). With an average of
252 21.54±2.85 g per testicle, and despite a high body weight, human testicular mass is
253 similar to that of most *Macaca* species (mean *Macaca*: 25.23±5.44 g) and inferior to
254 *Papio* species (mean *Papio*: 34.38±7.16 g) and some *Atelidae* (*Ateles paniscus*: 32.12 g,
255 *Brachyteles arachnoides*: 39.18 g – one data point per species). Among *Hominidae*,
256 humans have heavier testicles than gorillas (12.84g ±1.24 g) and orang-utans (17.65±1.2
257 g), but much lighter ones than *Pan* species.

258 When this mass is adjusted to body weight ([figure 1](#)), human appears to have relatively
259 small testicles and to be closer to polygynous species like *Gorilla* than to
260 polygynandrous species *Pan*, despite a closer common ancestor. Overall, we find that
261 polygynandrous primates have bigger relative testes mass than those found in other
262 mating systems, confirming results of previous studies (2016 Parker, 2018 Dixson) on
263 the relationships between relative testes sizes and mating systems (see section 2.1. for
264 discussion).

265 **1.4. Limitations**

266 While based on numerous independent sources, it should be kept in mind that all data
267 on primate sperm should be interpreted in regard to the main sources of possible
268 variation due to subspecies, populations, individuals, time collection and technical
269 differences. Indeed, variations are reported at the subspecies level (2009 Steinberg), but
270 also between populations of identical taxa but of different geographical locations (2014
271 Valle). Many environmental factors, such as season (2000 Gupta; 2002 Muehlenbein;
272 2002 Hernandez- Lopez; 2008 Hernandez-Lopez; 2009 Cerda Molina) and toxic

273 exposition (2007 Hung; 2011 Falzone; 2013 Nyachieo), may also play a role, as well as
274 individual factors, such as age (2006 Slotter), sexual maturity (1988 Marson), abstinence
275 time (1989 Marson, 2017 Alipour) and current health status. At a technical level, there is
276 no universal standard method for the analysis of primate sperm parameters (2010
277 Auger). Variations may therefore be due to the use of different procedures (2005
278 Hernandez-Lopez), such as the sperm recovery method (1995 Young; 1998 Yeoman;
279 2000 Kuederling; 2004 Schneiders) or sample conditions (fresh, washed, frozen,
280 contaminated; 1986 Katz). For example, despite the existence of WHO
281 recommendations in humans, many different stains are still used such as,
282 Haematoxylin/Eosin, Shorr,Papanicolaou, Bryan-Leishman, DiffQuik, Quickdip,
283 Harris-schorr and SpermBlue (2009 van der horst, 2010 Cooper, 2010 Maree), which
284 could explain in part the reported variations

285 **2. Factors of sperm diversity**

286 Here, we will review some of the most important variables (e.g. mating-system
287 variables, life-history traits, ecological variables) influencing sperm form, function, and
288 competition across primates.

289 **2.1. Mating systems**

290 Sperm characteristics in group-living animals, such as primates, will depend on the
291 relative numbers of males and females mating with each other in a given social unit or
292 population i.e. on mating systems. Four types of mating systems are commonly found
293 among primates (2012 Dixson): monogamy (one male - one female), polygyny (one
294 male – multifemale, also often called harem systems), polyandry (one female –
295 multemale, mostly in cooperatively breeding primates) and polygynandry (i.e.
296 multemale-multifemale, MMMF). Concerning polygyny, the extent and exclusiveness of

297 this mating system will be affected by the distribution of mating opportunities in space
298 and time (dispersion of females and synchronicity of their fertile periods; see further
299 details on seasonality), in interaction with female behavior, i.e. the ability to monopolize
300 them (see below for further details on sexual monopolization and coercion). The
301 strength of intra-sexual selection in male primates, via sperm competition, correlates
302 with the mating system, with higher levels of selection in MMMF systems (such as
303 macaques, baboons and chimpanzees) and then bigger relative testes size (i.e. greater
304 investment in sperm production) and mass (figure 1) than in monogamous (e.g., owl
305 monkeys and gibbons) or polygynous (e.g., proboscis monkeys, gorillas and geladas)
306 mating systems (2016 Parker, 2018 Dixson). Sperm competition does seem to be the
307 primary agent of testes size evolution in primates with large testes being adaptive under
308 conditions where females mate with multiple partners during their fertile period
309 (because they usually contain a greater volume of seminiferous tissue). Testes size in
310 humans occupy an intermediate position between gorillas and chimpanzees (2014 van
311 der Horst & Maree). As suggested by Dixson (2018), this relatively small testes size
312 does not seem to provide evidence for a significant role of sperm competition during
313 human evolution.

314 Besides testes size, some other traits have been under positive selection, via sperm
315 competition (and/or cryptic female choice, see below), in polygynandrous primates (and
316 more generally polygynandrous mammals): faster rates of spermatogenesis, greater
317 capacity to sustain high sperm counts, copulatory plug formation, etc... (2018 Dixson).
318 Indeed, increased levels of sperm competition are expected to result in increased sperm
319 numbers (increased semen volume and sperm concentration; 1990 Parker, 2012
320 Montoto, 2013 Lupold), increased sperm length (figure 2), and a higher percentage of

321 sperm with normal morphology (figure 2), progressive motility, and viability (2009
322 Pitnick). For instance, ejaculate size should increase with the incidence of rapid female
323 polyandry (i.e. the rate of mating relative to the duration of sperm survival in the female
324 reproductive tract), such as in polygynandrous species compared to monogamous
325 species with extra-pair matings and slower female polyandry (2016 van Schaik). Sperm
326 length has also been linked to the intensity of sperm competition, with males producing
327 longer (and faster swimming) sperm in species with promiscuous females, which are
328 probably adaptations to reach the ova first (1991 Gomendio & Roldan). Other
329 morphological parameters, such as the size of sperm midpiece (indicator of
330 mitochondrial loading and thus motility), are larger in primate species whose females
331 mate polyandrously and males have larger testes in relation to body weight (2004
332 Dixson & Anderson, 2011 Maree), with human sperm having smaller midpiece volumes
333 than any of the 40 primate species measured by Anderson et al. (2005) (with the
334 exception of the common marmoset). Sperm kinematic parameters (swimming
335 characteristics) might also be related to mating systems, with sperm from MMMF
336 primate species swimming faster and with greater force than sperm from polygynous
337 primate species (2008 Nascimento). Nevertheless, as discussed previously (section
338 1.2.3.), these findings have to be taken with caution because the sample size was small
339 and semen samples from each species were prepared using different methods. Semen
340 quality parameters, such as the percentage of normal sperm in the ejaculate, are also
341 related to the levels of sperm competition experienced by the different species (figure
342 2). The high incidence of pleiomorphism in Human and Gorilla, associated with the
343 striking similarities between other sperm traits (e.g. ejaculate volume, sperm
344 concentration and motility, table 2), support the view of a very low risk of sperm

345 competition in humans compared to other primates (2018 Dixson). Finally, there is also
346 evidence that male copulation frequencies and frequencies of ejaculation (ejaculatory
347 mounts and masturbation) are significantly higher in MMMF systems than in
348 polygynous and monogamous systems, including humans (1995 Dixson) whose
349 reproductive system does not seem to be adapted to sustain high sperm counts during
350 periods of high sexual activity. Such findings can be interpreted as indicating that
351 “masturbation is more likely to occur in multimale-multifemale primate groups because
352 males possess neuroendocrine specialization for greater sexual arousal and performance
353 in such mating systems” (2004 Dixson). However, the question of why there are so
354 frequent masturbations in some primate species remains unresolved. One hypothesis is
355 that regular masturbation would have a positive physiological effect on the general
356 quality of spermatogenesis.

357 **2.2. Interplay between pre- and post-copulatory selection**

358 Male secondary sexual characters are traits that bias mating success because their
359 expression influences the outcome of male-male contests over access to females
360 (weapons) or renders males more attractive to females (ornaments). There are evidence
361 that weapons (e.g. canines) and ornaments (e.g. the red chest patches of geladas
362 (*Theropithecus gelada*), the red face and genital sex skin in mandrills (*Mandrillus*
363 *sphinx*) and Japanese macaques (*Macaca fuscata*), the hair capes of hamadryas baboons
364 (*Papio hamadryas*), the cheek flanges of orangutans (*Pongo* spp.), enlarged noses of
365 proboscis monkeys (*Nasalis larvatus*), the beards of men, etc. (see 2012 Dixson))
366 evolved under pre-copulatory sexual selection. When these attributes do not contribute
367 to have a better access to mates, sexual selection will be on the ability to find and reach
368 the fertile females (mobility, sensory abilities) and/or to fertilize her. Thereby, when

369 females have multiple mating partners, as it is the case in many groups of primates,
370 sexual selection will continue after mating in the form of sperm competition (1970
371 Parker) and through cryptic post-copulatory female choice (1996 Eberhard), i.e. females
372 selecting sperm with particular characteristics (see section 2.4.). Theoretical models of
373 sperm competition predict a trade-off between expenditure on the acquisition of mates
374 (pre-mating sexual selection) and expenditure on post-copulatory traits (testes size,
375 sperm number and quality) that promote fertilization success (post-mating sexual
376 selection), i.e. an increased expenditure on testes and sperm should be associated with a
377 decreased expenditure on the weapons and ornaments (2010 Parker and Pizzari).

378 Numerous comparative analyses have investigated the evolutionary associations
379 between weapons and testes in a wide range of taxa (see Simmons et al. 2017 for a
380 review). In general, the covariance between these sexual traits changes from positive to
381 negative as male-male competition and female monopolization increase within animal
382 taxa (2014 Lüpold, 2017 Simmons). Across primates, there is an increase in size-
383 corrected testes mass with the number of males within breeding groups (2019 Lüpold),
384 which is in accordance with predictions of sperm competition models (2016 Parker).

385 Similarly, primate species characterized by a higher female monopolization show a
386 decreased investment in testes size (2019 Lüpold). In a previous study, Lüpold et al.
387 (2014) estimated that the proportion of species within each taxon where males
388 monopolize females was about 20% in their primate sample (e.g. species with
389 monogamous and multimale mating systems were classified as low monopolization
390 while single-male mating systems were classified as high monopolization), showing that
391 female monopolization is not very common in this Order. Given that, one should predict
392 a general positive relationship between weapons and testes at the Order level (as shown

393 in a comparative study of gregarious primate species by Lüpold et al. 2019: testes mass
394 increases with increasing sexual dimorphism of the canines), with some taxon-specific
395 associations depending on additional life-history, ecological and mating-system
396 variables. For example, in polygynous species like gorillas, male body size/canines are
397 under very intense sexual selection and greatly exaggerated, suggesting that those very
398 costly traits will be more likely to trade off evolutionarily against investment in sperm
399 production, which could explain their relatively small testicles compared to their body
400 size.

401 Most of the studies investigating the evolutionary trade-off between pre- and post-
402 copulatory traits have focused on the associations between weapons and testes, and very
403 little attention has been paid to the patterns of covariation between ornaments and post-
404 copulatory traits. At the within-species level, studies on visual sexual signaling traits,
405 such as nose size in proboscis monkeys (2018 Koda) or face redness in mandrills (2001
406 Setchell & Dixson), showed that there was a positive relationship between the strength
407 of these ornaments and testes size. However, at the interspecific level, it has been shown
408 that species who invested most in the acoustic ornaments (enlargement of the larynx and
409 hyoid allowing males to broadcast low formant-frequency vocalizations) used during
410 male pre-mating competition in the genus *Alouatta* (howler monkeys), had smaller
411 testes (2015 Dunn). Moreover, a very recent comparative study in more than 100
412 primate species documented an evolutionary trade-off between pre-mating ornaments
413 (e.g. fleshy swellings, skin color, hairy traits etc) and testes mass (2019 Lüpold). The
414 authors suggested that “if male ornaments function as badges of status, with privileged
415 mating opportunities for highly ranked males similar to female monopolization by the
416 most successful males in contest competition, investment in male ornaments should also

417 lower the level of sperm competition and relax selection on sperm production”.

418 Therefore, the contrasting evolutionary trajectories between weapons/testes (positive
419 relationship) and ornaments/testes (negative relationship) reported in primates could be
420 driven by differential selection, functional constraints or temporal patterns of metabolic
421 investment between the different types of sexual traits (2019 Lüpold). There is a need
422 for more research on the trade-offs between weapons/ornaments and ejaculate traits in
423 primates (sperm number, viability, swimming speed and size; see meta-analysis by
424 Mautz et al. 2013: positive but non-significant relation between male secondary sexual
425 characters and ejaculate quality across taxa), as most studies until now focused almost
426 exclusively on testes size as a proxy for post-copulatory sexual selection. Similarly,
427 studies in sensory ecology and ecophysiology that focus on the evolutionary trade-off
428 between ejaculate expenditure and mate-searching (linked to sensory abilities and
429 multimodal sexual communication), rather than direct male-male contest, would be a
430 productive avenue for future research.

431 **2.3. From the male’s perspective: Mate guarding and copulatory plugs**

432 There is considerable evidence that males have evolved behavioral adaptations, such as
433 mate guarding, that function to prevent competitor males from gaining access to
434 reproductively active females (1994 Andersson), thereby limiting the extent of sperm
435 competition (1998 Birkhead and Møller) and increasing their chances of fertilizing the
436 egg. Mate guarding is widespread among polygynous primates, where it has been
437 described in detail for about 20 species of New and Old World monkeys (2012 Dixson).
438 Given the costs associated with mate guarding (e.g. reduction in foraging time, Alberts
439 et al. 1996; physiological costs, Girard-Buttoz et al. 2014), one should expect that males
440 would invest in mate guarding if the reproductive benefits outweigh the costs associated

441 with this activity. However, the extent to which male primates may adjust their relative
442 use of mate guarding compared to the opposite tactic, which is the engagement in sperm
443 competition through an increased expenditure on the ejaculate, remains largely
444 unexplored. In one of the rare studies examining the relationship between mate guarding
445 and ejaculate quality, Leivers et al. (2014) showed that men who performed more mate
446 guarding behaviors produced lower quality ejaculates, with a lower concentration of
447 sperm, a lower percentage of motile sperm and sperm that swam slowly and erratically.
448 Concerning male non-human primates, there is a paucity of empirical data on the costs
449 of this behavior and its effectiveness does not seem to be absolute but rather dependent
450 on its timing relative to the moment of ovulation. Moreover, whether a correlation
451 between mate guarding and ejaculate quality exists in non-human primates remains to
452 be investigated.

453 Another adaptation for the avoidance of sperm competition and an increase in male
454 fertilization success is the use of coagulated ejaculate that forms sperm plugs (also
455 called copulatory plugs). These copulatory plugs are found in many species of primates,
456 but especially in those having polygynandrous mating systems (e.g., ring-tailed lemurs,
457 muriquis, chimpanzees; 2002 Dixson and Anderson). Two main hypotheses have been
458 proposed to explain the evolution of pronounced sperm plugs in polygynandrous
459 primate species: it promotes the passage of highly motile sperm through the cervix
460 (2008 Hernandez-Lopez), buffers pH, and raises the temperature of the vagina which
461 improve sperm survival in the vagina and its transcervical transport; it obstructs semen
462 deposition and sperm transport by a second male. This second hypothesis seems less
463 supported by the empirical data, and even if plugs tend to close the entry to the female's
464 genital tract, they do not prevent her from subsequently mating with other males in

465 primates (2017 Parga). Indeed, several studies have shown that penile morphology, such
466 as spines, found in different primate species may facilitate the removal or displacement
467 of coagulated semen and plugs deposited by previous matings, and hence reduce
468 potential sperm competition (1993 Hershkovitz, 2003 Parga). Moreover, males and
469 females (see section 2.4. below) can also manually and/or orally remove these plugs,
470 with semen ingestion being also reported (Garcia, personal observations in olive
471 baboons and Japanese macaques).

472 **2.4. Female choice & sexual conflict (sexual coercion)**

473 Whenever polyandrous matings occur, sperm competition will inevitably arise, setting
474 up selection on males (quantity and quality of sperm that improve their chances to
475 fertilize the ova) but also on females to select sperm with particular characteristics and
476 circumvent male control of reproduction (i.e. cryptic post-copulatory female choice;
477 1996 Eberhard). There will be also antagonistic selection on males and females due to
478 sexual conflict.

479 Post-copulatory female choice is expected to occur more often in species in which
480 females have little direct control over choice of mating partners or in which female mate
481 choice is especially costly. This is particularly the case in species characterized by a
482 high level of sexual dimorphism, and/or in species in which males are aggressive
483 towards females in the context of mating (e.g. chimpanzees, pigtailed macaques, etc). In
484 cases of sexual conflict, some traits that benefit males oppose with the female's interests
485 and vice versa. For example, some conflicts can emerge in species where penile
486 morphology might damage the female's genital structures during intromission (e.g.
487 spines in galagos). They can also occur in species where females show prominent sexual
488 swellings (e.g. chimpanzees, baboons – serving to attract multiple partners and

489 encourage the likelihood of mating and sperm competition; 2012 Dixson) that could
490 influence the distance that males must cover during mating and sperm transport, and
491 then increase the chances of being fertilized by males with longer penises. This conflict
492 can also take the form of sexual coercion (review by Smuts & Smuts 1993 and Muller et
493 al. 2011) with direct (females are compelled to copulate more frequently with their
494 aggressors) and indirect coercion (females are prevented from mating with other males).
495 Until recently, post-copulatory female choice had received little attention in the primate
496 literature, especially because of practical difficulties of conducting such experiments in
497 this Order, and more generally in mammals. There is therefore little evidence for
498 differential fertilization chances of sperm of different males once inside the female
499 reproductive tract. Nevertheless, there is ample reason to consider that, as in a number
500 of insects and birds, there are anatomical, physiological and behavioral adaptations for
501 post-copulatory female choice in primates. Here are a few examples of indirect evidence
502 of possible cryptic female choice in primates.

503 At the anatomical level, after their deposition in the vagina during ejaculation,
504 spermatozoa have to cross numerous barriers, such as the cervix or the uterotubal
505 junction, before reaching the oviduct. There is a huge filtering in the number of
506 spermatozoa from the vagina to the oviduct, with only about 200 being found in the
507 human oviduct whereas 280 million sperm were initially released (2018 Dixson).
508 Moreover, it seems that elongated oviducts may serve to “test” the relative fitness of
509 gametes from rival males and thus represent a mechanism of cryptic female choice in
510 mammals, with longer and more convoluted oviducts being associated with higher
511 relative testes size and sperm midpiece volumes (2006 Anderson). There are
512 unfortunately not enough data on the anatomy of these potential physical barriers in

513 non-human primates to assess the differential effects of the female's anatomical
514 structures as selective filters upon sperm transport and then fertilization success and a
515 lot more comparative studies are needed in this area of research.

516 At the physiological level, Hernandez-Lopez et al. (2008) have shown that there is a
517 buffering effect of seminal fluid on vaginal pH in the spider monkey, which increased
518 sperm motility in the vagina. Even if these results did not provide a distinct proof of
519 female cryptic choice in this species, they still suggest that sperm selection could start
520 as early as the vagina, with females relying on cues provided by the seminal coagulum
521 in favoring or opposing sperm migration.

522 At the behavioral level, it has been suggested that female copulation calls (i.e. auditory
523 signal occurring after mating) in Old World monkeys and apes are a form of post-
524 copulatory female choice that encourages post-copulatory mate guarding by preferred
525 males and minimize the probability of sperm competition by non-preferred males (2005
526 Maestriperi & Roney). By calling after copulation with certain males, females express
527 their preferences for these males and their sperm; whereas by not calling after
528 copulation with other males, they do not encourage mate guarding by these males,
529 which leaves the possibility that other males will mate with them and engage in sperm
530 competition. Another behavioral mechanism that could be used to choose among
531 different males is the active manipulation of their ejaculates. It has been shown that in
532 chickens, females can expel the sperm from matings with low-ranking roosters
533 immediately after insemination (cited in van Schaik 2016). Nevertheless, so far, we still
534 do not know whether primate female's behavior might actively bias the fate of
535 spermatozoa originating from different males, and if so, how.

536 Therefore, the question of how the primate female's reproductive system preferentially

537 receives and influences processes associated with sperm transport, storage and viability
538 remains to be investigated in more details.

539 **2.5. Seasonality & Climatological factors**

540 Reproductive activity of many primates is more or less seasonal, resulting in an
541 increased frequency of matings during a relatively short period, which may select for
542 increased sperm production, compared to year-round breeders (1977 Short). In this case,
543 we might expect a decrease in optimal ejaculate size as sperm production rates increase.
544 Indeed, this sperm depletion could be promoted by oestrus synchronization, which
545 reduces the male-bias in the operational sex ratio (i.e. the ratio of the number of fertile
546 adult males to the number of potentially fertile females in a group at a given time;
547 definition in van Schaik 2016) during the breeding season and forces males to mate at a
548 higher rates than if oestrus was not synchronous (2011 Stockley and Bro-Jørgensen).
549 Different studies have reported a negative relationship between the ratio of oestrous
550 females to males and conception rates in both geladas and hamadryas baboons (1983
551 Dunbar & Sharman, 1994 Zinner). Similar findings suggested some sperm limitation in
552 gorillas (i.e. a species where males can only sustain relatively low mating rates, 1979
553 Short), with females receiving fewer copulations when other females were
554 simultaneously in oestrus (1990 Watts).

555 Climatological factors have been invoked as causes of seasonal variation in the
556 frequency of intercourse within human populations and could have a direct influence on
557 human reproductive physiology and thereby on human fecundity. One of the main
558 factors most often raised to explain these relations is temperature. Indeed, the process of
559 spermatogenesis in primates, and mammals in general, is temperature-sensitive and
560 optimized at temperatures slightly below the core body temperature. This temperature

561 sensitivity has been a selective force in primate evolution resulting in external testes
562 (cited in Ellison et al. 2015) and leads to ask whether high ambient temperatures, such
563 as the ones encountered by most tropical non-human primates or humans living in
564 hottest environmental places, could compromise male fecundity by affecting sperm
565 quality and/or quantity. Most studies relating heat and damage to spermatogenesis
566 focused on general seasonal variation in sperm concentration and total sperm count (e.g.
567 with summer values being much lower than the ones found during winter times; in
568 Durairajanayagam et al. 2015) or used experimental approaches with induced-
569 hyperthermia to evaluate whether different frequencies of heat exposure caused
570 different degrees of damage to spermatogenesis (2015 Rao et al.: reversible decrease in
571 sperm concentration and motility with transient scrotal hyperthermia). However, to our
572 knowledge, studies examining the effects of living in very hot environments on human
573 spermatogenesis and the resultant spermatozoa are lacking. There is also a scarcity of
574 data in non-human primates, with one study showing that high temperatures could
575 reduce 80% of the original sperm count in cynomolgus monkeys (2005 Liu). Therefore,
576 clear evidence of a relationship between high ambient temperature and defects in male
577 reproductive physiology in wild populations of primates is lacking and would deserve
578 more attention.

579 **2.6. Social constraints**

580 Optimal sperm investment within species and within animal populations is expected to
581 vary predictably with respect to male roles in the society, as defined within theoretical
582 models known as sperm competition games (2010 Parker & Pizzari). Sperm
583 competition theory predicts that males should progressively invest more resources in
584 their germline as their mating costs increase. When access to fertile females is

585 determined by social dominance (e.g. dominant males being more likely to ejaculate at
586 an optimal time relative to ovulation, i.e. a favored role), allocation trade-off hypothesis
587 (soma vs. germline) predicts that semen characteristics and within-male variance in
588 sperm design should be affected by the social environment, with subordinate males (i.e.
589 the disfavored phenotype) investing more in ejaculate expenditure (1990 Parker, 1998
590 Parker). Many studies have investigated the effects of social environment and social
591 status on ejaculate characteristics in birds and some mammals, with some conflicting
592 results regarding the theoretical predictions of sperm competition (e.g. 2007 Cornwallis
593 & Birkhead and 2007 Pizzari et al.: ejaculates of lower quality and reduced swimming
594 speeds of sperm in socially dominant male fowls, who experience reduced levels of
595 sperm competition; 2009 Kruczek & Styrna: higher motility of sperm in dominant bank
596 voles; 2012 Lemaître et al.: dominant male bank voles invest more sperm per ejaculate
597 than subordinates; 2015 Burger et al.: higher sperm numbers and velocity in stallions
598 exposed to other stallions than exposed to mares; 2017 Rojas Mora et al.: ejaculates
599 with higher levels of within-ejaculate variation in sperm design in dominant house
600 sparrows compared to subordinate ones). There are much less information on the
601 influence of social status on non-human primate sperm features and sperm competition;
602 even though there has been a considerable literature on the effects of social constraints
603 on male mating and reproductive success in different primate species (1991 Cowlshaw
604 & Dunbar, 2004 van Noordwijk & van Schaik, 2005 Setchell) and a few papers on the
605 relationships between social rank and testicular physiology (e.g. smaller relative testes
606 in subordinate males than in dominant ones in mandrills or sifakas; 1992 Wickings,
607 2009 Lewis). This is even truer in human populations with very few studies venturing
608 out on this touchy topic and showing solid results. For example, Latif et al. (2018)

609 suggested that semen quality was not explained by socio-economic status, but due to the
610 limited sample size and the fact that participants did not represent the general
611 population (i.e. they were referred for infertility assessment), these results need to be
612 further confirmed in future studies. There are therefore avenues for further research on
613 the role of social status on fertilization outcomes in human and in a range of primate
614 species.

615 Besides social status, there are some other social constraints than could have an
616 influence on sperm competition and sperm features. For example, an increased
617 population density might reduce the efficiency of male-male contests in securing
618 females and increase its cumulative costs, thus leading to scramble competition (2013
619 Parker). In marine invertebrates, it has been shown that males experimentally allocated
620 to high-density groups, where sperm competition is more likely, produced longer and
621 more motile sperm that swam for longer periods of time than did males in low-density
622 treatment groups (2008 Crean). Another study in amphibians also showed that across
623 geographically isolated populations of chorusing frogs, the density of males in choruses
624 was positively associated with testes mass and sperm production (2010 Dziminski).
625 However, whether this pattern of covariation is also found in primate species and if
626 there is a phenotypic plasticity in male allocation to ejaculates in response to fluctuating
627 male densities remain to be investigated.

628 **2.7. Androgens and sperm competition**

629 Testosterone drives the process of male genital development, supports sperm production
630 (2004 Weinbauer, 2012 Dixson) and has a wide range of effects that plausibly function
631 to support male competitive behavior, for example the development and maintenance of
632 the armaments and ornaments that males employ in mating competition. The “Challenge

633 hypothesis”, first developed from studies in birds (1990 Wingfield), states that the
634 temporal patterns of circulating testosterone are closely associated with aggressive
635 mating competition (2017 Muller). Observations from a range of wild primates support
636 this hypothesis, which is also highly relevant for understanding social interactions in
637 humans (2017 Wingfield). Mean levels of testosterone in MMMF primate species are
638 higher than in uni-male mating systems and there is a positive correlation between
639 testosterone levels and relative testes sizes (indicative of multiple partner matings by
640 females and sperm competition among males) for the Order Primates, as a whole (2000
641 Whitten; 2004 Dixson). Muller (2017) reviewed the relationship between testosterone
642 and mating effort in primates, with specific emphasis on the ways in which testosterone
643 promotes male-male competition: “in both seasonally and non-seasonally breeding
644 species, males increase testosterone production primarily when competing for fertile
645 females. In species where males compete to maintain long-term access to females,
646 testosterone increases when males are threatened with losing access to females [...].
647 And when male status is linked to mating success, and dependent on aggression, high-
648 ranking males normally maintain higher testosterone levels than subordinates,
649 particularly when dominance hierarchies are unstable”. Low testosterone levels of
650 subordinate males have also been reported in other mammal species, with some extreme
651 cases in which the investment in ejaculate and reproductive capabilities of subordinates
652 could even be suppressed in the presence of dominant individuals (cited in 2012
653 Lemaître et al.). Regarding the correlation between testosterone levels and semen
654 characteristics, Burger et al. (2015) found that blood testosterone levels in horses were
655 positively correlated with both the mean sperm number (after exposure to mares but not
656 after exposure to stallions) and curvilinear sperm velocity (after exposure to stallions),

657 suggesting that testosterone levels during exposure to a mare can be an indicator for a
658 stallion's willingness to invest into costly semen production. However, to our
659 knowledge, such studies examining the links between testosterone levels and sperm
660 features in non-human primates are currently lacking and this topic needs further
661 attention.

662

663 **CONCLUDING REMARKS AND FUTURE DIRECTIONS**

664 This review has discussed the different selection pressures involved in the evolution of
665 primate sperm diversity. We considered especially how sexual selection (pre- and post-
666 copulatory), acting via mating competition, sperm competition and cryptic female
667 choice, has influenced the evolution of primate reproductive systems and sperm
668 parameters. Cryptic female choice is still poorly studied in mammals and in primates in
669 particular, and this topic deserves more attention. More detailed investigation is also
670 required to determine the evolutionary trade-off between ejaculate expenditure and
671 mate-searching across a broad range of primate taxa. Further studies are also needed to
672 determine how social conditions explain variation in sperm morphology and parameters.
673 In conclusion, further research in this field offers much exciting potential to advance our
674 current understanding of primate reproductive system evolution.

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1491 **FIGURE LEGENDS**

1492 Figure 1. Relative testes mass to body mass for 71 primate species displayed by family
 1493 (A) or mating system (B). Each dot refers to a single species. If several data were
 1494 available, mean is presented.

1495 References : Aotidae : 1938 Schultz, 1981 Harcourt, 2004 Dixson ; Atelidae : 1925
 1496 Hrdlicka, 1938 Schultz, 1981 Harcourt, 1998 Parker, 2004 Dixson, 2019 Arakaki ;
 1497 Callitrichidae : 1925 Hrdlicka, 1981 Harcourt, 1987 Dixson, 1993 Soini, 1999 Birkhead,
 1498 2004 Dixson 2004 ; Cebidae : 1960 Hill, 1972 Middleton, 1981 Harcourt, 1998 Parker,
 1499 1999 Birkhead 1999, 2004 Dixson ; Cercopithecidae : 1938 Schultz, 1941b Kennard,
 1500 1960 Kinsky, 1966 Hill, 1970 Hill, 1976 Amann, 1981 Harcourt, 1986 Amann, 1987
 1501 Dixson, 1991 Harcourt, 1992 Wickings, 1993 Bercovitch, 1998 Parker, 1999 Birkhead,
 1502 2000 Gupta, 2004 Dixson ; Cheirogaleidae : 1964 Petter-Rousseaux, 1998 Parker, 2002
 1503 Aslam, 2004 Dixson ; Galagidae : 1964 Butler, 1987 Dixson, 1998 Parker, 2004 Dixson
 1504 ; Hominidae : 1938 Schultz, 1962 Hall-Craggs, 1981 Harcourt, 1986 Amann, 1998
 1505 Parker, 1999 Birkhead, 2004 Dixson ; Hylobatidae : 1938 Schultz, 1941a Kennard,
 1506 1946 Harrison-Matthews, 1981 Harcourt, 1998 Parker, 1999 Birkhead, 2004 Dixson ;
 1507 Indriidae : 1964 Petter-Rousseaux ; Lemuridae : 1964 Petter-Rousseaux, 1977 Bogart,
 1508 1993 Morland, 1998 Parker, 2004 Dixson ; Lorisidae : 1967 Ramakrishna, 1981
 1509 Harcourt ; Pitheciidae : 1960 Hill, 1995 Harcourt.

1510 Figure 2. Relationships between total sperm length, abnormal morphology and mating
 1511 system of 66 primate species. Total sperm length is presented according to the species
 1512 mating system (A) and percentage of sperm with normal morphology is presented
 1513 according to the mean total sperm length of the species (B) or mating system (C). Each
 1514 dot refers to a single species with data presented as mean if several sources. Black

1515 horizontal line is the mean of each mating system. **Gorilla gorilla* and ***Callithrix*
 1516 *penicillata*.

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 1520 Vidal, 2009 Da Silva, 2013 Poches, 2013 Valle, 2014 Valle, 2016 Swanson, 2017
 1521 Arakaki, 2018 Arakaki ; Cebidae : 1968 Ackerman, 2002 Barnabe, 2011 Oliveira, 2015
 1522 Leao, 2015 Nakazato, 2015 Oliveira, 2016a Oliveira, 2016b Oliveira, 2017 Sampaio ;
 1523 Cercopithecidae : 1968 Ackerman, 1980 Wickings, 1988 Cranfield, 1989 Schaffer,
 1524 1992 Thomson, 1998 Kyaligonza, 1999 Chan, 1999 Gago, 2000 Cseh, 2000 Kholkute,
 1525 2004 Mdhluli, 2012 Nyacheio, 2014 Thomsen, 2019 Zainuddin ; Hominidae : 1968
 1526 Ackerman, 1977 Seuanez, 1980 Platz, 1982 Gould, 1982 Seager, 1983 Bader, 1986
 1527 Jeyendran, 1988 Marson, 1997 Ombelet, 1997 Pope, 1998 Aziz, 2001 Kusunoki, 2003
 1528 Soler, 2005 O'brien, 2007 Aziz, 2010 Cooper, 2012 Thilagavathi, 2018 Yu ;
 1529 Hylobatidae : 1968 Ackerman.

1530

1531 TABLES

1532 Table 1. Sperm morphometric data of 76 primate species.

Species	Head					Flagellum				Total length (μM)				
	Length (μM)	Width (μM)	Perimeter (μM)	Area (μM ²)	Volume (μM ³)	Ellipticity (L/W)	Elongation (LW)/(L+W)	Roughness (4π(A/P ²))	Regularity (π(LW/4A))		Midpiece length (μM)	Principal piece length (μM)	Terminal piece (μM)	Flagellum length (μM)
Aotidae family														
<i>Aotus lemurinus</i>	2.8	4.7	-	-	19.3	0.60	-0.25	-	-	6.60	-	-	45.70	55.10
Atelidae family														
<i>Alouatta caraya</i>	4.8	3.1	13.2	12.3	37.5	1.57	0.22	0.88	132.6	3.56	-	-	-	55.01
<i>Ateles belzebuth</i>	5.2	2.7	-	-	38.2	1.93	0.32	-	-	6.56	-	-	-	70.83
<i>Ateles chamek</i>	5.2	3.3	-	-	45.6	1.58	0.22	-	-	7.34	-	-	-	64.09
<i>Ateles geoffroyi</i>	4.5	2.8	-	-	29.6	1.62	0.24	-	-	-	-	-	-	-
<i>Ateles paniscus</i>	5.8	3.3	-	-	45.0	1.56	0.22	-	-	8.71	-	-	48.50	124.61
Mean Aotidae	5.1	3.0	13.2	12.3	39.2	1.7	0.2	0.9	132.6	6.5	-	-	48.5	78.6
Callitrichidae family														
<i>Callimico goeldii</i>	5.0	3.1	14.3	14.8	40.3	1.57	0.21	0.90	181.0	-	-	-	-	-
<i>Callithrix geoffroyi</i>	5.0	2.5	-	-	32.7	2.00	0.33	-	-	6.00	-	-	62.00	73.00
<i>Callithrix jacchus</i>	5.2	3.3	14.6	15.2	44.1	1.55	0.21	0.89	214.9	4.15	-	-	47.22	52.31
<i>Cebuella pygmaea</i>	5.3	4.0	-	-	53.9	1.50	0.20	-	-	7.75	-	-	42.95	58.00
<i>Leontopithecus rosalia</i>	5.5	4.0	-	-	63.4	1.38	0.16	-	-	5.00	-	-	68.00	78.00
<i>Saguinus fuscicollis</i>	5.6	3.2	-	-	52.5	1.73	0.27	-	-	-	-	-	55.16	60.74
<i>Saguinus leucopus</i>	4.9	3.3	-	9.7	41.9	1.51	0.20	-	123.1	-	-	-	58.62	64.88
<i>Saguinus midas</i>	5.3	-	-	-	36.2	-	-	-	-	9.10	-	-	40.20	-
<i>Saguinus oedipus</i>	5.1	3.3	-	-	42.9	1.67	0.25	-	-	11.20	-	-	49.17	64.96
Mean callitrichidae	5.2	3.3	14.4	13.2	45.3	1.6	0.2	0.9	173.0	7.2	-	-	52.9	64.6
Cebidae family														
<i>Cebus albifrons</i>	9.0	-	-	-	59.4	-	-	-	-	13.20	-	-	58.20	-
<i>Saimiri boliviensis</i>	5.9	4.0	-	-	74.0	1.47	0.19	-	-	11.35	-	-	62.00	74.10
<i>Saimiri collinsi</i>	6.2	4.2	-	-	84.5	1.48	0.19	-	-	-	-	-	70.50	76.80
<i>Saimiri sciureus</i>	5.4	3.5	-	-	46.3	1.46	0.19	-	-	9.83	55.34	-	58.08	71.42
<i>Saimiri vanzolinii</i>	6.8	4.8	-	-	116.2	1.42	0.17	-	-	-	-	-	69.20	76.10
<i>Sapajus apella</i>	7.5	3.5	-	-	60.5	1.64	0.24	-	-	10.96	-	-	64.00	75.97
<i>Sapajus cay</i>	6.1	3.9	-	-	77.0	1.57	0.22	-	-	8.67	-	-	-	65.06
<i>Sapajus libidinosus</i>	5.9	3.7	-	-	67.1	1.58	0.22	-	-	8.53	-	-	-	67.26
<i>Sapajus nigrinus</i>	6.3	4.1	-	-	85.1	1.53	0.21	-	-	9.35	-	-	-	66.27
Mean Cebidae	6.6	4.0	-	-	74.5	1.5	0.2	-	-	10.3	55.3	-	63.7	71.6
Cercopithecidae family														
<i>Allenopithecus nigroviridis</i>	5.6	3.3	-	-	54.9	1.69	0.26	-	-	9.32	-	-	57.54	66.49
<i>Cercocebus galeritus</i>	6.8	-	-	-	-	-	-	-	-	13.30	-	-	73.00	93.10
<i>Cercopithecus lhoesti</i>	4.0	2.5	-	-	20.9	1.60	0.23	-	-	9.00	-	-	41.00	54.00
<i>Cercopithecus nictitans</i>	5.3	-	-	-	46.2	-	-	-	-	12.30	-	-	40.50	-
<i>Cercopithecus petaurista</i>	5.7	3.0	-	-	41.4	1.67	0.25	-	-	9.60	-	-	38.95	73.00

<i>Eulemur fulvus</i>	5.6	-	-	-	35.1	-	-	-	-	11.00	-	-	62.30	-
<i>Eulemur macaco</i>	6.5	4.5	-	-	89.9	1.58	0.22	-	-	10.68	37.30	-	45.10	54.90
<i>Eulemur mongoz</i>	6.0	-	-	-	43.2	-	-	-	-	13.50	-	-	43.20	55.30
<i>Lemur catta</i>	4.9	4.6	-	-	55.7	1.13	0.06	-	-	11.27	42.10	-	52.20	55.87
<i>Varecia variegata</i>	7.5	3.6	-	-	106.0	2.08	0.35	-	-	20.70	76.60	-	83.50	104.87
Mean Lemuridae	6.1	4.2	-	-	66.0	1.6	0.2	-	-	13.4	52.0	-	57.3	67.7
Lepilemuridae family														
<i>Lepilemur mustelinus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	52.00
Lorisidae family														
<i>Nycticebus coucang</i>	7.7	5.6	-	-	152.4	1.52	0.21	-	-	13.63	67.90	-	72.28	90.00
Tarsiidae family														
<i>Cephalopachus bancanus</i>	9.0	-	-	-	-	-	-	-	-	9.90	-	-	-	-
Mean primates	5.8	3.6	14.5	14.4	56.6	1.5	0.2	0.9	204.3	10.1	50.4	3.7	55.1	70.7

1533

1534 All measurements are presented uncritically and as mean when multiple sources. References: Aotidae : 1938 Schultz, 1981 Harcourt, 2004 Dixson ; Atelidae :
1535 1925 Hrdlicka, 1938 Schultz, 1981 Harcourt, 1998 Parker, 2004 Dixson, 2019 Arakaki, 2019 Steinberg ; Callitrichidae : 1925 Hrdlicka, 1981 Harcourt, 1987
1536 Dixson, 1993 Soini, 1999 Birkhead, 2004 Dixson, 2019 San Diego Zoo ; Cebidae : 1960 Hill, 1972 Middleton, 1981 Harcourt, 1998 Parker, 1999 Birkhead, 2004
1537 Dixson ; Cercopithecidae : 1938 Schultz, 1941 Kennard, 1960 Kinsky, 1966 Hill, 1970 Hill, 1976 Amann, 1981 Harcourt, 1986 Amann, 1987 Dixson, 1991
1538 Harcourt, 1992 Wickings, 1993 Bercovitch, 1998 Parker, 1999 Birkhead, 2000 Gupta, 2004 Dixson, 2019 San Diego Zoo ; Cheirogaleidae : 1964 Petter-
1539 Rousseaux, 1998 Parker, 2002 Aslam, 2004 Dixson ; Galagidae : 1964 Butler, 1987 Dixson, 1998 Parker, 2004 Dixson ; Hominidae : 1938 Schultz, 1962 Hall-
1540 Craggs, 1981 Harcourt, 1986 Amann, 1998 Parker, 1999 Birkhead, 2004 Dixson, 2019 San Diego Zoo ; Hylobatidae : 1938 Schultz, 1941 Kennard, 1946
1541 Harrison-Matthews, 1981 Harcourt, 1998 Parker, 1999 Birkhead, 2004 Dixson ; Indriidae : 1964 Petter-Rousseaux ; Lemuridae : 1964 Petter-Rousseaux, 1977
1542 Bogart, 1993 Morland, 1998 Parker, 2004 Dixson ; Lorisidae : 1981 Harcourt, 1967 Ramakrishna ; Pitheciidae : 1960 Hill, 1995 Harcourt, 2019 San Diego Zoo.

1543 Table 2. Semen analysis of 43 primate species.

Species	Collection method	n	Semen analysis									
			pH	Mean volume (μL)	Volume range	Mean concentration (10 ⁶ /mL)	Concentration range	Mean motility (%)	Motility range (%)	Mean intact membrane (%)	Mean intact acrosome (%)	Normal morphology (%)
Aotidae family												
<i>Aotus lemurinus</i>	EE	3	-	-	-	-	-	-	-	-	-	67.1
Atelidae family												
<i>Alouatta caraya</i>	ES	41	7.97	88.4	10-218	748.4	7-5400	74.43	5-95	57.84	58.96	59.45
<i>Ateles geoffroyi</i>	ES	21	-	3300	210-8000	102.48	18-301	62.2	7-65	53.8	-	62.83
<i>Brachyteles arachnoides</i>	ES	5	7.7	353	303-402	144	-	82.5	70-95	64.5	81	-
Callitrichidae family												
<i>Callimico goeldii</i>	ES	16	7.61	26.9	-	143.18	-	83.33	-	36.38	66	47.8
<i>Callithrix jacchus</i>	ES	48	7.56	35.1	8-200	139.2	0.1-710	47.7	10-90	76.48	-	50.4
<i>Callithrix jacchus</i>	EE	26	-	-	-	28	2.2-85.8	57.47	43.5-90	83.21	74.5	89.83
<i>Callithrix jacchus</i>	PVS	107	7.54	26.62	2-78	492.62	32.4-3557	65.52	20-95	67.22	80.44	44.33
<i>Callithrix jacchus</i>	VW	12	-	-	-	19	0.3-114	71.65	20-95	84.4	-	91.9
<i>Callithrix penicillata</i>	PVS	10	7.53	16.83	-	1.47	-	56.67	-	62.83	76.67	30.17
<i>Leontopithecus chrysomelas</i>	ES	10	-	11.9	-	-	-	-	-	-	-	67.29
<i>Saguinus leucopus</i>	PVS	-	7.5	24	-	87.62	-	97.1	-	93.7	-	69.3
Cebidae family												
<i>Saimiri boliviensis</i>	ES	20	-	202.5	200-205	2.8	-	57.05	44.1-70	-	-	-
<i>Saimiri boliviensis</i>	EE	1	-	-	-	-	-	-	-	-	-	98.3
<i>Saimiri boliviensis</i>	PVS	20	-	418	400-436	77.1	-	80.2	79.8-80.6	-	-	-
<i>Saimiri cassiquiarensis</i>	ES	10	-	120	60-180	-	-	61.5	43-80	76	-	86
<i>Saimiri collinsi</i>	ES	48	7.43	285.97	10-1100	92.64	20-121	73.67	16-100	65.88	-	75.32
<i>Saimiri macrondon</i>	ES	10	-	500	-	-	-	90	-	98	-	93
<i>Saimiri sciureus</i>	ES	12	-	243.68	37-500	298.24	0.1-847.1	65.85	20-90	70.3	-	57
<i>Saimiri vanzolinii</i>	ES	18	-	168.37	-	-	-	89	-	74.33	-	92
<i>Sapajus apella</i>	ES	74	-	911.4	200-2600	791.85	38.7-1810	52.51	15-83	64.57	-	64.8
Cercopithecoidea family												
<i>Cercocebus galertus</i>	ES	4	8.3	57.4	20-150	1989	100-4100	89.8	-	-	-	83.8
<i>Cercopithecus neglectus</i>	ES	3	8.4	39.2	3.6-80	64.1	15-180	76.8	-	-	-	71
<i>Chlorocebus aethiops</i>	EE	1	-	-	-	230.7	-	32	-	-	-	-
<i>Chlorocebus aethiops</i>	ES	81	7.82	700	600-1200	134.69	0.2-280	56.11	28-80	63.13	57.39	64.02
<i>Chlorocebus aethiops</i>	M	5	-	1540	1300-1900	3.14	2.3-3.9	46.4	30-67	-	-	-
<i>Erythrocebus patas</i>	ES	8	-	-	-	226.2	6.5-445.9	45	5-56	45.5	-	59.5
<i>Lophocebus aterrimus</i>	ES	1	-	337.5	50-750	1.45	0.3-3	62.5	30-90	78.85	83.79	-
<i>Macaca arctoides</i>	ES	6	-	-	-	264	11-509	35	5-60	49	-	70
<i>Macaca fascicularis</i>	EE	24	-	-	-	23	-	75.33	64-82	78.9	63.5	-
<i>Macaca fascicularis</i>	ES	31	-	576.25	50-3000	551.46	10-2430	75.15	35-91	67.72	91.09	74.75
<i>Macaca fascicularis</i>	VW	4	-	530	300-800	275	120-870	-	-	82.4	-	-
<i>Macaca fuscata</i>	ES	2	-	-	-	-	-	50	40-55	-	-	-
<i>Macaca fuscata</i>	M	32	7.1	2200	100-5000	529.4	12.5-990	-	-	59.6	-	94.4
<i>Macaca mulatta</i>	ES	117	7.25	411	20-7200	433.75	6-4040	74.24	30-98	73.15	88.59	60.94
<i>Macaca mulatta</i>	EE	19	-	-	-	920	9-218	83	50-95	-	-	-

<i>Macaca nemestrina</i>	ES	10	7.82	1298.5	80-2600	168.15	4-705	77.43	44-90	82.01	-	70.57
<i>Macaca nigra</i>	ES	4	-	-	-	31.15	3.6-57.6	71.3	58-82.2	-	-	96.95
<i>Macaca radiata</i>	ES	7	-	780	200-3000	249	116-799	78.3	60-94	78	91.4	87.2
<i>Macaca silenus</i>	ES	23	8.5	900	10-4000	144.2	38-800	58.35	30-95	-	-	50
<i>Papio anubis</i>	ES	54	7.53	413.65	150-3220	65.21	0.2-239.2	57.59	0.1-98	72.25	53.88	63.99
<i>Papio cynocephalus</i>	ES	2	-	4000	3000-5000	840	600-1080	75	70-80	-	-	-
<i>Papio hamadryas</i>	EE	2	-	-	-	-	-	42.5	-	-	59.5	-
<i>Papio ursinus</i>	ES	10	-	900	-	212.5	-	73.4	-	-	-	-
<i>Theropithecus gelada</i>	ES	1	-	-	-	-	104	-	20	22	-	81
Cheirogaleidae family												
<i>Microcebus murinus</i>	ES	16	-	-	-	-	-	48.4	37-64	66.4	-	-
Hominidae family												
<i>Gorilla gorilla</i>	ES	57	8.3	548.33	10-1850	111.33	0.1-1300	25.33	0-90	45	-	42.5
<i>Gorilla gorilla</i>	M	2	-	2100	-	91.7	-	-	-	-	-	23.75
<i>Homo sapiens</i>	M	2580	7.8	2500	1400-6000	39	12-200	32	0-90	58	-	32.22
<i>Pan paniscus</i>	ES	1	-	-	-	-	-	-	-	-	-	98
<i>Pan troglodytes</i>	ES	34	-	1860	100-5400	493.45	1-2900	-	0-84	52	-	81.9
<i>Pan troglodytes</i>	EE	2	-	-	-	-	-	87.5	82.5-89.5	96.95	88.73	95.5
<i>Pan troglodytes</i>	M	69	-	2471.43	100-4400	775.88	61-11300	73.5	3-93.2	72.13	82.75	69.58
<i>Pongo abelli</i>	M	1	-	6100	-	164	6-312	60	38-70	-	-	-
<i>Pongo pygmaeus</i>	ES	4	-	1100	200-3200	61	10-128	47	32-62	59	-	98.5
<i>Pongo pygmaeus</i>	M	1	-	2000	-	60	-	-	-	-	-	-
Hylobatidae family												
<i>Hylobates lar</i>	ES	3	-	-	-	293	34-552	10	5-15	29.5	-	55.5

1544

1545 All measurements are presented uncritically and as mean when multiple sources. EE: epididymal extraction (aspiration or dissection) ; ES: Electrostimulation
1546 (rectal probe or electrodes) ; M: Masturbation (manual or artificial vagina) ; PVS : penile vibrostimulation ; VW: vaginal washing (flushing or pipetting) ; n:
1547 number of individuals (as some authors did not give the number of individuals included in their studies, these numbers should be considered as minima).

1548 References: Aotidae : 2015 Nakazato ; Atelidae : 2001 Moreland, 2002 Hernandez-Lopez, 2004a Valle, 2004b Valle, 2008 Hernandez-Lopez, 2009 Cerda
1549 Molina, 2012 Flores-Herrera, 2013 Valle, 2013 Silva, 2014 Carvalho, 2016 Swanson, 2019 Arakaki ; Callitrichidae : 1991 Cui, 1996 Cui, 1996 Kuederling, 1996
1550 Morell, 1997a Morell, 1997b Morell, 2000 Kuederling, 2000 Pudritz, 2003 O'brien, 2004 Schneiders, 2005 Hernandez-Lopez, 2005 Valtonen, 2007 Vidal, 2008
1551 Valle, 2009 Da silva, 2013 Poches, 2013 Valle, 2014 Valle, 2016 Swanson, 2017 Arakaki, 2018 Arakaki ; Cebidae : 1967 Bennett, 1968 Ackerman, 1976 Denis,
1552 1983 Nagle, 1997 Yeoman, 1998 Yeoman, 2002 Barnabe, 2009 Araujo, 2011 Oliveira, 2015 Leao, 2015 Nakazato, 2015 Oliveira, 2016a Oliveira, 2017 Lima,
1553 2017b Oliveira ; Cercopithecidae : 1963 Mastroianni, 1965 Weisbroth, 1967 Hoskins, 1967 Roussel, 1968 Ackerman, 1968 Roussel, 1969 Kraemer, 1970
1554 Valerio, 1973 Cho, 1974 Zamboni, 1976 Fléchon, 1980 Wickings, 1988 Cranfield, 1989 Schaffer, 1990 Lanzendorf, 1990 Tollner, 1992 Thomson, 1993 Mahony,
1555 1994 Conradie, 1994 Sankai, 1996 Mahony, 1998 Kyaligonza, 1998 Ramesh, 1999 Chan, 1999 Gago, 1999 Hiyaoaka, 1999 van der Horst, 2000 Cseh, 2000
1556 Kholkute, 2000 Mahony, 2000 Sanchez-Partida, 2000 Si, 2001 Feradis, 2003 Amboka, 2003 O'brien, 2004 Mdhluli, 2004 Vandervoort, 2005a Li, 2005b Li, 2007
1557 Hung, 2007 Leibo, 2007 Sparman, 2008 Gagliardi, 2008 Dong, 2009 Dong, 2010 Nyachieo, 2011 Maree, 2011 Yang, 2012 Nyachieo, 2013 Nyachieo, 2014

1558 Thomsen, 2017 Dubaut, 2018 Devilliers, 2019 Gadea, 2019 Zainuddin ; Hominidae: 1967 Roussel, 1968 Ackerman, 1974 Hardin, 1974 Warner, 1977 Seuanez,
1559 1980 Platz, 1981 Srivastava, 1982 Gould, 1982 Seager, 1983 Bader, 1986 Jeyendran, 1988 Marson, 1989 Gould, 1989 Marson, 1991 Schaffer, 1993 Vandevoort,
1560 1993 Gould, 1995 Young, 1995 Joslin, 1997 Ombelet, 1997 Pope, 1998 Aziz, 1998 Younis, 2001 Kusunoki, 2003 O'brien, 2003 Soler, 2004 Kuehl, 2005 Agca,
1561 2005 O'brien, 2006 Slotter, 2007 Aziz, 2010 Cooper, 2010 Maree, 2011 Maree, 2012 Thilagavathi, 2013 Mossman, 2018 Yu ; Hylobatidae : 1968 Ackerman.

1562

1563 Table 3. Computer assisted sperm analysis of 9 primate species.

Species	VAP (μM)	VCL (μM)	VSL (μM)	ALH (μM)	References
Callitrichidae family					
<i>Callithrix jacchus</i>	97.5	125.2	82.7	6.2	1996 Morell, 1997 Morell, 1998 Morell, 2004 Schneiders, 2005 Hernandez-Lopez
Cercopithecidae family					
<i>Chlorocebus aethiops</i>	227.7	201.5	167.8	3.8	1999 van der Horst, 2004 Mdhluli, 2011 Maree
<i>Macaca fascicularis</i>	-	152.7	140.0	6.3	1990 Tollner, 1993 Mahony, 1996 Mahony
<i>Macaca mulatta</i>	182.0	222.1	163.9	4.6	2006 Baumber, 2007 Hung, 2011 Maree
<i>Papio ursinus</i>	357.2	367.7	337.8	3.4	2011 Maree
Cheirogaleidae family					
<i>Microcebus murinus</i>	-	145	20.2	-	2002 Aslam
Hominidae family					
<i>Homo sapiens</i>	75.2	98	69.9	2.7	1990 Mortimer, 2006 Slotter, 2011 Maree
<i>Pan troglodytes</i>	138.0	110.3	34.3	5.2	1993 Gould, 1998 Younis, 2018 Nascimento, 2018 Yu

1564

1565 All measurements are presented uncritically and as mean when multiple sources. VAP: average path velocity; VCL: curvilinear velocity; VSL: straight-line
1566 velocity; ALH: head lateral amplitude.

1567

1568 Table 4. Mean total weight of both testis for 71 primate species.

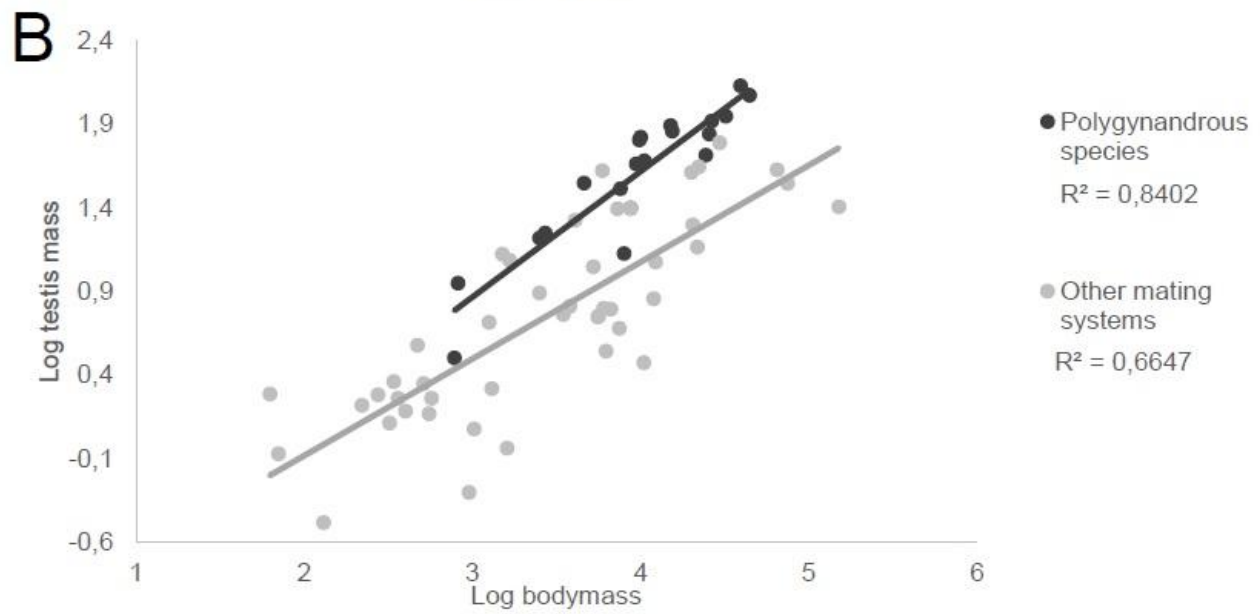
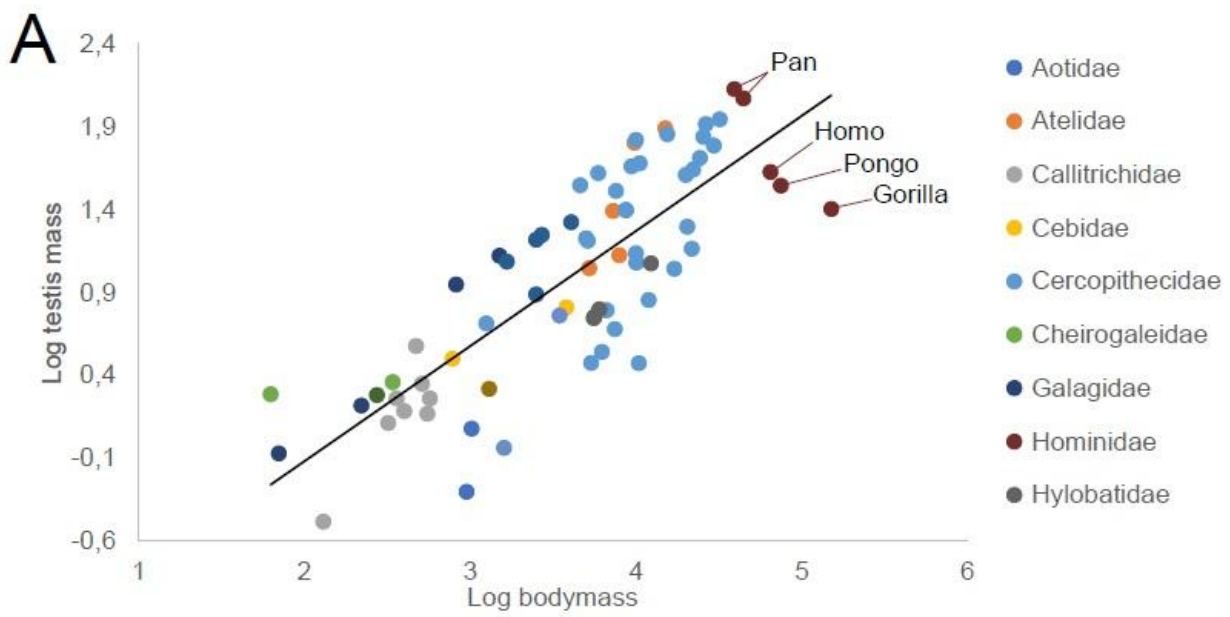
Species	Total weight (gr)	References
Aotidae family		
<i>Aotus lemurinus</i>	0.500	2004 Dixson
<i>Aotus trivigatus</i>	1.200	1938 Schultz, 1981 Harcourt
Atelidae family		
<i>Alouatta palliata</i>	24.950	1925 Hrdlicka, 1981 Harcourt
<i>Ateles geoffroyi</i>	13.400	1938 Schultz, 1981 Harcourt
<i>Ateles paniscus</i>	64.230	1998 Parker
<i>Brachyteles arachnoides</i>	78.350	2019 Arakaki
<i>Lagothrix lagotricha</i>	11.200	1938 Schultz, 1981 Harcourt
Mean Atelidae	38.426	
Callitrichidae family		
<i>Callithrix jacchus</i>	1.300	1981 Harcourt, 1999 Birkhead, 2004 Dixson
<i>Cebuella pygmaea</i>	0.330	1993 Soini
<i>Leontopithecus rosalia</i>	1.480	1987 Dixson
<i>Mico argentatus</i>	1.830	1987 Dixson
<i>Saguinus fuscicollis</i>	1.530	2004 Dixson
<i>Saguinus midas</i>	1.830	1987 Dixson
<i>Saguinus nigricollis</i>	3.800	1987 Dixson
<i>Saguinus oedipus</i>	2.440	1925 Hrdlicka, 1981 Harcourt, 1999 Birkhead
Mean callitrichidae	1.818	
Cebidae family		
<i>Saimiri sciureus</i>	3.185	1972 Middleton, 1981 Harcourt, 1999 Birkhead, 2004 Dixson
<i>Sapajus apella</i>	6.870	1960 Hill, 1998 Parker, 2004 Dixson
Cercopithecidae family		
<i>Allenopithecus nigroviridis</i>	16.960	1966 Hill
<i>Cercocebus atys</i>	25.100	1966 Hill
<i>Cercocebus torquatus</i>	25.100	1941 Kennard
<i>Cercopithecus ascanius</i>	3.000	1966 Hill
<i>Chlorocebus aethiops</i>	16.800	1960 Kinsky, 1981 Harcourt, 1999 Birkhead, 2004 Dixson
<i>Colobus guereza</i>	2.980	1987 Dixson
<i>Colobus polykomos</i>	12.200	1960 Kinsky, 2004 Dixson
<i>Erythrocebus patas</i>	7.200	1991 Harcourt, 1998 Parker, 2004 Dixson
<i>Lophocebus aterrimus</i>	13.780	1966 Hill
<i>Macaca arctoides</i>	48.200	1981 Harcourt, 1999 Birkhead, 2004 Dixson
<i>Macaca fascicularis</i>	35.450	1938 Schultz, 1981 Harcourt, 1999 Birkhead, 2004 Dixson
<i>Macaca fuscata</i>	72.300	2004 Dixson
<i>Macaca mulatta</i>	49.565	1938 Schultz, 1976 Amann, 1981 Harcourt, 1986 Amann, 1993 Bercovitch, 1999 Birkhead, 2000 Gupta, 2004 Dixson
<i>Macaca nemestrina</i>	66.700	1938 Schultz, 1981 Harcourt, 1999 Birkhead, 2004 Dixson
<i>Macaca radiata</i>	38.950	1938 Schultz, 1981 Harcourt, 2000 Gupta, 2004 Dixson
<i>Macaca silenus</i>	42.000	1998 Parker, 2004 Dixson
<i>Mandrillus leucophaeus</i>	41.050	1970 Hill
<i>Mandrillus sphinx</i>	61.907	1992 Wickings, 1998 Parker, 2004 Dixson
<i>Miopithecus talapoin</i>	5.200	1987 Dixson
<i>Nasalis larvatus</i>	14.700	1938 Schultz
<i>Papio anubis</i>	83.447	1981 Harcourt, 1998 Parker, 2004 Dixson
<i>Papio cynocephalus</i>	52.000	1981 Harcourt
<i>Papio hamadryas</i>	49.700	1960 Kinsky, 1981 Harcourt, 1999 Birkhead, 2004 Dixson
<i>Papio papio</i>	88.900	1981 Harcourt
<i>Papio ursinus</i>	69.760	1981 Harcourt, 2004 Dixson
<i>Presbytis rubicunda</i>	3.500	1938 Schultz, 1981 Harcourt
<i>Semnopithecus entellus</i>	11.100	1981 Harcourt, 2004 Dixson
<i>Theropithecus gelada</i>	20.033	1960 Kinsky, 1970 Hill, 1999 Birkhead
<i>Trachypithecus cristatus</i>	6.250	1938 Schultz, 1981 Harcourt
<i>Trachypithecus obscurus</i>	4.800	1981 Harcourt
Mean Cercopithecidae	32.954	
Cheirogaleidae family		
<i>Cheirogaleus major</i>	2.300	1964 Petter-Rousseaux
<i>Microcebus murinus</i>	2.098	1964 Petter-Rousseaux, 1998 Parker, 2002 Aslam, 2004 Dixson
Galagidae family		
<i>Galago senegalensis</i>	1.660	1964 Butler
<i>Galagoides demidovii</i>	0.850	1987 Dixson
<i>Otolemur crassicaudatus</i>	13.320	1998 Parker, 2004 Dixson
<i>Otolemur garnetti</i>	8.930	2004 Dixson
Mean Galagidae	6.190	

Hominidae family		
<i>Gorilla gorilla</i>	25.673	1962 Hall-Crags, 1981 Harcourt, 1999 Birkhead, 2004 Dixson
<i>Homo sapiens</i>	43.080	1938 Schultz, 1981 Harcourt, 1986 Amann, 1999 Birkhead, 2004 Dixson
<i>Pan paniscus</i>	135.200	1998 Parker, 2004 Dixson
<i>Pan troglodytes</i>	118.800	1938 Schultz, 1999 Birkhead, 2004 Dixson
<i>Pongo pygmaeus</i>	35.300	1938 Schultz, 1999 Birkhead, 2004 Dixson
Mean Hominidae	71.611	
Hylobatidae family		
<i>Hylobates agilis</i>	6.320	1946 Harrison-Mattews
<i>Hylobates lar</i>	5.705	1941 Kennard, 1981 Harcourt, 1999 Birkhead, 2004 Dixson
<i>Hylobates moloch</i>	5.600	1938 Schultz, 1981 Harcourt
<i>Hylobates syndactylus</i>	11.950	1998 Parker, 2004 Dixson
Mean Hylobatidae	7.394	
Indriidae family		
<i>Avahi laniger</i>	2.090	1964 Petter-Rousseaux
Lemuridae family		
<i>Eulemur fulvus</i>	7.780	1964 Petter-Rousseaux
<i>Eulemur macaco</i>	16.650	1977 Bogart, 1998 Parker, 2004 Dixson
<i>Eulemur mongoz</i>	12.250	1998 Parker, 2004 Dixson
<i>Lemur catta</i>	17.800	1998 Parker, 2004 Dixson
<i>Varecia variegata</i>	21.735	1993 Morland, 2004 Dixson
Mean Lemuridae	15.243	
Lorisidae family		
<i>Loris tardigradus</i>	1.920	1967 Ramakrishna, 1981 Harcourt
Pitheciidae family		
<i>Cacajao calvus</i>	5.800	1995 Harcourt
<i>Pithecia pithecia</i>	0.920	1960 Hill
Mean primates	24.096	

1569

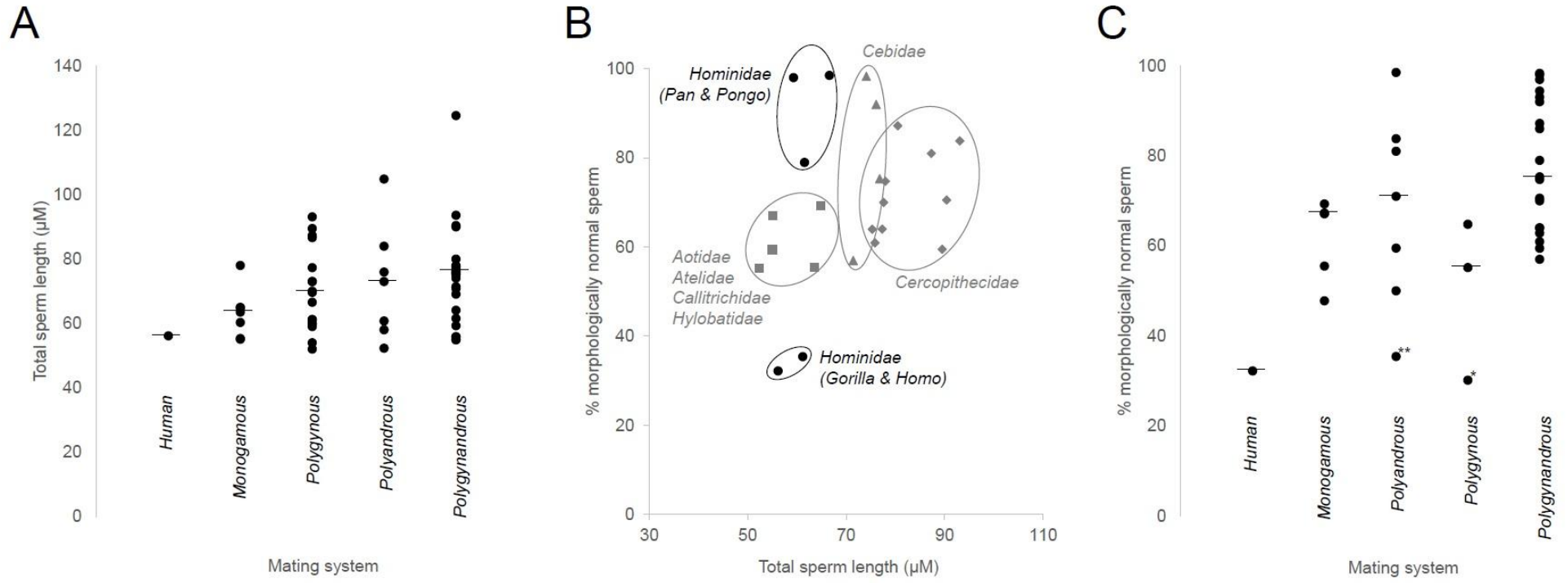
1570 All measurements are presented uncritically and as mean when multiple sources.

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