Testing the biomechanical optimality of the wall thickness of limb bones in the red fox (*Vulpes vulpes*)

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Abstract

The optimum for the ratio K of the internal to external diameter of a marrow-filled tubular bone with minimum mass designed to withstand a given type of strength (yield/fatigue, stiffness, fracture or impact) depends on $Q = \rho_m/\rho_b$ only, where ρ_m and ρ_b are the densities of marrow and bone. With computer-assisted evaluation of radiographs of 62 femurs in the red fox (*Vulpes vulpes*) we measured the values of K. The mean and standard deviation of K are 0.68 and 0.036, and K changes in the rather wide range from 0.59 to 0.74. Accepting the assumption of earlier authors that $Q = 0.50$ or 0.44, our data would support the hypothesis that the fox femurs are optimized to withstand yield, fatigue or stiffness strengths. However, since the Q-values are unknown, the possibility cannot be excluded that any studied fox bone with an appropriately selected Q-value is optimized for any strength type. Assuming $Q = 0.50$ or 0.44, the relative mass increments μ of the investigated fox bones are smaller than 5% under all four mechanical conditions. The evolutionary relevance of such tiny μ-values is questionable.
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1. Introduction

The long bones in the limbs of mammals are hollow tubes with an approximately circular cross section filled with marrow. One of their geometrical variables is the ratio K of the internal to external diameter. These bones have to resist forces and torques which bend and twist them. On the basis of biomechanical studies mammalian limb bones have been concluded to be optimum structures (e.g. Alexander, 1982, 1983, 1996); it became a wide-spread view that the wall thickness of mammalian long bones is optimal for strength and stiffness with lightness. According to Alexander (1982, 1983, 1996), lightness is a particularly desirable property for limb bones because limbs have to be accelerated and decelerated in every step. The less the mass of a limb,

the less the work needed to accelerate it. Assuming the cross sections of long bones to be circular, Pauwels (1980), Currey (1982), Alexander (1982, 1983, 1996) and Currey and Alexander (1985) derived theoretically different biomechanical optima for the value of K, which ensure that a marrow-filled tubular bone has a minimum mass per unit length and is strong enough to withstand a given mechanical load (yield, or fatigue, or fracture, or bending, or impact). In other words, those values of K were derived which are the optimum for different strengths with lightness. The optima of K depend on the ratio $Q = \rho_m/\rho_b$, where ρ_m and ρ_b are the densities of marrow and bone, respectively (Appendix A).

Bending moments are generally the most important causes of stress in bones, optimal stiffness of long bones allows minimizing the mass of muscles necessary to move the limbs (Alexander et al., 1990). On the other hand, the special situation of flying impose great torsion load on the limb bones of flying animals (Swartz et al., 1992). In the case of bending and torque load the bone

mass is minimal if $K = 0.63$ (Alexander, 1982, 1996). This minimum is, however, a shallow one: a marrow-filled bone with $K = 0.63$ is only 10% lighter than a solid bone of the same strength, and only very slightly lighter than equivalent bones with $K = 0.4$ or 0.7. Thus Alexander (1982, p. 16; 1983, p. 131; 1996, p. 19) expected to find that tubular bones have evolved to have $K \approx 0.6$.

Alexander (1982) and Currey (1982) measured the value of K at the mid-point of the shaft of one humerus and one femur of a hare, a fox, a lion, a camel and a buffalo (Table 1), and concluded that most of them are less than 0.6, but all of them lie in the range from 0.4 to 0.7. Currey and Alexander (1985) carried out a much larger survey to investigate which groups do, and which do not fulfill expectations based on theory: the variation of wall thickness of long bones among species was examined by surveying K-values of 240 long bones from single individuals of 70 species. The numerous data surveyed by Currey and Alexander (1985) were gathered from various sources: measurements by calipers (i) on the cross section of large bones, (ii) on projected images of small bones, (iii) on drawings of bone cross sections made with *camera lucida* by another author, or (iv) performed by other authors. Interspecific variation of K-values was found to be high, but most values lie in the range from 0.4 to 0.8.

Bone structure in mammals could vary because of different way of life of different species. However, biological relevance of optimization of the wall thickness in long bones in a given species should be supported by low intraspecific variance of K. In earlier studies the value of K was measured only at one humerus and/or femur and/or tibia and/or metatarsus and/or metacarpus of a given animal species, and thus the mean and variance of K of a given bone type could not be determined in any species. Since the exact values of the relative density Q, which may be species specific and/or could change during the life of the animal, are unknown, Alexander (1982, p. 14; 1996, p. 19) assumed $Q_1 = 0.50$, while Currey and Alexander (1985, p. 455) supposed $Q_2 = 0.44$. A detailed investigation on the variance of Q would be essential in the future to study the optimality of the wall thickness of marrow-filled limb bones.

Since there have been derived at least four different optima for K (Appendix A), and the existence of a

general Q-value among mammals is questionable, measurement of the K-value of a limb bone in numerous individuals of particular species should be performed to test optimality reliably. Therefore it is necessary to investigate the optimality of mammalian limb bones using a (possibly homogeneous) data basis composed of numerous K-values (measured with the same reliable technique if possible) in a given species.

Here, we present an experimental study on the femur of the red fox (*V. vulpes*). This species was chosen because on the one hand its limb bones were easily available in large numbers from the Hungarian Natural History Museum as well as from a hunter, and on the other hand $K = 0.63$ of a single fox femur (Table 1) published by Alexander (1982, p. 16; 1996, p. 21) is exactly the same as one of the eight theoretical optima (Appendix A and Tables 1 and 2). Theoretical optima K_y, K_s, K_i, K_f were derived using the assumption that the cross sections of marrow-filled tubular bones are circular. However, most long bones have protuberances supporting muscle attachments, and their cross section are rather elliptical. In mammals, femurs have the most circular mid-shaft cross section (Cubo and Casinos, 1998), thus femur is the most appropriate bone-type to test biological relevance of the mentioned theoretical optima.

With computer-assisted evaluation of the radiographs of 62 limb bones we measured the K-values and their standard deviation. The measured K-values were compared with the theoretical optima for K. Using these data, we calculated the optimal values of Q which would allow that the mass of the fox bones designed to withstand four different strengths is minimal. We calculated also the mass increments of the investigated fox bones relative to the minimum mass for two different Q-values.

2. Materials and methods

A total of 62 limb bones of the red fox (*V. vulpes*) were collected from three sources: (i) A Hungarian hunter, Mr. Sen. Mihály Gasparik provided wild-living animals hunted during the autumn shooting season in 2001. Animals were skinned, and the hind limbs were separated from the body in the field; only frozen limbs were transferred to the laboratory. Majority of flesh was cut off manually, then all remaining soft tissues were removed from the bones after cooking for 6 h. To

Table 2
Optimal K-values calculated from (A.1) to (A.4) for $Q_1 = 0.50$ and $Q_2 = 0.44$

| $Q_1 = 0.50$ | $K_{y1} = 0.63$ | $K_{s1} = 0.71$ | $K_{f1} = 0.50$ | $K_{i1} = 0.52$ |
| $Q_2 = 0.44$ | $K_{y2} = 0.67$ | $K_{s2} = 0.75$ | $K_{f2} = 0.56$ | $K_{i2} = 0.55$ |

Table 1
Values of the ratio K of the internal to external diameter measured at the mid-points of the shafts of various mammal bones (after Table 2.1 of Alexander 1982 on p. 16 and 1996 on p. 21)

	Hare	Fox	Lion	Camel	Buffalo
Femur	0.57	**0.63**	**0.56**	0.62	0.54
Humerus	**0.55**	0.59	0.42	0.66	0.51

Those numerical data are printed in boldface, which are exactly the same as one of the eight optimal K-values in Table 2.

remove fat the bones were immersed for 24 h in domestic detergent solution containing hypochlorite. Prepared bones were dried on room temperature and stored in plastic bags with zeolite sorbent until the radiographic study was performed. (ii) Mammal Collection of the Department of Zoology of the Hungarian Natural History Museum: the red fox bones originated from different sources collected during the last 20 years. Their preparation followed the same protocol as described above. (iii) From the Palaeovertebrate Collection of the Department of Geology and Palaeontology of the Hungarian Natural History Museum we examined the following specimens (first datum is the inventory number): V.58.600, one femur fragment from the Kálmán Lambrecht cave; V.58.937, two femurs (one is fragment) from the Kálmán Lambrecht cave; V.61.1318, one femur fragment from the Remete cave; G.57.570, two femurs (one is fragment) from level B of the Szelim cave. The age of the specimens is Late Pleistocene. In case of the bones from the Kálmán Lambrecht cave the age is about 75000−80000 years. The bones were turned up from cave deposits (clay), they were collected manually in situ from the clay, their preparation was performed also manually without using any chemical.

Latero-medial and cranio-caudal radiographs were taken from every examined fox femur (Fig. 1) at the Department and Clinic of Surgery and Ophthalmology of the Faculty of Veterinary Science, Szent István University Budapest (EUREKA Diamond 150, CEA OGA green sensitive). After standard chemical development of the radiographs, they were digitized using an AGFA Arcus 1200 scanner with a resolution of 400 dpi. Using a computer program developed by ourselves (Horváth, 2001), a rectangular part of a digitized picture was selected including the mid-point of the shaft of the investigated limb bone (Figs. 1A and B). To filter the inevitable small signal noise of the digitized picture, the digital value of the intensity I of a pixel in a given row and column was replaced by the arithmetical mean i of the I-values of pixels of the same column in the neighbouring ± 10 rows. Thus the intensity function $i(x)$ was obtained in every row of the filtered image, where x is the pixel number (Fig. 2A). Forming the differential quotient $i'(x) \equiv \mathrm{d}i/\mathrm{d}x$ (Fig. 2B) and smoothing it with a normalized Gaussian function, we obtained the smoothed version $i'(x)_{\mathrm{smoothed}}$ of $i'(x)$ (Fig. 2C). The function $i'(x)_{\mathrm{smoothed}}$ has sharp maxima and minima at the external and internal walls of a marrow-filled tubular bone (Fig. 2C) as is shown in Appendix B (Horváth, 2001). Thus, the external and internal walls of the investigated limb bone were recognized by the detection of the positions of maxima and minima of $i'(x)_{\mathrm{smoothed}}$ (Fig. 2D). Then the ratio K of the internal to external diameter of the bone was calculated in every row of the picture for both the latero-medial and cranio-caudal radiographic views (Fig. 2E). The arithmetical mean of these two K-values was considered as the average K-value of the bone in a given row of the
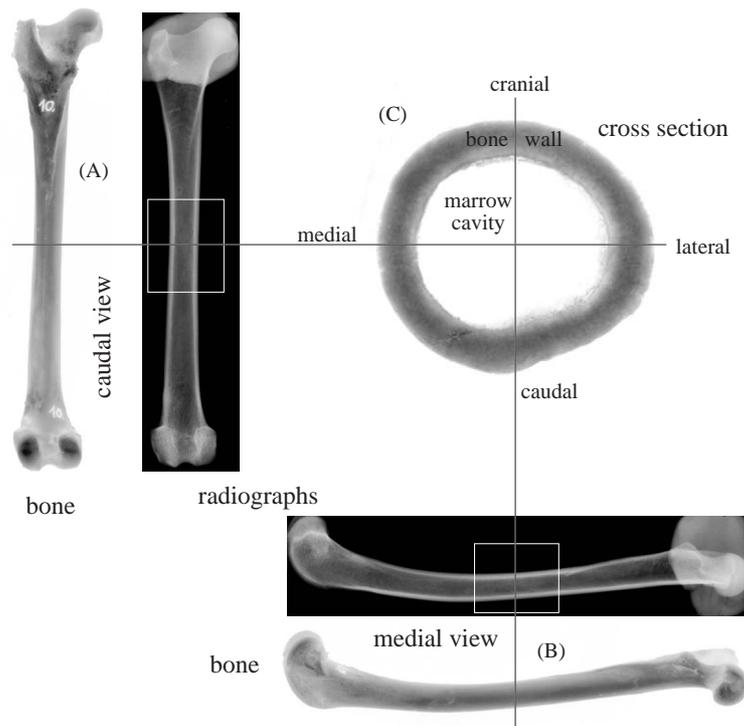
Fig. 1. (A, B) Photographs and radiographs taken from the femur of a red fox (*V. vulpes*) from latero-medial and cranio-caudal views, where the rectangular parts demarcated by white line are selected for further computer-assisted evaluation. C: Photograph of a cross section of the bone. The horizontal (lateral/medial) line marks the cross section, at which the functions $i(x)$ and $i'(x)$ in Figs. 2(A)–(C) are presented.
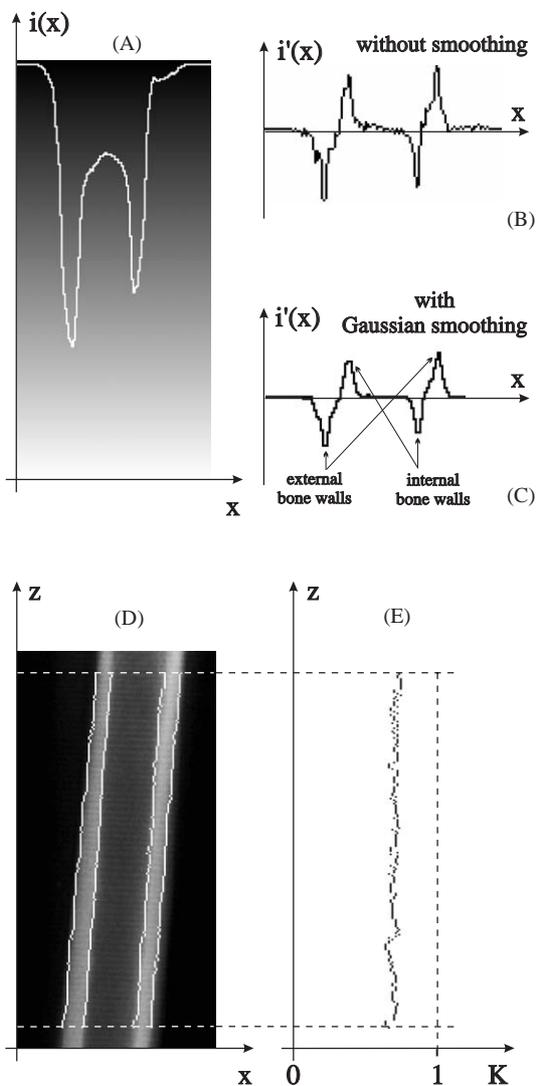
Fig. 2. (A) Change of the relative intensity $i(x)$ of X-ray transmitted through a bone versus the radial distance x along a cross section. (B) The differential quotient $i'(x) \equiv \mathrm{d}i/\mathrm{d}x$ of $i(x)$. (C) $i'(x)$ smoothed by a normalized Gaussian function. (D) Contours of the external and internal bone walls recognized by means of the detection of maxima and minima of the smoothed $i'(x)$. (E) Change of the ratio K of the internal to external diameter of the bone along the selected section calculated on the basis of the recognized positions of the bone walls.

picture. Finally, we obtained the change of K along the selected mid-section of the bone. The reliability of this method was tested by comparison of computationally obtained K-values with data measured directly by a caliper square. Our method based on the computer evaluation of radiographs of tubular bones can measure the K-value with an accuracy of $\pm 1\%$.

To test the difference between intraspecific and interspecific variation of bone wall thickness the variance of mean K-values measured in single fox femurs and K-values in femurs of terrestrial mammalian species given by Currey and Alexander (1985) were

compared using two-tailed F-test. From earlier studies only data originating from caliper measurements were used, data from drawings and the outlying elephant femur were excluded.

3. Results

Table 3 contains the K-values of 62 red fox femurs. Measuring both from the caudal and medial views was possible in the case of 36 bones. Fig. 3 shows the frequency of the mean K-values of these 36 bones. Among the investigated bones there are several ones, the K-value of which is exactly the same as one of the theoretical optima K_{y1}, K_{y2} and K_{s1} (Tables 2 and 3). However, bones with K-values equal or near to one of the theoretical optima $K_{f1}, K_{f2}, K_{i1}, K_{i2}$ (Table 2) do not occur (Table 3). The minimum, maximum, mean and standard deviation of K are $K_{min} = 0.59$, $K_{max} = 0.74$, $K_{mean} = 0.681$ and $\Delta K = 0.036$. Since the age of the foxes was unknown, furthermore for many fox bones the sex of the animal was unknown, possible age-dependent and/or sex-specific differences in the K-values could not be established. Similarly, no difference in K could be established between the fossil bones and recent ones due to the small number ($N = 6$) of the former. Hence, the investigated fox bones seem to be optimized either for yield/fatigue or for stiffness. Intraspecific variation of K among the fox femurs studied by us was significantly lower than the interspecific variation of K among terrestrial mammalian species given by Currey and Alexander (1985): F-test: $F_{(25,35)} = 37.06$; $F*_{(0.005,25,35)} = 2.58$; $p < 0.01$.

Since the exact value of the relative density Q ($=$ marrow to bone density) is unknown, we calculated the optimal values of Q_y, Q_s, Q_f and Q_i (Appendix C) which allow the total mass of the investigated fox bones to be minimized under yield/fatigue, stiffness, fracture and impact strength at the measured K-values in Table 3. Fig. 4 shows the frequencies of Q_y, Q_s, Q_f, Q_i, and Table 4 contains the minima Q_{min}, maxima Q_{max}, means Q and standard deviations ΔQ. In the case of yield/fatigue and stiffness strengths the two values of $Q_1 = 0.50$ and $Q_2 = 0.44$ used by Alexander (1982, 1996) and Currey and Alexander (1985) are near to the mean $Q_s = 0.52$ and $Q_y = 0.41$, respectively, obtained by us. However, for fracture and impact strengths Q_1 and Q_2 fall quite out of the ranges $Q_{min} \leqslant Q \leqslant Q_{max}$. Under all four mechanical conditions the standard deviations ΔQ are about 5%, and the values of $Q_{max} - Q_{min}$ equal approximately to 19%.

Figs. 5 and 6 show the frequencies of the values of the relative mass increment μ (Appendix D) calculated with the use of the measured K-values in Table 3 for $Q_1 = 0.50$ and $Q_2 = 0.44$ assumed by Alexander (1982, 1996) and Currey and Alexander (1985), while Table 5

Table 3
K-values of 62 red fox (*V. vulpes*) femurs measured with computer-assisted evaluation of their radiographs

Origin	Caudal view	Medial view	Mean	Sex	Origin	Caudal view	Medial view	Mean	Sex
FO	0.68	—	—	U	MU	0.74	—	—	U
FO	0.66	—	—	U	MU	**0.67**	—	—	M
FO	**0.67**	—	—	U	MU	0.66	—	—	M
FO	**0.71**	—	—	U	MU	0.64	0.66	0.65	U
FO	—	0.65	—	U	MU	0.65	0.68	0.66	U
FO	**0.71**	—	—	U	MU	**0.71**	0.68	0.69	U
HU	0.66	**0.67**	0.66	M	MU	0.72	0.70	**0.71**	U
HU	0.68	**0.67**	**0.67**	M	MU	0.69	**0.63**	0.66	U
HU	—	0.61	—	M	MU	**0.67**	**0.67**	**0.67**	U
HU	0.70	0.65	**0.67**	M	MU	0.70	0.69	0.69	U
HU	0.70	0.73	0.72	U	MU	—	**0.67**	—	U
HU	0.68	—	—	U	MU	0.72	0.61	**0.67**	U
HU	0.74	0.72	0.73	F	MU	0.61	0.69	0.65	U
HU	0.74	0.66	0.70	F	MU	0.73	0.70	0.72	U
HU	0.72	0.72	0.72	F	MU	0.69	0.70	0.69	U
HU	0.69	0.72	**0.71**	F	MU	0.72	0.68	0.70	U
HU	**0.71**	0.72	**0.71**	M	MU	0.72	0.73	0.72	U
HU	**0.71**	**0.71**	**0.71**	M	MU	0.66	0.65	0.65	U
HU	0.68	—	—	F	MU	—	0.61	—	U
HU	0.60	0.62	0.61	F	MU	**0.71**	0.62	**0.67**	U
HU	0.61	**0.67**	0.64	M	MU	0.73	0.70	**0.71**	U
HU	**0.67**	**0.52**	0.59	M	MU	0.70	0.69	0.69	U
MU	**0.63**	—	—	M	MU	0.69	0.70	—	U
MU	0.61	—	—	M	MU	—	0.70	—	U
MU	0.70	—	—	F	MU	0.66	—	—	U
MU	**0.71**	—	—	F	MU	0.70	0.72	**0.71**	U
MU	0.68	—	—	M	MU	0.70	0.70	0.70	U
MU	0.70	—	—	M	MU	0.62	0.59	0.60	U
MU	**0.67**	—	—	U	MU	0.65	0.61	**0.63**	U
MU	—	0.70	—	U	MU	0.73	**0.67**	0.70	U
MU	0.73	—	—	F	MU	0.74	**0.67**	0.70	U

Those numerical data are printed in boldface, which are exactly the same as one of the eight optimal K-values in Table 2. FO, fossil, HU, hunted, MU, museum, M, male, F, female, U, unknown sex.
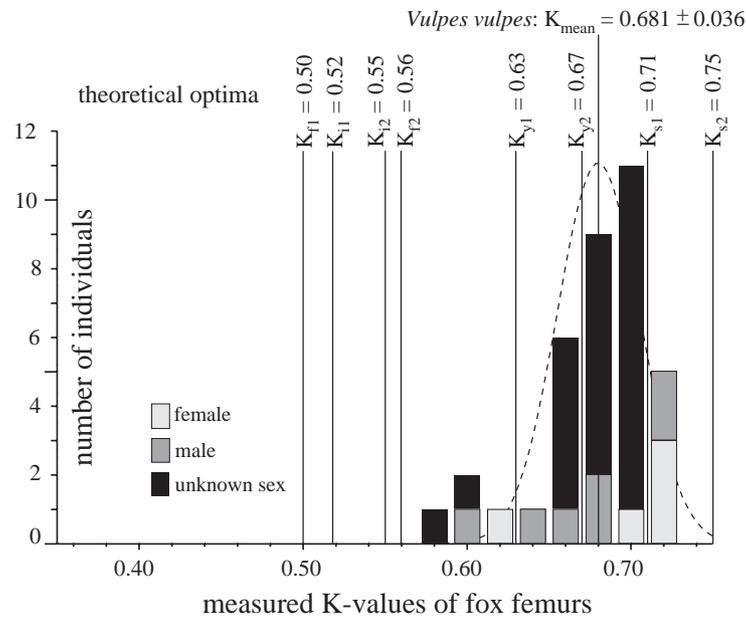
Fig. 3. Diagram showing the frequency of the mean K-values of the 36 fox femurs for which measurements both from the caudal and medial views were possible with computer evaluation of their radiographs and given in Table 3. Vertical lines represent the eight theoretical optima $K_{y1}, K_{y2}, K_{s1}, K_{s2}, K_{f1}, K_{f2}, K_{i1}, K_{i2}$ in Table 2.
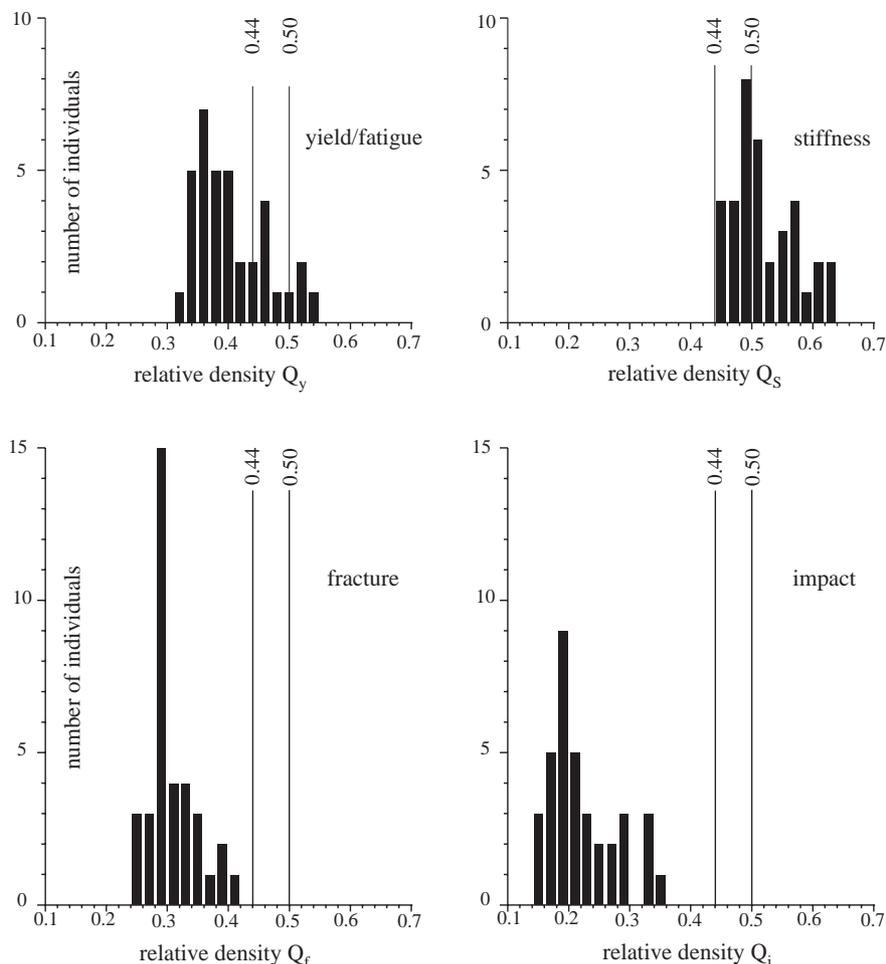
Fig. 4. Diagram showing the frequencies of the optimal values of Q_y, Q_s, Q_f and Q_i calculated from (C.1)–(C.4) with the use of the measured K-values in Table 3. Vertical lines represent $Q_1 = 0.50$ and $Q_2 = 0.44$ assumed by Alexander (1982, 1996) and Currey and Alexander (1985). The maximum, minimum, mean and standard deviation of Q_y, Q_s, Q_f and Q_i are given in Table 4.

Table 4
Minimum (Q_{min}), maximum (Q_{max}) and mean (Q) as well as standard deviations (ΔQ) of the Q-values calculated from (C.1) to (C.4) with the use of the measured K-values in Table 3 (see also Fig. 4)

	Q_{min}	Q_{max}	Q	ΔQ
Q_y (yield/fatigue), Eq. (C.1)	0.33	0.54	0.41	0.06
Q_s (stiffness), Eq. (C.2)	0.45	0.64	0.52	0.05
Q_f (fracture), Eq. (C.3)	0.26	0.40	0.31	0.04
Q_i (impact), Eq. (C.4)	0.15	0.36	0.23	0.06

contains the minima μ_{min}, maxima μ_{max}, means μ and standard deviations $\Delta \mu$ under four mechanical conditions. In the case of yield/fatigue and stiffness strengths the maximum μ_{max} is always smaller than 3.5%, while for fracture and impact strengths μ_{max} is never higher than about 10%. Thus, the relative mass increments of the investigated fox bones are tiny ($\mu \leqslant 1\%$) in the case of yield/fatigue and stiffness strengths and they are small ($\mu \leqslant 5.4\%$) for fracture and impact strengths. The reason for this is that the functions $\mu(K)$ have a very low slope

around their minimum as shown in Fig. 7. In other words, considerable deviations of K from the optimum result in only small increments of the mass relative to its minimum.

4. Discussion and conclusion

Currey and Alexander (1985) demonstrated that it was reasonable to consider that a wide variety of amniote long bones were optimized for minimum mass in relation to the ratio K of total marrow cavity radius to the total bone radius. They showed, from a large collection of bones, that (i) the K-values for land mammals centred on $K \approx 0.5$; (ii) the K-values for gas-filled bird bones were considerably greater than those of marrow-filled bird bones; (iii) flightless birds had K-values similar to those of land mammals; (iv) aquatic animals tended to have very low K-values; (v) pterosaurs had extremely high K-values. All but the last observation could be predicted from theoretical
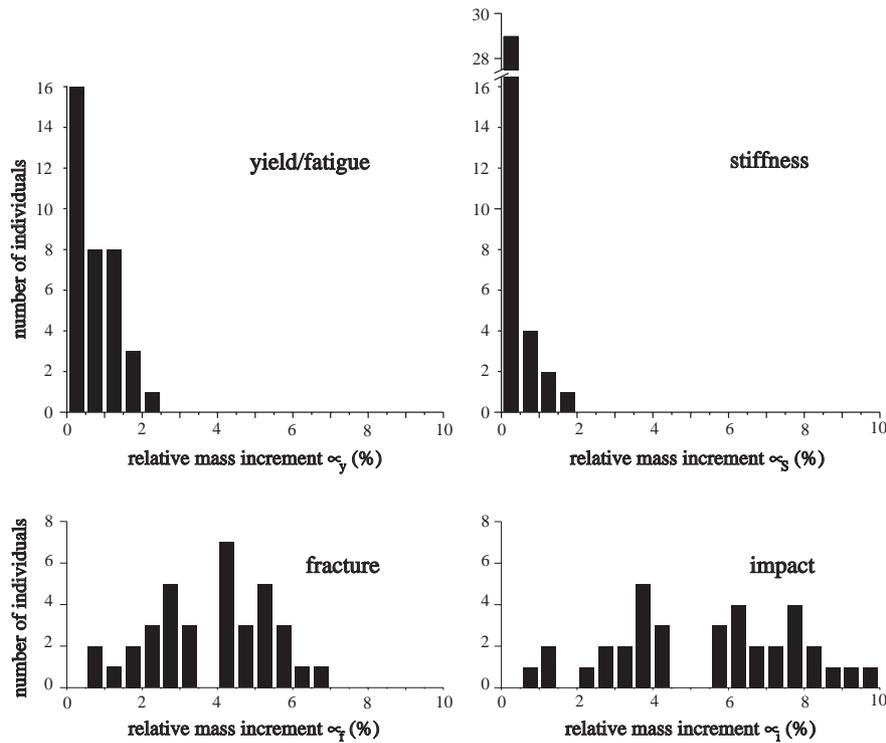
Fig. 5. Diagrams showing the frequencies of the values of the relative mass increments μ_y, μ_s, μ_f and μ_i calculated from (D.2) to (D.5) with the use of the measured K-values in Table 3 for $Q_1 = 0.50$ assumed by Alexander (1982, 1996). The maximum, minimum, mean and standard deviation of μ_y, μ_s, μ_f and μ_i are given in Table 5.

calculations performed by Currey and Alexander (1985). This was the first theory to account for the variation in hollowness found in amniotes. It could explain a large number of disparate observations, and could be tested empirically.

In this work, we tested one small but important part of the theory of Currey and Alexander (1985): we studied what K-values would best minimize the mass of the bones under different mechanical strengths. Using radiographic methods to determine values of K, we examined many specimens of one bone of one species, the femur of the red fox *V. vulpes*, and found the population variation. We calculated the change in mass needed to bring the K-value to the optimum for a variety of loading systems, and also explored the effects of varying the ratio Q of marrow to bone density, an important variable in the theory.

We established that the mean and the standard deviation of K of the femur in *V. vulpes* is $K = 0.681 \pm 0.036$, and K changes in the rather wide range from 0.59 to 0.74 (Fig. 3 and Table 3). Note that three theoretical optima for K (K_{y1}, K_{y2} and K_{s1} in Table 2) fall in this range with the assumption that Q equals to 0.50 or 0.44. With these Q-values our data support the hypothesis that the red fox femurs are optimized to

withstand yield/fatigue or stiffness strengths. Since the values of Q in the fox are unknown, the possibility cannot be excluded that any studied fox bone with an appropriately selected Q-value is optimized for any strength type (Appendix C, Fig. 4, Table 4). However, the variance of K measured in fox femurs would demand too high variance of Q to secure optimal wall thickness. Although the femur of the red fox may be optimized for yield, fatigue or stiffness the possible changes in Q would allow the bones to be optimized for almost all of the situations envisaged by Currey and Alexander (1985).

In the study of optimality of marrow-filled tubular bones the biologically most relevant parameter is the relative mass increment μ if the K-value of a bone differs from its optimum (Appendix D, Figs. 5–7, Table 5). If the relative mass increment have evolutionary relevance, selection should keep the K-value of the long bones near one of the theoretical optima. However, assuming $Q = 0.50$ or 0.44, the relative mass increments of the investigated fox bones are small (μ smaller than about 5%) under all four mechanical conditions. Considerable deviations of K from the optimum value result in only small mass increments. This may be the reason for the great variation of K in the fox femur (Fig. 3, Table 3).

relative mass increment ∝ for $Q_2 = 0.44$
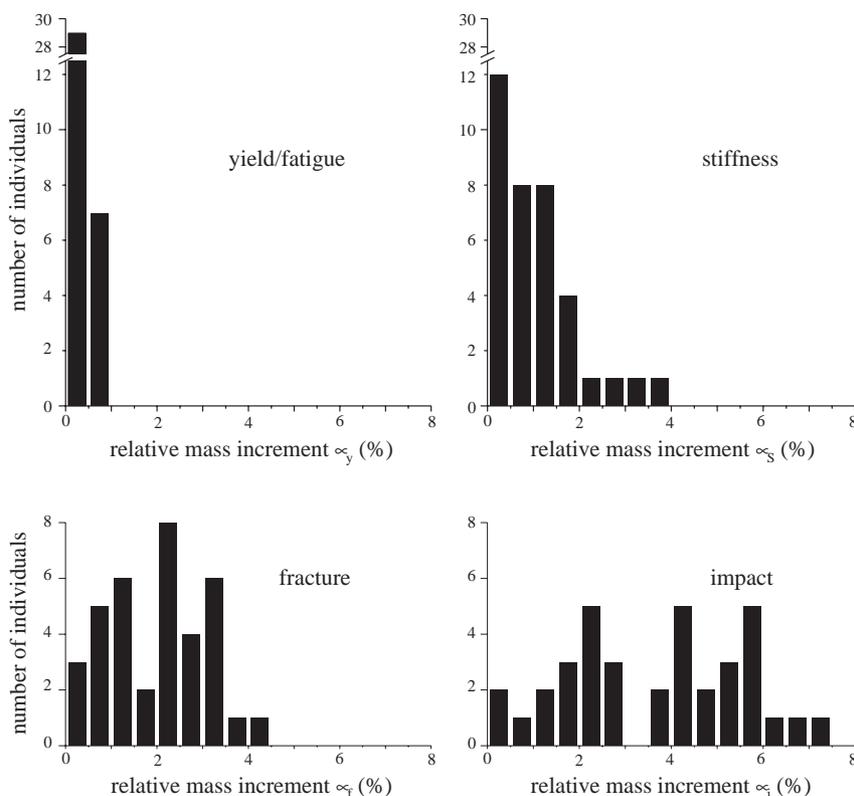
Fig. 6. As Fig. 5 for $Q_2 = 0.44$ assumed by Currey and Alexander (1985).

Table 5
Minimum (μ_{min}), maximum (μ_{max}) and mean (μ) as well as standard deviations ($\Delta\mu$) of the relative mass increment μ calculated from (D.2) to (D.5) for $Q_1 = 0.50$ and $Q_2 = 0.44$ (see also Figs. 5 and 6)

		Yield/fatigue	Stiffness	Fracture	Impact
$Q_1 = 0.50$	$\mu_{min}(\%)$	0.0	0.0	0.7	0.8
	$\mu_{max}(\%)$	2.0	1.6	6.6	9.9
	$\mu(\%)$	0.7	0.3	3.7	5.4
	$\Delta\mu(\%)$	0.6	0.4	1.6	2.4
$Q_2 = 0.44$	$\mu_{min}(\%)$	0.0	0.1	0.1	0.2
	$\mu_{max}(\%)$	0.8	3.5	4.0	7.3
	$\mu(\%)$	0.2	1.0	1.9	3.6
	$\Delta\mu(\%)$	0.2	0.9	1.0	1.9

K can change in a wide range independently of the strength type, and the evolutionary relevance of the small relative mass increments is questionable.

Due to this great variability of K of fox femurs, in Table 3 individual bones could be easily found, the K-value of which is exactly the same as one of the three theoretical optima K_{y1}, K_{y2} and K_{s1}. By measuring only one bone any of this three optima could be corroborated by chance. Since earlier studies did not focus on the intraspecific variability of the wall thickness of marrow-filled tubular bones, they did not have the chance to verify the biological relevance of the optimal wall thickness by the necessary demonstration of low intraspecific variance of K within any species. Inter-specific variance of K could be high either because the different ways of life may demand optimization for different mechanical loads, or because of the biological irrelevance of optimization of the wall thickness due to the too tiny values of the relative mass increment μ. Therefore studies without measurements on numerous bones of particular species support only the possibility of an optimization process. Further research is necessary to investigate the mean and standard deviation of K-values of tubular bones also in other species, on which the paradigm of optimal bone structure has been based until now.

According to Appendix A, the optimum K-value of a marrow-filled tubular bone depends on the relative density of marrow to bone (Q) and on the type of strength (e.g. yield/fatigue, stiffness, fracture, or impact). If one wishes to test whether the structure of a marrow-filled tubular bone in a species is designed to withstand a given strength type with minimum mass, one has (i) to measure (with the same method) the K-values of many bones of a given species, the number of which is large enough for statistical analysis; (ii) to measure (with the same method) the relative density Q in all bones; (iii) to compare the mean of the measured
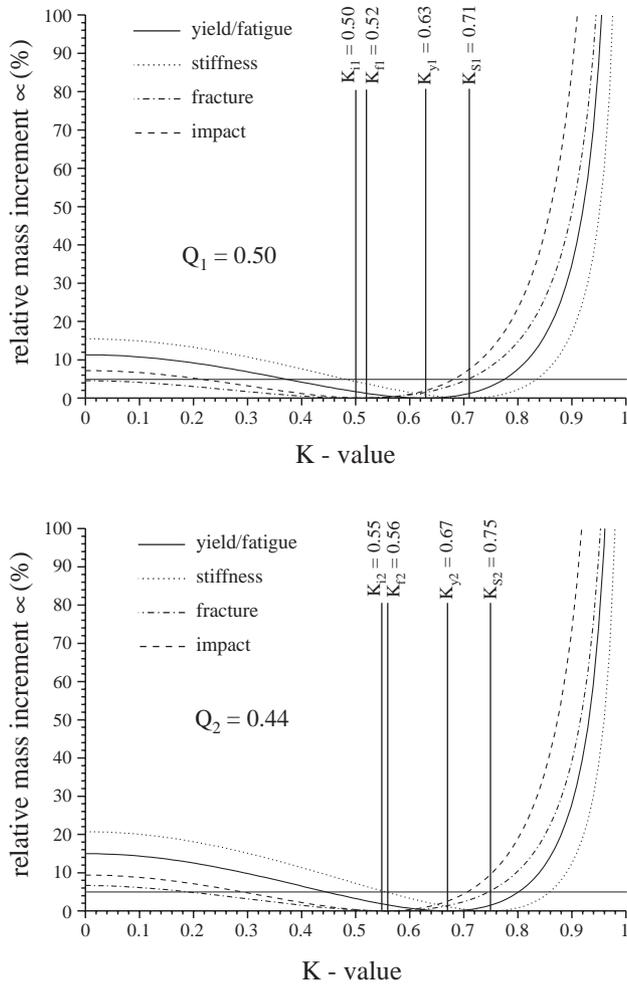
Fig. 7. The relative mass increment μ as a function of K calculated from (D.2) to (D.5) for $Q_1 = 0.50$ and $Q_2 = 0.44$ assumed by Alexander (1982, 1996) and Currey and Alexander (1985). Vertical lines represent the eight theoretical optima $K_{y1}, K_{y2}, K_{s1}, K_{s2}, K_{f1}, K_{f2}, K_{i1}, K_{i2}$ (Table 2) at which the functions $\mu(K)$ are minimal (zero).

K-values with the theoretical optima $K(Q)$ calculated for different strength types. The measurement of Q should be performed in fresh bones, since after freezing or a longer storage the density of both marrow and bone changes due to material destruction and loss of water.

Since the values of Q were/are unknown in all earlier studies (Pauwels, 1980; Currey, 1982; Alexander, 1982, 1983, 1996; Currey and Alexander, 1985) and the present investigation, the optimality of the bone structure could not/cannot be decided. We conclude that the wall thickness of fox femurs may be optimized, however, the minimal relative mass increment μ due to deviation of K from the optima and the considerable intraspecific variance of K make it probable that the accurate optimization of wall thickness has no relevance in the fox. Since sections of different parts of the limb bones of mammals have different shapes, a more complex analysis could explain geometry of tubular bones.

Finally, we would like to emphasize that it is not obvious that any relative mass increment μ is trivial in selective terms. Currey (2002, pp. 208–209) had an argument suggesting that a saving of 10% in the mass of the bone of a distal segment will produce a 5% saving in the power required for running. This would obviously be of considerable selective importance. Reducing the mass saving produces a proportional decrease in the power saving, but even a 1–2% saving in power may be not trivial.

Acknowledgements

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

In the optimization calculations by Alexander (1968, 1982, 1983, 1996) and Currey and Alexander (1985) it was assumed that the cross section remains circular when the marrow-filled tubular bone is bent. This assumption is justified unless the ratio K of the internal to external diameter of the bone is very nearly 1. If the ratio of the density ρ_m of marrow and the density ρ_b of bone is $Q = \rho_m/\rho_b$, according to Currey and Alexander (1985) the four different optima for K which allow the total mass of bone and marrow to be minimized under different mechanical conditions are the following:

Yield/Fatigue: If the bone with minimum mass is designed to withstand yield and fatigue strengths, it should have the following optimum K:

$$K_y(Q) = \{[2 - (1 - 3Q^2 + 6Q)^{1/2}]/(1-Q)\}^{1/2}. \quad (A.1)$$

Stiffness: If the bone is stiff enough in bending, the optimum for K is

$$K_s(Q) = (1-Q)^{1/2}. \quad (A.2)$$

Fracture: If the bone is designed not to fracture, the optimum for K is:

$$K_f(Q) = 1 - Q. \quad (A.3)$$

Impact: If the bone is strong enough in bending under impact loading, the optimum for K is:

$$K_i(Q) = \{[1 - (2Q - Q^2)^{1/2}]/(1-Q)\}^{1/2}. \quad (A.4)$$

$Q_1 = 0.50$ was assumed by Alexander (1982, p. 14; 1996, p. 19) while $Q_2 = 0.44$ by Currey and Alexander (1985, p. 455). Table 2 contains the numerical optimum K-values calculated from (A.1) to (A.4) for Q_1 and Q_2.

Appendix B. Radial change of X-ray intensity transmitted through a marrow-filled tubular bone

Let the intensity of X-ray incident perpendicularly to the long axis of a marrow-filled tubular bone be I_0 (Fig. 8). The intensity $I(x)$ of X-ray transmitted through the bone and detected by the photoemulsion changes as a function of the radial distance x from the axis due to the exponential absorbtion by the marrow and bone. The relative intensity $i(x) = I(x)/I_0$ has a breaking point at the external ($x = r$) and internal ($x = Kr$) bone walls (Figs. 9A and B). On the basis of Fig. 8 we can write

$$S(x) = (r^2 - x^2)^{1/2}, \quad H(x) = (K^2 r^2 - x^2)^{1/2},$$
$$L(x) = (r^2 - x^2)^{1/2} - (K^2 r^2 - x^2)^{1/2}. \tag{B.1}$$

The relative intensity of X-ray transmitted through the tubular bone in the radial range $0 \leqslant |x| \leqslant Kr$ is (Figs. 8 and 9A and B):

$$i_1(0 \leqslant |x| \leqslant Kr) \equiv I_1/I_0 = \exp\{-2[a_b L(x) + a_m H(x)]\}, \tag{B.2}$$

where a_b and a_m are the extinction (or absorption) coefficients of bone and marrow (Horváth, 2001). The relative intensities at the long axis ($x = 0$) and inner wall
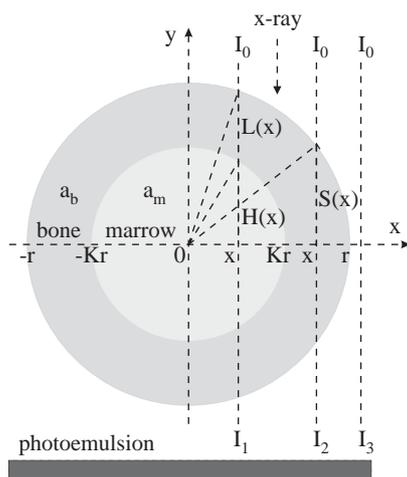
Fig. 8. Geometry of the cross section of a marrow-filled tubular bone with external and internal radii r and Kr ($0 \leqslant K < 1$). I_0 is the intensity of X-ray incident perpendicularly to the long axis of the bone, while I_1, I_2 and I_3 are the intensities transmitted by different radial parts of the bone: (i) bone wall/marrow/bone wall; (ii) bone wall; (iii) outside the bone.

($x = Kr$) of the bone are

$$i_1(x = 0) \equiv j_1 = \exp\{-2[a_b - (a_b - a_m)K]r\},$$
$$i_1(x = Kr) \equiv j_2 = \exp\{-2a_b r(1 - K^2)^{1/2}\}. \tag{B.3}$$

The differential quotient of the relative intensity is (Figs. 9C and D):

$$i_1'(x) = 2x[a_b/(r^2 - x^2)^{1/2} - (a_b - a_m)/(K^2 r^2 - x^2)^{1/2}]$$
$$\times \exp\{-2[a_b(r^2 - x^2)^{1/2} - (a_b - a_m)$$
$$\times (K^2 r^2 - x^2)^{1/2}]\}. \tag{B.4}$$

The values of $i_1'(x)$ at the long axis and inner wall of the bone are:

$$i_1'(x = 0) = 0, \quad i_1'(x = Kr) = \text{signum}\{a_m - a_b\} \infty. \tag{B.5}$$

We can see that

$$j_1 > j_2, \quad \text{if } a_m/a_b < [(1 - K^2)^{1/2} + K - 1]/K \equiv P,$$
$$0 < P \leqslant 1. \tag{B.6}$$

The above characteristics of the relative intensity of X-ray transmitted through the bone in the radial range $Kr \leqslant |x| \leqslant r$ are (Figs. 8 and 9)

$$i_2(Kr \leqslant |x| \leqslant r) \equiv I_2/I_0 = \exp\{-2a_b S(x)\},$$
$$i_2(x = Kr) = j_2,$$

$$i_2(x = r) = 1,$$
$$i_2'(x) = [2x a_b/(r^2 - x^2)^{1/2}]\exp\{-2a_b(r^2 - x^2)^{1/2}\},$$

$$i_2'(x = Kr)$$
$$= [2a_b K/(1 - K^2)^{1/2}]\exp\{-2a_b r(1 - K^2)^{1/2}\} \geqslant 0,$$
$$i_2'(x = r) = +\infty. \tag{B.7}$$

Finally, the relative intensity of X-ray transmitted through the tubular bone in the radial range $r \leqslant |x|$ is (Figs. 8 and 9):

$$i_3(r \leqslant |x|) \equiv I_3/I_0 = 1. \tag{B.8}$$

Fig. 9A and B show how the relative intensity $i(x)$ of X-ray transmitted through the bone and detected by the photoemulsion changes radially. Figs. 9C and D display the radial change of the differential quotient $i'(x)$.

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

If Q is expressed from (A.1) to (A.4) as a function of K, we obtain

Yield/Fatigue:

$$Q_y(K) = (K^4 - 4K^2 + 3)/(K^4 + 3), \tag{C.1}$$

Stiffness:

$$Q_s(K) = 1 - K^2, \tag{C.2}$$
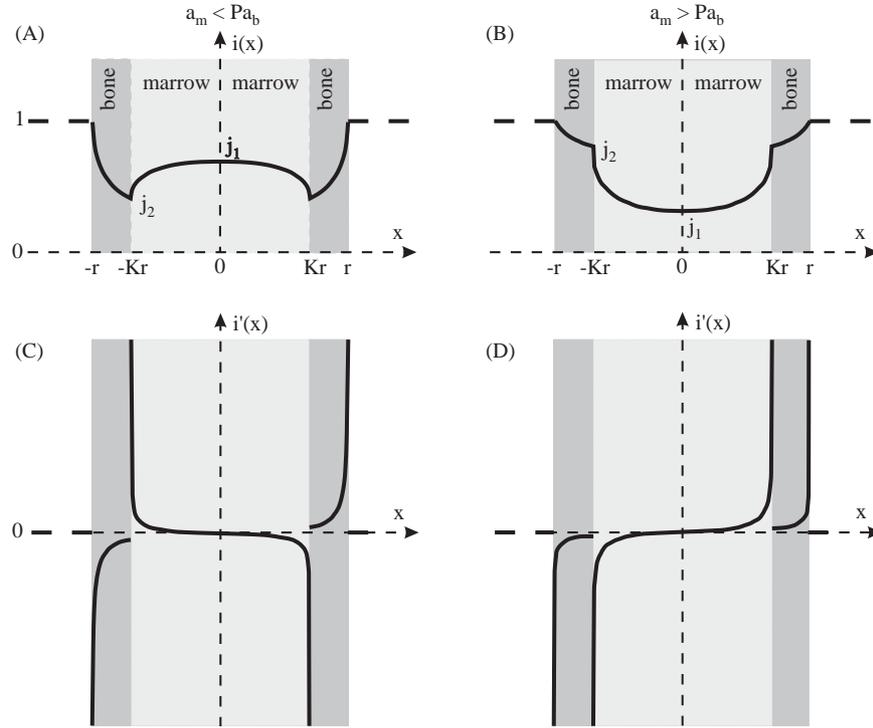
Fig. 9. Radial change of the relative intensity $i(x) = I(x)/I_0$ (A, B) and its differential quotient $i'(x)$ (C, D) calculated for X-ray transmitted through a marrow-filled tubular bone and detected by a photoemulsion, if $a_m < Pa_b$ (A, C) and $a_m > Pa_b$ (B, D), where $P = [(1 - K^2)^{1/2} + K - 1]/K$ (Appendix B). x is the radial distance from the long axis of the bone. The expressions of the local extrema j_1 and j_2 are given in (B.3).

Fracture:

$$Q_f(K) = 1 - K, \tag{C.3}$$

Impact:

$$Q_i(K) = (1 - K^2)^2/(1 + K^4). \tag{C.4}$$

These optimal Q-values allow the total mass of bone and marrow to be minimized under different mechanical conditions at a fixed K-value.

Appendix D. Relative mass increment μ of tubular bones with non-optimal K

If the K-value of a marrow-filled tubular bone is optimal, that is, it is equal to the optimum $K_y(Q)$, or $K_s(Q)$, or $K_f(Q)$, or $K_i(Q)$ given by (A.1)–(A.4), the total bone mass m (the sum of bone and marrow) is minimal: $m = m_{min}$. If the K-value is different from the optimum, the bone mass $m(K)$ is always larger than m_{min}. The relative mass increment μ of a bone with non-optimal K is

$$\mu = [m(K) - m_{min}]/m_{min} = m(K)/m_{min} - 1. \tag{D.1}$$

Using the calculations of Currey and Alexander (1985), the dependence of μ on K, Q and the optimum K-value is the following under different mechanical conditions:

Yield/Fatigue:

$$\mu_y(K, Q, K_y) = [1 - (1 - Q)K^2](1 - K_y^4)^{2/3}$$
$$/[1 - (1 - Q)K_y^2](1 - K^4)^{2/3} - 1, \tag{D.2}$$

Stiffness:

$$\mu_s(K, Q, K_s) = [1 - (1 - Q)K^2](1 - K_s^4)^{1/2}$$
$$/[1 - (1 - Q)K_s^2](1 - K^4)^{1/2} - 1, \tag{D.3}$$

Fracture:

$$\mu_f(K, Q, K_f) = [1 - (1 - Q)K^2](1 - K_f^3)^{2/3}$$
$$/[1 - (1 - Q)K_f^2](1 - K^3)^{2/3} - 1, \tag{D.4}$$

Impact:

$$\mu_i(K, Q, K_i) = [1 - (1 - Q)K^2](1 - K_i^4)$$
$$/[1 - (1 - Q)K_i^2](1 - K^4) - 1. \tag{D.5}$$

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