

ANELASTICITY IN BONE AND ECHINODERM SKELETONS

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INTRODUCTION

A considerable amount of work has been done on some of the mechanical properties of bone. Chief among these are its strength (Evans, 1957) and its modulus of elasticity (Dempster & Liddicoat, 1952). Most of the strength tests have been static, but some work has been done on the dynamic and fatigue strength of bone (Evans, Lissner & Lebow, 1958; Lease & Evans, 1959). However, it cannot be said that we know a great deal about these latter properties at the moment.

In contrast to bone, in which the organic component is about one-third by weight, the skeleton of echinoderms is made of relatively large crystals of dolomite (calcium and magnesium carbonate) with very little, if any, organic component within the skeletal matrix itself, although all the skeletal elements are in the form of a three-dimensional network with soft tissues filling the spaces. It would be interesting to compare bone and echinoderm skeleton, particularly their mechanical properties, to see how such very different materials are adapted to their particular functions. Unfortunately almost nothing is known about the mechanical properties of echinoderm skeletons. Part of the reason for this is that the skeletal elements are so irregular in shape and usually so small that it is difficult to prepare specimens for testing. There is, however, one property, anelasticity, that is reasonably simple to study, both in echinoderm skeletons and bone, because its determination does not depend on precise knowledge of the dimensions of the test-piece, and which, because of the nature of the different materials, would be likely to be different in the skeletons of the two groups.

Anelasticity is a recoverable strain appearing over a period of time. Most materials show this phenomenon, though often only to a slight extent. The final strain occurring in steel may, after a few months of loading, be about 30% greater than the initial strain (Lubahn & Felgar, 1961). On loading, these substances show an immediate strain; as time passes further strain is observed, the rate of appearance of strain falling with time. On unloading, the material immediately loses the strain that appeared initially, but the extra, *anelastic* strain remains, although it starts to disappear at once, which it does at an ever-decreasing rate. Considerable anelasticity is typically shown by materials in which there are networks of 'flabby' molecules held together by bonds with a large range of stabilities. Under stress the less stable bonds break, through thermal agitation and the applied stress, and re-form 'downstream'. Endless flow is prevented by the holding firm of the more stable bonds (Alfrey, 1948).

Bone, having a large amount of fibrous protein, probably held together to a large extent by hydrogen bonding, is a substance that might be expected to show anelasticity. On the other hand echinoderm skeleton, being composed of few, large crystals, would not be expected to show such effects, certainly not to the same extent as bone.

If the anelasticity of bone produced large strains, it might be necessary for bones to be larger and heavier than they would be otherwise. An effective reduction in the stiffness of the bone, which is what is entailed by the phenomenon of anelasticity, does not in itself lead directly to a loss of strength, but if the bone is loaded as a column, and is at all slender, the load at which it will fail is a linear function of the stiffness (Singer, 1962), and so stiffness is, in some circumstances, of more importance than strength. Anelasticity or the lack of it might be an important biological difference between the two types of skeleton.

Smith & Walmsley (1959) reported that bone showed elastic after-effect (i.e. anelasticity). They said that the final anelastic strain was sometimes as great as 10% of the initial anelastic strain.

The purposes of the present investigation were: (a) to determine the anelastic behaviour of bone and echinoderm spines; (b) to investigate whether such behaviour is of biological importance.

MATERIALS AND METHODS

(a) Bone

The test-pieces were machined from the tibiae and metacarpal bones of cattle. The metacarpals were taken from the slaughterhouse a few hours after death. The tibiae were obtained from a butcher. They had not been frozen, and were presumably 2 or 3 days *post mortem*. During machining the test-pieces were kept moist, and care was taken to see that they never became hot.

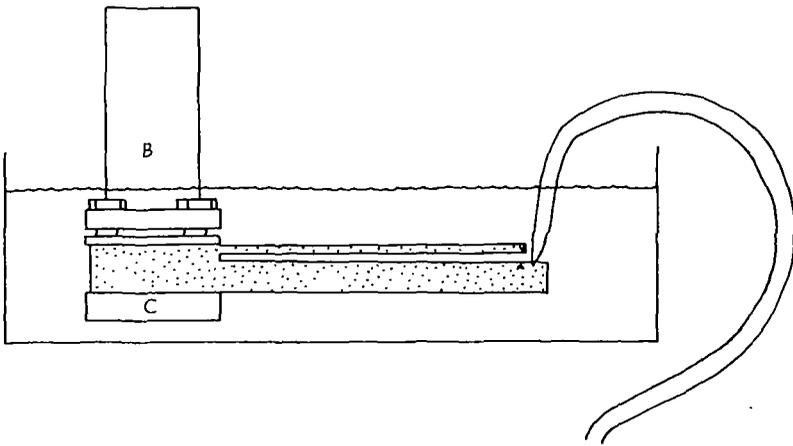


Fig. 1. Diagram of the loading apparatus. The bone test-piece, stippled, is held in a clamp C, attached to a bracket B, which is itself attached rigidly to a bench. The bone is loaded by a swan-necked hook. The support for the water-bath is not shown.

The pieces were loaded as cantilevers, divided along the free portion horizontally with only the lower portion loaded (Fig. 1). The cantilever was loaded by means of a weight attached to a swan-necked hook, the upper end of which was filed into a knife-edge and inserted into a groove cut in the cantilever. Reference marks were made on the loaded and unloaded parts of the cantilever, and the deflexion on the loaded part was determined by measuring, with a Baker travelling microscope,

variations in the vertical distances between these marks. This enabled any deflexion or rotation of the support when the bone was loaded to be discounted, since it would effect the loaded and the unloaded portions equally.

The mechanical properties of wet bone differ considerably from those of dry bone (Evans, 1957). Therefore in these experiments the bone was immersed in a bath of physiological saline. Fungal and bacterial attack were prevented by putting a crystal of thymol in the water. The properties of the test-pieces seemed not to vary with time of immersion, so it is to be supposed that the thymol is effective. The cells in the bone would, of course, have died very quickly, but there is much evidence that bone protected from bacterial attack is very stable, and indeed collagen can survive for hundreds of millions of years (Isaacs, Little, Currey & Tarlo, 1963). Because of the danger of corrosion of pumps the tests at elevated temperatures had to be performed in tap-water, not physiological saline. Some tests were performed to compare the effects of the bathing solutions. No significant or consistent differences were found either in the modulus of elasticity or the anelasticity when the same piece of bone was immersed in these different fluids.

The test-pieces were loaded so that the plane of bending would be tangential to the curvature of the shaft wall of the long bone from which the pieces were taken. Care was taken to see that the bones were not loaded into the plastic range, about 10,000 p.s.i. Except where stated to the contrary the tests took place at room temperature, which varied from about 12 to 19° C.

The shortest practicable time in which careful measurements can be made using the apparatus described above is 2 min. Therefore I shall call the strain after 2 min. the immediate strain although, of course, anelastic strain could be appearing during the first 2 min. In these experiments no strains are measured directly, only deflexions, but since the deflexions are small they will be proportional to the strains in the test-pieces.

(b) *Echinoderm spines*

The large spines of the echinoid genus *Heterocentrotus* were used. These spines are about 70–100 mm. long, and sufficiently large to be capable of being divided down most of their length in a way similar to the bone specimens. As living specimens of this tropical genus were not available the spines were taken from dried specimens. The base of each spine was embedded in an epoxy resin, and the spine and resin were immersed in sea water for 24 hr. The spine was then clamped in the same way and loaded in the same way as the bone specimens. The spine was loaded in sea water, which was at a temperature of about 16° C.

EXPERIMENTS AND RESULTS

Bone

If a piece of material is loaded for a long time and shows an extra deflexion beyond the initial one. there are in general three things that could have brought this about: (a) irrecoverable plastic flow; (b) a decrease in the stiffness of the material; (c) anelasticity. These effects could, of course, be all present together. If the extra deflexion is produced solely by plastic flow, then the piece would show a permanent set when the load is removed. If the extra deflexion is caused solely by a decrease in stiffness of the material, then the piece will immediately recover *all* the extra deflexion.

If, therefore, we wish to exclude the first two possibilities, we must show that all the deflexion is recoverable, that on unloading the bone will immediately recover the initial deflexion, but not the extra deflexion, and that the elastic properties are unaltered.

Tests were first performed on two test-pieces to see whether immersion in physiological saline for a period of 4 days had an effect on the modulus of elasticity. No large or consistent changes were found. This finding was confirmed by all later work.

Demonstration of anelasticity

A test-piece from a tibia was loaded for a long time (10 days) to see whether any extra deflexion occurred. The immediate deflexion was 1.66 mm. At the end of 10 days it was 2.20 mm., an increase of 33% over the original deflexion. The load was then removed. After 2 min. the residual deflexion was 0.55 mm. This is in good

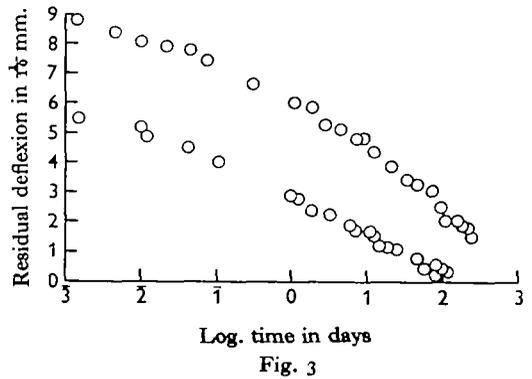
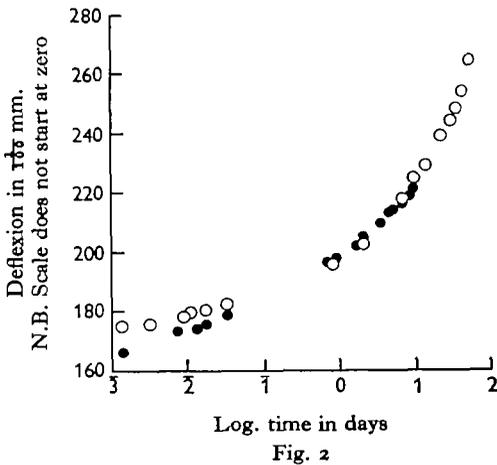


Fig. 2. Deflexion/time curves for the same piece of bone as in Fig. 1, loaded twice at room temperature. ●, First experiment; ○, second experiment.

Fig. 3. Relaxation curves for the same piece of bone as in Fig. 1, loaded twice at room temperature. The lower line of circles refers to the first experiment, the upper line to the second.

agreement with the extra deflexion that had occurred between the first loading and the time when the load was removed (0.54 mm.). The residual deflexion then started to disappear approximately exponentially; when plotted against log. time a fairly straight line is obtained (Fig. 3). However, after about 60 days the curve became irregular. At 100 days the residual deflexion was 0.04 mm., approximately 8% of the extra deflexion. There is no reason for supposing that even this small residual deflexion might not eventually have disappeared. This experiment indicated, therefore, that at least a very large part of the extra deflexion appearing on prolonged loading is recoverable, and that the total extra deflexion could be more than 30% of the original deflexion.

The experiment was repeated on the same piece of bone. Fig. 2 shows that there was good agreement between the two loading curves, the maximum difference in the deflexions being only 5% initially, and becoming almost nothing later. The loading in this experiment was continued for 55 days. In this time extra deflexion had become

53% of the initial deflexion. When the load was removed the residual deflexion after 2 min. was 0.89 mm., which is close to the extra deflexion, 0.92 mm. The residual deflexion after 234 days was 0.15 mm., 17% of the residual deflexion after 2 min. Although, as can be seen from the form of the recovery curve after 10 days' loading, it is probable that little of the residual deflexion is irrecoverable, the time required for full recovery would be very great.

It is clear from these results that at least the greater part of the considerable extra deflexion caused by prolonged loading is indeed true anelasticity, and is not plastic flow nor is it caused by a change in the elastic properties of the bone. It is striking what little effect prolonged immersion *in vitro* has on the stiffness of the bone. It can also be seen that the total amount of extra deflexion is much greater than the 10% or so reported by Smith & Walmsley, who observed the deflexion for only about half an hour. The extra deflexion after the immediate deflexion will be called 'anelastic' from now on in this paper, although it is probable that there is a very small plastic component.

The effect of drying on the anelasticity of bone

The mechanical behaviour of dry bone is different from that of wet bone (Evans, 1957). Amprino (1958), however, has shown that, in respect of hardness at least, the change is reversible. The following experiments were performed to see to what extent anelastic behaviour differs in wet and dry bone.

A test-piece of metatarsal was loaded wet until the anelastic deflexion was 10% of the immediate deflexion. It was then unloaded and allowed to recover nearly all its anelastic deflexion, dried at room temperature for a week, and again loaded with the same weight. The whole process was then repeated. Fig. 4 shows the loading curves,

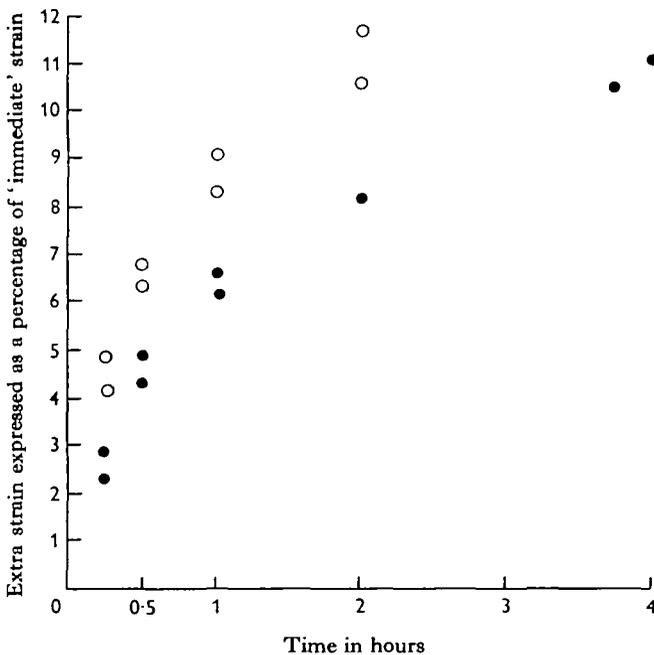


Fig. 4. Deflexion/time curves for the same piece of bone as in Fig. 1, loaded twice wet and twice dry with the same weight. O, Wet loading; ●, dry loading.

with the anelastic deflexion expressed as a percentage of the original deflexion. The two curves for dry bone are very similar, and the two curves for wet loading are also quite similar. The curves for wet and dry bone are, however, very different. These results show that drying out does not have a very marked irreversible effect on the anelastic behaviour of bone.

Proportionality to load

It is important for two reasons to test whether the anelastic phenomena of bone are proportional to load. First, the nature of the molecular processes producing anelasticity make this proportionality very likely (Alfrey, 1948), and if bone did not show this proportionality it would be necessary to consider whether it was behaving differently from other anelastic materials. Secondly, if anelasticity became disproportionately greater with increased stress, then its biological importance would be greatest near to the elastic limit. For obvious reasons the tests performed in this paper were carried out well below the elastic limit, and therefore any extrapolations from observed behaviour to behaviour near the elastic limit would be suspect if anelasticity increased disproportionately with stress.

A single specimen was loaded with weights of 0.5, 1.0, 1.5 and 2.0 kg. (called hereafter A, B, C, and D) three times. The piece was loaded with a weight, the immediate deflexion and the deflexion after 4 hr. were measured, the piece was unloaded for 2 days and then loaded with another weight. The gap of 2 days was to allow the major part of the anelastic strain to disappear. The order of the application of the weights was A B C D D C B A D C B A.

The initial deflexions showed extremely good proportionality to load. The anelastic deflexions were, in millimetres:

| | | Weight | | | |
|------|--|--------|-------|-------|-------|
| | | A | B | C | D |
| | | 0.04 | 0.10 | 0.12 | 0.14 |
| | | 0.04 | 0.04 | 0.09 | 0.10 |
| | | 0.03 | 0.08 | 0.10 | 0.16 |
| Mean | | 0.037 | 0.073 | 0.103 | 0.133 |

Although there is a fair amount of spread in the deflexions, the means show a good approximation to the expected proportionality.

It is probable therefore that anelastic deflexions appear at a rate proportional to the stress, and that no special mechanism must be invoked for bone. Tests performed at fairly low loads are probably applicable to the situation at stresses near the elastic limit.

The effects of temperature

All the experiments described so far were carried out at room temperature, which varied from 12 to 19° C. In the following experiments a greater range of controlled temperatures was employed. The temperature of the water was controlled thermostatically; in the short-term experiments it never varied by more than 1° C., but in the longer experiments the temperature did vary occasionally by a few degrees, but never for very long.

In the first experiments the effects of different temperatures on the anelasticity and

elasticity of one piece of bone were determined. The bone was loaded with the same weight ten times. It was loaded, and the immediate deflexion and the deflexion after 2 hr. were measured. The temperatures at which the bone was loaded, and their order were, in degrees centigrade: 37, 18, 37, 16, 3, 49.5, 2.5, 50, 19 and 48. After loading, the bone was subjected to reversed loading for a short time to reduce quickly part of the anelastic strain, and was then allowed to recover for a day at room temperature.

The results are shown in Figs. 5 and 6. Both the elastic and the anelastic deflexion increase with temperature. Smith & Walmsley (1959) reported that the elastic strain varied approximately linearly between 9 and 43° C., and that the increase was about 0.51% per degree. The present results give a figure of approximately 0.4% per degree. The difference in slope is probably not important, considering the different conditions of the experiments. The anelastic deflexion does not increase linearly with temperature, but increases more at higher temperatures. This is also true of the 'immediate' deflexion, but it is possible that the deflexion appearing immediately on

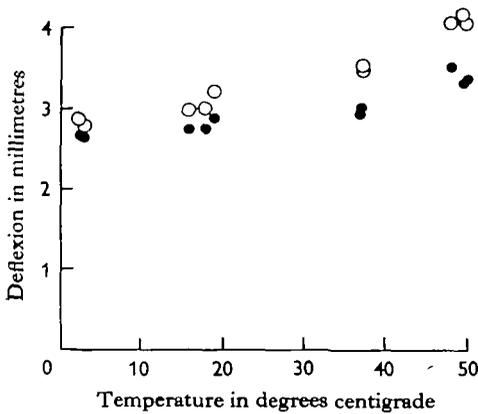


Fig. 5

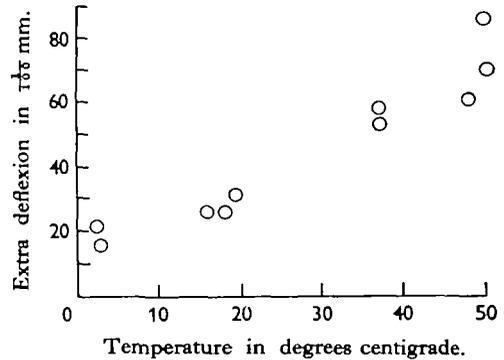


Fig. 6

Fig. 5. Deflexion/temperature experiments. ●, 'Immediate' deflexion; ○, deflexion at the end of 2 hr.

Fig. 6. Deflexion/temperature experiments. ○, The extra deflexion after 2 hr. loading at various temperatures.

loading does vary linearly with temperature, and that the non-linear component is caused by unmeasured anelastic deflexion appearing within the first 2 min.

The increase in immediate deflexion between 3 and 49° is about 24%, while the corresponding increase for the anelastic deflexion is about 300%. The increase in anelastic deflexion between room temperature (16–18° C.) and blood heat is about 100%. Because these experiments were carried out on the same piece of bone they are open to the objection that during all experiments after the first one the bone was still recovering from the previous experiments, which would confuse the situation. However, this effect is unlikely to be important, because the amount of recovery occurring between 24 and 26 hr. after unloading is very small compared with the amount of anelastic deflexion appearing in the first 2 hr. of loading. Certainly there was no evidence from the data that the later experiments showed consistently lower values for the anelastic deflexion than the earlier ones. Rigby, Hirai, Spikes & Eyring (1959) report that the anelastic behaviour of collagen changes markedly at about

40° C., and that much of the strain appearing at this temperature and above it is irreversible. No such irreversible effect was found with bone at temperatures of about 49° C.

It is clear that anelasticity in bone is to a large extent a function of temperature. What does not emerge from these experiments is whether the effect of raising the temperature is to increase the rate at which the final equilibrium (if such exists) is approached, or whether the strain at equilibrium is itself increased. The following experiment shows that it may in practice be exceedingly difficult to get any idea of the equilibrium value at which anelastic movement ceases.

A test-piece was loaded at 37° C. The initial deflexion was 2.53 mm. At the end of 54 days the deflexion had increased to 5.99 mm., an increase of 136%. The plot of strain against log. time showed no sign of having reached the point of inflexion as would be expected if equilibrium was being approached (Fig. 7). Probably therefore the final deflexion at equilibrium could be at least twice the observed deflexion, if it were all recoverable. If, on the other hand, the strain were partly plastic, the bone would

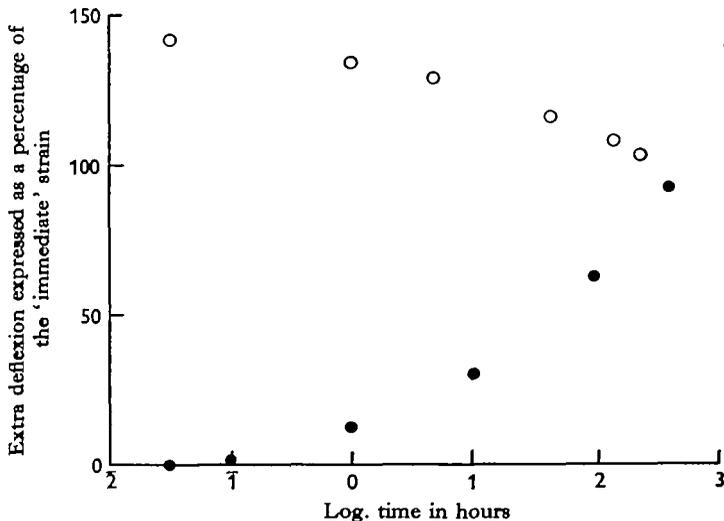


Fig. 7. Long loading at 37° C. ●, Loading curve; ○, relaxation curve.

continue to bend until it broke. The experiment was discontinued in order to see whether the observed extra deflexion was all recoverable, and a longer loading time would have made the recovery time many years. The recovery curve, as far as it went, indicated that at least a considerable part of this very large deflexion might have been recoverable. Unfortunately the experiment had to be stopped when the thermostat broke and the bone dried.

A further experiment on a different test-piece was performed at 37° C. On this occasion the bone was loaded for only 24 hr. (Fig. 8). The extra deflexion, expressed as a percentage of the immediate deflexion, appeared rather more rapidly in this experiment than in the previous one. At the end of a day the extra deflexion was 40.6% of the original deflexion. The recovery curve shows that after 79 days, when the experiment was stopped, 92% of the extra deflexion had been recovered, and presumably after a very long time nearly all of it would disappear.

The experiments at elevated temperatures show that the magnitude of the anelastic effects alters very much with temperature. However, the deflexions are probably all recoverable as at low temperatures, and it is probable that the experiments carried out at room temperature showing that anelastic effects are proportional to load are also applicable to higher temperatures.

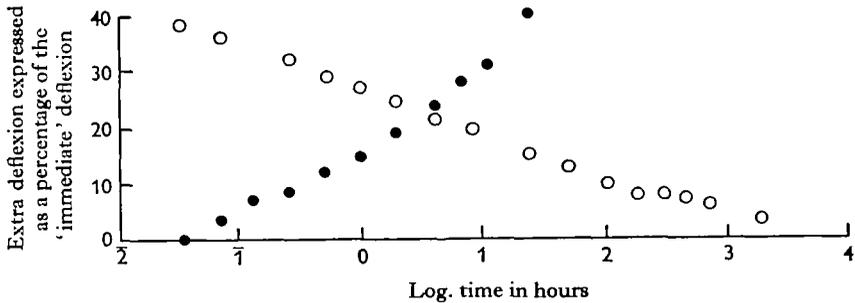


Fig. 8. Loading for 24 hr. at 37° C. ●, Loading curve; ○, relaxation curve.

The biological significance of anelasticity in bone

The experiments described above give some idea of the magnitude of anelastic effects on bone, and of the factors that are likely to affect them. It remains to be discussed whether effects of this magnitude will be of importance in the life of vertebrates.

1. *Impact.* At the moment virtually nothing is known about the resistance of bone to impacts. To a large extent the ability of materials to resist impact is inversely proportional to the modulus of elasticity, because the energy that can be absorbed is proportional to the reciprocal of the stiffness. Calculations of the impact-resisting properties of bone are likely to be seriously in error if the modulus of elasticity is taken to be that derived from the 'immediate' strain. For, if bone shows anelastic effects over several minutes, it is possible that the modulus of elasticity calculated from the strain observed after a second or even less after loading may be considerably too low if the effective modulus of elasticity is that obtaining during the first few milliseconds. In other words, it is possible that bone is very stiff indeed for a very short period of time, but that it quickly starts to show a reversible further strain. This is by no means certain, but it does point to the need for investigations into the impact properties of bone by experiment, rather than by theory.

2. *Static loading.* Birds that roost on one leg, flamingos for instance, may do so for many hours. The slenderness of the leg of a bird would certainly make it behave as a slender column, and so its strength in compression would not be determined by the strength of bone in compression, but by its modulus of elasticity. Therefore anelasticity, since it effectively reduced the modulus of elasticity with time, would in effect reduce the strength of legs loaded in this way. However, in cases such as this the load acting over a long period of time cannot be greater than the animal's weight. But the limb bones must be built to have a safety factor to resist at least modest dynamic loads, and these will be of much greater danger to the bone than the bird's own weight acting statically. If therefore a flamingo did nothing but stand on its slender legs roosting, the design of the legs would have to include a safety factor for anelasticity. However, the

stresses imposed on the leg during walking, take-off and landing will be so much greater than those imposed simply by the static weight of the animal that safety factors allowing for the former activities would necessarily include the latter. In general it can probably be safely concluded that the anelastic behaviour of bone under static loading is probably never significant in determining the design of the bone.

3. *Cyclical loading.* If a bone is loaded cyclically and symmetrically about zero stress, then (apart from hysteresis effects) each half-cycle will cancel the effects of the previous half-cycle. If, however, the loading is asymmetrical, in regard either to time or the amount of loading, then the effects of anelasticity must be considered. In life a common stress régime is one in which a stress varies from zero to some positive stress to zero again, cyclically. Such a stress will be borne, for instance, by the metapodial bones of ungulates and wolves when running, and by the arm bones of migratory birds. The number of cycles performed without rest may be very great, probably hundreds of thousands in the case of some migratory birds.

The strain occurring because of anelasticity in a material can be described by a polynomial of the form:

$$\frac{S}{a_1}(1 - e^{-t/T_1}) + \frac{S}{a_2}(1 - e^{-t/T_2}) \dots + \frac{S}{a_n}(1 - e^{-t/T_n}),$$

where S is the stress, t is the time of application of the load, a is a constant and T is a relaxation time (the time needed to reach $1/e$ of the equilibrium strain) (Lubahn & Felgar, 1961). There are in fact an infinite number of corresponding values of a and T , but the behaviour of many metals, for example, is for practical purposes adequately described by about six terms with t varying by six orders of magnitude. Probably the same would be found to be true of bone if sufficient tests were performed. The relaxation times of interest here are those that are long compared to the length of the cycle—those in respect of which the bone will be far from equilibrium after it has been stressed for about a second or less.

Boltzmann's superposition principle is applicable here. It states that the final strain after a series of loadings and unloadings is the strain that would remain if the whole series of *changes* of stress were considered to be acting from the moment they were applied. Let us suppose that a load S is applied for a time t , which is short in relation to T (for simplicity only one value of T will be considered), and is then removed. After a further time t' the residual strain will be

$$\frac{S}{a}(1 - e^{-(t+t')/T}) - \frac{S}{a}(1 - e^{-t'/T}).$$

As t' becomes very large with respect to t the difference between $e^{-t'/T}$ and $e^{-(t+t')/T}$ will become very small, but in theory there will always be a small residual strain caused by the initial loading. One can show (Appendix) that if an anelastic material is subjected to an infinite series of loadings and unloadings of equal length, then the strain will approach half what would have been obtained had the material been loaded continuously. If the loading part of the cycle is shorter than the unloading part then the final strain will be reduced correspondingly, but will not disappear.

It is therefore possible to arrive at quite large anelastic strains after repeated loading and unloading. Furthermore, in life the maximum stress may be a large one, unlike

the situation in which a static load is applied for a long time. In the last experiment described above an anelastic deflexion of 20% of the original deflexion was reached after 2 hr. If the bone had been subjected to intermittent loading, the deflexion would have been a little less than 10%. (How much less than 10% would depend on the exact form of the stress relaxation curve.)

It would seem, then, that under natural régimes of cyclical loading anelastic strains of a magnitude that could make them biologically significant could occur, especially in bones loaded as columns. However, these large strains would appear only after a considerable time. The majority of strains in continuously swimming fish are completely reversed every cycle, but compressive stresses in the vertebra are likely to be cyclical but not reversed. Here, however, the strains involved are so small that they can be ignored.

From the considerations given above it seems unlikely that anelastic strains can often be important in bones in nature, although, for instance, they may perhaps influence very slightly the design of long bones of wolves, and the arm bones of migratory birds may perhaps be a little more bulky because of the phenomenon of anelasticity than they would be otherwise.

Echinoderm spines

Two spines were tested. The initial deflexion in the first specimen was 0.24 mm. and remained at this or 0.23 mm. for the next 26 hr. On removal of the load the residual deflexion was -0.01 mm. and remained at this for the succeeding hour. Within the limits of the accuracy of the observations (about 0.01 mm. each way) there was no anelasticity. Bones tested at this temperature for 26 hr. would have shown an anelastic deflexion of about 0.04 mm., which would certainly have been measurable.

A second experiment with a longer spine was performed in order to increase the sensitivity of the experiment. The initial deflexion was 1.13 mm. At the end of 24 hr. the deflexion was apparently 1.12 mm. When the load was removed the residual deflexion was -0.01 mm. Again, therefore, there was no change within the limits of accuracy of the observations. Bones, similarly treated, would have shown an anelastic deflexion of about 0.20 mm.

There is no evidence from these experiments that echinoderm spines show any anelasticity at all at temperatures that are biologically meaningful. Unfortunately the spines used were not fresh, and so there is the slight possibility that, had there been fresh tissue within the spine, it would in some way have permitted anelasticity to be shown. But it seems likely that the dolomitic material of the spines does not contain any organic component between the crystals (Raup, 1959, 1962).

The known organic material in spines is the living tissue within the mesh of the spine. This could hardly convert the elastic behaviour of the dolomitic part of the spine into anelastic behaviour of the spine as a whole except by virtue of its own anelasticity. But the modulus of elasticity of the living components must be at least two orders of magnitude lower than that of the dolomite, and therefore their effect can be ignored.

As echinoderm spines show no anelasticity, it is clear that it can have no biological significance within them. It is reasonable to suppose that the other skeletal elements in echinoderms would behave in the same way as the spines, since they are built on the same general plan and made of the same material.

DISCUSSION

The anelastic properties of bone and echinoderm skeleton are what would be expected from a knowledge of their constitution. The anelasticity of bone is presumably caused by the reorientation of the organic components and the migration of water under stress. Not a great deal is known about the anelastic properties of collagen. Rigby *et al.* (1959) show that stress relaxation still occurs in rat tail tendon up to 24 hr. after the load is applied, but it is uncertain how much of this strain is recoverable; some of it certainly is, but some at least is not. Harkness & Harkness (1959) show that the non-pregnant uterus of the rat shows anelasticity, and this is approximately linear with time. However, they continued loading for only 2 hr., so it is not known how much strain would have occurred.

Not all natural long-chain polymers used as skeletal elements show anelasticity. Weis-Fogh (1960) has shown that resilin, a rubbery protein found in insects and other arthropods, shows no measurable anelasticity at all. This is probably brought about by the very precise arrangements of the cross-links between the constituent molecules. There are several uses to which resilin is put that would make anelasticity disadvantageous (Jensen & Weis-Fogh, 1962), and it is clear that this lack of anelasticity is adaptive. Chief amongst these uses is that in which resilin forms a hinge at the base of the wings to store the kinetic energy of the wings as strain energy so that the wing muscles do not have to decelerate the wings as well as accelerating them. Anelasticity would lead to the loss of some of the stored energy as heat. Analogous energy losses would seem not to be important in bone because the elasticity of bone is not used for storing energy except in very exceptional circumstances.

The anelasticity of bone is imposed on it by its construction. I have argued elsewhere (Currey, 1962, 1964) that the combination of collagen and apatite in bone is highly adaptive, producing a material stronger than either of the components are alone. The fact that this composition necessarily produces anelasticity has been shown in this paper to be of only marginal biological significance. Attempts to understand the adaptive significance of the differences between bone and echinoderm skeletons must, then, involve consideration of other differences between the two skeletal types—probably their strength, their moduli of elasticity and their metabolic activity.

SUMMARY

1. Bones and echinoderm skeletons have been tested for anelasticity.
2. Bone shows considerable, largely anelastic strains, continuing for at least 54 days, by which time the extra deflexion may be 130% of the original deflexion. The rate at which the anelastic deflexion appears is proportional to the applied stress.
3. Between 2 and 50° C. there is a 300% increase in the rate at which anelastic deflexions in bones appear. Drying seems not to affect irreversibly the anelastic properties of bone.
4. Echinoderm spines show no anelastic deflexion on prolonged loading.
5. The mechanical behaviour of the skeletal materials of the two phyla investigated are such as would be expected from their constitution.
6. The biological significance of these findings is discussed. It is concluded that

anelasticity will, except perhaps in a few special cases, be of only marginal importance in vertebrates in life.

7. The adaptive significance of the difference between bone and the skeletal tissue of echinoderms is as yet unknown. It does not lie in their anelastic properties.

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APPENDIX

The effect of intermittent loading

The total strain ϵ is given by a series of terms of the general form $(S/a)(1 - e^{-t/T})$, where S is the stress applied for a time t , T is a relaxation time, and a is a constant. If the stress is applied for a time t and then released for a time t , then the strain at the end of time $2t$ is

$$\epsilon(2) = (S/a)(1 - e^{-2t/T}) - (S/a)(1 - e^{-t/T}).$$

For $n/2$ loadings and $n/2$ unloadings, i.e. at the end of time nt , the strain is given by

$$\begin{aligned} \epsilon(n) &= (S/a)(1 - e^{-nt/T}) - (S/a)(1 - e^{-(n-1)t/T}) \dots + \dots - (S/a)(1 - e^{-t/T}) \\ &= (S/a) \left[\sum_{k=1}^{\frac{1}{2}n} e^{-(2K-1)t/T} - \sum_{k=1}^{\frac{1}{2}n} e^{-2Kt/T} \right]. \end{aligned}$$

The sum up to the p th term of a geometric series,

$$a + ax + ax^2 + \dots + ax^{p-1} = \sum_{r=1}^p ax^{r-1} = S_p$$

is given by

$$S_p = \frac{a(1-x^p)}{1-x}$$

For the series

$$\sum_{k=1}^{\frac{1}{2}n} e^{-(2k-1)t/T},$$

$$a = e^{-t/T}, \quad x = e^{-2t/T}.$$

Therefore

$$S_{\frac{1}{2}n} = \frac{e^{-t/T}(1-e^{-n t/T})}{1-e^{-2t/T}}.$$

Similarly the series

$$\sum_{k=1}^{\frac{1}{2}n} e^{-2kt/T},$$

$$S_{\frac{1}{2}n} = \frac{e^{-2t/T}(1-e^{-n t/T})}{1-e^{-2t/T}}.$$

Therefore

$$\begin{aligned} \epsilon(n) &= (S/a) \left[\frac{e^{-t/T}(1-e^{-n t/T})}{1-e^{-2t/T}} - \frac{e^{-2t/T}(1-e^{-n t/T})}{1-e^{-2t/T}} \right] \\ &= (S/a) \left[\frac{1-e^{-n t/T}}{1+e^{t/T}} \right] \quad (n \text{ always even}). \end{aligned}$$

In the limit

$$\lim_{n \rightarrow \infty} \epsilon(n) = (S/a) \left[\frac{1}{1+e^{t/T}} \right].$$

If t/T is very small, $e^{t/T} \simeq 1$. Therefore

$$\lim_{n \rightarrow \infty} \epsilon(n) \simeq \frac{S}{2a}.$$