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Do femoral biomechanical properties follow locomotor changes in primates? An ontogenetic study of olive baboons (*Papio anubis*)

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Abstract

Objectives

The locomotor repertoire of the olive baboon (*Papio anubis*) evolves during ontogeny from a diversified pattern in infancy to a stereotyped pattern in adults. On the assumption that the cortex of the femoral diaphysis registers variations in the loading regime, we aimed to evaluate the impact of locomotor changes on femoral biomechanical properties during the development of olive baboons.

Materials and methods

We used the cross-sectional geometry of 65 3D-reconstructed femora of an ontogenetic sample including individuals from birth to 28 years of age and belonging to a single social group. Cross-section parameters and cortical thickness maps were produced for 60% of femoral length.

Results

Newborns show a symmetrical longitudinal distribution of cortical thickness and antero-posterior orientation of their sections at midshaft. From this condition, infants evolve quickly to an adult pattern characterized by a proximal shift in cortical thickness and a more mediolateral orientation of load resistance.

Discussion

As soon as locomotor autonomy is established and despite a combination of several significant locomotor modes, quadrupedalism has a predominant impact on the biomechanical pattern of the femoral shaft. We therefore advise caution when inferring complex locomotor behaviour from femoral biomechanical properties.

Keywords

biomechanics, locomotion, quadrupedalism, ontogeny, primates

1 Introduction

The positional repertoire (i.e. the combination of both postural and locomotor modes) has an influence on bone modeling and remodeling by imposing variations in the loading regime on the appendicular skeleton (Jungers & Burr, 1994; Marchi et al., 2016; Shaw & Ryan, 2012). In this respect, the cortical bone of the femoral shaft is known to be one of the best indicators of biological response to mechanical stresses: for example, a large cortex is associated with grounded locomotion while a thinner and less robust cortex is generally associated with aerial or arboreal behaviour (Habib & Ruff, 2008; Hansen, Bredbenner, Nicolella, Mahaney, & Havill, 2009; Kimura, 2002; Ruff & Hayes, 1983).

Among mammals, primates represent the order with the greatest known diversity in their positional repertoire (Napier, 1967; Gebo, 1989; Hunt et al., 1996). For this reason, they are the most relevant group to explore biomechanical properties in relation to locomotion (Schaffler & Burr, 1984). For example, cercopithecoid leapers have high bending resistance and a high remodeling index (Lad, Pampush, McGraw, & Daegling, 2019; Ruff, 2019). As knuckle-walkers, African apes display mediolaterally oriented resistance (Burgess, 2018; Morimoto, De León, & Zollikofer, 2011a; Puymerial, 2011). Bipedal humans have a particular pattern with bending resistance reinforced anteroposteriorly at midshaft and mediolaterally at the extremities (Puymerial, 2011; Ruff, Burgess, Ketcham, & Kappelman, 2016; Trinkaus & Ruff, 2012).

Besides these predominant modes in adults, the positional repertoire of primates evolves as they develop. From a general point of view, the repertoire is composed of several significant modes during infancy and becomes more stereotyped in adults. During the last decade, studies of ontogenetic modifications of femoral cortical properties in relation to locomotion have expanded (Burgess et al., 2016; Burgess, 2018; Canington, Sylvester, Burgess, Junno, & Ruff, 2018; Ruff, 2003; Ruff, 2013; Sarringhaus, MacLatchy, & Mitani, 2016; Swan, Ives, Wilson, & Humphrey, 2020). For example, in chimpanzees, femoral strength increases relatively to the humerus, which is linked to the development of more terrestrial locomotion with age (Sarringhaus et al., 2016). With regard to femoral cortical properties, these changes are reflected for example by the mediolateral reinforcement of the femoral diaphysis during growth (Burgess, 2018). In humans, the increasing strength of the femur has been related to the development of an autonomous bipedal gait (Ruff, 2003; Swan et al., 2020). These changes are materialized in particular by the emergence of the femoral pilaster.

Here, we investigate this relationship between the biomechanical properties of the femur and locomotion in an ontogenetic sample of olive baboons (*Papio anubis*), whose positional repertoire (e.g. Druelle & Berillon, 2013; Rose, 1977), morphology (Druelle, 2017; Leigh, 2009; Raichlen, 2005b) and gait biomechanics (Berillon et al., 2010; Patel & Wunderlich, 2010) are well known.

1.1 The baboon model

Like many mammals, *Papio* are described as primarily terrestrial quadrupeds (Hunt, 1992; Polk et al., 2000; Rose, 1977). However, unlike in other quadrupedal mammals of comparable size such as carnivores (Bekoff, 1989; Taylor, 1989; Iwaniuk, Pellis, & Whishaw, 1999), their locomotion evolves through development, their locomotion evolves as they develop. During the first months of life, they mainly grasp their mother around the waist; locomotor autonomy

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3 appears very early (Altmann, 1980), with a varied positional repertoire (Anvari, 2013; Druelle
4 85 & Berillon, 2013; Druelle, Aerts, & Berillon, 2016; Raichlen, 2005a). In *Papio anubis*, at
5 around 0.5 years, quadrupedalism (60.2% of locomotion) is associated with climbing (27.5%),
6 leaping (5.4%) and several other modes including bipedalism (1.9%) (Druelle et al., 2016). By
7 1.75 years, the locomotor repertoire has evolved: the proportion of bipedalism is stable (2.1%),
8 but leaping (2.2%) and climbing (9.6%) are drastically reduced while quadrupedalism has
9 increased (76.7%) (Druelle et al., 2016). Adults spend most of their time in a quadrupedal
10 90 position (Rose, 1977; Hunt, 1992; Druelle & Berillon, 2013). Their repertoire includes an
11 extreme predominance of quadrupedalism, (98.7%) while climbing decreases (1%) and leaping
12 and bipedalism disappear from field observations (Hunt, 2016). Overall, baboons spend more
13 and more time on the ground during their development.

14
15
16 95 With regard to femoral properties, Ruff (2003) noted few differences in the pattern of
17 proportionate strength in limb-bones during ontogeny when compared to humans. Hansen *et*.
18 *al* (2009) highlight the importance of heritability in cross-sectional properties and Puymerrail
19 (2011) noted a posterior reinforcement and thin distal cortex in adults of different species.
20 However, the link between biomechanical properties and locomotor development in baboons
21 100 has been unclear so far. In parallel with the locomotor repertoire, their morphotypes change
22 during ontogeny, with a proximal shift of the center of mass (CoM) of the limbs (Druelle, Aerts,
23 D'Août, Moulin, & Berillon, 2017; Raichlen, 2005a, 2005b). This variation of the limb CoM
24 position, linked with loading regime fluctuations, might also have an impact on the
25 biomechanical properties of bones.

30 105 1.2 Study objectives

31
32 The objective of this study is to test whether femoral biomechanical properties reflect locomotor
33 changes. This would allow us to refine the current view of the relationship between the loading
34 regime caused by locomotion and the biomechanical properties of the femoral shaft. We studied
35 the cross-sectional geometry of a group of olive baboons for which a substantial body of
36 110 knowledge is available (Berillon et al., 2010; Druelle, 2017; Boulinguez-Ambroise et al., 2021),
37 including on their positional repertoire through age (Druelle et al., 2016). This makes it possible
38 for the first time, to cross-reference the biomechanical properties of the femur and the
39 locomotor repertoire of a single social group housed in the same controlled environment.

43 1.3 Hypotheses

44
45 115 During prenatal development, fetuses are exposed to various loads that affect bone properties
46 (Henstock, Rotherham, Rose, & El Haj, 2013; Nowlan, 2015). These loads are primarily due to
47 fetal movements which are the main mechanical signals in the osteogenesis process (Carter,
48 Van der Meulen, & Beaupré, 1996a; Grieve, Myers, & Stark, 1994). This loading regime should
49 lead to a biomechanical pattern in newborns that is representative of intra-uterine development.
50 120 Newborns can be characterized as passive individuals in terms of locomotion, and we argue
51 that the properties of femoral sections follow a theoretical pattern that is *de facto* not constrained
52 by locomotor practices. Following the pattern of primary ossification, the cortex is expected to
53 be thicker around the ossification centre at midshaft than in surrounding areas (Carter &
54 Beaupré, 2000; Ryan & Krovitz, 2006).

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3 125 In adults, due to their almost exclusively quadrupedal gait, we expect a specific and derived
4 pattern of biomechanical properties in agreement with a highly specialized and reduced
5 locomotor repertoire.
6

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8 Between these two periods, we expect changes in biomechanical properties related to variations
9 in the locomotor repertoire previously described. In infants, grasping the mother's waist is the
10 130 first locomotor mode observed in baboons (Altmann, 1980; Anvari et al., 2014). Although the
11 group studied showed great aptitude for grasping (Boulinguez-Ambroise et al., 2021; Druelle,
12 Young, & Berillon, 2018), this behaviour mostly concerns the distal extremities of the limbs.
13 Therefore, we do not see how this behaviour, which is involved only in an indirect mode of
14 locomotion, could impact the biomechanical pattern of the femur. We thus consider that only
15 135 changes in "direct locomotion" can be expected to permanently alter the loading regime at the
16 thigh segment. Considering the acquisition of locomotor autonomy and the emergence of varied
17 modes around 0.5 years of age, we expect this period to be significant in the development of a
18 new stressful loading regime and therefore to involve major changes in biomechanical
19 properties. Until weaning (1.8 years on average), the number of independent displacement
20 140 events does not change significantly (Druelle et al., 2016). After weaning, juveniles are
21 completely independent from the mother for locomotion, and are more specialized in
22 quadrupedal walking and running. Due to this transition to adult-like locomotor behavior, we
23 expect a transitional pattern for specimens between weaning and the end of growth.
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28 To summarize, we expect:

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30 145 (H1) The femora in newborns to present a theoretical pattern that would match the primary
31 ossification process and not be affected by locomotor-related stresses.
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35 (H2) Adult femora to present a biomechanical pattern with little variation that would reflect
36 their typical locomotor repertoire dominated by quadrupedalism.
37

38 150 (H3) Infant femora to present a biomechanical pattern differing significantly from that of
39 newborns and adults and reflecting their expanded locomotor repertoire.
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45 (H4) Juvenile femora to present an intermediate biomechanical pattern between those of infants
46 155 and adults due to the decreasing diversity of their locomotor repertoire.
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49 2 Material and Methods

50 2.1 *Papio anubis* sample

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54 We studied a sample of 65 femora representing 65 individuals housed at the CNRS primatology
55 centre (UPS 846) at Rousset-sur-Arc (France); details of the samples are given in Table 1. The
56 160 48 females represent the 5 main developmental stages based on the growth rate of the thigh
57 segment and locomotor repertoire development (see Druelle et al., 2016, 2017; Leigh, 2009):
58 newborns (less than 2 days in our sample), young infants (less than 0.5 years), infants (0.5 to
59
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3 1.8 years) juveniles (1.8 to 4.75 years) and adults (more than 4.75 years). Two newborn males
4 were added to the newborn sample for statistical processing; previous studies on this sample
5 165 have shown that no sexual dimorphism exists at this stage (Moulin, Berillon, & Bocquet-Appel,
6 2013). The other 15 were treated separately in order to avoid any bias due to sexual dimorphism
7 and used when required.

8
9 The study was approved by the Performance, Financing and Contractualization service with
10 research organizations of the “Département des pratiques de recherches réglementées” and the
11 170 “Cellule Animaux utilisées à des fins Scientifiques (AfiS)” from the french Ministère de
12 l’Enseignement Supérieur, de la Recherche et de l’Innovation.
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15 2.2 Virtual data

16
17 3D models of complete femurs were constructed from CT-scan (mean of slice thickness:
18 175 0.6mm) using Avizo 8.1 (Thermo Fisher Scientific) and ImageJ (National Institutes of Health,
19 USA) software. The segmentation was performed using Half Maximum Height thresholding
20 method (Spor, Zonneveld, & Macho, 1993). Table A in the supplementary material presents
21 details of individuals information about the sample and CT scan origins.
22
23
24

25 2.3 Cross-sectional geometry

26
27 180 Cross-sections were positioned by using the alignment and biomechanical length proposed by
28 Ruff for bones with advanced epiphyseal fusion (see Ruff, 2002). For infants, we used the
29 maximum diaphyseal length (without epiphyses) parallel to the diaphyseal long axis according
30 to Canington et al., (2018) and Swan et al. (2020) on catarrhines. For the following, the term
31 *length* will be used in both cases (see Ruff, 2003). Measurements were calculated using the
32 morphomap package (Profico, Bondioli, Raia, O’Higgins, & Marchi, 2020) on R (R Core
33 185 Team). The bones were cut virtually into 61 regularly spaced sections from 20% (distal) to 80%
34 (proximal) of the length, as in previous studies (Puymeraul, 2011; Puymeraul et al., 2012).
35 Geometry parameters were calculated for each cross-section.
36
37
38

39 These parameters include the percentage of cortical area (%CA), the second moments of area
40 190 relative to the anteroposterior (Ix) and mediolateral (Iy) axes. In addition, we used the section
41 moduli relative to the anteroposterior (Zx) and mediolateral (Zy) axes. The %CA reflects the
42 compressive strength in the longitudinal axis (Ruff, Trinkaus, Walker, & Larsen, 1993). By
43 giving indications about the shape of the sections, the second area moments and section moduli
44 are proportional to bending rigidity and strength. In order to erase allometry, we used these
45 195 parameters as ratios: %CA = cortical area / subperiosteal area; Ix/Iy; Zx/Zy (Trinkaus & Ruff,
46 2012; Rodríguez, 2018; Swan et al., 2020).
47
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50 We also produced individual cortical thickness maps (Bondioli et al., 2010; Profico et al., 2020),
51 which provide an overview of the dispersion of cortical thickness variations on the diaphysis
52 so that the evolution of the parameters can be correlated with a precise position on the
53 200 mediolateral and anteroposterior axes. We also generated consensus maps for all stages, each
54 representing the average map for the relevant stage.
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57 2.4 Statistics

58
59 To evaluate the parameters as a function of age and length, we performed ordinary least squares
60 (OLS) regressions. Bivariate plots show the mean values for each group along the longitudinal

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3 205 axis. Differences across stages in females for specific locations were statistically tested every
4 5% of the length with non-parametric tests. Kruskal-Wallis tests were performed to identify
5 where differences occurred between groups and Wilcoxon pairwise tests were used to identify
6 which stage was involved in these differences. Boxplots are used to illustrate intra-group
7 variation for sections at 35%, 50% and 65% of femoral length. Finally, to compare the
8 individual cortical thickness maps, we performed principal component analysis on pixel
9 210 coordinates. All the statistical analyses were performed using R with a significance level at
10 0.05.
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15 3 Results

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17 For all statistical test results, please refer to Table B in the supplementary material.
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20 215 3.1 Resistance to compression

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22 Resistance to compression along the longitudinal axis can be assessed by measuring the relative
23 cortical area (%CA). The Kruskal-Wallis test revealed a %CA divergence between groups
24 below 65% of length. This parameter is presented in Figure 1.
25

26
27 In newborns, the mean values of %CA are higher than in all the other stages (Figure 1a). This
28 220 difference is significant in every section except the most proximal one. Values are maximal at
29 midshaft and lower at both extremities of the diaphysis. As in all groups, the curve shows a
30 single peak of maximal %CA (%CA max). In newborns, this is at 51% of length (%CA max =
31 97.58%). %CA values for the femora of young infants (n=2) are close to both newborns and
32 6-7 month-old infants and could be considered as an intermediate pattern.
33

34
35 225 In infants, the mean %CA values are lower than in newborns for each section, with significant
36 differences at every level except at 65% and 80%. Comparisons with older stages show
37 differences with adults only at 60%. The pattern for infants is less symmetrical longitudinally
38 than in newborns, with %CA max located at 65% (%CA max = 86.46%). Individuals between
39 6 and 7 months of age (n=2) are in an intermediate position between newborns and 18-19
40 230 month-old individuals (n=5) (Figure 1b). In juveniles and adults, %CA is similar with a higher
41 %CA in the proximal than in the distal extremity of the diaphysis. %CA max is reached at 73%
42 in juveniles (%CA max = 83.28%) and at 74% in adults (%CA max = 83.15%).
43
44

45
46 %CA variability is higher in infants and adults than in juveniles and newborns (Figure 1c), and
47 235 ontogenetic evolution of this parameter across the sample shows that 1.5 year-old specimens
48 already have values matching the adult variation (%CA never reaches 90% after 1.5 years in
49 both sexes, see Figure 5a).
50

51 The location of %CA max shifts proximally with age until the juvenile stage (Table 2). This
52 proximal drift is correlated with age in both females and males (Figure 2).
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3.2 Bending rigidity and strength

240 The ratios of area moment of inertia (I_x/I_y) and section moduli (Z_x/Z_y), relative to bending axes describe whether bending rigidity is oriented more mediolaterally (ratio < 1) or more anteroposteriorly (ratio > 1). These ratios are presented in Figure 3 and 4.

245 In newborns, both ratios indicate a mediolateral orientation of the cortex in the distal third and an anteroposterior orientation in the midshaft and the proximal part of the diaphysis. The femora of young infant specimens are in the upper range of values for newborns, and even sometimes present a more anteroposterior orientation (see both ratio at 50% in Figures 3b, 4b).

In infants, juveniles and adults, these parameters indicate a mediolateral orientation in the distal half and no specific orientation in the proximal ends (mean ratio ~ 1).

250 The Kruskal-Wallis test indicates differences between groups in the distal part and at midshaft, but more occasionally in the proximal part. For both parameters, newborns appear distinctive at midshaft compared to other stages (at 40%, 45%, 55% and 60%). Juveniles also differ from infants and adults in the distal ends (at 20% and 25% for both parameters). In the proximal part of the diaphysis, adults only differ from newborns at 65% and 75% for both parameters, and from infants at 80% for Z_x/Z_y .

255 Concerning intra-group distribution, boxplots for I_x/I_y indicate that adults have the lowest variability at midshaft and in the proximal third (Figure 3b), while the Z_x/Z_y boxplots indicate that intra-group distribution is more homogenous along the diaphysis (Figure 4b). Table 3 shows the overall variability for each parameter and for each stage and confirms that adults have the lowest intra-group variability in both ratios.

260 Bivariate plots of both parameters also indicate decreasing variability with age and the occurrence of values that fall within the variability of adults from an early age (Figure 5b, c).

3.3 Distribution of thickness along the diaphysis

265 The consensus maps show a gradual evolution of the distribution of cortical thickness in the diaphysis between newborns, infants and juveniles (Figure 6). In newborns, the maximum thickness is located in a posterior position at midshaft. The rest of the diaphysis is quite homogeneous, with an average thickness around 0.5 (normalized scale). In young infants, the extension of the thickest zone is more limited in the mediolateral axis and the extremities are thinner. In infants, we observe an area of maximum thickness that is smaller and less wide in the mediolateral axis. The distal part of the diaphysis is relatively thinner than in newborns. In juveniles, the area of maximum thickness extends in length along the longitudinal axis of the bone, especially by lengthening in the proximal part. This area splits in two towards its proximal end. The distal part is characterized by a small thickness. Adults show a similar pattern to juveniles. We also note the emergence of a separate high-thickness zone in the posteromedial region in infants. This second zone of thickness is separated from the posterolateral zone and extends proximally with age along the longitudinal axis.

275 Principal component analysis reveals that the distribution of thickness is very similar between infants, juveniles and adults (Figure 7). Newborns and young infants are in the same range.

4 Discussion

4.1 The newborn condition

280 We hypothesized that newborns would show a theoretical pattern of ossification with no
285 influence of biomechanical stresses due to locomotor activities (H1). Our results confirm this
hypothesis.

The distribution of cortical bone in the femur of newborns is longitudinally symmetrical with
respect to a point of maximum thickness at midshaft. This observation fits with the intra-uterine
285 ossification model of the femur, with primary ossification spreading from the midshaft
ossification center to the extremities (Carter & Beaupré, 2000). This observation also concerns
the shape of the sections, which are more oriented along the anteroposterior axis at midshaft
than at both ends. Therefore, it is likely that no specific stress drives the biomechanical
properties.

290 The large relative abundance of cortical bone in newborns distinguishes them from older
individuals. The same observation can be made in humans (Swan et al., 2020) and in
chimpanzees (Morimoto et al., 2011) which reinforces the idea of an initial pattern that seems
to be common to all primates (Morimoto, Nakatsukasa, Ponce de León, & Zollikofer, 2018;
Morimoto, Ponce de León, & Zollikofer, 2014). According to Young *et al.* (2010), bone
295 robusticity in young specimens can be explained by an increase in the safety factor to avoid
fractures of an immature skeleton. This allows us to define a primary model, which seems to
be genetically predetermined, from which the ontogenetic changes in the biomechanical
properties of the femoral diaphysis can be described.

4.2 Quadrupedal pattern of adults

300 We hypothesized that adults would present a pattern with little variation due to the 98% of the
quadrupedal mode in their locomotor repertoire (Hunt, 2016) (H2). Our results are consistent
with this hypothesis.

Adults present a diaphysis with small cortical area in the cross-sections, and a clear orientation
of resistance to bending stresses along the mediolateral axis in the distal half. This difference
305 indicates that bending stresses have a greater influence than compressive stresses in the
development of the biomechanical properties of the distal diaphysis. The proximal half has no
clear orientation and is thicker, probably due to the dominance of compression rather than
bending in this region.

According to Polk *et al* (2000) body mass considerably increases the cortical area in the cross-
sections. Our results suggest that in the proximal part, which supports the body mass, the
cortical area is therefore larger, and this probably overrides the effect of bending stresses, which
on the other hand appear to be dominant in the distal part. We noted that proximal reinforcement
results in the presence of two posteromedial and posterolateral pillars as seen in the cortical
thickness maps (Figure 6). The distinctive position of these reinforcements extends the cortex
315 along both the mediolateral and anteroposterior axes, which results in a neutral value in the
 I_x/I_y and Z_x/Z_y parameters. The diaphysis of the adults shows a balanced, but derived, load
resistance pattern compared to the initial condition of newborns.

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3 In terms of variability, CSG parameters as well as the cortical thickness maps show little
4 variation in the adult stage (Figure 7, Table 3). This reduced diversity of patterns in adults
5 indicates adaptation of the femoral biomechanical properties in agreement with the stable
6 320 loading regime of a stereotyped locomotor repertoire. As noted by Ruff (1987), we observed a
7 strong similarity in the adaptation of resistance to mechanical stresses at the intra-species level.
8
9

10 The pattern described is consistent with previous studies on adult baboons (M. Loring Burgess
11 et al., 2016; Puymerrail, 2011). Although Puymerrail noted (2011), in specimens of different
12 325 baboon species, more anteroposterior bending resistance than we do, the evolution of parameters
13 along the longitudinal axis is similar to our observations. Mediolateral orientation of the cortex
14 also characterizes the femoral diaphysis of carnivorous quadruped mammals (Puymerrail, 2011;
15 Sumner, Devlin, Winkelman, & Turner, 1990). It can therefore be claimed that this feature
16 reflects the increased mediolateral strains in the terrestrial quadruped mode, as suggested by
17 Yates *et al* (2010). In baboons, this mediolateral orientation is erased in the proximal part by
18 330 the predominance of compressive stresses and the presence of posterior reinforcements. These
19 reinforcements in quadrupedal carnivores are either absent or more laterally located (Puymerrail,
20 2011).
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24 We also note that the femoral properties of olive baboons differ from those of arboreal
25 335 macaques, whose distal and proximal diaphyses present equivalent resistance (Burr, Ruff, &
26 Johnson, 1989). This can be interpreted by strengthening of the distal part in association with
27 an arboreal substrate that requires more distal control of movement. This latter characteristic is
28 also found in prosimians, which are largely arboreal (B. Demes & Jungers, 1993). The femoral
29 pattern in baboons also differs from that of African knuckle-walkers that present even more
30 mediolaterally oriented bending rigidity (Morimoto et al., 2018; Nadell, 2017; Puymerrail,
31 340 2011). Our results also largely differ from the modern human bipedal condition characterized
32 by a very pronounced posterior pilaster that gives a clear anteroposterior orientation in sections
33 at midshaft (Rodríguez, 2018; Trinkaus & Ruff, 2012). From these comparisons, it seems clear
34 to us that the pattern described in adults corresponds to an adaptation to the ground-living
35 quadruped condition, as opposed to the less oriented sections observed in several arboreal
36 345 species (B. Demes & Jungers, 1993; Brigitte Demes, Jungers, & Selpien, 1991; Patel, Horner,
37 Thompson, Barrett, & Henzi, 2013).
38
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42 While multi-directional strains (i.e. arboreal behaviour such as suspension) tend to be
43 materialized in more radial sections (Carlson, 2005), the baboon's stereotypical repertoire
44 350 results in low-diversity stresses, giving the sections a shape that respond better to stresses along
45 the axis of these strains. However, a study by biomechanical simulation of the distribution of
46 mechanical strains in the femur that are specific to the quadrupedal gait would allow this
47 hypothesis to be tested.
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51 4.3 Changes in biomechanical patterns during ontogeny

52
53 355 Considering the development of several autonomous locomotor modes during the first months
54 of growth, we hypothesized that infants would have a singular pattern that reflects this
55 locomotor diversity (H3).
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57 The biomechanical pattern of the two young infants studied falls directly into the range of the
58 pattern for newborns. This can be explained by the fact that at two months of age, locomotor
59 360 activities are not constraining enough to impose bone remodelling. It is also possible that the
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3 time necessary for bone remodeling (3-5 months for complete remodelling in humans according
4 to Carmona et al., 2004) has not been reached and that the influence of new stresses is not yet
5 expressed in the bone tissue.
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8 In infants, the pattern clearly differs from these early stages. Changes result in a reduction of
9 365 the cortical area and in the mediolateralisation of load resistance in the distal and midshaft
10 femur as early as 0.5 years of age, when individuals are at least partially autonomous in terms
11 of locomotion. This pattern is therefore very similar to that of adults. The close similarity to
12 adults does not allow us to conclude that the observed pattern fully reflects the diversity of
13 locomotor modes in infants, and thus to maintain the hypothesis (H3). However, the high
14 370 variability within the infant group (Figure 7, Table 3) may indicate that definitive
15 biomechanical adaptation to quadrupedalism, although it occurs early, does not occur at the
16 same time in every individual.
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20 In juveniles, the pattern is very similar to that of infants and adults despite a transitional
21 locomotor repertoire. The absence of a clear transitional pattern between infants and adults
22 375 leads us to reject our hypothesis of intermediate biomechanical properties in juveniles (H4).
23 The variability observed in this group is relatively low when compared to the other stages, even
24 considering our small sample size, which might indicate that adaptation is fully completed at
25 this stage, unlike in infants.
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28 Thus, when compared with the initial pattern of newborns, the major changes during ontogeny
29 380 are a gradual reduction of the cortical area and early mediolateralisation of bending rigidity.
30 These changes are preserved until adulthood, which confirms the observation of Burgess *et al.*
31 (2016) of a relatively stable bending rigidity pattern during ontogeny in female baboons. As
32 suggested by Sarringhaus *et al.* (2016) for chimpanzees, our results on baboons also show
33 differences in synchronization between behavioural and biomechanical developments during
34 385 juvenility. To summarise, we observed that biomechanical changes occur before the onset of
35 definitive locomotor behaviour.
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39 At the interspecies level, the mediolateralisation of bending rigidity, also observed in *Gorilla*,
40 *Pan*, *Pongo* and to a lesser extent in *Hylobates* and *Macaca* (Nadell, 2017), appears during
41 infancy and therefore seems to be established later and more progressively than in baboons,
42 390 highlighting the distinctive pattern of the latter. This is confirmed by other studies on gorillas
43 and chimpanzees where changes in the biomechanical properties of limb bones appeared much
44 later than in our baboon sample (Ruff, 2013; Sarringhaus et al., 2016). Conversely, our results
45 are more closely related to the changes observed in humans, who present early modifications
46 in cross-sectional shape and strength, as early as the emergence of locomotor autonomy (around
47 395 one year in humans, around five months in baboons), in two specific cases that present an
48 extremely stereotyped locomotor repertoire in adults (Cowgill, 2010; Swan et al., 2020). These
49 findings confirm the high variability of developmental patterns of biomechanical properties
50 among Catarrhines (Ruff, 2003; Sarringhaus et al., 2016).
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54 4.4 Influence of growth and development

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56 400 Despite differences during ontogeny in the locomotor repertoire of infants, juveniles and adults,
57 growth and development also drive bone (re)modeling and therefore have an influence on the
58 evolution of femoral biomechanical properties (Dennis R. Carter, 1987; D.R. Carter, Van der
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3 Meulen, & Beaupré, 1996b). However, when we compared growth rates with the evolution of
4 biomechanical parameters of the femur, we noted that they are not synchronized.
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6 405 According to Leigh (2009) and Druelle et al. (2017), the growth of the thigh segment in baboons
7 does not show evident spurts, although the growth rate is faster during the first month of life,
8 and stops at around 5 years of age in females. However, we show that bending resistance
9 parameters stabilize much earlier (around 0.5 years), during the period of fastest growth. There
10 is therefore a very early development of biomechanical properties that are more correlated to
11 the timing of locomotor development (especially the emergence of locomotor autonomy) than
12 410 to growth. Our results nevertheless support the work of Druelle *et al* (2017) on the same
13 population of females, in which the main changes in thigh segment length and mass appear
14 early in development (1.65 years for segment length and 1.11 years for segment mass).
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18 However, the transitional pattern suggested by the progressive decrease in cortical area from
19 415 newborns to young infants and 6-7 month-old infants (Figure 1c; Figure 6) corresponds better
20 to a continuous development of the thigh, as suggested by the absence of growth spurts. This
21 may indicate that %CA is influenced more by growth than by bending rigidity. In this respect,
22 bending rigidity parameters seem to better inform on the stresses resulting from locomotor
23 behaviour than cortical area, as suggested by Duda *et al.* (1998).
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26 420 Growth and development are therefore probably inseparable from the establishment of
27 biomechanical properties in the femur, but they do not explain the early age of their
28 establishment, unlike the emergence of locomotor autonomy.
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31 4.5 Influence of proximal musculature 32

33 Our results show a clear shift in the position of the point of maximal cortical thickness towards
34 425 the proximal extremity of the diaphysis (Figure 2), as also seems to be the case in chimpanzees
35 (Mary Loring Burgess, 2018; Morimoto et al., 2011), despite great differences in the adult
36 pattern of the two taxa. This proximal displacement of cortex thickening is in agreement with
37 the proximalization of the CoM in the limbs already observed in *Papio*, which is intrinsically
38 linked to the shift of muscle mass towards the hip (Raichlen, 2005b; Druelle et al., 2017).
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41 430 Concerning the muscles, the cortical thickness maps (Figure 6) also seem to concur with the
42 detailed muscle-bone maps in Swindler and Wood's atlas (see plate 145 in Swindler & Wood,
43 1973). In this respect, the location of the attachments of *musculus pectineus*, *m. adductor*
44 *longus*, *m. adductor brevis* and *m. adductor magnus* are almost the same as the location of the
45 thickest areas of the diaphysis in adults. These muscles are adductors, rotators and extensors of
46 the thigh and the hip flexors. As musculature has a strong influence on bone remodelling of the
47 435 proximal femur (Duda et al., 1998; Bitsakos, Kerner, Fisher, & Amis, 2005), it is likely that the
48 early development of the hip joint (or proximal thigh) musculature influences biomechanical
49 properties via locomotion. Dissections show that the muscles of the posterior thigh region are
50 particularly well developed in baboons (ongoing research, see also (Swindler & Wood, 1973).
51 440 These muscles control the sagittal movements of the thigh and the trunk, but also the
52 mediolateral balance of the body, which appears to be a major requirement during the diagonal
53 sequence gait (DSDC), which is the main quadrupedal pattern in baboons (Shapiro & Raichlen,
54 2006, Druelle et al, 2021). Also, the diagonal quadrupedal gait develops strongly at around 5
55 months; our observations of an early emergence of the quadrupedal biomechanical pattern in
56 the femur are consistent with this behavioural observation.
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5 This study presents original results on young individuals and provides insights into the impact
6 of behavioural diversity on the biomechanical characteristics of limb bones. Based on
7 behavioural data on the locomotor repertoire of a well known population of captive olive
8 baboons, we predicted that the patterns of locomotion and biomechanical properties would co-
9 450 evolve. Our results suggest that the pattern in newborns reflects the primary ossification of the
10 femur, and that adults present biomechanical characteristics of the quadrupedal condition. We
11 propose an early transition of biomechanical properties from the newborn condition to an adult-
12 like pattern as soon as locomotor autonomy is established at around 0.5 years of age. Thus, the
13 455 impact of modifications in the locomotor repertoire on the biomechanical pattern of the femur
14 appears to be limited by the predominant influence of quadrupedal locomotion. We suggest that
15 simulation of biomechanical stresses during quadrupedal walking would provide a suitable way
16 to test our hypothesis.
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51 475 Conflict of interest

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53 The authors declare no competing interest.
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Data Availability Statement

The datasets supporting this article are available from the corresponding author on reasonable request.

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26 720 Figure legends

27
28 Figure 1: Percentage of cortical area in the femoral diaphysis. (a) mean by stage: newborns
29 (n=4), young infants (n=2), infants (n=8), juveniles (n=6) and adults (n=30); (b) mean of
30 percentage of cortical area in infants: 6-7m (n= 2), 18-19m (n=5); (c) boxplots (min, Q1, mean,
31 Q3, max) for each stage.
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33
34 725 Figure 2: Location of peak of cortical area during ontogeny in females (n=18) and males (n=8),
35 the ordinary least square regression line for both sexes is represented in black.
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37 Figure 3: Ratio of anteroposterior and mediolateral second moment of area in the femoral
38 diaphysis. (a) mean by stage: newborns (n=4), infants (n=8), juveniles (n=6) and adults (n=30);
39 (b) boxplots (min, Q1, mean, Q3, max) for each stage.
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41 730 Figure 4: Ratio of anteroposterior and mediolateral section moduli in the femoral diaphysis. (a)
42 mean by stage: newborns (n=4), infants (n=8), juveniles (n=6) and adults (n=30); (b) boxplots
43 (min, Q1, mean, Q3, max) for each stage.
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46 Figure 5: Bivariate plots of biomechanical parameters (a: percentage of cortical bone, b: area
47 moments of inertia, and c: section moduli) vs. age; for 3 locations, all specimens are
48 735 represented.
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50 Figure 6: Consensus femoral thickness maps of the five stages, heatmaps are scaled from 0
51 (thinnest point of the map) to 1 (thickest point of the map). Sides are noted A (anterior), M
52 (medial), P (posterior) and L (lateral).
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55 740 Figure 7: Principal component analysis based on 2D maps coordinates and thickness values for
56 the five groups (n=48).
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3 Table 1: *Papio anubis* sample details.
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5 Table 2: Wilcoxon-test for each pair to compare the position of peak of cortical area section (*:
6 p-value >0.05).
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8 Table 3: Standard deviation in stages for each parameter along the diaphyseal cross-sections.
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12 745 **Supplementary material**
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14 Table A: Details of the study individuals.
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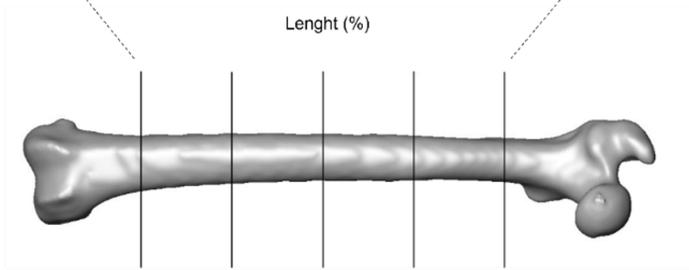
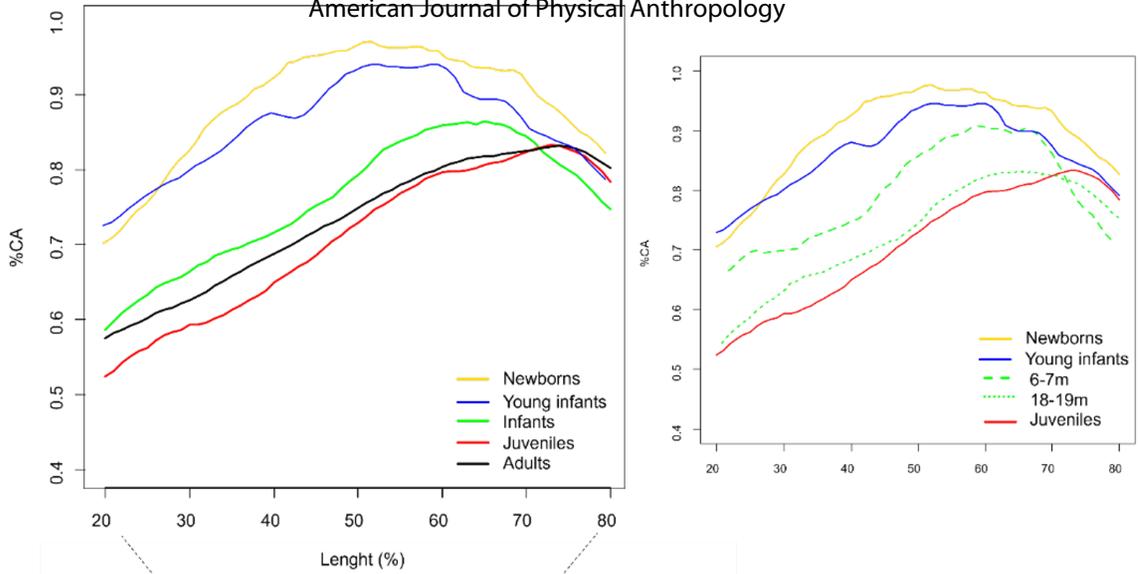
16 Table B: Statistical analysis of stage differences for each parameter, every five sections:
17 Kruskal-Wallis and Wilcoxon paired-test. Statistical significances are presented in in grey and
18 bold with a level of 0.95.
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20 750 Table C: Cross-section geometry parameters, mean by stages.
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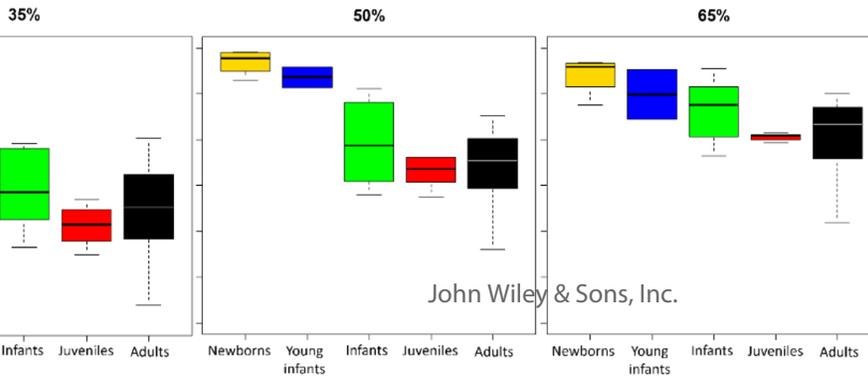
Table 1 : *Papio anubis* sample details.

Stages	Age range	Sex	N
Newborns	0 - 2 days	F	2
		M	2
Young infants	< 0.5 years	F	2
		M	1
Infants	0.5 -1.8 years	F	8
		M	2
Juveniles	1.8 - 4.75 years	F	6
		M	2
Adults	> 4.75 years	F	30
		M	9

(a)



(c)



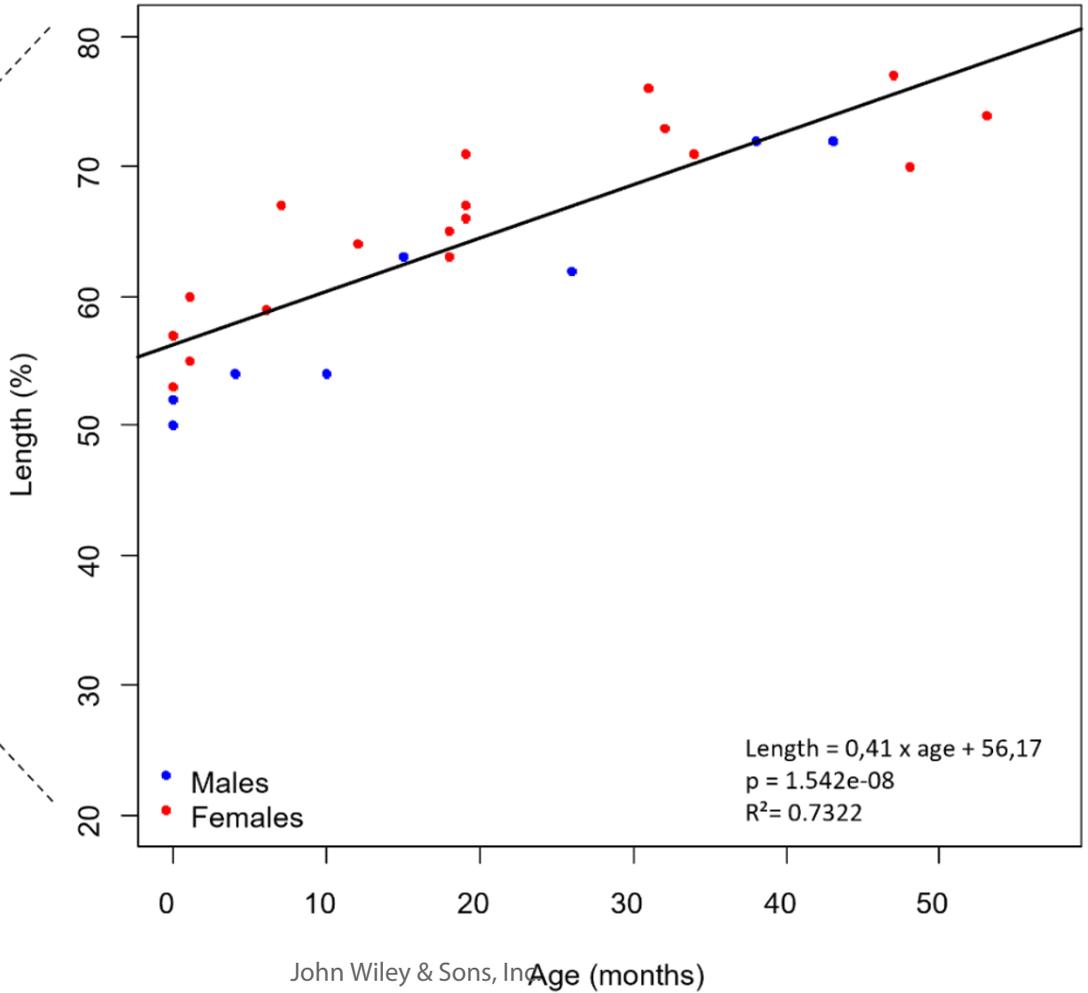
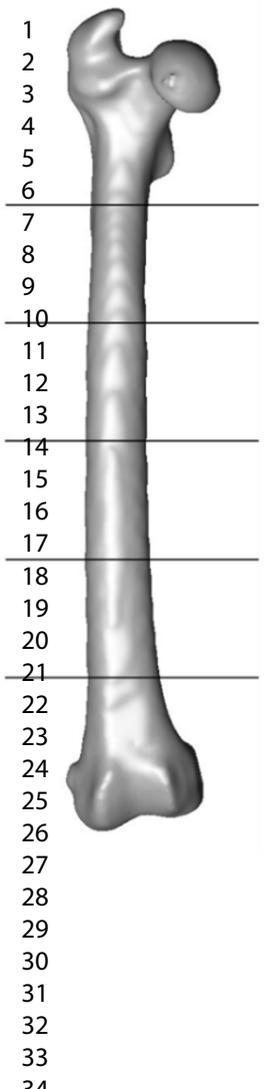
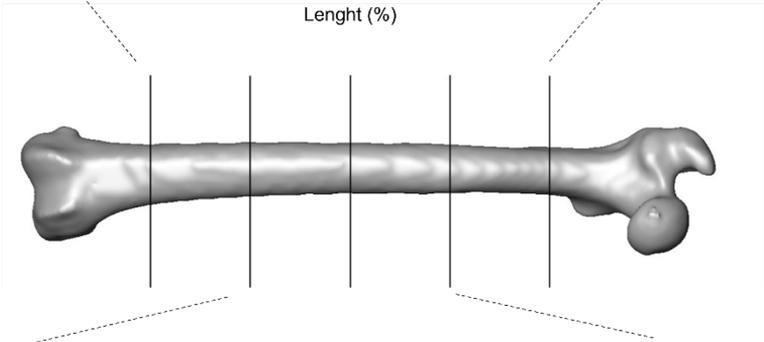
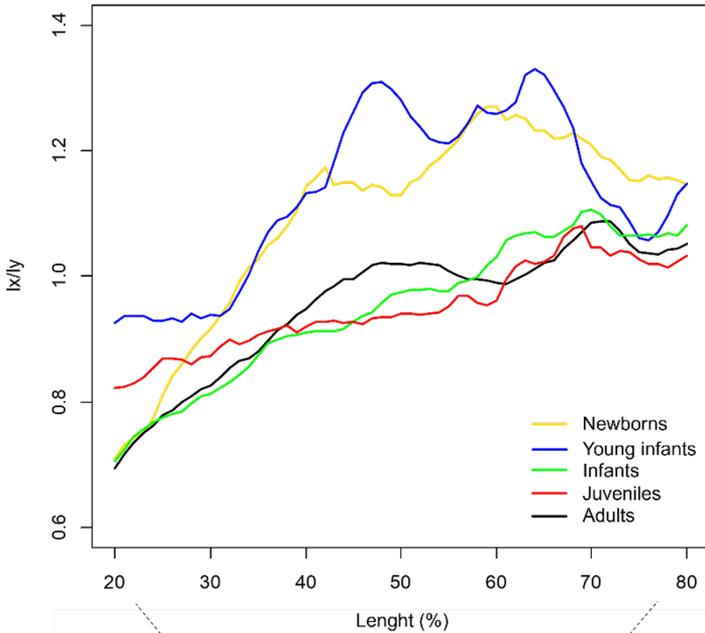


Table 2: Wilcoxon-test for each pair to compare the position of peak of cortical area section (*: p-value >0.05).

Wilcoxon paired-test (p-value)	Newborns	Infants	Juveniles	Adults
Newborns	X	X	X	X
Infants	0.00836*	X	X	X
Juveniles	0.01587*	0.008237*	X	X
Adults	0.001669*	0.001004*	0.4913	X

(a)

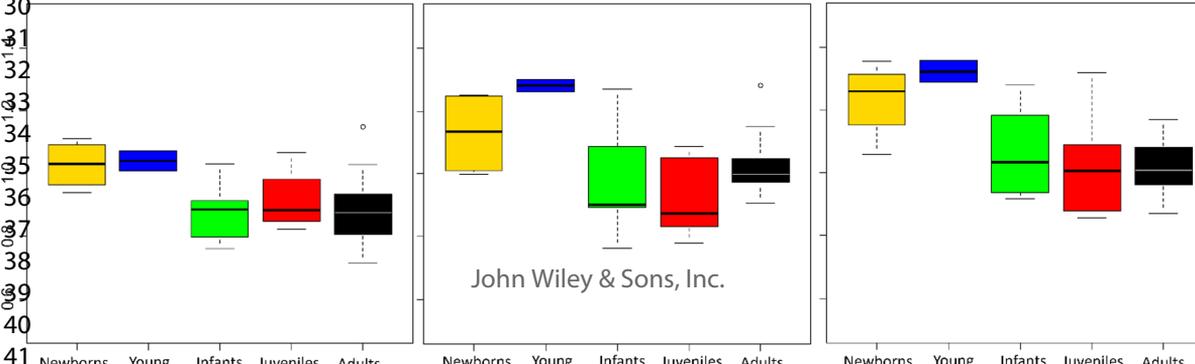


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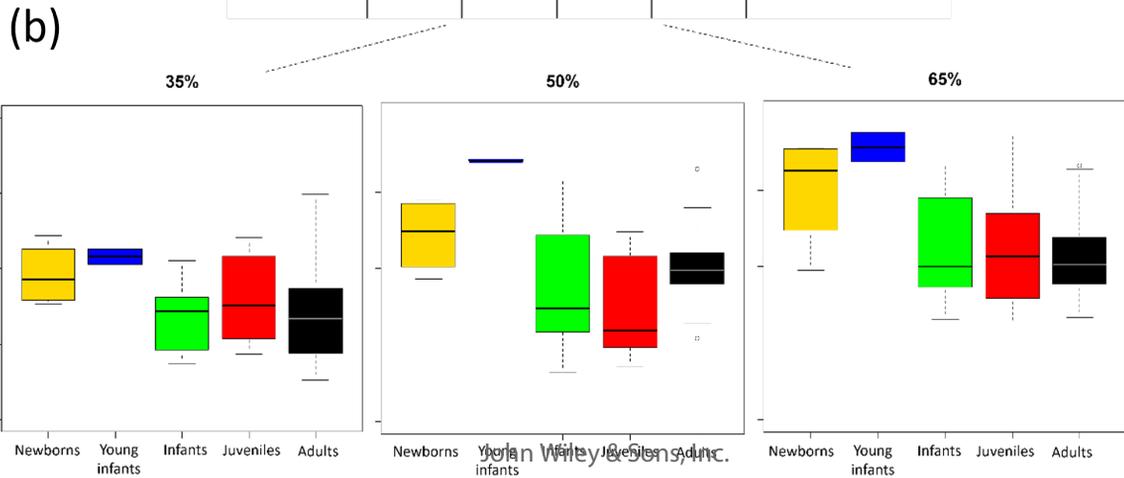
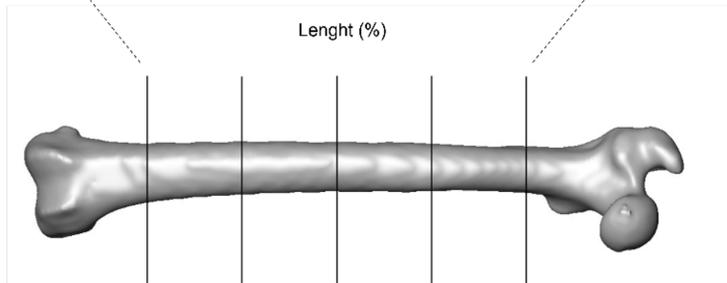
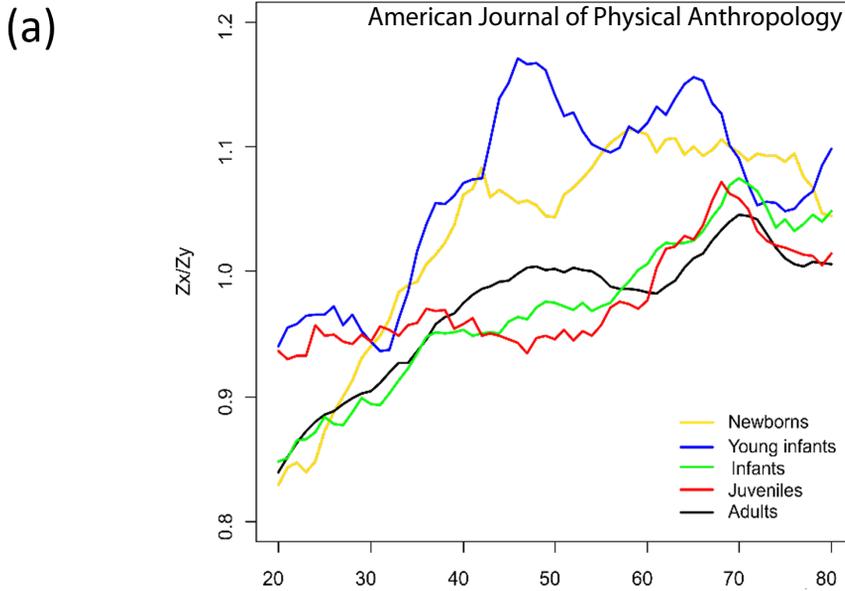
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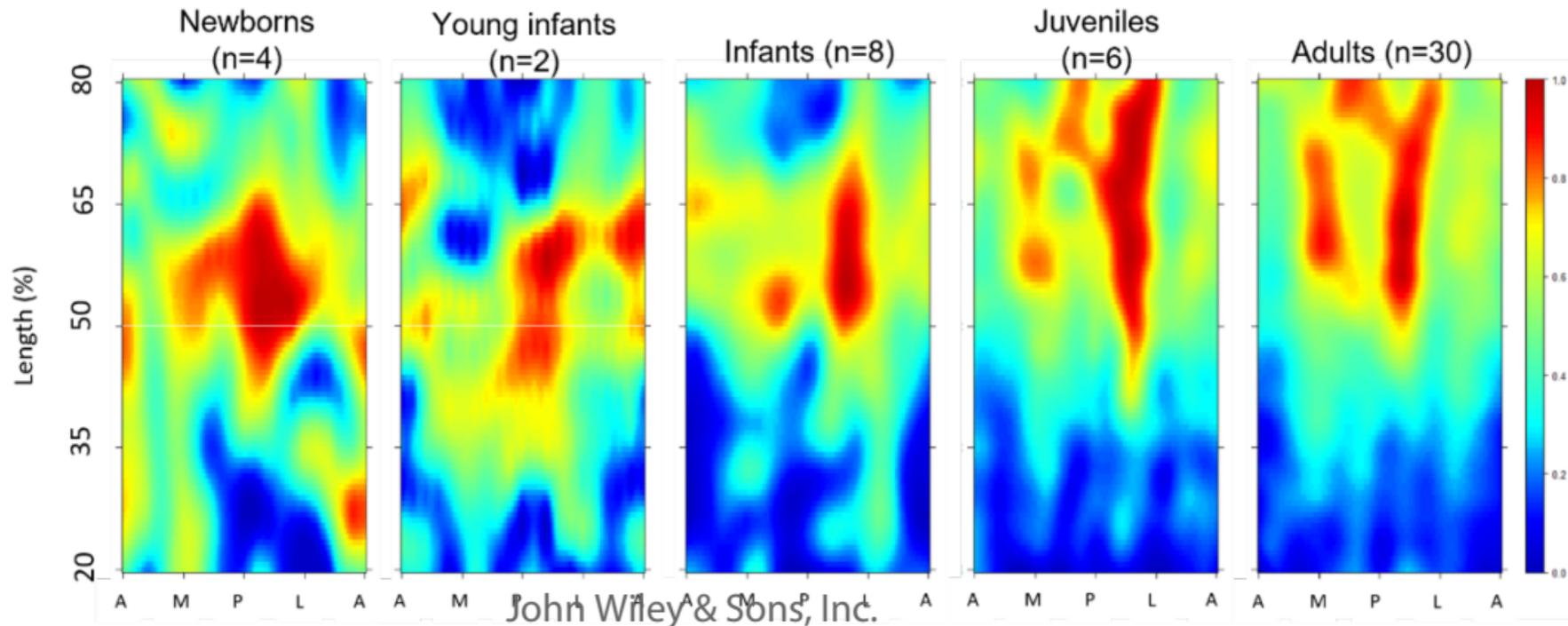
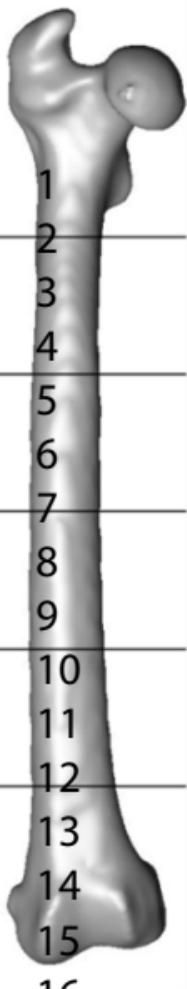
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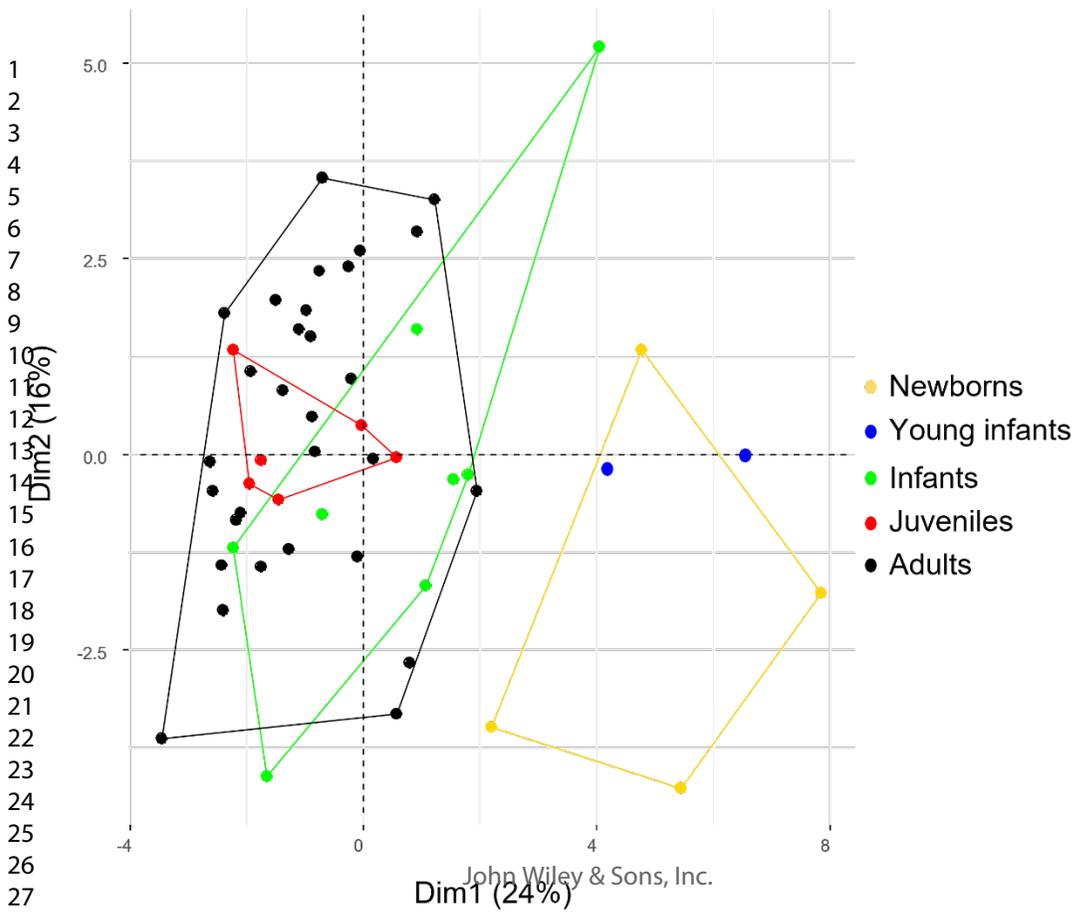


Table 3: Standard deviation in stages for each parameter along the diaphyseal cross-sections.

Mean of sd on the 80 sections	%CA	lx/ly	Zx/Zy
Newborns	0.03124942	0.07769159	0.0377664
Infants	0.06157985	0.08891268	0.05002496
Juveniles	0.02762963	0.08823692	0.05080078
Adults	0.05933164	0.06476197	0.0359473