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1 **Title:**

2 Sexual dimorphism in postcranial skeletal shape suggests male-biased specialization for physical
3 competition in anthropoid primates

4

5 **Short title:**

6 Sexual dimorphism in anthropoid primates

7

8 **Authors:**

9 Jeremy S. Morris¹

10 Christopher B. Cunningham²

11 David R. Carrier³

12

13 **Author affiliations:**

14 ¹Department of Biology, Wofford College, 429 N. Church Street, Spartanburg, SC 29303, USA

15 ²Department of Biosciences, Swansea University, Swansea SA2 8PP, Wales, UK

16 ³Department of Biology, University of Utah, 257 S 1400 E, Salt Lake City, UT 84112, USA

17

18 **Corresponding author:**

19 Jeremy S. Morris

20 ¹Department of Biology, Wofford College, 429 N. Church Street, Spartanburg, SC 29303, USA

21 (864) 597-4523

22 morrisjs@wofford.edu

23

24 **Abstract.**

25 Sexual dimorphism often arises as a response to selection on traits that improve a male's ability
26 to physically compete for access to mates. In primates, sexual dimorphism in body mass and
27 canine size are more common in species with intense male-male competition. However, in
28 addition to these traits, other musculoskeletal adaptations may improve male fighting
29 performance. Postcranial traits that increase strength, agility, and maneuverability may also be
30 under selection. To test the hypothesis that males, as compared to females, are more specialized
31 for physical competition in their postcranial anatomy, we compared sex-specific skeletal shape
32 using a set of functional indices predicted to improve fighting performance. Across species, we
33 found significant sexual dimorphism in a subset of these indices, indicating the presence of
34 skeletal shape sexual dimorphism in our sample of anthropoid primates. Mean skeletal shape
35 sexual dimorphism was positively correlated with sexual dimorphism in body size, an indicator
36 of the intensity of male-male competition, even when controlling for both body mass and
37 phylogenetic relatedness. These results suggest that selection on male fighting ability has played
38 a role in the evolution of postcranial sexual dimorphism in primates.

39

40 **Key words:**

41 aggression, anatomy, functional morphology, sexual selection

42

43 **Research Highlights**

44 Sexual dimorphism is present in the postcranial skeleton of anthropoid primates. This
45 dimorphism increases with the intensity of male-male competition and has likely evolved in
46 response to selection on male aggressive performance.

47

48

49 **Introduction.**

50 Sexual dimorphism is common among primates. The multifactorial nature of this phenomenon
51 reflects a variety of disparate pressures on both males and females (Plavcan, 2001). Sexual
52 selection is thought to play a major role in the evolution of male-biased sexual dimorphism by
53 acting on traits that improve a male's ability to compete for mates and produce offspring
54 (Andersson, 1994; Darwin, 1871). In many species, the mating opportunities of males, through
55 the means of resource control, social dominance, or mate guarding, are determined by
56 performance in agonistic contests (e.g., Campagna & Le Boeuf, 1988; Clutton-Brock, Guinness,
57 & Albon, 1982; Le Boeuf, 1974). Though most encounters between males do not lead to physical
58 fighting, the importance of fighting performance has led to the evolution of male-biased sexual
59 dimorphism in traits that improve fighting performance (Clutton-Brock, 1985; Crook, 1972;
60 Darwin, 1871; Ford, 1994; Kappeler, 1990, 1991; Kay, Plavcan, Glander, & Wright, 1988;
61 Leutenegger & Kelly, 1977; Lindenfors & Tullberg, 1998; Martin, Willner, & Dettling, 1994;
62 Plavcan, 2001; Plavcan & van Schaik, 1992, 1997). For example, body mass has a strong
63 influence on the outcome of male-male contests in many species because it confers the
64 advantages of increasing absolute force and momentum that may be used against a competitor
65 (Andersson, 1994; Darwin, 1871). Because of this, male body mass is positively correlated with
66 reproductive success within many mammalian species (Clinchy, Taylor, Zanette, Krebs, &
67 Jarman, 2004; Clutton-Brock, Albon, & Guinness, 1988; Fisher & Lara, 1999; Kruuk, Clutton-
68 Brock, Rose, & Guinness, 1999; Zedrosser, Bellemain, Taberlet, & Swenson, 2007). Likewise,
69 in primates, body mass dimorphism is more pronounced in species with more intense male-male
70 competition (Alexander, Hoogland, Howard, Noonan, & Sherman, 1979; Clutton-Brock, Harvey,
71 & Rudder, 1977; Gaulin & Sailer, 1984; Mitani, Gros-Louis, & Richards, 1996; Plavcan, 1999,

72 2004; Plavcan & Van Schaik, 1997; Puts, 2010, 2016). Similarly, canine teeth are primary
73 weapons in male-male contests in many species. As with body mass, canine size dimorphism
74 increases with levels of male-male competition in some primate taxa (Kay et al., 1988;
75 Leutenegger & Kelly, 1977; Plavcan & van Schaik, 1992), though not when analyzed using
76 phylogenetic comparative methods (Plavcan, 2004; but see Thorén, Lindenfors, & Kappeler,
77 2006).

78 In addition to body mass and canine teeth, other musculoskeletal adaptations may
79 improve male fighting performance. Traits that improve strength, agility, and maneuverability
80 (i.e., whole-organism performance capacities) may also be under positive selection in males
81 (Carrier, 2002, 2007; Clutton-Brock & Harvey, 1977; Kappeler, 1990, 1991, 1996; Lailvaux &
82 Irschick, 2006, 2007; Lawler, 2009; Lawler, Richard, & Riley, 2005; Leutenegger & Kelly,
83 1977; Lindenfors, 2002). In several lizard species, for example, winning in male contests is best
84 predicted by sprint speed (Garland, Hankins, & Huey, 1990; Robson & Miles, 2000) or jumping
85 ability (Lailvaux, Herrel, Vanhooydonck, Meyers, & Irschick, 2004), traits that likely reflect the
86 importance of agility during combat. Recently, we found widespread sexual dimorphism in
87 postcranial skeletal traits related to male-male competitive performance in a sample of 26
88 Carnivora species. Phylogenetic model selection analyses on a variety of life history traits
89 provided strong support that the evolution of this dimorphism was associated with sexual
90 selection on male fighting performance (Morris & Carrier, 2016).

91 Anthropoid primates are a useful group to examine postcranial specialization for male-
92 male competition because of the variation of competition intensity across this taxon in addition
93 to a well-resolved phylogeny. In addition to biting, fighting between male primates involves
94 dynamic actions of the postcranial musculoskeletal system. In chimpanzees, for example,

95 fighting consists of grappling, striking with the hands, kicking and stomping with the feet, and
96 lifting and then slamming an opponent to the ground (Goodall, 1986). Fighting between male
97 orangutans involves grappling and biting that occurs both in the trees and on the ground
98 (Galdikas, 1979). In mountain gorillas, striking with the hands, kicking, dragging, and pinning
99 opponents to the ground occurs (Rosenbaum, Vecellio, & Stoinski, 2016). Striking, grappling, or
100 wrestling also occur in male contests in other anthropoid primates: gray langurs (Sugiyama,
101 1965), toque macaques (Dittus, 1977), red howler monkeys (Sekulic, 1983), olive baboons
102 (Owens, 1975), southern muriqui (Talebi, Beltrão-Mendes, & Lee, 2009), and red colobus
103 monkeys (Struhsaker, 2010).

104 Male fighting may result in severe injuries or death. Fractures to skull and limb bones
105 have been reported for a variety of primate taxa (Brain, 1992; Crockett & Pope, 1988; Fossey,
106 1983; Goodall, 1986; Jurmain, 1997; Kay et al., 1988; Valero, Schaffner, Vick, Aureli, &
107 Ramos-Fernandez, 2006). Injuries related to aggression are much more common in males than in
108 females (Smuts, 1987). Similarly, death resulting from intraspecific aggression has been reported
109 in many primate species (Brain, 1992; Crockett & Pope, 1988; Daly, 2016; Dittus, 1977; Enquist
110 & Leimar, 1990; Goodall, 1986; Huntingford & Turner, 1987; Lindburg, 1971; Packer, 1979;
111 Setchell, Wickings, & Knapp, 2006; Sherrow, 2012; Southwick, 1970; Wich et al., 2007;
112 Wrangham & Peterson, 1996; also see references above). Higher rates of male mortality have
113 resulted in female-biased adult sex ratios, particularly in polygynous species with intense male
114 aggression (Clutton-Brock, 1991; Clutton-Brock et al., 1977; Kappeler, 1999; Setchell et al.,
115 2006).

116 Coalitional killing, an extreme form of lethal intraspecific competition that is typically
117 carried out by males, is also widespread among primates (Wrangham, 1999). Though individual

118 aggressive performance may be less critical than overall group aggressive performance in these
119 events, the role of inflicting damage may nonetheless select for morphological traits that improve
120 a male's ability to do so. For example, coalitionary killing has been reported in gray wolves
121 (Mech & Boitani, 2003), lions (Grinnell, Packer, & Pusey, 1995), and African wild dogs (Creel
122 & Creel, 2002), species that also exhibit sexual dimorphism in postcranial skeletal traits
123 associated with aggression (Morris & Carrier, 2016). In summary, though physical fighting is
124 likely avoided during most male-male encounters (e.g., through bluffs, sounds displays, etc.),
125 when fighting does occur, it is dynamic, injurious, and likely imposes high demands on the body
126 of combatants. Indeed, the pervasiveness of aggression and violence among males across primate
127 taxa has led to the suggestion that these are general characteristics of the Primates order (Talebi
128 et al., 2009; Wrangham & Peterson, 1996).

129 Sexual dimorphism in postcranial anatomy received much attention prior to the arrival of
130 modern phylogenetic-informed comparative methods. Those early studies showed that
131 postcranial dimorphism was present but typically interpreted these patterns as a correlated
132 response to increases in male body mass ("size-required" allometry; Leutenegger & Larson,
133 1985; Wood, 1976). However, more recent studies have shown that phylogenetic-informed
134 analyses are crucial to understanding patterns of primate postcranial anatomy. For example, long
135 bone metrics show significant phylogenetic signal both before and after adjusting for body mass
136 (O'Neill & Dobson, 2008). Similarly, the intermembral index, a measurement of relative
137 forelimb to hindlimb length commonly associated with primate locomotor mode, was previously
138 shown to be positively correlated with body mass across species (Jungers, 1984; Martin, 1990).
139 When performing the same analysis using phylogenetic independent contrasts, however, this
140 association is nearly absent ($R^2 = 0.04$; Nunn, 2011). Thus, there is a need to examine patterns of

141 sexual dimorphism in the postcranial skeleton of primates while incorporating phylogenetic
142 relatedness.

143 Here, we evaluate the postcranial skeletal anatomy of 11 anthropoid primate species
144 using a set of functional indices that are predicted to reflect specialization for improved
145 performance in physical competition (Morris & Brandt, 2014; Morris & Carrier, 2016). Greater
146 values in these functional indices are associated with the following traits: (1) broader distal ends
147 of limbs that increase surface area for muscle attachment (Swindler & Wood, 1973) and increase
148 safety factors (Alexander, 1981); (2) greater mechanical advantages across limb joints to
149 increase force output (Maynard Smith & Savage, 1956); and (3) relatively broader scapulae to
150 house larger muscles associated with stabilizing the shoulder joint (Larson, 1993) when using the
151 forelimbs (e.g., for striking or grappling with a competitor). Together, these traits function to
152 increase forces that may be applied to a competitor, increase stability and acceleration capacity,
153 and increase safety factors to resist high limb loading in variable directions that may occur when
154 fighting (Morris & Brandt, 2014; Morris & Carrier, 2016; Pasi & Carrier, 2003). Thus, for each
155 index, values are expected to increase with a greater degree of specialization for physical
156 competition.

157 Based on the behavioral and life history data above, we predicted that males, as compared
158 to females, would have greater values in these functional indices. We test this by examining
159 functional index values for sex-based differences among species. We also predicted that mean
160 skeletal shape sexual dimorphism (calculated as the mean sexual dimorphism of all functional
161 indices) would increase with both sexual dimorphism in body mass (size sexual dimorphism;
162 SSD) and canine height (canine sexual dimorphism; CSD). The degree of sexual dimorphism in
163 both body mass and canine size are general indicators of the intensity of male-male competition

164 and sexual selection. We examine these relationships using both standard and phylogenetic-
165 informed methods. Because both SSD and CSD are correlated with body mass (Leutenegger,
166 1982; Smith & Cheverud, 2002), we use data adjusted for body mass using residual analysis.
167 However, we also evaluate uncorrected data because of the suggestion by Plavcan (2004) that
168 adjusting sexual dimorphism values for body mass also removes variation in the causal variable
169 (sexual selection).

170

171 **Materials and Methods.**

172 We measured male ($n = 74$) and female ($n = 63$) skeletons from specimens housed at the
173 Smithsonian Institution National Museum of Natural History (Washington, D.C.), the British
174 Natural History Museum (London), and the American Museum of Natural History (New York).
175 All specimens were osteologically mature, as determined by fusion of epiphyses of the long
176 bones. Specimen identification information is provided in the supplementary (Table S1). From
177 physiological length (distance between articular surfaces) and width measurements, we
178 calculated nine functional indices that are associated with increased specialization for physical
179 competition (Table 1; Morris & Brandt, 2014; Morris & Carrier, 2016).

180 To test for sexual dimorphism across the species in our data set, we compared ln-
181 transformed male and female functional index values using both standard paired t -tests as well as
182 phylogenetic paired t -tests (Lindenfors, Revell, & Nunn, 2010). We calculated sexual
183 dimorphism in each functional index (SD_{FI}) as male mean/female mean when the male mean was
184 greater and $2 - \text{female mean/male mean}$ when the female mean was greater (Lovich & Gibbons,
185 1992; Smith, 1999). SD_{FI} values for each species were calculated separately and then ln-
186 transformed.

187 To test the prediction that skeletal shape sexual dimorphism increases with the intensity
188 of male-male competition, we examined the relationships between mean skeletal shape sexual
189 dimorphism (SD_{SHAPE} ; calculated separately for each species by taking the mean of all nine SD_{FI}
190 values) and SSD and CSD. We obtained SSD and CSD values from the literature (SSD data:
191 (Kingdon et al., 2013; Smith & Jungers, 1997); CSD data: Plavcan, 2004). We took four
192 approaches to evaluate the relationships between SD_{SHAPE} , SSD, and CSD. First, In-transformed
193 species values of SD_{SHAPE} were regressed against In-transformed SSD or CSD. Second, we
194 corrected data for body mass by calculating least-squares residuals of SD_{SHAPE} , SSD, and CSD
195 on female body mass. Following this, body mass residuals of SD_{SHAPE} were regressed against
196 body mass residuals of SSD and CSD. Third, we adjusted data for phylogenetic relatedness by
197 calculating phylogenetic independent contrasts (PIC; Felsenstein, 1985) for SD_{SHAPE} , SSD, and
198 CSD. PIC values for SD_{SHAPE} were then regressed against PIC values for SSD and CSD. Fourth,
199 to adjust for both phylogenetic relatedness and body mass simultaneously, we calculated body
200 mass residuals of PIC values of SD_{SHAPE} , SSD, and CSD. For this, we regressed PIC values of
201 SD_{SHAPE} , SSD, and CSD against PIC values of female body mass using least-squares regression
202 with the intercept restricted to zero (Garland, Harvey, & Ives, 1992). We then regressed body
203 mass residuals of SD_{SHAPE} PIC values against body mass residuals of SSD and CSD PIC values.
204 For all phylogenetic-informed analyses, we used a recent species-level Primates supertree
205 (Perelman et al., 2011). PIC values were calculated using the `pic()` function in the *ape* package
206 (Paradis, Claude, & Strimmer, 2004). All analyses were carried out in the R statistical
207 programming environment (R Development Core Team, 2016).

208 To graphically summarize the data, we plotted SD_{FI} values for each species onto the
209 phylogeny used in the analysis. We plotted a given SD_{FI} value only when a univariate analysis of
210 variance (ANOVA) indicated sexual dimorphism was present ($p < 0.05$).

211

212 **Results.**

213 Among the 11 species of anthropoid primates in the analysis, sexual dimorphism was found in 4
214 of 9 functional indices (Table 2). Results from the non-phylogenetic and phylogenetic paired t -
215 tests differed slightly, with 3 of 4 significant differences ($p < 0.05$) being in the same functional
216 indices (humerus epicondyle index, olecranon mechanical advantage, and ischium mechanical
217 advantage). The styloid width index was significant in the non-phylogenetic test and was
218 marginally significant in the phylogenetic test ($p = 0.052$). Conversely, the femur epicondyle
219 index was significant in the phylogenetic test and trended the same way in the non-phylogenetic
220 test ($p = 0.089$). The hindlimb malleolus index trended toward dimorphism in both the non-
221 phylogenetic ($p = 0.074$) and phylogenetic tests ($p = 0.093$). In all significant and trending
222 results, males had greater functional index values.

223 Across species, SD_{SHAPE} was positively correlated with SSD when using species values,
224 PIC values, and body mass residuals of PIC values, but not when using body mass residuals of
225 species values (Table 3; Figure 1). SD_{SHAPE} was positively correlated with CSD only when using
226 PIC values (Table 3; Figure 1). A graphical summary of the data set showing the presence ($p <$
227 0.05 ; ANOVA) and degree of dimorphism in SD_{FI} values for each species is presented in Figure
228 2. Means, standard deviations, sample sizes, and descriptive statistics for SD_{FI} values are
229 provided in the supplementary (Table S2).

230

231 **Discussion.**

232 In our sample of 11 anthropoid primate species, we found sexual dimorphism in a subset (4 of 9)
233 of postcranial functional indices associated with morphological specialization for physical
234 competition. Consistent with our predictions, sexual dimorphism was male-biased in all
235 significant and trending results. Mean sexual dimorphism in skeletal shape (SD_{SHAPE}) was
236 positively correlated with SSD. When controlling for species relatedness using phylogenetic
237 independent contrasts, evolutionary change in SD_{SHAPE} is strongly associated with evolutionary
238 change in SSD ($R^2 = 0.659$); when adjusting contrasts for body mass, this relationship remains
239 moderately strong ($R^2 = 0.534$). SD_{SHAPE} was correlated with CSD only when using phylogenetic
240 independent contrasts and resulted in a weaker but significant correlation ($R^2 = 0.334$). Together,
241 these results indicate the presence of sexual dimorphism in skeletal shape within the anthropoid
242 lineage and that this dimorphism increases with the intensity of male-male competition (using
243 SSD as a proxy).

244 These results are in agreement with previous studies investigating the relationship
245 between sexual selection and sexual dimorphism in anthropoid primates. Numerous studies have
246 shown a strong association between SSD or CSD and the degree of sexual selection as measured
247 by mating system, the frequency and intensity of male-male competition, or the operational sex
248 ratio (Clutton-Brock et al., 1977; Ford, 1994; Gaulin & Sailer, 1984; Harvey, Kavanagh, &
249 Clutton-Brock, 1978; Kay et al., 1988; Leutenegger, 1982; Leutenegger & Kelly, 1977;
250 Lindenfors & Tullberg, 1998; Mitani et al., 1996; Plavcan, 1999, 2004; Plavcan & van Schaik,
251 1992, 1997). The results of the present study extend these by showing that sexual selection may
252 be acting on specific components of the musculoskeletal system in addition to body and canine
253 size.

254 Sexually dimorphic traits in the forelimb identified in our analysis include a relatively
255 broader humeral epicondyle and greater mechanical advantage associated with the triceps muscle
256 (olecranon mechanical advantage) in males. These traits increase surface area for muscle
257 attachment of forelimb muscles that flex the wrist and digits and increase force output from the
258 triceps during forearm extension. Similar male-biased sexually dimorphic traits have been found
259 in western lowland gorillas (*Gorilla gorilla*), in which males have greater forelimb mass
260 (Zihlman & McFarland, 2000), a trait that is likely explained by selection on striking ability that
261 frequently occurs during male-male contests (Rosenbaum et al., 2016) . Male-biased sexual
262 dimorphism in forelimb skeletal robusticity has also been identified in australopiths (McHenry,
263 1986, 1991, 1996) and greater muscle mass is present in the arms of male humans (Abe et al.,
264 2003; Fuller et al., 1992; Lassek & Gaulin, 2009; Nindl et al., 2002). Additionally, males in our
265 study had a broader styloid in the forelimb. This trait, along with a broader humerus, increases
266 safety factors which improve the ability to resist high loading in variable directions that may
267 occur during aggressive interactions (e.g., during grappling). Together, this suite of traits allow
268 for greater force delivery for striking, grappling, and wrestling, behaviors that occur during male-
269 male contests in most of the species (or closely related species) in this study. Similarly, male
270 kangaroos fight by grappling and striking with their forelimbs (Ganslosser, 1989) and they also
271 exhibit male-biased sexual dimorphism in forelimb muscle mass (in shoulder adductors, arm
272 retractors, and elbow flexors) that functions to improve performance in fights (Jarman, 1983,
273 1989; Richards, Grueter, & Milne, 2015; Warburton, Bateman, & Fleming, 2013).

274 In the hindlimbs, males in our study had a greater ischium mechanical advantage, which
275 increases force output of muscles that retract the hindlimb, allowing greater acceleration of the
276 body mass and greater ability to push a competitor when grappling. Males also had a broader

277 hindlimb malleolus, which indicates greater robusticity of the distal hindlimb and may increase
278 stability. These hindlimb traits are also sexually dimorphic in carnivore species in which males
279 compete aggressively for females (Morris & Carrier, 2016). Specialization for aggressive
280 behavior may also have played a role in the evolution of short hindlimbs and the derived
281 plantigrade foot posture of Hominoidea (Carrier, 2007; Carrier & Cunningham, 2017).

282 The different manifestations of sexual dimorphism within and among groups of primates
283 may depend, in part, upon the dynamics of male-male combat (Carrier & Morgan, 2015; Lassek
284 & Gaulin, 2009; Morgan & Carrier, 2013). For example, Kappeler (1996) suggested that the lack
285 of sexual dimorphism in body mass or canine size in strepsirrhine primates, despite high levels of
286 male-male aggression, may be due to the lack of importance of these traits during fights (in
287 contrast to haplorrhine primates). Instead, agility and maneuverability may be more important for
288 male fighting performance (Clutton-Brock & Harvey, 1977; Kappeler, 1990, 1996; Lawler,
289 2009; Lawler et al., 2005; Leutenegger & Kelly, 1977; Lindenfors, 2002).

290 The environmental substrate where male-male contests occur may also influence which
291 traits improve performance (Kappeler, 1990, 1991; Lawler, 2009; Lawler et al., 2005). This may
292 be especially salient in primarily arboreal species. Lawler et al.'s (2005) study of Verreaux's
293 sifaka (*Propithecus verreauxi*) provides a relevant example. This species is sexually
294 monomorphic in both body and canine size yet males compete in sustained, violent contests
295 involving chasing, lunging, grabbing, and biting, all of which occurs arboreally (Richard, 1978,
296 1992). In this case, the importance of arboreal agility may be greater than that of body size.
297 Analysis showing that males of intermediate body size have the greatest reproductive fitness
298 supports this assertion (Lawler et al., 2005). This may also explain the combination of high
299 intensity male-male competition and low level of sexual dimorphism found in other strepsirrhine

300 primates (Kappeler, 1990, 1991, 1996; Lawler et al., 2005; Lindenfors, 2002; Richard, 1992).
301 Indeed, arboreal locomotion is thought to constrain the evolution of body size sexual dimorphism
302 more strongly than terrestrial locomotion in primates (Clutton-Brock et al., 1977; Harvey et al.,
303 1978; Lawler et al., 2005; Leutenegger & Kelly, 1977; Lindenfors & Tullberg, 1998; Plavcan &
304 Van Schaik, 1997). In our data set, the two primarily terrestrial species (*Gorilla gorilla* and
305 *Papio anubis*) had pronounced skeletal shape and body size dimorphism. However, *Pongo*
306 *pygmaeus*, an arboreal species, had the highest degree of shape dimorphism of any species in the
307 study. In addition to limiting body size sexual dimorphism, a functional trade-off between
308 locomotor performance and aggressive performance may also constrain the evolution of sexual
309 dimorphism in the musculoskeletal system (Carrier, 2002; Kemp et al., 2005; Morris, Ruff, Potts,
310 & Carrier, 2017; Pasi & Carrier, 2003). Additional studies examining patterns of sexual
311 dimorphism in skeletal shape and muscle distribution in other taxa could provide resolution to
312 this issue.

313 In summary, we found evidence of sexual dimorphism in postcranial skeletal shape
314 among a sample of 11 anthropoid primate species. A subset of functional morphological traits
315 that are predicted to improve physical competition performance are sexually dimorphic in our
316 sample, allowing males to have greater surface areas for attachment of limb muscles, greater
317 safety factors in the limb bones, and greater force output. Though the dimorphism identified in
318 our analysis was restricted to 4 of 9 functional indices, overall mean shape dimorphism (all
319 indices included) was significantly positively correlated with dimorphism in body size, a
320 common proxy for the intensity of male-male competition. Despite among-species differences
321 associated with fighting dynamics, substrate use, and possible coalition-forming behaviors, our
322 analysis indicates a small but significant degree of sexual dimorphism in postcranial skeletal

323 shape among the species in this study. In conclusion, our results suggest that selection on male
324 fighting ability has played a role in the evolution of postcranial sexual dimorphism in primates.

325

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332

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- 632
- 633

634 **Table 1.** Postcranial morphological indices, definitions, and functional interpretations associated
 635 with morphological specialization for aggression.

636

Index	Definition
Scapula width index	Width of scapula along medial border relative to length of scapula along spine. Indicates relative size of surface area for attachment of muscles involved in stabilizing the shoulder joint during arm movements (supraspinatus, infraspinatus, subscapularis; Larson, 1993).
Forelimb proportions index	Length of humerus relative to length of radius. Indicates degree of morphological specialization for producing large out-forces in the forelimb (Maynard Smith & Savage, 1956). Note: this is the inverse of the “brachial index” (Mivart, 1867; Napier & Napier, 1967).
Humerus epicondyle index	Humerus epicondyle width relative to humerus length. Indicates relative surface area for attachment of wrist and digit flexor, extensor, pronator, and supinator muscles (Swindler & Wood, 1973; Williams et al., 1995).
Olecranon mechanical advantage	Length of olecranon process relative to length of radius. Indicates anatomical mechanical advantage of triceps brachii, the main extensor of the elbow (Maynard Smith & Savage, 1956; Rose, 1993).
Styloid width index	Width of distal end of articulated radius/ulna relative to radius length. Indicates relative robusticity of distal forelimb.
Ischium mechanical advantage	Length of ischium relative to length of hindlimb (femur length + tibia length). Indicates anatomical mechanical advantage of main hindlimb retractor muscles (biceps femoris, semimembranosus, semitendinosus; Emerson, 1985; Swindler & Wood, 1973; Williams et al., 1995).
Hindlimb proportions index	Length of femur relative to length of tibia. Indicates degree of morphological specialization for producing large out-forces in the hindlimb (Maynard Smith & Savage, 1956). Note: this is the inverse of the “crural index” (Mivart, 1867; Napier & Napier, 1967).
Femur epicondyle index	Femur epicondyle width relative to femur length. Indicates relative surface area for attachment of knee flexor and foot plantarflexor muscles (e.g., gastrocnemius; Swindler & Wood, 1973; Williams et al., 1995).
Hindlimb malleolus index	Width of distal end of articulated tibia/fibula relative to tibia. Indicates relative robusticity of distal hindlimb.

637

638

639

640 **Table 2.** Mean sexual dimorphism in functional indices (SD_{FI}) and T-test results for 11
 641 anthropoid primate species. Statistics for both non-phylogenetic and phylogenetic two-tailed
 642 paired *t*-tests are given. See Table 1 for description of variables.

643

Index	Mean SD_{FI} (std. dev.)	Paired <i>t</i> -test		Phylogenetic paired <i>t</i> -test	
		<i>t</i>	<i>p</i> -value	<i>t</i>	<i>p</i> -value
Scapula width index	1.010 (0.020)	-1.67	0.125	-1.26	0.241
Forelimb proportions index	0.992 (0.025)	1.03	0.329	0.64	0.542
Humerus epicondyle index	1.067 (0.035)	-6.54	< 0.001*	14.00	< 0.001*
Olecranon MA	1.075 (0.056)	-4.58	0.001*	-3.13	0.014*
Styloid width index	1.035 (0.040)	-2.86	0.017*	-2.23	0.057
Ischium MA	1.047 (0.070)	-2.27	0.047*	-2.33	0.048*
Hindlimb proportions index	1.000 (0.016)	0.01	0.989	-0.09	0.929
Femur epicondyle index	1.025 (0.044)	-1.88	0.089	-2.73	0.034*
Hindlimb malleolus index	1.027 (0.045)	-2.02	0.071	-1.80	0.115

644

645 MA, mechanical advantage

646 * $p < 0.05$; bold type *p*-values indicate variables that remained significant after correction for
 647 multiple comparisons using the false discovery rate procedure (Benjamini & Hochberg, 1995).

648

649

650

651 **Table 3.** Analyses of the relationships between mean sexual dimorphism in skeletal shape
 652 (SD_{SHAPE}) and sexual dimorphism in body mass (SSD) or canine height (CSD) for 11 anthropoid
 653 primate species.

654

	Species values		Body mass residuals		PIC		Body mass residuals of PIC	
	R^2	p -value	R^2	p -value	R^2	p -value	R^2	p -value
SD_{SHAPE} versus SSD	0.388	0.024*	0.153	0.128	0.659	0.003*	0.534	0.010*
SD_{SHAPE} versus CSD	0.076	0.210	-0.085	0.654	0.334	0.047*	0.188	0.117

655

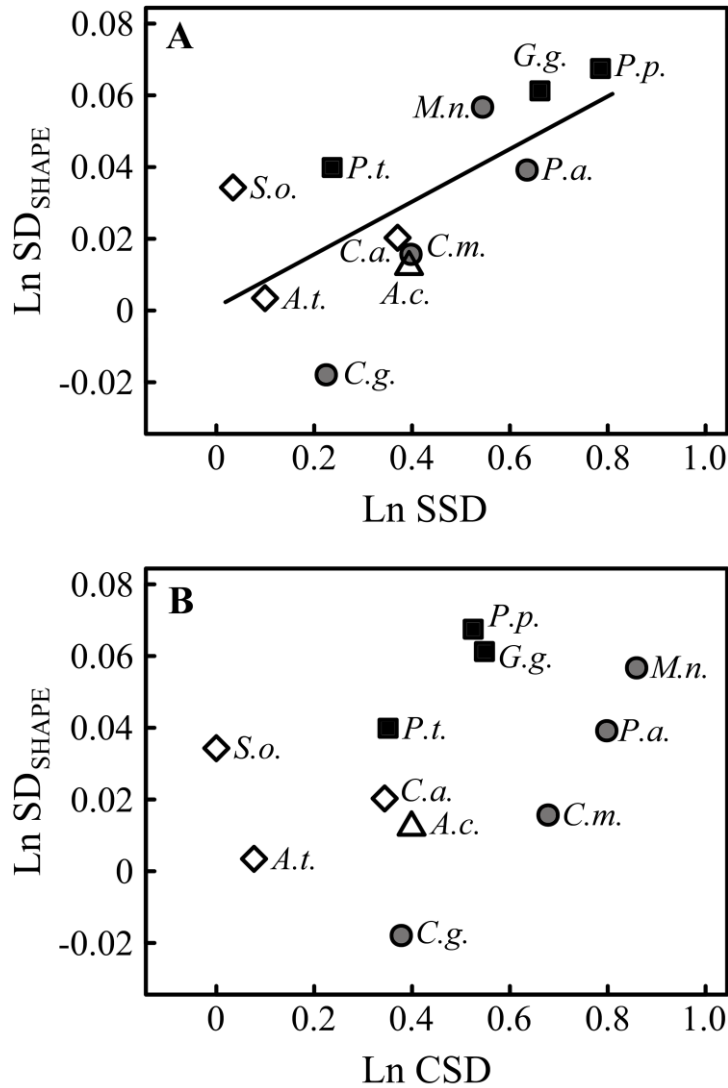
656 *Slope of regression significant ($p < 0.05$)

657 PIC: phylogenetic independent contrasts

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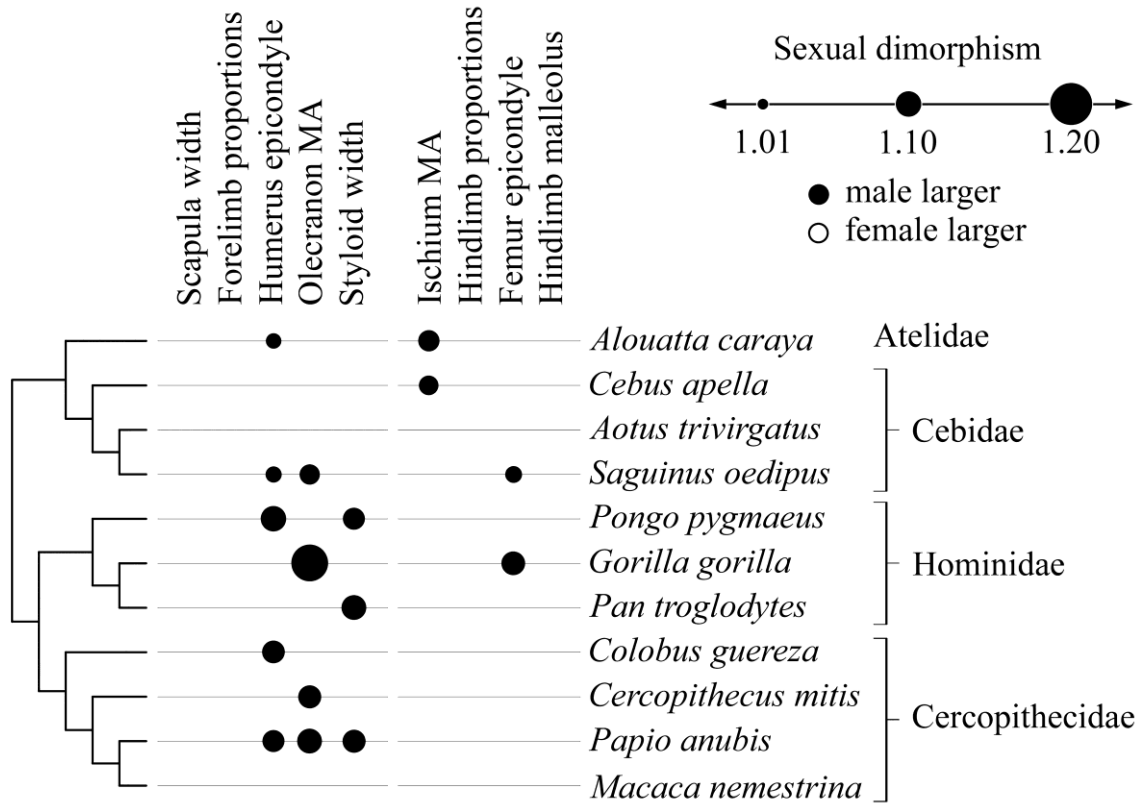


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662 **Figure 1.** Regressions of mean sexual dimorphism in skeletal shape (SD_{SHAPE}) on (A) sexual
 663 dimorphism in body mass (SD_{MASS}) and (B) sexual dimorphism in canine height (SD_{CANINE}) for
 664 11 anthropoid primate species. Unique symbols represent families: Cebidae (diamonds),
 665 Cercopithecidae (circles), Hominidae (squares), Atelidae (triangle). Initials indicate species
 666 names (see Figure 2 for phylogeny and full species names). A regression line is shown for a
 667 significant linear regression equation ($p < 0.05$).

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671 **Figure 2.** Graphical summary of data from 11 anthropoid primate species used in the analysis.

672 Plotted points indicate SD_{FI} values that were sexually dimorphic ($p < 0.05$; ANOVA). The size

673 of a point indicates the degree of sexual dimorphism (see scale). The phylogeny was pruned from

674 a recent Primates supertree (Perelman et al., 2011).

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