

This is a repository copy of *Notch sensitivity of mammalian mineralized tissues in impact*.

White Rose Research Online URL for this paper:

<https://eprints.whiterose.ac.uk/1266/>

Article:

Brear, K., Zioupos, P. and Currey, J.D. (2004) Notch sensitivity of mammalian mineralized tissues in impact. *Proceedings of the Royal Society B: Biological Sciences*. pp. 517-522. ISSN 1471-2954

<https://doi.org/10.1098/rspb.2003.2634>

Reuse

Items deposited in White Rose Research Online are protected by copyright, with all rights reserved unless indicated otherwise. They may be downloaded and/or printed for private study, or other acts as permitted by national copyright laws. The publisher or other rights holders may allow further reproduction and re-use of the full text version. This is indicated by the licence information on the White Rose Research Online record for the item.

Takedown

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing eprints@whiterose.ac.uk including the URL of the record and the reason for the withdrawal request.

Notch sensitivity of mammalian mineralized tissues in impact

John D. Currey^{1*}, Kevin Brear^{1†} and Peter Zioupos²

¹Department of Biology, University of York, York YO10 5YW, UK

²Department of Materials and Medical Sciences, Cranfield University, Shrivenham SN6 8LA, UK

The toughness of bone is an important feature in preventing it from fracturing. We consider the notch sensitivity in impact, and the associations between brittleness, notch sensitivity and post-yield energy absorption of mammalian mineralized tissues. Specimens of bone-like tissues covering a wide range of mineralization were broken, either notched or un-notched, in impact. The greater the mineral content, the greater was the notch sensitivity. Also, the more brittle tissues dissipated the least post-yield energy and were the most notch sensitive. It is suggested that since antler bone, the least mineralized of all known mammalian mineralized tissues, seems to be notch insensitive in impact, no adaptive purpose would be served by having mineralized tissues of a lower mineralization than antler. This may explain the lower cut-off in mineralization seen in mammals.

Keywords: bone; mineral content; toughness; energy absorption; impact strength; notch sensitivity

1. INTRODUCTION

Amniote mineralized tissues have a range of mineralization, from *ca.* 220 mg g⁻¹ (milligrams of calcium per gram dry bone) to *ca.* 300 mg g⁻¹ (Currey 1999). There are some bony tissues, mainly bones associated with the ear, that exceed this upper limit (Lees *et al.* 1996; Zioupos *et al.* 1997). However, there seem to be no tissues having less than *ca.* 220 mg g⁻¹. There is presumably no chemical or developmental reason why tissues with a lower mineralization could not be formed. It is reasonable therefore to consider whether such tissues would have poorly adaptive mechanical properties. This is the theme of the present article.

When assessing the adaptive significance of features of bone tissues by using mechano-biological arguments, one needs to have a clear idea as to what actually matters in life, or what that tissue is designed (by natural selection) to avert. Quite often the conclusions are similar. Animals are designed to survive and tissues are designed to avert failure. Failure can be avoided either by the design of the whole structure or by the design of the bone material, or by a combination of these two. As regards the material, one may argue that strength, toughness or extensibility at failure is most important. Consider, for instance, a tensile test specimen (with no pre-cracks, other than inherent internal flaws) of linearly elastic material. At the point of yield the specimen will have absorbed energy according to its elastic resilience, that is: energy per unit volume = $(1/2)\sigma_y\varepsilon_y = (1/2)\sigma_y^2/E = (1/2)\varepsilon_y^2E$, where σ_y is the yield stress at yield, ε_y is the yield strain, and E is Young's modulus of elasticity. The desirable qualities for an elastically resilient material would appear therefore to be either: (i) a high yield stress σ_y ; or (ii) for a constant yield stress σ_y ; a low Young's modulus, or contrarily (iii) if yield strain ε_y does not vary greatly (as found for bone and similar

mineralized tissues by Zioupos & Currey (1996) and Currey (1999)) a high Young's modulus E .

However, quite often (Currey & Butler 1975; Zioupos & Currey 1994) it is the toughness properties of bone-like tissues (Behiri & Bonfield 1980) that matter the most for the survival of the material and the host. During normal service, bones are presumably designed to be loaded only in the range in which they are elastically resilient, that is, where they incur no internal damage, because if any part of the bone passes the yield point it will undergo damage, which can be repaired only by remodelling. Nevertheless, occasionally the bone may be loaded so much that it is in danger of breaking. Under those conditions the bone should be able to absorb as much energy as possible, even at the expense of undergoing considerable damage. In this case the relationship between bone behaviour *pre-yield*, *post-yield* and *during* fracture is of critical importance in determining its overall toughness (Zioupos 1998).

In general, the energy absorption to failure of many amniote mineralized tissues *decreases* remarkably both in impact and in quasi-static loading, with the amount of mineralization and with Young's modulus (Currey 1979, 2004; Currey *et al.* 1996; Les *et al.* 2002; present paper). In quasi-static tests, the pre-yield energy absorption (resilience) *increases* somewhat with Young's modulus and mineral content. The implication is therefore that with an increase in mineralization the reduction in post-yield energy absorption outweighs the increase in resilience. It is likely that in impact also the difference in energy absorption between high- and low-impact strength mineralized tissues is due mainly to differences in the post-yield region.

There is a general relationship between the toughness, the nonlinear behaviour (see Appendix A), the post-yield energy absorption and the notch sensitivity of a material. The ability of a material to accommodate an insult to its structure (whether this is a machined notch or an inherent flaw) determines how brittle it is. Impact specimens are usually notched. The function of notching is to

* Author for correspondence (jdc1@york.ac.uk).

† Deceased 4 November 2002.

Table 1. Mean properties of the specimens; sample sizes are given in parentheses.

('Deer antler': red deer *Cervus elaphus*; 'narwhal dentine, narwhal cement': from tusk of male narwhal *Monodon monoceros*; 'tiger femur': young tiger *Panthera tigris*; 'walrus humerus': *Odobenus rosmarus*; 'human femur': adult, age unknown; 'cheetah femur': *Acinonyx jubatus*; 'deer femur': fallow deer *Dama dama*. No animals were killed for the purposes of this study. 'Mineral content': mg Ca g⁻¹ dry bone; 'Young's modulus': GPa; 'energy': kJ m⁻²; 'notch sensitivity' calculated from mean values of all specimens of the tissue type: 100% × [1 - (energy notched/energy un-notched)].)

specimen	mineral content	Young's modulus	un-notched energy	notched energy	notch sensitivity
deer antler	223.8 (8)	9.0 (8)	—	—	—
narwhal dentine	235.3 (13)	8.9 (14)	69.4 (7)	21.0 (6)	70
narwhal cement	248.1 (6)	8.0 (6)	31.4 (3)	21.7 (3)	31
tiger femur	249.2 (8)	14.7 (8)	30.9 (4)	5.1 (3)	83
walrus humerus	254.6 (8)	11.1 (8)	20.4 (4)	5.2 (4)	74
human femur	260.7 (8)	16.8 (8)	10.9 (4)	2.2 (4)	80
cheetah femur	263.4 (6)	19.6 (6)	31.1 (3)	2.0 (3)	93
deer femur	271.2 (8)	26.0 (8)	14.7 (4)	1.8 (4)	87
bos femur	271.6 (6)	21.5 (6)	12.6 (3)	1.5 (3)	88

concentrate the strain at the root of the notch and thus minimize the dissipation of energy elsewhere in the sample, that is, in places other than where the fatal fracture develops. The total energy absorption of a brittle specimen, and often the strength in quasi-static loading, will be severely reduced by a notch; that of a tough specimen will be less reduced. Consequently, brittle materials are 'notch sensitive'.

The aim of the work described here was to examine the effect of variations in mineral content and Young's modulus on the notch sensitivity in impact of some mammalian mineralized tissues, and to discuss its implications for the variation of mineralization in nature.

2. MATERIAL AND METHODS

(a) *The dataset*

It is possible to test amniote mineralized tissues with a wide range of mineralization levels and Young's moduli only by taking a wide range of types of material. The provenance and mechanical information regarding the tissues used in this study are displayed in table 1. The tissues are arranged in order of increasing mean mineral content. The choice of tissues was eclectic, and the tissues vary in their histology. No animals were killed for the purpose of this study. All specimens were machined so that their long axis was along the long axis of the whole structure, and their depth was in the radial direction of the structure. In each tissue specimens were tested notched and un-notched in equal numbers.

(b) *Mechanical testing*

Specimens were kept wet at all times, during preparation and testing. They were 35 mm long, 4 mm wide and either 4 mm or 2 mm deep, depending on whether they were to be tested later notched or un-notched. The Young's modulus was determined in three-point bending in an Instron 1122 tensile testing machine (Instron, High Wycombe, UK), using crosshead travel as a measure of specimen mid-point deflection. The deformation rate was 0.5 mm min⁻¹. The deflection was such that the maximum strain in the specimen was well below the yield strain. Machine compliance was allowed for. The depth of the specimens that were to be notched was approximately twice as great as that of the un-notched specimens. The doubling of the strain rate thus imposed by a constant machine deflection rate will not

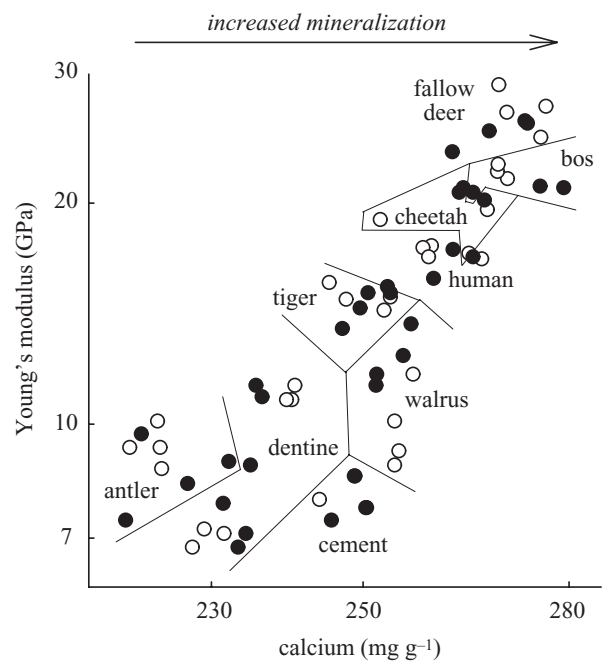


Figure 1. Relationship between Young's modulus and calcium content. Filled circles, un-notched; open circles, notched. Note that because the axes are logarithmic, the scale cannot start at zero.

produce a noticeable difference in modulus, since modulus is approximately proportional to (strain rate)^{0.05} (Carter & Caler 1983). However, differences in depth-to-length ratio may produce some difference in the calculated value of Young's modulus because of the greater importance of shear effects in deeper specimens (Spatz *et al.* 1996). Inspection of figure 1 suggests that this effect is unimportant in our specimens; the values of Young's modulus of notched and un-notched specimens are intermingled. After determination of Young's modulus, specimens to be tested notched had a slot cut in them with an Exakt metallurgical band saw (Exakt, Otto Herrmann, Denmark). The slot was *ca.* 400 µm wide, 2 mm deep with a semi-circular end, and the ligament remaining was also 2 mm deep.

All specimens were then tested, wet, in a Hounsfield impact-testing machine (Tensometer Ltd, Croydon, UK). This is essentially a falling pendulum, whose loss of kinetic energy in fracturing the specimen is measured. The energy lost is assumed to be

used in creating the two fracture surfaces, though in fact a small amount of energy is lost in giving kinetic energy to the fragments, and energy lost in this way will be relatively greater in brittle specimens. The periosteal side of the specimen was loaded in tension, and the notch, if present, was on the periosteal side. The impact energy absorption is the loss of kinetic energy divided by twice the area of the fractured ligament. The calcium content (mg g^{-1}) of bone shavings from close to the fracture site was determined using the method of Sarkhar & Chauhan (1967).

(c) Pre-yield versus post-yield work

The difference in energy absorption between high- and low-energy absorption mineralized tissues lies mainly in differences in the post-yield region (Currey 1999, 2004). The specimens reported there, although mainly of different species from those on which the present impact tests were done, covered a similar range of mineral contents. The original measurements reported there of the work under the stress-strain curve in tension did not distinguish between pre-yield and post-yield work, and the raw data are no longer available.

Nevertheless, one can estimate the two components of work from information available on yield stress and strain and post-yield stress and strain. Assume that the load deformation area for bone comprises a pre-yield triangle and a post-yield rectangle with a triangle on top. This is approximately true. Given this, the pre-yield work (resilience) is: $(\text{yield stress} \times \text{yield strain}/2)$ and post-yield work is $(\text{post-yield strain increase} \times \text{yield stress} + \text{post-yield strain increase} \times \text{post-yield stress increase}/2)$.

The total work calculated thus was plotted against work under the curve as originally determined from the computer output. The relationship was linear, with very few outliers, and the correlation coefficient was 0.965. Therefore, the calculated pre- and post-yield work can be considered a good approximation to what would have resulted from the original measurements. Of course, these measurements apply to quasi-static loading, and the situation is undoubtedly somewhat different in impact loading.

3. RESULTS

(a) Quasi-static tests

Figure 2 shows the relation between the total energy absorption and post-yield energy absorption for a wide variety of bones tested quasi-statically in tension, and is derived from data in Currey (2004). The dotted line is the line of equality and specimens lying very close to the line have a negligible contribution to total energy from pre-yield energy. Some specimens had no post-yield energy, and to allow all specimens to appear on a graph with logged axes all values of energy have been increased by 0.1 MJ m^{-3} . Therefore the block of specimens around '0.5' total energy on the right-hand ordinate in fact had a total energy of *ca.* 0.4 and no post-yield energy (they were entirely brittle). The great majority of specimens, however, absorbed considerably more energy in the post-yield region and in general the total energy is dominated by post-yield energy.

(b) Impact tests

In the present study, we have the following information for each specimen: its provenance, Young's modulus in bending, calcium content and impact energy absorption

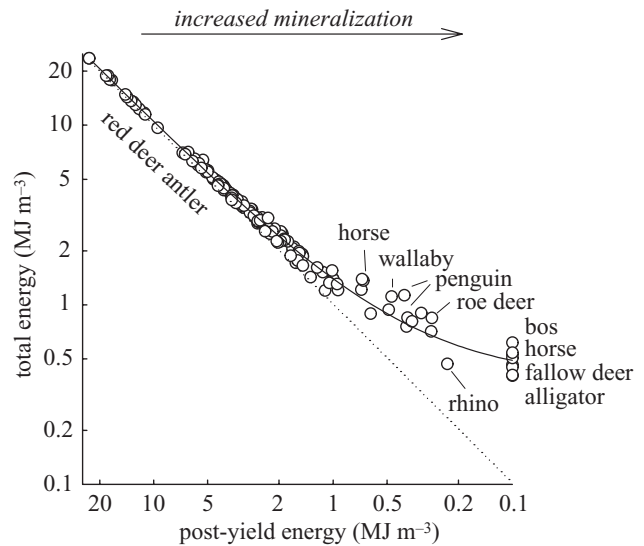


Figure 2. Relationship between total energy and post-yield energy. All values have been increased by 0.1 kJ m^{-2} to allow the zero values to be represented on the logarithmic axis. The figure is derived from the data of tensile specimens described in Currey (1999). The solid, curved line is the linear regression for the untransformed data. The dotted line is the line of equality. The closer a point is to the dotted line the less, proportionally, is the energy derived from pre-yield behaviour. Names giving the provenance of some of the more extreme specimens are shown. The arrow labelled 'increased mineralization' shows the general trend of mineralization. Note that because the axes are logarithmic, the scale cannot start at zero.

(table 1). All figures and regressions hereafter are on logarithmic scales and values, because the un-logarithmic relationships are somewhat curvilinear.

We have already shown, in figure 1, the relationship between the calcium content and the Young's modulus, for both notched and un-notched specimens. The distribution for the notched specimens (open circles) is essentially the same as for the un-notched specimens. This is to be hoped: equations (1) and (2) in table 2 are not significantly different; indeed they are very similar. There is therefore no indication that the notched specimens had a Young's modulus biased by being tested on deeper specimens. Also, table 2 shows that the relationship is nonlinear with the Young's modulus increasing as a power law function, the exponent being approximately 5.5. This effect may be somewhat affected by the cement (two notched values of which are hidden in figure 1 under nearly identically placed filled circles). Nevertheless, if cement is removed from the dataset the exponent for the power law exponent is reduced by only 0.1; to 5.4.

Figure 3 shows the relationship of energy absorption and calcium. The filled circles represent un-notched specimens, open circles notched. The antler specimens, both un-notched and notched, could not be fully broken in impact. They distorted into a bow but never broke. They are therefore neither shown in the figures nor included in the statistical analysis. Their *minimum* values for energy were, however, greater than those of any of the other specimens tested. This notch insensitivity of antler bone in impact is important, and will be discussed below. The figure shows two distributions, both approximately

Table 2. Linear regression equations for the various relationships.

(R^2 allows for the degrees of freedom. 'Slopes different?': F -value and associated probability for the analysis of covariance for difference in slope between equations (1) and (2), (3) and (4), and (5) and (6).)

dependent variable	constant	regression	R^2 (%)	p	slopes different?
(1) log E (notched)	-11.6	5.29 log Ca	64	< 0.0005	$F_{1,58} = 0.22$, n.s.
(2) log E (un-notched)	-12.6	5.71 log Ca	74	< 0.0005	
(3) log total energy (notched)	42.0	-17.2 log Ca	73	< 0.0005	$F_{1,58} = 13.8$, $p = 0.0005$
(4) log total energy (un-notched)	21.0	-8.15 log Ca	47	< 0.0005	
(5) log total energy (notched)	3.18	-2.18 log E	82	< 0.0005	$F_{1,58} = 21.0$, $p < 0.0005$
(6) log total energy (un-notched)	2.32	-0.83 log E	29	0.001	

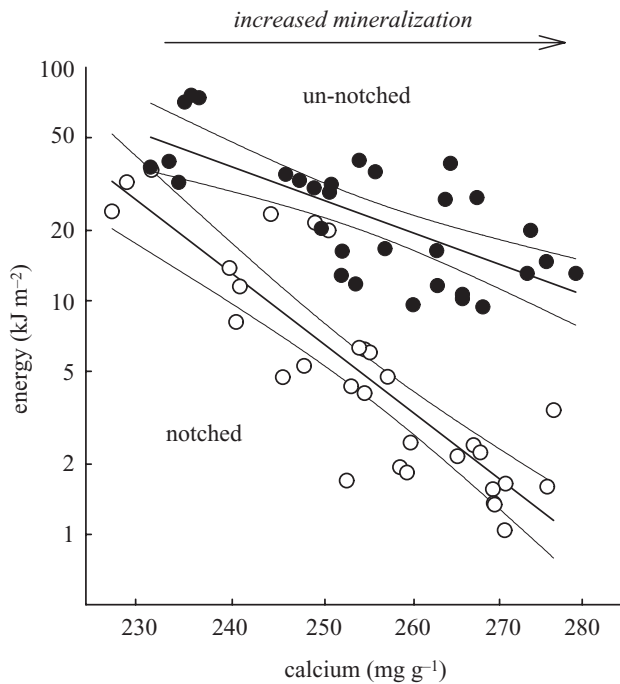


Figure 3. Relationship between total energy absorbed in impact and calcium content. The regression lines and their 95% confidence limits are shown. Note that because the axes are logarithmic, the scale cannot start at zero.

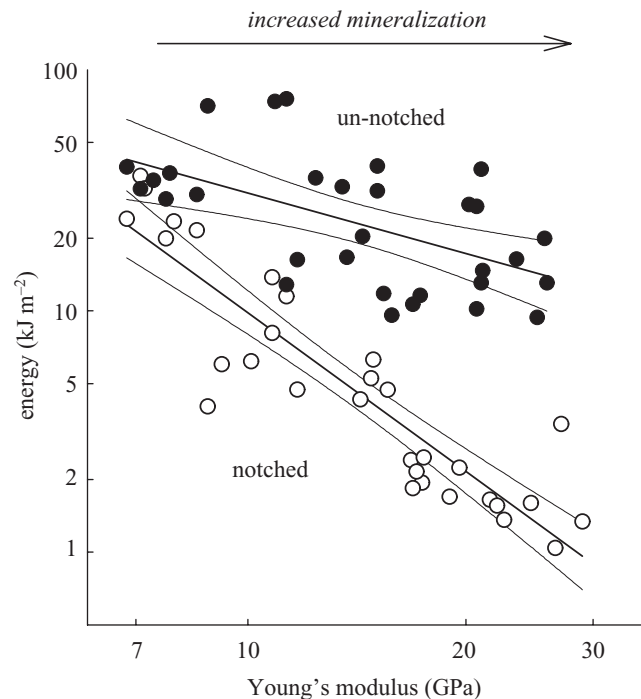


Figure 4. Relationship between total energy absorbed in impact and Young's modulus. The regression lines and their 95% confidence limits are shown. Note that because the axes are logarithmic, the scale cannot start at zero.

linear and highly significantly negative. They almost intermingle at low calcium values, but diverge at higher values, the un-notched specimens being apparently much less affected by an increase in calcium content. The regression equations are given in table 2 (equations (3) and (4)). Analysis of covariance (Snedecor & Cochran 1989) shows the slopes to be highly significantly different.

Figure 4 shows the relationship between energy absorption and Young's modulus. Since Young's modulus and mineral content are related, it is not surprising that the pattern is similar: at low Young's moduli, the notched and un-notched values are more intermingled. Again, the slopes are highly significantly negative and highly significantly different.

4. DISCUSSION

This paper deals with two interconnected issues: (i) the relationship between the Young's modulus, resilience, post-yield energy absorption, toughness and calcium content of bone-like tissues; and (ii) the effects of low calcium

content in producing tissues that achieve high failure strains and high levels of post-yield energy dissipation (shown to be due to extensive microcracking by Zioupos & Currey (1994)). This paper offers new data and examines the notch sensitivity behaviour of bone-like tissues, how it originates and what it may mean in adaptive terms.

The present work suffers from the minor limitation that, in order to test specimens with a large range of mineral contents, it was necessary to use specimens of different histological types. Antler and cement are rather unusual types of bony tissue, though not histologically particularly extreme. Narwhal cement has a low Young's modulus for its calcium content (figure 1) and the notched specimens absorb more energy, given their calcium content, than would be expected (figure 3, not explicitly labelled) though the un-notched specimens are unexceptional, so it has a rather low notch sensitivity. Its energy absorption as a function of Young's modulus is unexceptional. Dentine, though having a composition similar to that of bone, is histologically distinct. Nevertheless, if the results are considered to refer to 'mammalian mineralized tissues'

without regard to their origin, they are very striking and very consistent.

Whether one deals with 'simply brittle' or 'simply ductile' materials, their behaviour in the presence of a notch shows how tough these materials are. Conventionally the 'notch sensitivity' of a material refers to a reduction in the strength of specimens with different notch depths. A completely notch-insensitive material loaded in tension would show a reduction in strength equal only to the reduction in cross-sectional area, whereas a notch-sensitive material would show a disproportionate decline (Kelly & Macmillan 1986). For nonlinear materials in particular, the determination of notch sensitivity may be more complex (Purslow 1991) and may be related to the shape of the stress-strain curve. If we assume that the stress-strain characteristics observed macroscopically by testing whole specimens also apply at the microlevel in the vicinity of a notch then one can demonstrate (Appendix A) that stress-strain curves that are concave to the right, such as those seen in the toughest bone-like biological examples, produce a rapid stress reduction away from a notch and thus enhance the notch insensitivity of a material. This hints at a more profound relationship between three variables: nonlinear stress-strain characteristics, high amounts of post-yield energy dissipation and notch insensitivity (which is also indicative of toughness).

In the present article we define notch sensitivity (NS) in terms of its effect on the energy absorbed in impact, of notched specimens, given the same ligament depth:

$$NS = 100\% \times (1 - [\text{energy notched} \div \text{energy un-notched}]).$$

That is to say, if the specimen is completely brittle, the energy in the notched state is very small compared with that in the un-notched state, and the notch sensitivity approaches 100%. If notching has little effect, the notch sensitivity is close to zero. The notch sensitivity of mineralized tissues increases markedly with mineral content and with Young's modulus. According to the predictions of the equations in table 2, over the range of mineral contents of 230–275 mg g⁻¹ calcium, the notch sensitivity increased from 47% to 89%. Over the roughly equivalent range of Young's moduli, 7–25 GPa, the increase was from 48% to 91%. Furthermore, the antler specimens, which have the lowest mineral content, and which do not contribute to the regressions, are effectively notch insensitive. In the orientation that they and the other specimens were loaded, that is normal to the long axis of the fibres, the antler specimens could not be broken in impact, whether or not they were notched.

One could extrapolate the regressions slightly to lower values of calcium, to the point where the notched and un-notched specimens would have the same values for energy absorption. In reality, of course, this would be an improper exercise, both because one should never extrapolate regression lines beyond the data, and because to continue the linear regressions *beyond* the point at which they meet would produce the unreasonable outcome that notched specimens have higher energy absorptions than the un-notched ones. Despite all this, it is interesting that the lines meet at a calcium value of 214 mg g⁻¹, not far below the mean value for antler (224 mg g⁻¹).

The fact that the antler specimens could not be broken in impact under the conditions of the experiments does not, of course, mean that they never can be. In life, red deer antlers quite frequently break during fights (Clutton-Brock *et al.* 1979) though it is not clear whether this occurs during impact or during the pushing match that follows the original impact. The impact tests used here probably load the antler material in the optimum way, that is, normal to the grain of the tissue.

Nevertheless, if one can assume that notch sensitivity gives a good idea of toughness under service conditions, an interesting conclusion follows. Among mature tissues antler has the lowest mineral content known; there seem to be no mammalian mineralized tissues intermediate between antler and tendon. In general, in mineralized tissues, mineral content is associated positively with Young's modulus, but negatively with toughness. There is presumably no developmental reason why tissue more poorly mineralized than antler could not be produced. Even if antler bone *is* notch sensitive (and there are indications that in quasi-static loading it is), the fact that the antler specimens could not be fractured in impact even if notched means it is not possible to measure this sensitivity, and its value must be small. It appears probable therefore that antler bone is almost as tough in impact as it is possible to make mineralized tissue. Any reduction in mineral content would still further reduce Young's modulus, which in general is unadaptive, but would barely increase toughness. This may explain the gap in mineralization between that found in antler and the zero mineralization of tendon and similar collagenous tissues.

It would be extremely interesting to examine the toughness characteristics of mineralized tissues with less mineralization than antler, should any be discovered.

APPENDIX A

The work of Purslow (1991) and Mai & Atkins (1989) has established a broad equivalence between the nonlinear shape of the stress-strain curves of biological materials and the degree of notch sensitivity of such tissues. In general nonlinear elastic stress-strain curves can be expressed in a simple power law relationship as

$$(\text{stress}, \sigma) = (\text{elastic constant}, k)(\text{strain}, \epsilon)^n. \quad (\text{A } 1)$$

When $n < 1$ the formula gives rise to r-shaped curves as seen in the hard bone-like tissues of figure 5 and when $n > 1$ the formula produces j-shaped curves as seen in soft biological materials (skin, mesentery, aortas etc.).

In a sample of length l , breadth b and thickness h , with a starter crack a , where the stress at fracture σ_f and strain at fracture ϵ_f , the total strain energy over the sample volume V_0 not affected by the notch is

$$U = \left(\int_0^{\epsilon_f} \sigma d\epsilon \right) \times V_0. \quad (\text{A } 2)$$

Assuming that the area/volume affected by the notch is semicircular around the crack a , then

$$U = k \frac{\epsilon_f^{n+1}}{n+1} h \left(bl - \frac{\pi a^2}{2} \right). \quad (\text{A } 3)$$

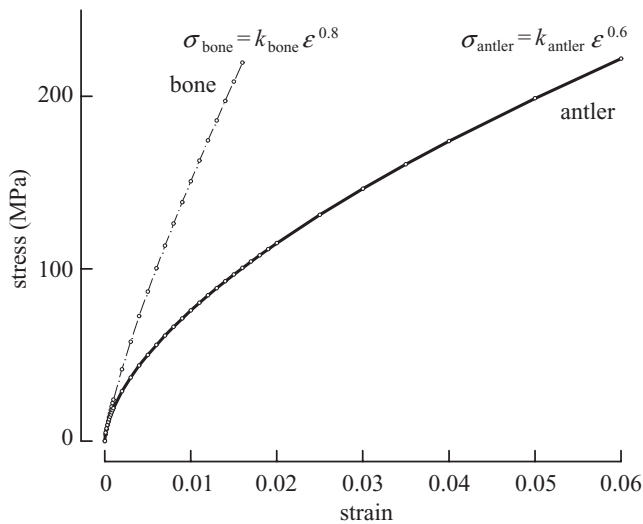


Figure 5. Nonlinear elastic stress–strain curves for normal bone and antler bone produced by using equation (A 1) and constants for bone: $k_{\text{bone}} = 6.0$ GPa, $n = 0.8$; and for antler: $k_{\text{antler}} = 1.2$ GPa, $n_{\text{antler}} = 0.6$.

Then toughness, in fixed grip configuration (constant displacement, u) is the energy release for a infinitesimally small cracked area ($A = ah$) growth:

$$R = - \left[\frac{dU}{dA} \right]_u = k \frac{\epsilon_f^{n+1}}{n+1} \pi a. \quad (\text{A } 4)$$

By using equation (A 1), equation (A 4) turns into

$$\sigma_f^{(n+1)/n} = \frac{R(n+1)}{k\pi a}, \quad (\text{A } 5)$$

and in a log–log form (taking R to be a material property constant),

$$\log \sigma_f = \left(\frac{n}{n+1} \right) \log \left(\frac{R(n+1)}{k\pi} \right) - \left(\frac{n}{n+1} \right) \log(a); \quad (\text{A } 6)$$

therefore, for the same increase in notch length a , the drop in failure stress σ_f increases as the value of n increases.

An example is shown in figure 5, where different exponents n were used to derive two different stress–strain curves for the semi-brittle bovine bone and for the tough antler bone. Tough bone-like tissues such as antler or dentine have lower strain exponents n , and drawn out curves. The previous analysis shows that in the hypothetical case of figure 5, a moderate increase of $n = 0.6$ to $n = 0.8$ increases the slope ($n/(n+1)$) and thus the notch sensitivity by 33%. However, this also means that for the same increase in notch size the failure stress $-\sigma_f$ in the case of the semi-brittle bovine bone decreases by the impressive amount of ca. 62%. This too compares well with the

differences between the extreme values produced by energy considerations alone shown in table 1.

REFERENCES

- Behiri, J. C. & Bonfield, W. 1980 Crack velocity dependence of longitudinal fracture in bone. *J. Mater. Sci.* **15**, 1841–1849.
- Carter, D. R. & Caler, W. E. 1983 Cycle-dependent and time-dependent bone fracture with repeated loading. *J. Biomech. Engng* **105**, 166–170.
- Clutton-Brock, T. H., Albon, S. D., Gibson, R. M. & Guinness, F. E. 1979 The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). *Anim. Behav.* **27**, 211–225.
- Currey, J. D. 1979 Changes in the impact energy absorption of bone with age. *J. Biomech.* **12**, 459–469.
- Currey, J. D. 1999 What determines the bending strength of bone? *J. Exp. Biol.* **202**, 2495–2503.
- Currey, J. D. 2004 Tensile yield in compact bone is determined by strain, post-yield behaviour by mineral content. *J. Biomech.* **37**. (In the press.)
- Currey, J. D. & Butler, G. 1975 The mechanical properties of bone tissue in children. *J. Bone Joint Surg.* **A 57**, 810–814.
- Currey, J. D., Brear, K. & Zioupos, P. 1996 The effects of ageing and changes in mineral content in degrading the toughness of human femora. *J. Biomech.* **29**, 257–260.
- Kelly, A. & Macmillan, N. H. 1986 *Strong solids*. Oxford: Clarendon Press.
- Lees, S., Hanson, D. B. & Page, E. A. 1996 Some acoustical properties of the otic bone of a fin whale. *J. Acoust. Soc. Am.* **99**, 2421–2427.
- Les, C. M., Stover, S. M., Keyak, J. H., Taylor, K. T. & Kaneps, A. J. 2002 Stiff and strong compressive properties are associated with brittle post-yield behavior in equine compact bone material. *J. Orthop. Res.* **20**, 607–614.
- Mai, Y. W. & Atkins, A. G. 1989 Further comments on J-shaped stress–strain curves and the crack resistance of biological materials. *J. Phys.* **D 22**, 48–54.
- Purslow, P. 1991 Notch-sensitivity of non-linear materials. *J. Mater. Sci.* **26**, 4468–4476.
- Sarkhar, B. C. & Chauhan, U. P. S. 1967 A new method for determining micro quantities of calcium in biological tissues. *Anal. Biochem.* **29**, 155–156.
- Snedecor, G. W. & Cochran, W. G. 1989 *Statistical methods*. Ames, IA: Iowa State University Press.
- Spatz, H. C., O’Leary, E. J. & Vincent, J. F. V. 1996 Young’s moduli and shear moduli in cortical bone. *Proc. R. Soc. Lond.* **B 263**, 287–294.
- Zioupos, P. 1998 Recent developments in the study of failure of solid biomaterials and bone: ‘fracture’ and ‘pre-fracture’ toughness. *Mater. Sci. Engng C* **6**, 33–40.
- Zioupos, P. & Currey, J. D. 1994 The extent of microcracking and the morphology of microcracks in damaged bone. *J. Mater. Sci.* **29**, 978–986.
- Zioupos, P. & Currey, J. D. 1996 Pre-failure toughening mechanisms in the dentine of the Narwhal tusk: microscopic examination of stress/strain induced microcracking. *J. Mater. Sci. Lett.* **15**, 991–994.
- Zioupos, P., Currey, J. D., Casinos, A. & De Buffrénil, V. 1997 Mechanical properties of the rostrum of the whale *Mesoplodon densirostris*, a remarkably dense bony tissue. *J. Zool. Lond.* **241**, 725–737.