

How does the relative wall thickness of human femora follow the biomechanical optima? An experimental study on mummies

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Summary

We studied how the ratio (K) of the internal:external diameter of human femora follows the biomechanical optima derived earlier by other researchers for marrow-filled tubular bones with circular cross section and minimum mass designed to withstand yield and fatigue, or stiffness, or bending fracture, or impact strengths. With evaluation of radiographs of 107 femora from 57 human mummies the values of K were measured. We found that $K_{\text{posterior}}=0.498\pm 0.085$ for the posterior radiographic view, and $K_{\text{medial}}=0.589\pm 0.070$ for the medial view with $K_{\text{min}}=0.345$ and $K_{\text{max}}=0.783$. The theoretical optima for K depend on the ratio (Q) of the marrow:bone density. Accepting the assumption of earlier authors that $Q=0.50$, our data show that human femora are optimised to withstand bending fracture, or yield and fatigue strengths.

There were no sex-, age- and length-specific differences in K , and the means of K of the right and left femora of individuals were statistically not significantly different. The biomechanical optimization for K of human femora is not finely tuned. Compared with fox femora, K of human femora follows the biomechanical optimum to a much lesser extent. Although the relative wall thickness $W=1-K$ of human femora are optimised, the very low relative mass increment due to deviation of K from the optimum and the considerable intraspecific variance of K make it probable that an accurate optimization of the relative wall thickness is irrelevant in humans.

Key words: marrow-filled tubular bones, optimum bone-wall thickness, human femora, mummies, bone mechanics.

Introduction

The diaphysis of human femora is a hollow tube with a nearly circular cross section filled with marrow. One of its characteristic variables is the ratio (K) of the internal:external diameter. Pauwels (1980), Currey (1982), Alexander (1968, 1982, 1983, 1996) and Currey and Alexander (1985) derived different biomechanical optima for K of tubular bones with a circular cross section. The optimum value of K , which allows the minimization of the mass of a marrow-filled bone, depends on whether the bone is selected principally for yield and fatigue strength, for ultimate strength, for impact strength, or for stiffness. Currey and Alexander (1985) showed that the change in mass as a function of relative wall thickness $W=1-K$ was quite gradual, suggesting that natural selection would not act strongly against relative wall thicknesses that were not very close to the optimum.

Legs have to be accelerated and decelerated in every step. Optimal K -values for leg bones will allow bones to have sufficiently thick walls to maintain mechanical integrity, while remaining sufficiently thin so as to moderate the energetic costs of limb acceleration (Pauwels, 1980; Currey, 1982; Alexander, 1968, 1982, 1983, 1996; Currey and Alexander,

1985; Lieberman et al., 2003). According to the biomechanical optimization theory of Alexander (1982), Currey (1982), Currey and Alexander (1985), the optima for K depend on the ratio Q of the marrow to bone density (see Equations 1–4 in the Materials and methods of the present work). Unfortunately, the exact values of Q are unknown. The density of human cortical bone ranges from 1700 to 2100 kg m⁻³, the density of yellow (fatty) marrow is about 930 kg m⁻³ (Ashman, 1989; Currey, 2002), suggesting that Q ranges between 0.44–0.55. Alexander (1982, 1996) assumed $Q=0.50$.

To test their biomechanical optimization theory, Alexander (1982), Currey (1982) and Currey and Alexander (1985) surveyed the K -values of 240 long bones from single individuals of 70 species. They found that the interspecific variation of K was high, most K -values ranged from 0.4 to 0.8, and there was a general correspondence between theoretical predictions and real life. In general, they examined only one or two bones from any species, and therefore had no estimate of within-species variation. To say something about the force of selection, it was necessary to determine the mean (K_{mean}) and standard deviation (σ_K) of K of leg bones within a species.

The first species in which K_{mean} and σ_K of a given bone type was measured is the red fox, *Vulpes vulpes*. With evaluation of radiographs of 62 femora of adult foxes, Bernáth et al. (2004) found that in fox femora $K=0.68\pm 0.036$ with $K_{\text{min}}=0.59$ and $K_{\text{max}}=0.74$. Accepting the assumption of earlier authors that $Q=0.50$, Bernáth et al. (2004) found that the fox femora are optimised for stiffness. The mass increment, μ , relative to the minimum mass of fox femora was smaller than 5% under all four mentioned mechanical conditions for $Q=0.50$. Currey (2002) has argued that such small differences are selectively important.

According to Alexander (1982, 1983, 1996), the long bones of mammals are optimum structures. Until now this hypothesis have been thoroughly tested only in the case of fox femora (Bernáth et al., 2004). The aim of this work is to understand whether the relative wall thickness of femora in humans (which may be subject to natural selection to a smaller extent than wild animals) corresponds to a biomechanical optimum. In spite of the intense study of human bones and bone mechanics (e.g. Ruff and Hayes, 1983; Cowin, 1989, 2001; Runestad et al., 1993; Ohman, 1993; Stock and Pfeiffer, 2001; Currey, 2002), this problem has not yet been investigated. In this work we present an experimental study on K of femora of human mummies. With evaluation of the radiographs of 107 human femora we measured the mean and standard deviation of K . The measured K -values were compared with the four theoretical optima for K derived by Currey and Alexander (1985).

We chose mummy femora because they were easily available in large numbers from the Anthropology Department of the Hungarian Natural History Museum. We studied femora because, in humans, the femora have the most circular mid-shaft cross section (Cubo and Casinos, 1998). Since the theoretical optima for K were derived by Currey and Alexander (1985) for circular cross sections of marrow-filled tubular bones, the femur is the most appropriate bone to test the optimality of K in human long bones. Since both sex and age of the investigated mummified persons were known, we could investigate the possible dependence of K of human femora on sex and age. For reason of duty towards the dead, femora of recent dead persons could not be investigated. Conversely, the radiographs of femora of living persons available from hospitals were not of appropriate quality for our evaluation. Furthermore, the radiographs obtained from hospitals showed anatomical changes (e.g. fractures, cracks, fissures, or pathological alterations) and partly that is why they were inappropriate for our biomechanical analysis.

Finally, we would like to emphasize that our major aim was only to test experimentally whether human femoral wall thickness matches one (or several) theoretical optima. Any speculation about bone adaptation governed by the loading conditions in human femora is beyond the scope of this work.

Materials and methods

Mummy femora and their evaluation

The investigated human femora originated from the mummy

collection of the Department of Anthropology of the Hungarian Natural History Museum. The individuals came from the Dominican Church, Vác, Hungary, and were buried during 1731–1838. Although most of them were naturally mummified, approximately 30% of them were skeletonised. Contemporary written records of the parish register of the church are available for many individuals and include date of death, age, sex and name (Pap et al., 1997).

We examined 57 specimens (28 females, 29 males). Contemporary archives enabled us to determine the age at death in the case of 48 individuals. In anthropology, the standard way of classifying ages is the so-called Martin method: ‘infans I’ age-group 0–7 years; ‘infans II’ 8–14 years; ‘juvenis’ 15–17 years; ‘adultus’ 18–39 years; ‘maturus’ 40–59 years; ‘senium’ above 59 years. Fifteen (7 females, 8 males) of the investigated mummies belonged to the infans I age-group, three (2 females, 1 male) to the infans II, and two 15-year old females to the juvenis. The distribution of grown-ups was: three females belonging to the adultus age-group, 14 specimens (8 females, 6 males) to the maturus, and 11 (4 females, 7 males) to the senium. For nine individuals (2 females, 7 males) age records were not available. Their age at the time of death was estimated using standard anthropological methods (1 adultus female, 5 adultus males, 1 senium female, 2 senium males). For statistical analyses the original Martin age-groups were drawn into the following three age-groups: (1) subadults, age 0–20 years (20 individuals; number of femora: $N_{\text{female}}=18$, $N_{\text{male}}=15$); (2) adults, age 21–50 years (14 individuals; number of femora: $N_{\text{female}}=18$, $N_{\text{male}}=10$); (3) old people, age above 50 years (23 individuals; number of femora: $N_{\text{female}}=16$, $N_{\text{male}}=30$).

To avoid the difficult transport of whole mummies and to minimize their damage, we tended to select skeletonised bodies, from which the femora could be separated. Taking radiographs from such detached femora was much easier. Both left and right femora of individuals were examined, if it was possible.

Detachable femora were individually packed and transported to the Department and Clinic of Surgery and Ophthalmology of the Faculty of Veterinary Science of the Szent István University in Budapest, where lateromedial and anteroposterior radiographs were taken from every femur using EUREKA Diamond 150 (CEA OGA, green sensitive). After chemical development, the radiographs were digitized using an AGFA Arcus 1200 scanner with a resolution of 400 dpi. The evaluation of the radiographs for the majority of the investigated human femora was as described in detail by Horváth (2001) and Bernáth et al. (2004). Our method is partly similar to the evaluation procedure of computer tomographs used by Spoor et al. (1993) to determine the thickness of human enamel and cortical bone. Biplanar radiographs are commonly used to obtain dimensions of limb bones: Ruff and Hayes (1983), Runestad et al. (1993), Ohman (1993) and Stock and Pfeiffer (2001), for example, have developed and applied such a technique.

After the evaluation we obtained the ratio K of the internal

to external diameter of the bone at the selected mid-section for both the lateromedial and anteroposterior radiographic views. The reliability of this method was tested by comparison of computationally obtained K -values with data measured directly by a caliper on bone cross sections. Our method based on the evaluation of radiographs of tubular bones can measure the K -value with an accuracy of $\pm 1\%$ (Bernáth et al., 2004).

Because some mummies had residual marrow or exhibited porous bone structure, the automatic evaluation of some bones was impossible. In these cases the following modification of the evaluation was necessary. The selected rectangular area on each radiograph (see the areas demarcated by white line in Fig. 1) was divided into five small rectangular horizontal zones. In each zone, lines were fitted to the inner and outer bone walls visually and manually. The computer program determined the distance between the appropriate lines in each row of the zone and calculated the K -value for the zone. The final K -value was calculated as the arithmetical mean of the K -values of the five zones. This method was compared with the automatic procedure on bones suitable for both kinds of evaluation. The differences were very small, and not biased in a particular direction. We could not evaluate the medial radiograph of a few subadult and old-people femora, because these radiographs were so contrast-poor (usually due to osteoporosis) that the bone walls could not be recognized computationally or visually.

To examine the differences between the measured K -values and the four theoretical optima for K , a two-tailed single t -test was used. The possible correlation between K and the bone length L was tested by calculating Pearson correlation coefficients for the L - and K -values obtained for the anteroposterior and lateromedial views. The difference between the mean K -values obtained for the anteroposterior and lateromedial views of the femora was confirmed using associated two-tailed paired t -test. Since the theoretical optima for K were derived by Currey and Alexander (1985) for circular cross sections of marrow-filled tubular bones, further statistical analysis was performed using the average of the K -values obtained for the anteroposterior and lateromedial views of the femora. A few incomplete bones with missing epiphyses were excluded from these tests. The

difference between the K -values of the left and right femora of individuals was examined using two-tailed paired t -test. The possible differences between the K -values of femora of women and men were tested using a two-tailed unassociated t -test. To avoid pseudoreplication, only single femora of individuals were involved in the statistics. The possible differences between the K -values measured in the three age groups were tested using one-way ANOVA. Statistical tests were performed with the statistical software StatSoft STATISTICA 6.1.

Optima for K of marrow-filled tubular bones with given Q

Let us designate the ratio of the marrow density ρ_{marrow} to bone density ρ_{bone} by $Q = \rho_{\text{marrow}}/\rho_{\text{bone}}$. If the cross section of the diaphysis remains approximately circular when a marrow-filled tubular bone is bent, the biomechanical optima for the ratio K of the internal to external diameter of the diaphysis under different mechanical strengths are the following (Currey and Alexander, 1985; Bernáth et al., 2004).

Stiffness. The optimum value for stiffness is:

$$K_S (Q = 0.5) = \sqrt{1 - Q} = 0.71 . \quad (1)$$

Yield and fatigue. The optimum value for K for a bone of minimum mass for yield strength and fatigue strength is

$$K_Y (Q = 0.5) = \sqrt{\frac{2 - \sqrt{1 - 3Q^2 + 6Q}}{1 - Q}} = 0.63 . \quad (2)$$

Impact. The optimum for impact loading is:

$$K_I (Q = 0.5) = \sqrt{\frac{1 - \sqrt{2Q - Q^2}}{1 - Q}} = 0.52 . \quad (3)$$

Bending fracture. If the bone is strong enough not to fracture, under the greatest bending moments likely to act on it, the optimum K -value is:

$$K_F (Q = 0.5) = 1 - Q = 0.50 . \quad (4)$$

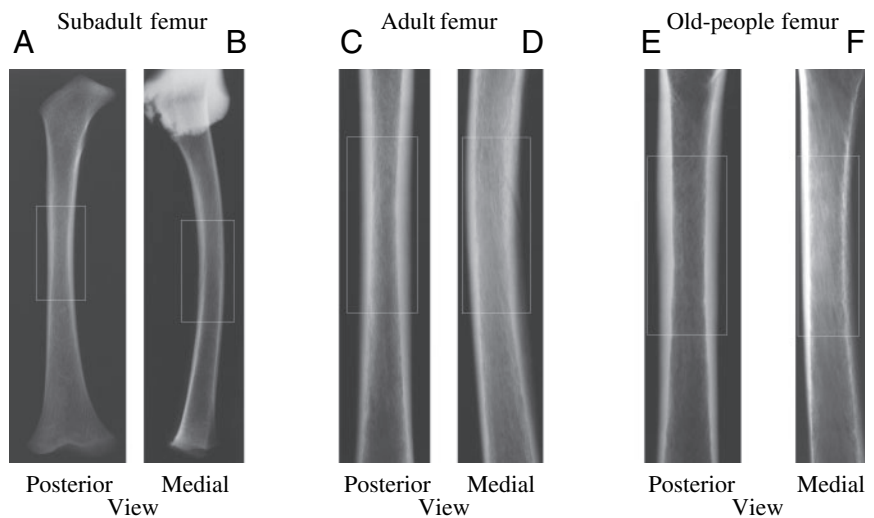


Fig. 1. Representative radiographs of human femora in posterior and medial views from the three age groups (subadults, adults and old people). Rectangular areas demarcated by white line show the regions selected for evaluation. (A,B) Right femur of a 5 year old boy (catalogue number: MTM-ET 190) in posterior ($K_{\text{mean}}=0.575$) and medial ($K_{\text{mean}}=0.636$) view. (C,D) Left femur of a 48 year old woman (MTM-ET 256) in posterior ($K_{\text{mean}}=0.461$) and medial ($K_{\text{mean}}=0.591$) view. (E,F) Left femur of a 58 year-old man (MTM-ET 146) in posterior ($K_{\text{mean}}=0.519$) and medial ($K_{\text{mean}}=0.678$) view.

These expressions were derived from the equations described by Currey and Alexander (1985). If the K -value of a marrow-filled tubular bone is equal to one of these four optima, the total mass of bone and marrow is minimal under the above-mentioned mechanical conditions. $Q=0.50$ was assumed by Alexander (1982, 1996). Table 1 contains the optimum K -values calculated from Equations 1–4 for $Q=0.50$.

Results

Fig. 2 shows the frequency of the K -values of all investigated human femora from posterior and medial views. Fig. 3 represents the frequency of the K -values of the femora of adults for both views. Table 2 contains the means K_{mean} , standard deviations σ_K , minima K_{min} and maxima K_{max} of the femora of subadults, adults and old people. $K_{\text{mean}}^{\text{posterior}}=0.498$ of (all investigated) human femora for posterior view is significantly smaller than $K_{\text{mean}}^{\text{medial}}=0.589$ for medial view (paired t -test: $t=-8.93$; d.f.=35; $P<0.001$). The difference between $K_{\text{mean}}^{\text{posterior}}$ and $K_{\text{mean}}^{\text{medial}}$ is smallest for subadult femora ($\Delta K_{\text{mean}}=0.036$) and greatest for adult femora ($\Delta K_{\text{mean}}=0.127$). The standard deviation σ_K of K is 0.085 and 0.070 for posterior and medial views, respectively. Depending on the age and radiographic view, σ_K ranges between 0.052 and 0.093, and K changes between the extrema $K_{\text{min}}=0.345$ and $K_{\text{max}}=0.783$. Due to this variation of K , within the sample of human femora, there were several individuals that exhibited K -values that were identical to each of the different theoretical optima K_Y , K_S , K_F , K_I given in Table 1. $K_{\text{mean}}^{\text{posterior}}=0.498$ is nearest to $K_F=0.50$ (optimum for bending fracture load), while $K_{\text{mean}}^{\text{medial}}=0.589$ is nearest to $K_Y=0.63$ (optimum for yield and fatigue strength). $K_{\text{mean}}^{\text{posterior}}=0.498$ does not differ significantly only from $K_F=0.50$ (single sample t -test: $t=-1.11263$, d.f.=47, $P=0.272$). $K_{\text{mean}}^{\text{medial}}=0.589$ is nearest to $K_Y=0.63$,

Fig. 2. Frequency diagram of the values of the ratio K of the internal to external diameter of all investigated human femora from posterior (left diagram) and medial (right diagram) views. The Gaussian curves are fitted to the measured K -values. A vertical arrow shows the mean K_{mean} . Vertical lines represent the four theoretical optima K_Y , K_S , K_F , K_I given in Table 1. There are fewer K -values for medial than for posterior view, because we could not evaluate the medial radiograph of a few subadult and old-people femora with osteoporosis (in the contrast-poor radiographs the bone walls could be recognized neither computationally, nor visually).

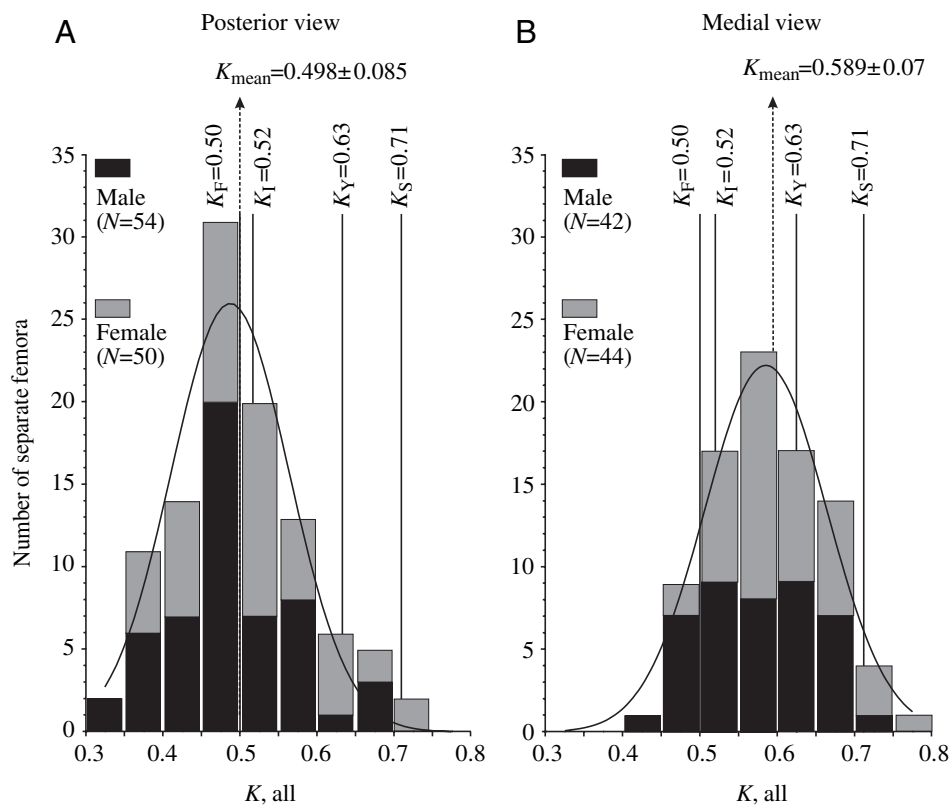


Table 1. Optimal values of the ratio K of the internal to external diameter of a marrow-filled tubular bone

Optimal for	Stiffness	Yield and fatigue	Impact	Bending fracture
$Q=0.5$	$K_S=0.71$	$K_Y=0.63$	$K_I=0.52$	$K_F=0.50$

Optimal values of the ratio K of the internal to external diameter of a marrow-filled tubular bone calculated from Equations 1–4 for $Q=0.50$, where $Q=\rho_{\text{marrow}}/\rho_{\text{bone}}$ is the ratio of the marrow to bone density ρ .

but it differs significantly from K_Y (single sample t -test: $t=-3.40844$, d.f.=36, $P=0.00162$). $K_{\text{mean}}^{\text{medial}}$ differs from K_F , K_S , K_I with significance levels lower by several orders of magnitude. Hence, the investigated human femora seem to be optimised either for bending fracture load or yield and fatigue strengths.

To reveal a possible difference in K between the left and right femora, we selected those mummies, in which both the left and the right femora could be investigated. Table 3 contains the mean, standard deviation, minimum and maximum of K of these femur pairs, for which the average $K=(K_{\text{left}}+K_{\text{right}})/2$ of the K -value of the left and right femur was calculated. Using paired t -test, we found that the means of K of the right and left femora of individuals were not significantly different (paired t -test: $t=0.961$; d.f.=35; $P=0.343$).

To test a possible difference in K of femora of female and male persons only the left or the right femur of a given

individual was used. The means of K of female ($K_{\text{female}}=0.560$) and male ($K_{\text{male}}=0.536$) femora were not significantly different (t -test for independent samples: $t=1.053$, $d.f.=34$, $P=0.299$). Hence, we could not establish a sex-specific difference in K . Similarly, the means of K of subadult, adult and old-people femora were not significantly different [one-way ANOVA: $SS=0.0112$, $MS=0.0056$, $F(2, 33)=1.525$, $P=0.233$]. Note the higher K -value in the posterior view of the subadult femora (0.549 for separate femora, and 0.541 for femur pairs) compared with that of the adult (0.462, 0.463) and old-people (0.485, 0.483) femora (Tables 2 and 3). In our opinion, this statistically non-significant difference between the subadult femora and the older ones is functionally not significant.

To test whether K is influenced by the bone length L , we investigated the correlation between them. We obtained that neither $K_{\text{mean}}^{\text{medial}}$, nor $K_{\text{mean}}^{\text{posterior}}$ depends on L (Pearson correlation between $K_{\text{mean}}^{\text{medial}}$ and L : $N=33$, $r=0.019$, $P=0.917$; while between $K_{\text{mean}}^{\text{posterior}}$ and L : $N=36$, $r=-0.18$, $P=0.28$). This was expected, because there were no age-specific differences in K . Among the investigated bones only the subadult femora differed significantly in length. If K were influenced by L , the mean K_{mean} of subadult femora should differ significantly from that of adult and old-people femora, but this was not observed.

Discussion

According to Currey and Alexander (1985), long bones can be solid, or very-thin walled (having values of K from 1 to, say, 0.1). However, except for those having special life styles (living in water, or having no marrow) they do not span that range, but their median is about 0.63. The reasons for this are the following.

(1) If the central bone cavity contains marrow, there will be an optimum value for K that produces a bone of minimum mass. The precise value of the optimum depends on what mechanical situation (or combination of them) for which the bone is optimised. The optimal value of K for stiffness is larger than that for bending strength, for instance.

(2) The curves of mass $m(K)$ as a function of K are rather flat near the optimum K_{opt} , so selection will not be acting strongly on the value of K_{opt} .

(3) The examination of actual values of K for land mammals and flightless birds shows them to be roughly where one would expect them to be, with perhaps a bias towards strength rather

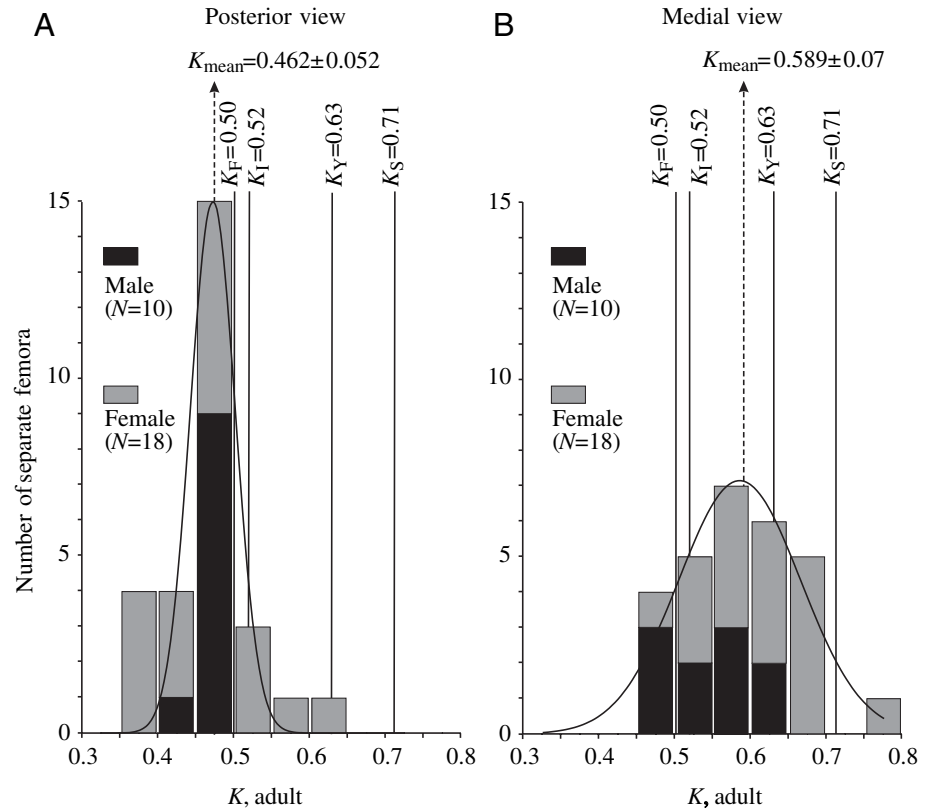


Fig. 3. As Fig. 2 for adult femora (age between 21 and 50 years).

than stiffness. Flying bird's bones, if anything, seem to be appropriate for stiffness rather than strength. The values of K for pterosaurs, marrowless bones of birds, and water-living vertebrates, deviate in the expected directions.

(4) This suggests that the hollowness of bones is to produce values of minimum mass for the bones.

Since the incidence of osteoporosis and osteoarthritis becomes greater and greater in human populations, bone wall thickness and bone density have become important subjects of quantitative investigations. These studies are focused on medical aims rather than on evolutionary relationships. As far as we know, human bones were not involved in interspecific comparative studies on the biomechanical optimality of the relative wall thickness of tubular bones.

The K -value of the femora in terrestrial mammals and flightless birds ranges from 0.26 (*Melursus ursinus*) to 0.73 (*Sorex araneus*, *Pedetes capensis*, *Litocranius walleri*, *Struthio camelus*) with a median of about 0.63 (Currey and Alexander, 1985). The mean, standard deviation, minimum and maximum of K of adult fox (*Vulpes vulpes*) femora are $K_{\text{mean}} \pm \sigma_K = 0.68 \pm 0.036$, $K_{\text{min}}=0.59$ and $K_{\text{max}}=0.74$ (Bernáth et al., 2004). Using the same method as Bernáth et al. (2004), in this work we established that $K_{\text{mean}}^{\text{posterior}} \pm \sigma_K^{\text{posterior}} = 0.462 \pm 0.052$, $K_{\text{mean}}^{\text{medial}} \pm \sigma_K^{\text{medial}} = 0.589 \pm 0.070$, $K_{\text{min}}=0.379$ and $K_{\text{max}}=0.783$ of adult human femora (Fig. 3, Table 2). The lack of sex-, age- and length-specific as well as right-left differences in K of human femora demonstrates well how robust and general are

Table 2. Mean (K_{mean}), standard deviation (σ_K), minimum (K_{min}) and maximum (K_{max}) of the ratio K of the internal to external diameter of separate human femora measured at the mid-points of the shafts with evaluation of their radiographs

	View	Separate human femora			
		K_{mean}	σ_K	K_{min}	K_{max}
All ($N=107=52f+55m$)	Posterior	0.498	0.085	0.345	0.732
	Medial	0.589	0.070	0.442	0.783
Subadults ($N=33=18f+15m$)	Posterior	0.549	0.075	0.379	0.685
	Medial	0.585	0.056	0.458	0.709
Adults ($N=28=18f+10m$)	Posterior	0.462	0.052	0.379	0.610
	Medial	0.589	0.070	0.480	0.783
Old people ($N=46=16f+30m$)	Posterior	0.485	0.093	0.345	0.732
	Medial	0.592	0.081	0.442	0.725

N , number of femora investigated (f, female; m, male). Subadults, age 0–20 years; adults, age 21–50 years; old people, age above 50 years. Note that after rounding of the numerical data, the mean and standard deviation for the medial view of adult femora are the same as the overall mean and standard deviation, for example. This is an accidental coincidence, and these identical values are real, and not the result of a typo.

Table 3. Mean (K_{mean}), standard deviation (σ_K), minimum (K_{min}) and maximum (K_{max}) of the ratio K of the internal to external diameter of human femur pairs measured at the mid-points of the shafts with evaluation of their radiographs

	View	Human femur pairs					
		K_{left}	K_{right}	K_{mean}	σ_K	K_{min}	K_{max}
All ($N=49=24f+25m$)	Posterior	0.487	0.496	0.491	0.075	0.349	0.718
	Medial	0.579	0.591	0.585	0.063	0.473	0.729
Subadults ($N=13=7f+6m$)	Posterior	0.533	0.549	0.541	0.061	0.450	0.640
	Medial	0.576	0.587	0.581	0.039	0.536	0.644
Adults ($N=14=9f+5m$)	Posterior	0.459	0.467	0.463	0.048	0.385	0.567
	Medial	0.599	0.580	0.589	0.067	0.491	0.729
Old people ($N=22=8f+14m$)	Posterior	0.480	0.485	0.483	0.086	0.349	0.718
	Medial	0.580	0.585	0.583	0.074	0.473	0.678

At every femur pair the average $K_{mean}=(K_{left}+K_{right})/2$ of the K of the left and right femur was calculated. N , number of femora investigated (f, female; m, male). Subadults, age 0–20 years; adults, age 21–50 years; old people, age above 50 years.

the biomechanical design and the structure of marrow-filled tubular bones in humans.

The major reasons for the statistically significant difference between $K_{mean}^{posterior}=0.498$ and $K_{mean}^{medial}=0.589$ are that: (1) the human femur is not exactly symmetrically circular; and (2) its wall thickness is not exactly uniform. Since circular cross section and uniform wall thickness are the prerequisites of the biomechanical optimization theory of Currey and Alexander (1985), the asymmetry of the cross section of the human femur makes it difficult to test the predictions of the theory for the optima of K . Until a more sophisticated theory is developed, it is only possible to analyse human femora. However, our conclusions remain valid in spite of the fact that the optima to which the human K -values are compared are based on the assumption of circular cross sections. Note that in comparison to other human long bones, the human femora possess the most circular mid-shaft cross section (Cubo and Casinos, 1998). More detailed explanation and functional interpretation of

our findings that $K_{mean}^{posterior}$ is significantly smaller than K_{mean}^{medial} could be the task of future research.

The human femur has considerably smaller K than the fox femur. Note that smaller K means greater relative wall thickness $W=1-K$. According to Currey and Alexander (1985), interspecific variance of K can be high either because the different ways of life may demand optimization for different mechanical loads and/or because of the biological irrelevance of optimization of the relative wall thickness due to the too tiny relative mass increments.

In our subadult group, 15 of the investigated mummies belonged to the infans I age-group (0–7 years), three to the infans II age-group (8–14 years), and two 15 year old females to the juvenis age-group (15–17 years). Thus, all subadult femora originated from subjects aged below 15 years, and the majority of the bones was not older than 7 years. Hence, these subadult bones were far from the borders of skeletal infancy and near-maturity, where considerable changes take place.

The standard deviation of K of adult human femora

($\sigma_{\text{adult}}^{\text{posterior}}=0.052$, $\sigma_{\text{adult}}^{\text{medial}}=0.070$) is 1.44–1.94-times higher than that of adult fox femora ($\sigma_K=0.036$). The maximal difference in K of adult human femora is $\Delta K=K_{\text{max}}-K_{\text{min}}=0.404$, which is 2.7-times as high as $\Delta K=0.15$ of adult fox femora. This relatively high variance in K in human femora explains why we could find several human femora that had similar K -values to each of the theoretical optima (K_Y , K_S , K_F , K_I ; Table 1). With the assumption of Alexander (1982, 1996) that $Q=0.50$, from our data ($K_{\text{mean}}^{\text{posterior}}$ and $K_{\text{mean}}^{\text{medial}}$) we conclude that the adult human femora are optimised to withstand bending fracture load, or yield and fatigue strengths. By comparison, fox femora are optimised for stiffness (Bernáth et al., 2004).

Note that considerable deviations of K from the optimum value result in only small mass increments (Bernáth et al., 2004), which could explain the relatively high variation of K in human femora (Fig. 1, Tables 2, 3). Currey and Alexander (1985) noted that the values around the minima do not result in large changes in the bone mass $m(K)$, suggesting that each effective optimum value K_{opt} may be best described as a range $\pm\Delta K$ of values around K_{opt} . However, at present there is no reliable estimation of the range $\pm\Delta K$ encompassed by the flat portions of each $m(K)$ curve.

The biological relevance of optimization of the relative wall thickness $W=1-K$ of the diaphysis in tubular bones in a given species should be reflected by low intraspecific variance of K . Since the standard deviation of K in human femora is 1.44–1.94-times higher than in fox femora, we conclude that the biomechanical optimization of K in human femora is not finely tuned. Compared with fox femora, K of human femora follows the biomechanical optimum to a lesser extent. Although the relative wall thickness of the diaphysis in human femora is optimised to withstand bending fracture load, or yield and fatigue strengths, the very low relative mass increments due to deviation of K from the optima and the relatively high intraspecific variance of K make it probable that an accurate optimization of the relative wall thickness is irrelevant in humans.

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