

## Chapter 1

# The Shape of Bones: Tension and Compression

### How It Started

I have been a solitary investigator in anatomical science for much of my life. Indeed my earliest investigations in 1952 involved dissections in the comparative anatomy of mammals. Dissection is a solitary activity.

Yet, for a better understanding of the human and animal morphologies into which dissection has lead me, I have found that collaborations or consultations with workers in other disciplines (mathematicians, physicists and engineers) and the use of physical, mathematical and engineering concepts and technologies not in those days available in anatomical laboratories are extremely important. Indeed, this idea gave me the title for my first book in 1973: *Form and Pattern in Human Evolution: Some Mathematical, Physical and Engineering Approaches*, University of Chicago Press.

Those first studies, extending what can be learnt from dissection, were much aided by my taking an experimental stress analysis course (using Timoshenko, 1955 as one of the texts) in 1960 in the Department of Mechanical Engineering at the Royal College of Advanced Technology at Salford (now the University of Salford). This was actually long before I ever heard the word biomechanics. Other students came to the practical classes with cold steel; I produced wet, warm and bloody bones from the local butcher. My mechanical engineering teachers were somewhat horrified at such material, but *very* intrigued.

Since those early days, it has become apparent to me that consultations and/or collaborations with scientists in the mathematical,

physical and engineering worlds, and usage of the many technologies in their laboratories are essential. These collaborations, moreover, involved not only scientists in universities but also those other scientists who were ‘out there’ in industry. Such industrial colleagues were usually acting altruistically — this was long before today’s miserable constraints of ‘user pays’.

Finding out about mechanics at first involved talking with individuals such as the late Ken Sharples, at Sharples Stress Analysis Inc., and using equipment from Westland’s Aircraft Ltd (in both cases, using photoelastic benches of different types that I employed for experimental stress analysis of bone forms). Photoelastic analysis is very attractive to biologists, providing, as it does, a pictorial representation of the mechanical efficiency of bone form. It has usually been aimed at studying the rather simple external shapes of bones and this is a matter for this chapter. It soon became clear that I could also use it for understanding more of the complex internal texture of bone (especially spongy bone, most evident in sections and radiographs of bones). That is a matter for the next chapter.

Finding out how bones, when loaded, bear stress and are strained was thus the problem. The photoelastic methods though useful initially were only able to give ‘ball-park’ answers. This was in part because they are mainly two-dimensional.

I did indeed attempt three-dimensional photoelasticity years ago. This involves what was called ‘frozen stress analysis’; the word ‘frozen’ was used because the fringes indicating the stresses were made permanent in a model of a whole bone, although not by freezing but by heating the model during loading. This fixes (freezes) the stress patterns in the model in three dimensions. These are then analysed, however, by carefully cutting the model into two-dimensional sections and looking at the stresses in each section. This turned out to be incredibly long-winded (as the reader can imagine) and I never managed to use the method to solve a real biological problem.

The usefulness of the photoelastic methods was also somewhat less because they assumed isotropic models of the bones (i.e. models of bones as though they were made of a uniform material). This too, could be allowed for by using models with plastic inserts having

different optical responses to mechanical loads. Likewise, however, though I was able to do this through examples, it was too complex for me to be able to tackle real biological problems.

Today, however, many of these difficulties and complexities have been overcome through the use of computational methods. At first this was with standard finite element analysis (FEA) on main-line computers (in collaboration with engineer and physical therapy doctoral student, Artyan Hsu). Though initially he did not speak English very well, Hsu spoke Mathematics extremely well, and carried out the first FEA of a section of bone in which I was very interested: the calcaneus (Hsu, 1989). Before that time many workers had assumed that the major stresses acting on the human calcaneus in walking and running were during heel strike. The very words ‘heel strike’ and the picture in the mind’s eye that they evoke seem to indicate powerful and violent loads as one rams the heel down. In contrast, Hsu’s studies quickly made it clear that by far the largest stresses in walking and running in humans were at the other end of the gait cycle: at ‘foot and then toe off’. It was to the stresses generated in this specific loading regime that we found the cancellous structure of the human calcaneus was most correlated (see next chapter).

Later studies came to involve applications of FEA that could be carried out on desktop computers. For me this involved fast Lagrangian analysis of continua (FLAC), thanks to colleagues (David Windsor and Wayne Robertson) in Geomechanics in Western Australia (Runnion, 1991). Their work was on how earthquakes shake buildings, but our application was on how muscles ‘shake’ bones. This collaboration was funded by the smallest research grant I have ever had (\$17,000) but it is the grant of which I am, perhaps, most proud because it was awarded by the Australian Commonwealth Scientific and Industrial Research Organisation to an old-fashioned medical anatomist!

This collaboration also allowed me to work with an ear, nose and throat surgeon (now Professor Francis Lannigan) together with another anatomist (also now Professor Paul O’Higgins) on the form of an ear-bone, the incus, how it works during hearing, and why it resorbs in some older men. Initially this work started with my arm-chair pencil

and paper guesses about stresses in the incus. Because that thinking raised a paradoxical possibility, we followed it by simplistic modelling of strain using a two-dimensional rubber sheet shaped like the incus. Because that, in turn, continued the paradoxical idea, the work was extended using FEA through a FLAC study of incudial form and function (I was to learn later that incudes contains the root and is the plural of incus!). The paradox was confirmed (see later in this chapter).

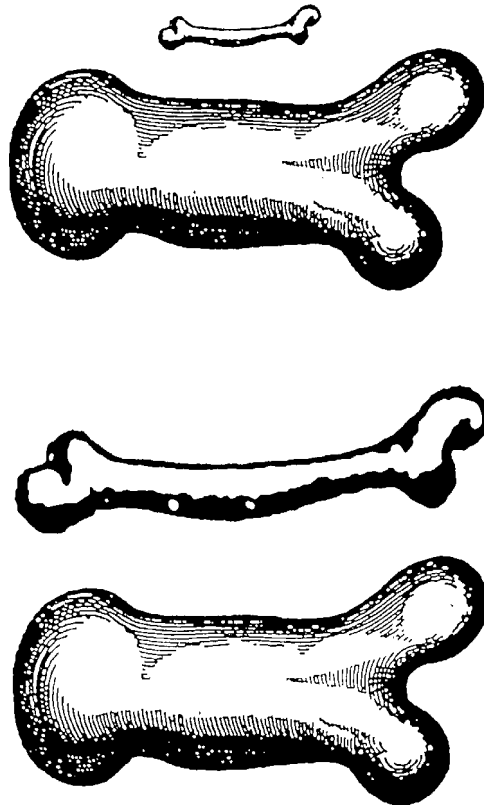
Today I am involved with bioengineering colleagues (at the Universities of Hull and York, and the Hull/York Medical School, UK) Michael Fagan, Catherine Dobson, Kornelius Kupczik and Paul O'Higgins, and with then graduate student Jens Hirschberg at the University of Western Australia (now senior lecturer at the university of Notre Dame, Fremantle). Their abilities in two-dimensional (Hirschberg *et al.*, 2000 and Hirschberg, 2005) and three-dimensional analyses (Kupczik *et al.*, 2007) promise to take us far beyond my initial ideas. As a result of all this I also hope to complete, with joint authorship of course, yet another book (but certainly not my last) to follow that first book written so many years ago. This one is tentatively entitled *The Bone–Joint–Fascia–Muscle Complex: Functional Anatomy and Mechanics*.

## The Nub of the Problem

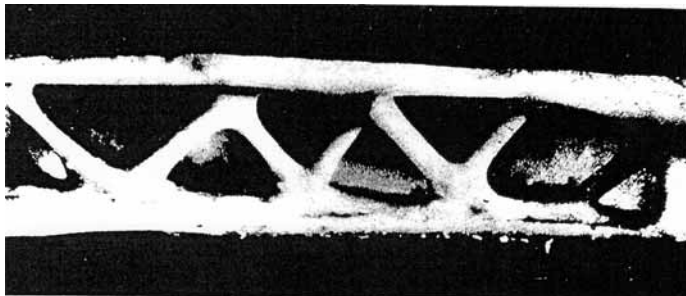
A very early mention of the mechanical significance of bone form was by Galileo (1638) who understood that bones in large animals were not simply scaled up versions of bones in small animals, but had also to be a different shape. Galileo explained it by the upper diagram in Fig. 1. But the differently scaled lower diagram makes the matter more obvious.

For me, however, the beauty of the significance of bone form was thrust upon me when, as a primary school student I saw D'Arcy Thompson's (1917) picture of the bracing struts inside the bone of a bird's wing. It was so similar to the struts and ties between the wings of the biplanes that I saw as a child before the Second World War (Fig. 2).

It was further enhanced when, as a medical student, I heard the story of the German engineer who, upon happening across a sagittal



**Fig. 1.** Top two bones: Galileo's (1638) comparison. Bottom two bones: the same comparison with the bones scaled to the same length.



**Fig. 2.** D'Arcy Thompson's (1917) figure of the interior of a vulture's wing bone.

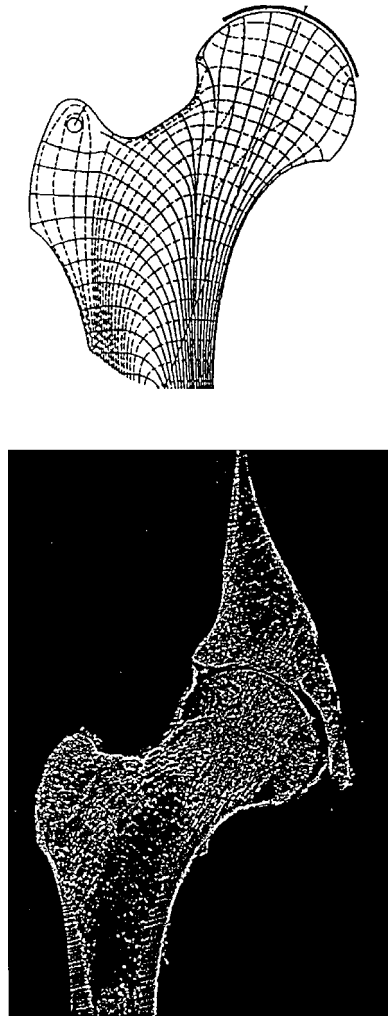
section of the upper end of the femur in the laboratory of a biologist colleague, is said to have uttered:

“Das ist mein crane!”

The relationship that he saw is pictured in Fig. 3 (Murray, 1934) where the pattern of principal stresses that he had calculated in a Fairbairn crane seemed so similar to the pattern of architectural bony spicules inside the head and neck of the human femur. This latter association between mechanics and anatomy, leading to the trajectorial theory of bone architecture as it has been called, so impressed itself upon me that I have taught it to generations of medical students as gospel truth. This, too, however, is a matter for the next chapter.

This all leads to a major problem in attempting to make evolutionary judgements on the basis of bony features, especially the features of fossils, that is, the question of their biological significance. One of the ways of dealing with whole bones is to observe their external features, such as tuberosities and pits, foraminae and fossae, grooves and ridges. These are often defined, in evolutionary studies, as ‘characters’. They are then often treated as ‘present’ or ‘absent’. Some workers recognise that they are really quantitative and use terms like ‘small’, ‘intermediate’ or ‘large’. The states of these characters are then assessed as primitive, shared derived, uniquely derived, etc., and they are employed in cladistic analyses as though they were genetically determined.

In actual fact, most of these architectural features are truly quantitative, and they are evidence of both the genetic and epigenetic plasticity of bone. Thus some such features may be initially generated by genetic factors with epigenetic contributions, for example genetically produced during early development and mechanically maintained and/or mechanically changed during later development and growth. Sometimes, even, they are produced *de novo* by functional change even as late as in the elderly adult. Some features (e.g. the head of a bone) usually appear in development long before mechanical function is established. However, many features of the head of a bone do not appear unless function commences (e.g. many processes around a



**Fig. 3.** The similarity between the stresses that can be computed as existing within a coronal section of a femoral head, and the actual spongy bone architecture that is displayed in the section (see Evans, 1957).

bone head for muscle attachment). There are even some features that do appear, only to disappear, if mechanical function is removed (e.g. Washburn, 1947; Avis, 1959; Moore, 1981). Some appear with early function (e.g. raising the head) then disappear or are replaced or

changed into other features as function develops (e.g. the curvatures of the vertebral column in the transition from raising the head, to sitting up, to crawling, to standing, walking and running). Some appear only if function is totally changed (e.g. bony ridges in relation to bone healing or surgical bone anastomoses). It is therefore important to know about these biomechanically related morphological features of bone before attempting evolutionary assessments.

The matter is yet more complex. Many such architectural features apparently exhibit opposite arrangements in different bones in the same creature. Why, for example is a whole bone, the incus, present in most mammals, yet a large portion of it may disappear in humans in certain situations (Oxnard *et al.*, 1995). Why are there tuberosities (often very large) on some bones where tendons or ligaments attach (e.g. the patellar ligament to the tibial tuberosity) when there are pits (sometimes very deep) where others attach (e.g. the insertion of the obturator externus tendon at the internal aspect of the greater trochanter of the femur)? Why, sometimes, are there both a tubercle and a pit present at certain tendinous attachments (e.g. the insertion of biceps tendon into the radial tuberosity)? Why are there sesamoid bones embedded in some tendons (e.g. the tendon of peroneus longus as it winds around the cuboid) but not in others (e.g. the tendon of obturator internus as it courses around the ischial spine) (Oxnard, 1993)?

Questions like these were at the heart of a series of initial biomechanical investigations that I have carried out over the years (Oxnard, 1991). I hope that their explication will improve the understanding of bone characters in evolution and illuminate important bone features within medicine.

Some of these mechanical questions seemed to revolve around a (now) quite old question: does overall tension exist in bone (Currey, 2002). Tension clearly does exist in many situations in bones at specific times, especially during reversals between tension and compression in cyclical bending induced by locomotor movements. This has been shown many times (especially in a series of investigations by Lanyon and Smith, 1970). But what happens when tension exists all the time or at least most of the time, or perhaps as some 'average' over time (though surely not a simple arithmetic average), is not clearly

understood. Some of this is a matter for this chapter on external bone form, some a matter for the next chapter on internal bone structure.

## **Is Bone Ever Subject to Tension Overall?**

When Currey (1962) first posed the question: “does overall tension exist in bone?” he was initially looking for a whole bone in overall tension. He was also not thinking of any instantaneous state of tension (which happens frequently), but a state of tension over the period of time relevant to architectural change. Indeed, Currey asked me on several occasions if I knew of bony situations where the main stresses might be tensile. He was thinking at that time about the possibility that the arm bones of gibbons might be principally in tension associated with their extreme form of locomotion that includes much hanging and swinging by the arms. He knew that I was interested in brachiation. My answer always was: given that the elbow joint functions during brachiation, net tension ought not to exist in gibbon elbows. I thought there would be compression at the elbow because it is a synovial joint and that type of joint operates under compression. However, Currey’s question was intriguing and at that time I started several investigations designed to discover if it were at all likely that tension might commonly exist in particular regions of bones, if not in whole bones. I initially employed simple thought experiments and then simple photoelastic analyses (Oxnard, 1972) in attempting to answer Currey’s question.

## **Zero Dimensions: Tension and Compression at a Point on a Bone**

My first thought was to look at the point of attachment on bone of powerful tendons. Surely Currey’s idea, overall tension, might predominate at such points (really, of course, rather small areas) when tendons are powerful, when the loads applied by them are large, and when the tendon/bone interface involves collagenous bundles (Sharpey’s fibres) that perforate the surface of the bone. These features are found in many places throughout the body. The histological

nature of such tendon/bone junctions may be quite complex, involving not only penetrating collagenous fibres, but also some degree of interpenetration of the fibres with hydroxy-apatite crystals, and often, too, an interface containing zones of fibro-cartilage and even, on occasion, mineralised fibro-cartilage.

The processes involved in fossilisation and in the preparation of dried bones for museums generally remove these non-osseous materials. For example, the attachment of the powerful temporalis tendon to the coronoid process of the mandible is first through a cap of fibro-cartilage (that is usually later converted into bone). In some dried mandibles (even in younger adults) this cap is lost. The loss may not be recognised; hence measurement involving the tip of the coronoid process as a landmark may be incorrect.

A similar phenomenon exists in many bony processes associated with ligamentous and tendinous attachment throughout the body. Other examples include the anterior and posterior clinoid processes around the pituitary fossa inside the skull, and the styloid and vaginal processes on the outside of the skull base (see later chapter). The styloid process of the skull is particularly obvious. The length of that process may totally depend upon how many of its four centres of ossification actually become incorporated into that part of the process that is attached to the skull base. Indeed one variation in humans exists where the styloid process completely links the skull base and the hyoid bone, and another can be found where none of the centres of ossification fuse with the result that, in the dried skull, the styloid process appears to be absent.

I originally studied this question of stress at a point at three levels. First, I used arm-chair analyses employing simple theoretical biomechanical concepts (Oxnard 1972). Second, I started to apply experimental investigations using actual biomechanical situations but through simplified photoelastic simulations (Oxnard, 1973). Finally, using FEA encompassing greater degrees of complexity, and with colleagues, I was able to take matters much further (Oxnard, 1983/1984).

The first level, biomechanical thinking, involved the following. Let us assume that the bone where the tendinous attachment occurs

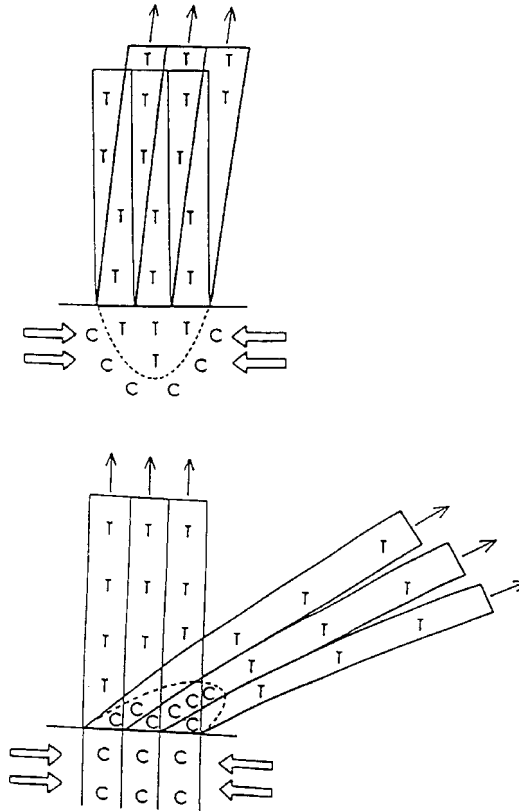
is flat. Let us assume, too, that there is a compression along the length of the bone due to the body weight. A tendon attached at close to right angles to the bony surface will be under tension due to contraction of the attached muscle. Somewhere within this structure there must be a junction where the compression in the bone grades into tension in the tendon. The question is: where is that junction located?

If, during the movement that is produced by the action of the muscle, the change in angulation of the tendon to the bone surface is small, then the state of tension may protrude some distance into the bone. This is because the load producing tension at the small region of attachment of a large tendon (of a powerful muscle) is very much greater than the load producing compression resulting from body weight.

If, however, during the movement that is produced by the action of the muscle, there is a large change in angulation of the tendon to the bone surface, then the situation may change. That is, though there will certainly be tension in the tendon some distance from the bone, this will be reduced close to the bone because the tendon fibres are under compression laterally, being constrained at their attachment. The larger the change in angulation during function, the more the fibres are squashed into a smaller cross-sectional area, and the greater the amount of compression of the fibres one against another. Depending upon the degree of this new compression it would be entirely possible for a region of compression to extend upwards into the tendon (Fig. 4).

If, therefore, the early ideas of Frost (1964) and Currey (1962) that overall compression induces bone apposition and overall tension bone resorption are correct, then a pit might be expected to develop in the first case and a tuberosity in the second.

One difficulty for this line of argument is raised by those instances mentioned above in which muscular (tendinous) attachments are to regions that exhibit both pits and tuberosities. For example, the area of origin on the skull of what must have been a very large and powerful temporalis muscle in sabre-toothed cats is undulating. It comprises both approximately circular concavities



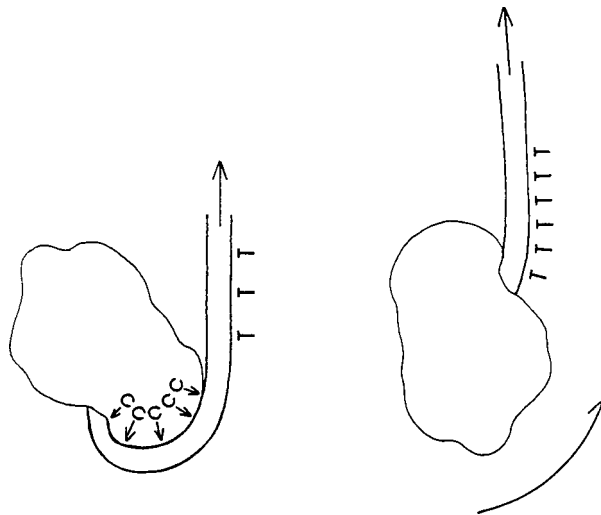
**Fig. 4.** Arm-chair analysis of the stresses existing in a tendon attached to the surface of a bone, upper frame, when the tendon changes angle to only a small degree during function, and lower frame, when the tendon changes angle to large degree. Arrows indicate loading in the tendon and the bone. T = tension, C = compression.

(pits) on generally raised convexities around the pits. However, though clues might be gained from dissections of present day cats, we do not actually know the precise tendinous relationships of this muscle in sabre-tooths.

Another somewhat simpler example is easier to understand, i.e. the attachment of the tendon of the biceps to the tuberosity of the radius in humans. This tuberosity is actually a complex structure with both a convexity and a concavity. The most ventral part of the

tubercle is convex but is quite smooth. It does not have any part of the biceps tendon attached to it. It is overlain by a bursa allowing friction free movement between the free tendon and this part of the bone when the radius is in the wound-up pronated position. It is not in contact with the biceps tendon in the unwound supinated position. A somewhat more dorsal part of the tuberos convexity (a tuberosity) is roughened, however, and bears part of the attachment of the biceps tendon. The dorsal-most part of the attachment of the tendon is actually a concavity (a pit). The biceps tendon (as the temporalis muscle in the prior example) thus attaches both to a tuberosity and a pit.

Let us now apply the same biomechanical thinking to this situation (Fig. 5). When the forearm is in the fully prone position, the biceps tendon is wound completely around the radial tuberosity. Although there is certainly tension in the free portion of the tendon, there ought to be mainly compression in the portion of



**Fig. 5.** Arm-chair analysis of the biceps tendon winding around the cross-section of the radius as it attaches to the radial tuberosity. Right frame: in the fully prone position of the forearm; left frame: in the fully supine position of the forearm. Arrows = directions of pull and movement; C = compression; T = tension.

tendon wound tightly around the bone. It is entirely possible that this additional compression will be great enough to outweigh the tension and to make the overall stress at this position compression. As supination occurs, the tendon unwinds from the tuberosity and the compression due to tight apposition against the tuberosity will gradually disappear as the previously wound portion of the tendon comes to move away from the tuberosity. However, the unwinding results in the more ventral fibres of the muscle markedly changing their angle of orientation in relation to the surface of the bone; from being initially parallel to the surface, they are no longer parallel. If the bony surface had been flat it would presumably have been associated with lateral compression of fibres and the development of compression extending into the base of the tendon. This would produce the observed convexity. In contrast, the more dorsal tendinous fibres remain in an unchanged orientation to the bone surface. The fibres do not press laterally against one another. This implies that compression is not generated and therefore the tension already in the tendon as a result of muscle contraction predominates. This could produce the observed concavity. The combination of these two situations could then conceivably lead to a combined sinuous convexity and concavity of the bone surface (which in fact exists).

The arm-chair thinking above has been tested by the second level of analysis: biomechanical analyses using simple photoelastic experimental stress analysis simulations. These employed the photoelastic method (as outlined by Frocht, 1941; Coker and Filon, 1957) and the results (Oxnard, 1972, 1991) tentatively confirmed these ideas.

However, that technique, involving a homogeneous model, is crude compared to the complex heterogeneity of the actual bio-architecture that exists. It is superseded by better simulations that involve the third level of study: finite element analyses (Hirschberg, 1997; Hirschberg *et al.*, 2000; Hirschberg, 2005) using computational methods. These involved testing the ideas computationally using FEA performed with FLAC technology (e.g., see Cundall and Board, 1988; Hoek *et al.*, 1990).

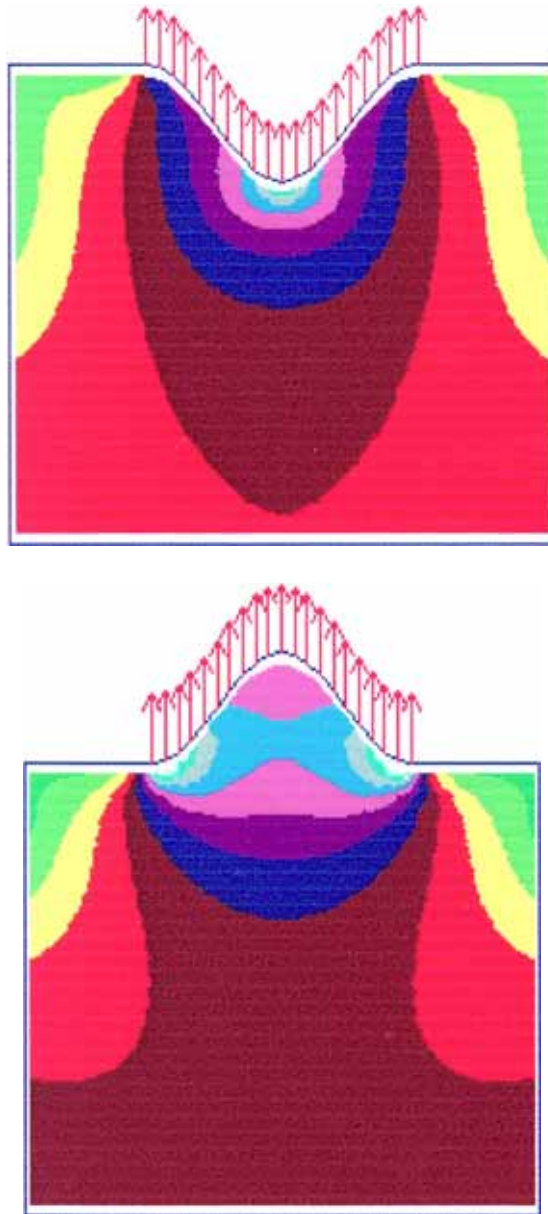
Thus, the compression due to body weight loading in the bone and the tension due to muscular pull on the tendon can be combined. The actual effect depends upon the proportion of these two sets of local stresses. Though generally such loads produce marked changes in stress (many different contours in the diagrams in Fig. 6) along the surface between tendon and bone (whether tubercle or pit), for any given size of tubercle or pit, there are particular combinations of applied forces that produce uniform values along the surface. These are the optimum efficiency solutions (Fig. 7). One might suppose that the final architectural result (height of tubercle, depth of pit) relates to that height or that depth necessary to render the optimum solution for the average set of loads acting upon the system over the response time of bone adaptation.

Even this situation can have further complexity. Consider the case where very large tendons have penetrating fibres. This can also be modelled and shows that, when there are penetrating fibres at the surfaces (of both tubercles and pits) peak tensions actually occur somewhat below the bone surface in both situations (Fig. 8). This fascinating result may explain why many tendon avulsions involve failure of bone beneath the tendon, not at the surface between tendon and bone, nor in the tendon itself. This is a phenomenon that makes it easier to perform orthopaedic repairs in such failure situations. It may be related too, to the phenomenon of cortical excavations that are of considerable interest to paleopathologists.

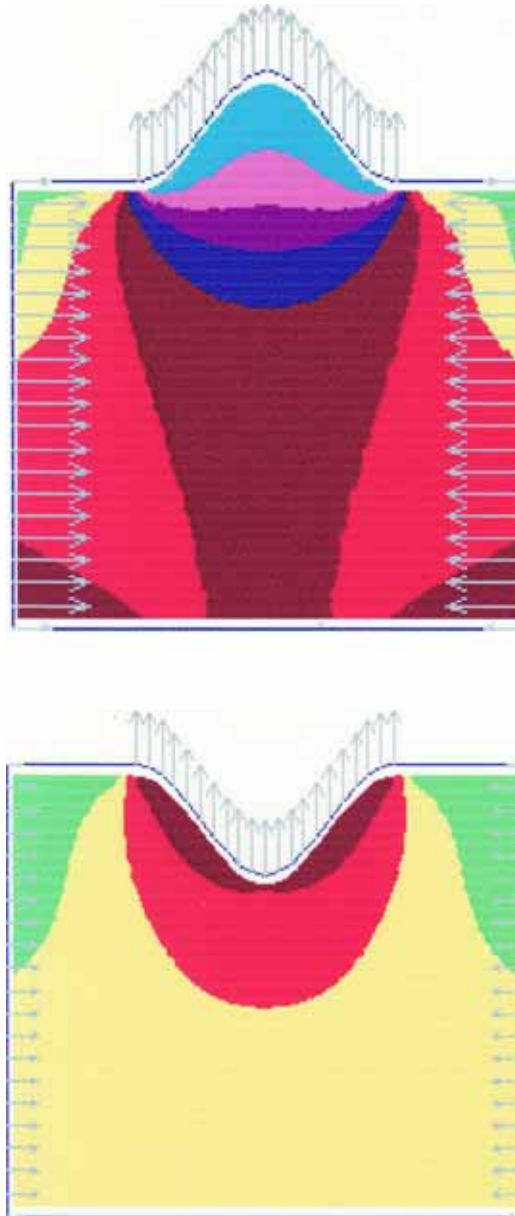
It is of special interest to note that the original explanation has been greatly extended. FLAC does indeed show that large changes in angulation of tendon fibres produces compression creeping up into the tendon (hence a tubercle). But the additional data about the balance of loads and about the effects of penetrating fibres are new.

## **One Dimension: Tension in a Linear Crest on a Bone**

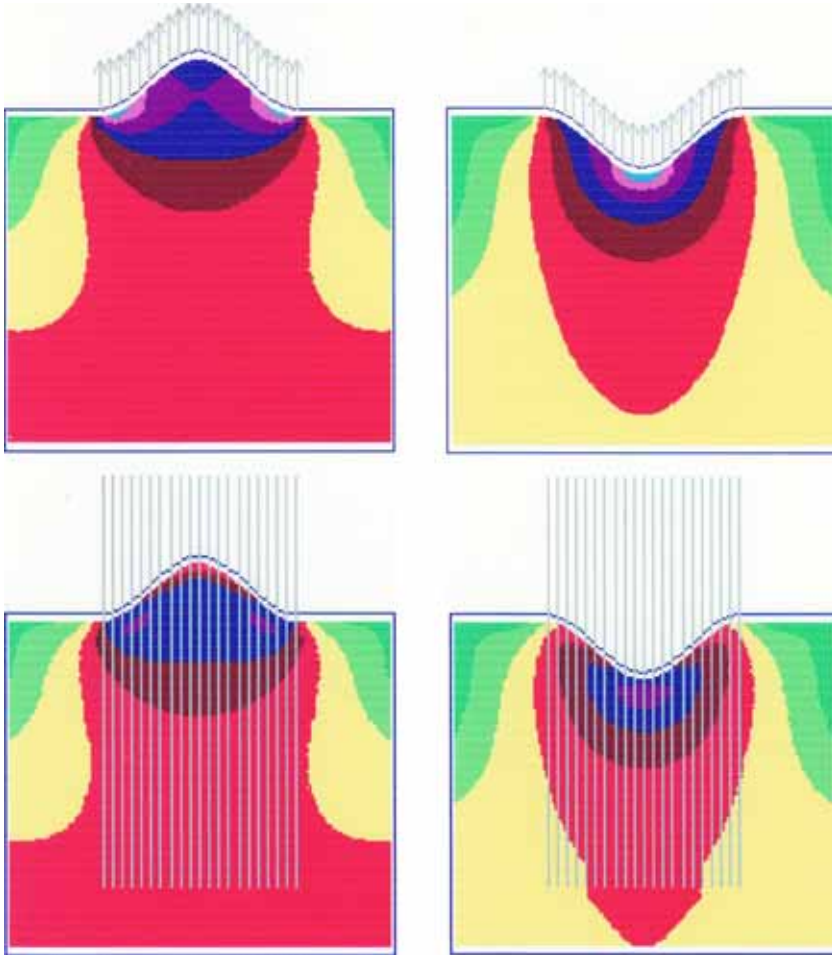
I also thought of a simple one-dimensional situation: a linear bony crest where muscles arise from opposite sides of the crest. This seems to imply that tension might exist in such a ridge. It would



**Fig. 6.** Stresses as calculated in a tendon attaching to a pit (top frame), and a tuberosity (bottom frame). There is a marked change of gradient (change in colours) across the surface of attachment in each case.



**Fig. 7.** Stresses as calculated in a particular pit and tuberosity showing that there are combinations of compressive and tensile loads that produce a constant gradient (same colour) over the bony surface (i.e. mechanically efficient).



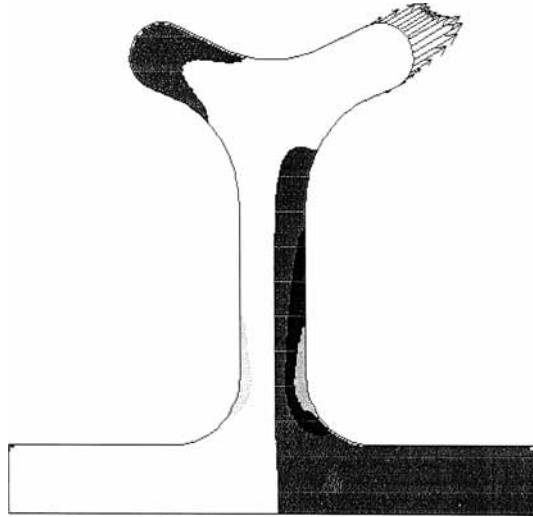
**Fig. 8.** Colour comparisons of tendon inserting into a pit and tuberosity where the attachment is on the surface (upper frames) and where tendon fibres go into the bone (lower frames). In the upper frames, the maximum stress is at the surface, the tendon bone junction. In the lower frames, the maximum stress is located at some distance into the bone below the surface.

require that the opposite muscles would have to contract at the same time. The midline cranial crests of gorillas, some chimpanzees and many australopithecine skulls have jaw closing muscles (temporalis) arising from each side of the cranium. Of course, though the

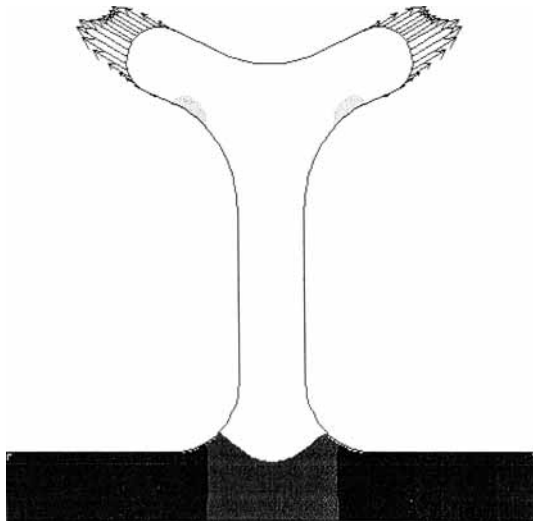
muscles on the two sides can co-contract during some jaw closing movements, they mostly contract alternately in the usual chewing cycles of these and most other mammals. As a result the predominant effect that they would have on the crest would be tension on one side and compression on the other in one phase of the chewing cycle with reversal in the other phase. A somewhat similar situation exists in the occipital crests of large primates, both living and fossil. These have jaw muscles originating from one side and extensor neck muscles from the other. Again, the effect on these crests would be mostly bending one way and then the other as the muscles function at different times and in different behaviours. The overall result would be that tension would not predominate for any significant period of time.

I was, however, thinking at the time of the crest on the scapula (the scapular spine) that gives attachment to portions of trapezius and deltoid muscles. It is easy to work out that, in the locomotor activities of most terrestrial creatures, these two muscles, like the two temporalis muscles in the masticatory example, do not usually co-contract in locomotion. Trapezius is a protractor of the limb, posterior deltoid a retractor. The scapular spine would be bent first one way and then the other. As in the cranial crests, compression and tension would alternate (Fig. 9). There would not be an extended period when tension alone would exist. If, however, one could find some animal in which these muscles did co-contract in locomotion then tension should exist in the spinal crest (Fig. 10).

It transpires that in some bats, these two muscles do frequently act together because, in acting together, they move the shoulder dorsally as in the upward movement of a wing. This upward movement is not simply produced by upwards air pressure (though that no doubt helps) but requires muscular activity to increase wing velocity to get it back for the start of the next power stroke. This effect of the action of two muscles co-contracting, should, one would think, produce tension in the scapular spine. This is complicated but further supported by the fact that in many bats the scapula is also strongly bent ventrally because it extends far out from the trunk like the first segment of a wing. This, too, might make the dorsal scapular spine act



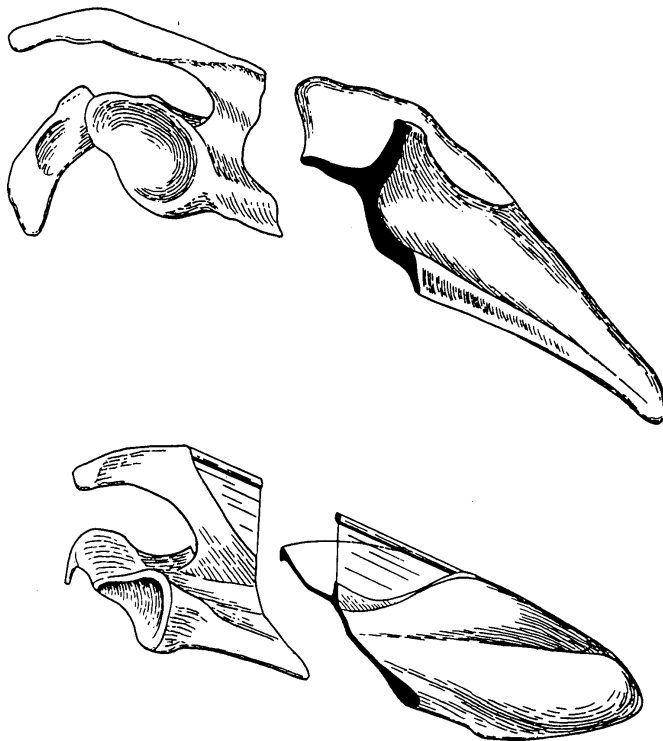
**Fig. 9.** Stresses in a simulacrum of a cross-section of the spine of the scapula on the scapular blade. A muscle is pulling on only one lip of the crest of the spine. The shaded contours show that the spine is undergoing bending.



**Fig. 10.** Stresses in a simulacrum of a cross-section of the spine of the scapula on the scapular blade. Muscles are pulling on both lips of the crest of the spine. The lack of contours show that the spine is in total tension.

like a dorsal tie taking up the tension on the outside of a ventrally bent scapula, rather than acting just as dorsal bony ridge strengthening a flat scapular plate.

I was therefore delighted when inspection of bat scapulae, dissections of bat shoulders, and discussion with my graduate student now Dr Timothy Strickler (who did his doctoral work on bats and flight, 1975) indicated that the bony crest is often replaced by a ligament and a fascial sheet (Fig. 11). In other words, in one situation where it is likely that the crest bears tension for most of the time, the crest is actually a powerful connective tissue ligament not bone.



**Fig. 11.** Cross-section of the scapular spine in a regular terrestrial mammal, above, and in a bat, below. In the bat most of the spine consists of a connective tissue sheet; the crest of the spine consists of a thick round ligament.

## Two Dimensions: Tension in a Flat Plate of Bone

I next took Currey's question into two dimensions: a flat two-dimensional bony plate. Again I had the scapula in mind. The arrangement of muscles originating from each side of the scapular blade implies that, at least in special cases where compression from the glenohumeral joint might be outweighed by tension from muscles (supraspinatus and infraspinatus on the one side, and subscapularis on the other), tension might exist in the scapular blade. This could not be fully tested because data about the actual sizes of the various loads were not available. However, using simulated loads, it did seem possible that this might sometimes occur, perhaps especially, in those primates with the largest scapulae like humans and gorillas. In humans the upper-limb does not participate in bearing the body weight so muscular forces producing tension might well outweigh forces due to compressive loads at the shoulder joint. In gorillas where the upper limb muscles are enormously powerful, again the muscles forces might well be the greater.

These species are, as it happens, the very species in which the scapular fossae are at their relative thinnest; holding the bone up to the light readily confirms this! On rare occasion in gorillas and humans a foramen is found in dried bone preparations (Fig. 12). Of course, this is not an open foramen in life. In life it is closed by the fusion of the two periosteal membranes from the two sides of the scapular blade lying across the foramen. It is this periosteal membrane, greatly strengthened by connective tissue fibres, that gives origin to the muscles on the two sides. It seems possible that in these cases there is no compression bearing bone but a tension-bearing collagenous membrane because overall tension exists.

A situation like this also obtains in the pelvic obturator foramen filled in by the obturator membrane and with the obturator internus and externus arising from each side of the membrane. It exists between the double forearm (radius and ulna) and leg (tibia and fibula) bones where the intervening space is infilled by the respective interosseous membranes with muscles arising from each side. In these cases of course, the membrane is permanent (as it were), in the scapula it only

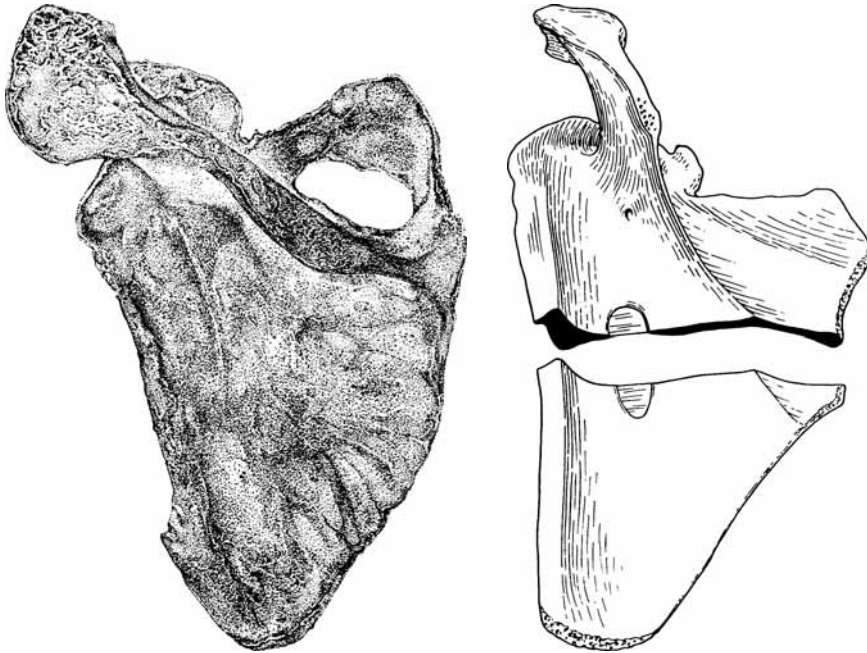


Fig. 12. Holes in bones: adult human and immature gorilla scapulae.

exists when there happens to be a scapular foramen. There are many other examples, even outside mammals (e.g. in reptile skulls), where bony foramina (or even just bony notches) are partially or completely infilled by fascial sheets that give rise to powerful muscles.

### **Three Dimensions: Tension in a Block of Bone**

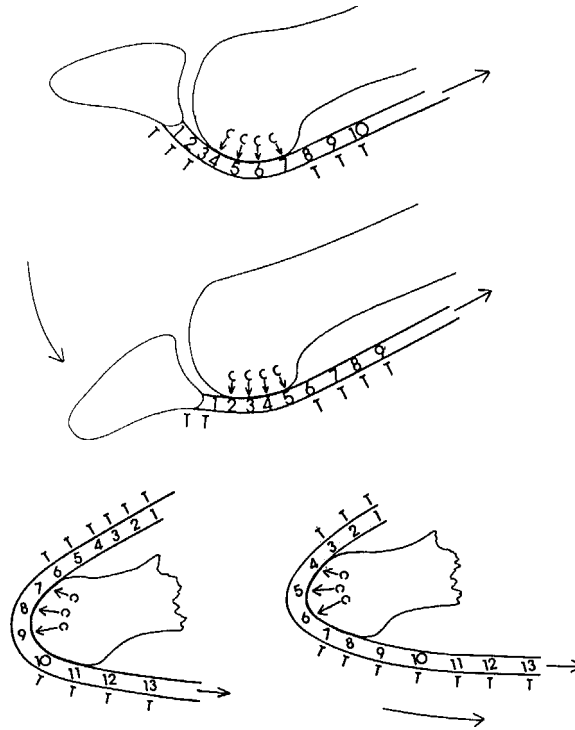
The problem was finally taken into three dimensions by examining the situation where two large and powerful tendons/ligaments arise from each side of a short more or less cubical bone, suggested again that they might generate, overall, tension in the bone. Take the case of a tendon winding around a bony pulley. It seems clear, on the basis of biomechanical thinking, that bone (a sesamoid) might exist in tendons where the degree of movement was small and a given portion of the tendon was in compression most of

the time (upper frame of Fig. 13 where the portion of the tendon labelled 4 and 5 is in compression at both extremes of the tendon movement). It seems equally clear that such bone should not exist in tendons where the degree of movement is great so that no either one portion of the tendon is ever always in compression (e.g. lower frame of Fig. 13 where none of the numbered parts of the tendon are in compression at both extremes of the tendon movement).

These two opposite examples model real situations in the human body. One of these is where the two tendons of the short big toe flexor muscle wind around the under-surface of the metatarsal head but with not much movement along the length of the tendons. Those tendons have sesamoids embedded in the internal surfaces of the tendons. The other is the tendon of obturator internus that winds around the ischial notch of the pelvis. The various movements of the femur on the pelvis dictate that the excursion of this tendon around the ischial notch will be very considerable so that no one part is in compression all the time. This tendon has no sesamoid.

An interesting intermediate case is the tendon of the peroneus longus muscle. This winds around the lateral malleolus at the ankle and again around the groove in the cuboid as it passes to its insertion under the foot. In both of these sites where the tendon changes direction by winding around a bony pulley the tendon is thickened and there is sometimes found a fibrocartilaginous pad (looking rather like a sesamoid bone but made of cartilage instead) embedded in the internal surface of the tendon and rubbing against the pulley. Sometimes, indeed, this fibrocartilaginous pad may actually be ossified so that it is truly a sesamoid bone. This ossification was at its largest in the foot of a Celebes monkey that had walked on two legs all of its life! It may well be that this is at the interface of the mechanical situation producing a sesamoid.

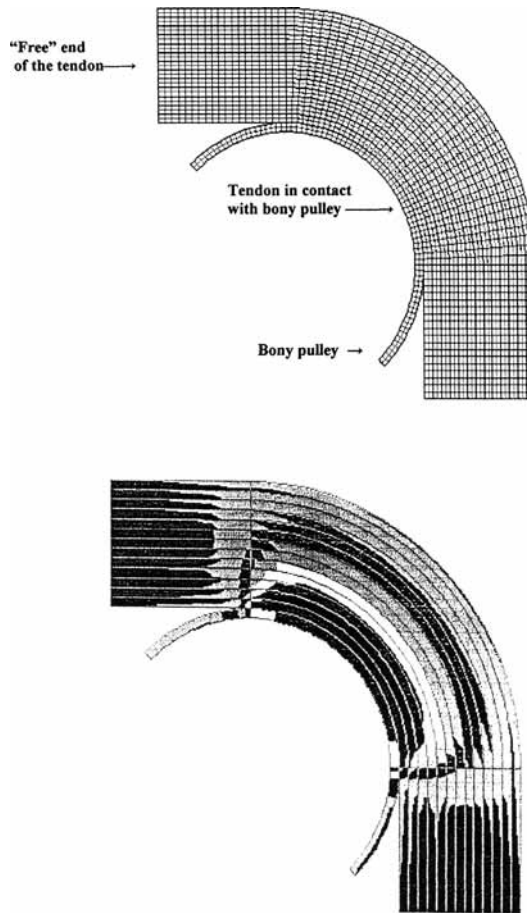
However, again, more extended analysis by Jens Hirschberg using FEA and FLAC was applied to the more specific case of the patella, a large sesamoid, but one which is pre-programmed in development. Yet there is also a biomechanical ontogenetic element. Even when the



**Fig. 13.** An arm-chair analysis of different types of tendons winding around bones. Top and middle frames: a tendon where the degree of movement is small. The points on the tendon, labelled 1, 2, ... are under the stresses indicated by the Ts (tension) and Cs (compression). Points 4 and 5 are always in compression. This is where a sesamoid should be found. Lower frame: a tendon where the degree of movement is large. The points on the tendon, labelled 1, 2, ... are under the stresses indicated by the Ts (tension) and Cs (compression). There are no points that are always in compression. A tendon like this should not have a sesamoid.

patella is removed surgically a new bony structure is formed in the patellar position.

The patella has a powerful quadriceps tendon attaching cranially and a powerful patellar ligament attaching distally. In this case, analysis to see whether perhaps tension might be present in the patella indicates fairly conclusively that the situation is primarily compressive



**Fig. 14.** FLAC of a tendon winding round a bone. The inner eleven contours are in compression, the outer four contours in tension. The compressive portion is where a sesamoid is found.

(Fig. 14). Such tension as exists is mainly located along the superficial surface of the bone; this surface, in life, is covered by a strong collagenous sheet that is the extra-patellar extension of the most superficial layers of the quadriceps tendon and patellar ligament. In the case of other smaller sesamoids, the bony pip is often totally embedded on the under-surface of the respective tendon. In other words, collagen, not

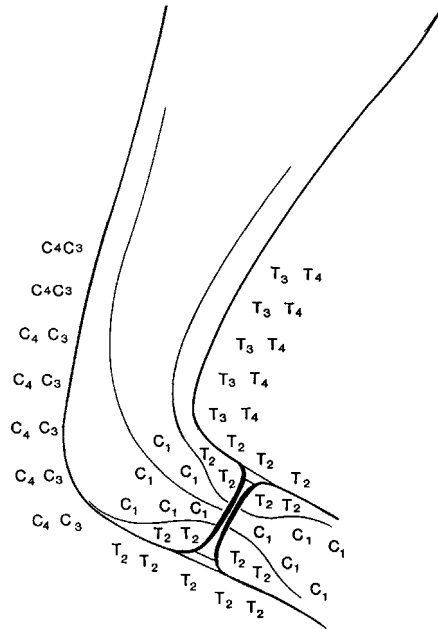
bone, exists where it can be shown that tension predominates; bone only exists where it can be shown that compression predominates.

## **The Case of the Disappearing Incus**

Further answers to this question arose through a chance meeting with an ear, nose and throat surgeon, Francis Lannigan who had, at that time, only just moved to Western Australia. He approached Paul O'Higgins (now at the University of York, UK but then at the University of Western Australia) and me with a request regarding the mechanical function of the human incus. How did we think that the human incus worked during hearing? Why did the human incus undergo resorption in certain situations? What might be the mechanical implication for bone grafts or artificial replacement of the incus in these clinical situations during life?

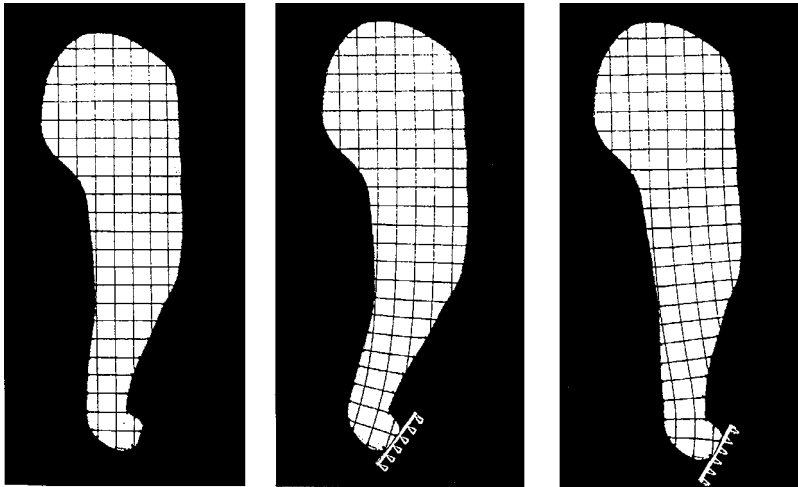
The best analysis of this situation, obtaining the real strains in the incus during function, obviously cannot be carried out. And in any case I was not about to make any great investment in the problem unless I had a little more evidence. I therefore made initial crude estimates by an arm-chair thinking examining the mechanical implications of the movements of the middle ear bones during function. Lannigan supplied me with accurate shape information in two dimensions for the incus ear ossicle. My assessments implied a paradoxical result: that a large portion of the bone must be under tension during both cycles of movement (Fig. 15). This is paradoxical, of course, because, in all other bones so far examined, if a major portion of the bone is strained in tension during one phase of a cyclical movement (e.g. during locomotion) that same portion is strained in compression during the opposite phase (e.g. Lanyon and Smith, 1970). To the degree that this last statement is true then overall tension (*sensu* Currey above) does not exist.

This result was so surprising that Paul O'Higgins and I tried a second (still very simple) estimation using a two-dimensional rubber model of the incus on which had been drawn an orthogonal grid. The distortions of the grid during simulated movement also implied that a portion of the incus could be in tension during both phases of its cycle during hearing (Fig. 16).



**Fig. 15.** An arm-chair analysis of the totality of stresses and strains in an object shaped like the lower end of an incus bone. C = compression, T = tension. The outer row of letters indicates stresses and strains when the incus taps against the stapes. The inner row indicates stress and strain when the incus distracts from the stapes. Movements like this do not usually occur in synovial joints.

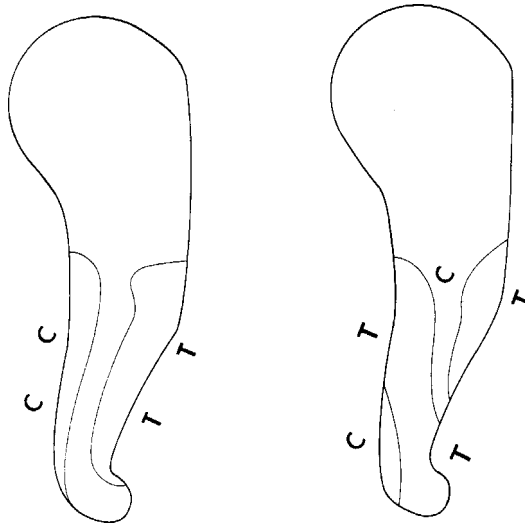
This meant we felt it was worth O’Higgins carrying out a more extensive study of the matter. This was done using the FEA carried out with FLAC obtained with help of the Geomechanics group as explained previously. That analysis showed what one normally expects, that one portion of the incus (the left-hand edge in Fig. 17) was in tension during one phase of the movement and compression during the other. But the analysis also confirmed that, indeed, there is a particular portion of the incus (the right-hand edge and concave face leading towards the joint between the head of the incus and the stapes in Fig. 17) that is under tension during both stages of the ear drum movements during hearing. In the normal individual, this is obviously compatible



**Fig. 16.** A rubber model of an incus with a grid inscribed. Left-hand side figure: no loading, the grid is rectangular, i.e. no distortion. Middle figure: loading of the head of the incus when the incus taps against the stapes. The distortion of the grid indicates tension on the right-hand side edge of the incus. Right-hand side figure: loading of the head of the incus when the incus pulls away from the stapes (i.e. in distraction, the incus taps against the stapes). The distortion of the grid again indicates tension on the right-hand side edge of the incus.

with normal structure of the incus. This implies that we have found a situation where tension seems to be compatible with the presence of bone.

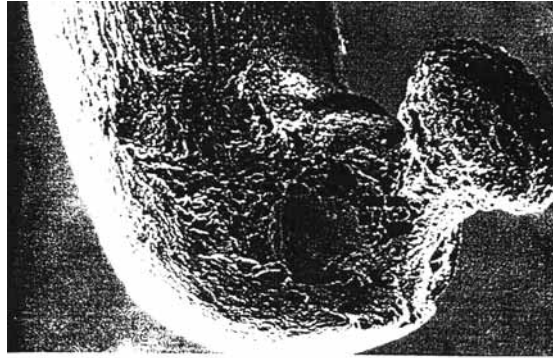
At that point Lannigan revealed to us the reason for his questions. It was indeed that it was exactly that portion of the incus that we identified as being under net tension that was sometimes resorbed (Fig. 18). This occurred particularly in older males working with noisy machinery, especially whistling and shushing sounds. It did not occur in individuals in rural environments. Lannigan had further noted that even when a small piece of bone was grafted in to replace the lost incus in these cases, it too, was shortly afterwards often resorbed. All of this had been established visually using scanning electron microscopy of includes in appropriate samples of individuals of different ages and sex. The visual results were



**Fig. 17.** A FLAC of the stresses in the incus during the tap against the stapes (left) and the distraction from the stapes (right). The lines indicate the contours of the stress differences. The left-hand side edge shows an alternation between tension T and compression C, the expected finding. The right-hand side edge shows tension T in both movements.

confirmed through morphometry of incudes (incus bones — Oxnard *et al.*, 1995).

I must add a caveat here. It could be that the determinant of bone existence or disappearance is not tension *per se* but some threshold level of tension above which bone is resorbed and, possibly some other threshold below which it is not. Under increased stresses induced by abnormal hearing situations (e.g. the continuously varying whistling and shushing sounds possibly existing in some work environments involving machinery, but not existing in normal situations) the degree of tension induced might be outside such thresholds. The bone on the inner curve of the incus might be being resorbed because tension of that higher degree existed there; the enclosing periosteum is still present as a kind of ligament. It is also likely that the height of the threshold differs whether one is going from compression to tension, or *vice versa*.



**Fig. 18.** SEM pictures of the head and neck of the incus showing marked resorption on bone. Upper picture, neck resorbed but head still present. Lower picture, head totally resorbed, large area of resorption of the neck and descending process on the concave side.

This situation in the incus is so far the only one I have found where tension seems to occur in a major portion of a whole bone. However, studies of small portions of bones: e.g. sites of tendon attachments, sesamoid bones within tendons and bony trabeculae in

cancellous bones as described above are also possible instances. Much of this work was carried out by Jens Hirschberg employed on my ARC grant at the University of Western Australia.

## Are Long Bones Always Hollow?

A final problem that may be worth examining relates to the long bones of the limbs. These are described in most anatomical texts as having a shaft and two ends. Though the ends contain cancellous bone (like a whole vertebra, the subject of the next chapter), the major portions of the shaft form a tube of cortical bone with a central hollow cavity (the marrow cavity). The biomechanical rationale behind the tubular shaft of a long bone is usually given as strength with lightness for efficiency in bending.

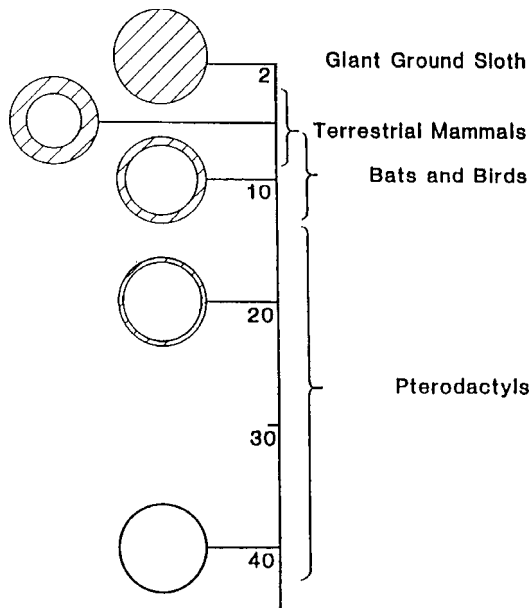
In the standard description of pure bending the highest stresses are at the surfaces of the tube with tension on the one side and compression on the other. There is a neutral axis through the centre where the stress is zero. If the bone were solid there would still be zero stress at the midline; in addition the bone close to the midline would bear very little stress. As a result, the absence of the central material, i.e. the presence of a marrow cavity, would scarcely weaken the bone at all. Certainly the slight increase in strength is not worth the high metabolic cost of maintaining bone in that position. This is the simplistic assumption around the tubular structure of bone.

In fact, this is a simplification of the real situation. In reality a bone is not under pure bending. There is pure bending due to a bone acting as a lever, to be sure, but this is combined with the axial compression of weight bearing. In addition, bones are rarely straight; axial loading of a curved bone produces bending (very few bones are completely straight, though some are almost straight; in humans, for example, the fibula).

Under this more complex circumstance the mechanical efficiency of a tube for bending depends upon an engineering quantity: the second moment of area. The architectural factor in that quantity is the diameter of the bone divided by the wall thickness. This gives information about efficiency in bending and compression, about 'bendability'

to coin a term. In theory the strongest column under pure bending with no axial compression is a tube that has an infinite diameter and an infinitesimal wall thickness; think of trying to bend a cooling tower in a power station! Of course, this is an engineer's abstraction. Likewise the strongest column in pure compression is one that is solid that is, has a diameter of twice the wall thickness when the wall thickness is the radius of the column. Equally, this is the practicality of an architect's column in a cathedral.

It is therefore possible to examine this measure in the limbs of a variety of animals (and this has been done by both Alexander, 1983 and Currey, 2002). Figure 19 shows the result. Where bending predominates then this ratio is large. Some pterodactyls have very large values (Fig. 19). In gliding, the wing bones bend, but because the animal glides, the wings are not flapped by muscular activity to anywhere near the degree in (say) birds, so that the compression along the length of the wing due to off-axial muscular activity is much



**Fig. 19.** Plot of values of limb bone diameter divided by limb bone wall thickness for a variety of animals.

smaller than in a true flying creature. Birds have a somewhat smaller ratio because of the powerful muscular forces compressing the wing bones as in Fig. 19 (but their mechanics is complicated by the presence of air sacs within their wings). Bats come next. Those terrestrial creatures that are smallest, lightest and most bouncy come next again; the heaviest creatures (with, therefore, greater degree of axial compression due to body weight though still with much muscular activity) are at the lower end of the axis.

The lowest figure that one can have is 2.0 (diameter divided by wall thickness when wall thickness is half diameter because there is no marrow cavity). The aforementioned columns in cathedrals have a value of 2.0: that is, they are solid. They do not move at all. They support the sometimes extremely heavy roofs of the earliest cathedrals. Are there any animals that are comparable? It turns out that there are: the giant ground sloths of the Californian tar pits have no marrow cavities (Fig. 20). Unfortunately, however, we do not actually know for certain how they moved though it is obvious that they were very large and heavy. If they were also very slow (as seems likely) then the major component acting on the limb bones would be, somewhat like the cathedral column, under great compression (even though muscular activity would produce some bending).

Giant ground sloths, however, are edentates. Could they have this feature for that reason? This is complicated by the fact that two living edentates (also extremely slow creatures, the two tree sloths) also have almost no marrow cavity. In these creatures, the marrow cavity has the dimensions of a needle; their diameter/wall thickness ratio is very close to 2. The fact that their limbs but not their bones bear weight by tension rather than compression does not deny the idea. However, this means that this could be an edentate characteristic and nothing to do with biomechanics at all.

Happily almost the first thing that occurred when I reached Australia was a trip to the West Australian museum.

“Have you any large slow marsupials?” I asked.

“Yes” said John Long, the curator.

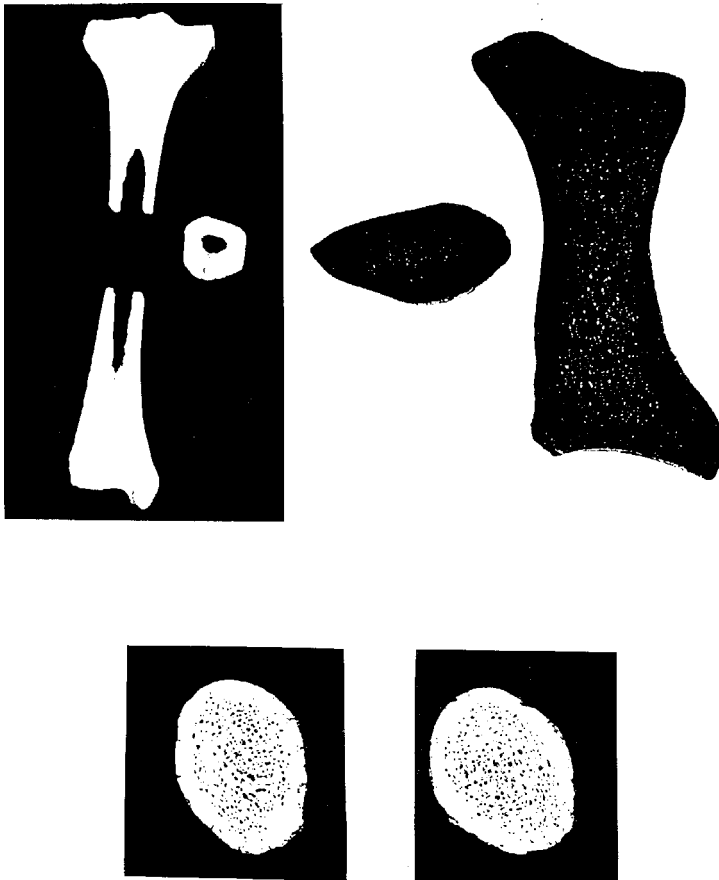


Fig. 20. Upper frames, longitudinal and cross-sections of tibiae of a human and a giant ground sloth. Lower frames, cross-sections of long bones of giant fossil marsupials (*Zygomaturus* and *Palorchestes*).

“Can I cut sections of their long bones?”

“No need for that” said John Long.

He opened a drawer. It contained many long bones of giant marsupials like *Zygomaturus* and *Palorchestes*. Many were broken across. They had no cylindrical marrow cavities (Fig. 20). It must be a biomechanical adaptation. It is not an edentate characteristic (Oxnard, 1993).

Again, therefore, we had evidence relating to the effects of tension on bone.

### **Question Again: Does Tension Ever Exist in Bone Overall?**

After all this do we now have an answer, even if only tentative, to Currey's question: does overall tension (in the sense of tension existing for the period of time influencing adaptation) ever exist in bone? Does this have implications for the mechanical adaptation of bone? The above discussion implies that: where overall tension is unlikely to exist, bone does; where overall tension probably does exist, bone does not. Yet it is clear that this is not the whole story. For further understanding of this problem we have to move on from macroscopic components of bone shape to microscopic elements of bone structure: the subject of the next chapter.

### **References**

- Alexander, RMcN, *Animal Mechanics*, 2nd ed., Blackwell, Oxford, 1983.
- Avis V, The relation of the temporal muscle to the form of the coronoid process, *Am J Phys Anthropol* **17**: 99–104, 1959.
- Coker EG, Filon LNG, *A Treatise on Photoelasticity*, 2nd ed., Revised by HT Jessop, Cambridge University Press, 1957.
- Cundall PA, Board M, A microcomputer program for modelling large-strain plasticity problems, in Swoboda S (ed.), *Numerical Methods in Geomechanics*, New York, 1988.
- Currey JD, The adaptation of bones to stress, *J Theor Biol* **20**: 91–106, 1962.
- Currey JD, *Bones: Structure and Mechanics*, Princeton University Press, Princeton, 2002.
- Evans FG, *Stress and Strain in Bones*, Thomas, Springfield, 1957.
- Frocht MM, *Photoelasticity*, Vols. 1 & 2, Wiley, New York, 1941.
- Frost HM, *The Laws of Bone Structure*, Thomas, Springfield, IL, 1964.
- Galileo, G, *Discourses and Mathematical Demonstrations Concerning Two New Sciences Pertaining to Mechanics and Motion*, Macmillan, New York, 1638 (Translated by H Crew and A de Salvio, 1933).

- Hirschberg J, A study of the effects of tubercles and pits on the stresses in bone at tendon attachments, MSc Thesis, University of Western Australia, 1997.
- Hirschberg J, Simulations of mechanical adaptations and their relationship to stress bearing in skeletal tissue, Doctoral Thesis, University of Western Australia, 2005.
- Hirschberg J, Milne N, Oxnard CE, Biomechanics of the tendon/bone interface, *Persp Human Biol* **5**: 55–68, 2000.
- Hoek E, Grabinsky M, Diederichs M, Numerical modelling for underground excavation design, *Short Course Lecture Notes on Ground Control Principles*, Ontario, Laurentian University, Geomechanics Research Centre, 17, 1990.
- Hsu A-T, Trabecular architecture and finite element analysis of the human calcaneus, Doctoral Thesis, University of southern California, 1989.
- Kupczik K, Dopson C, Fagan M, Crompton R, Oxnard CE, O'Higgins P, Assessing mechanical function of the zygomatic region in macaques: Validation and sensitivity testing of finite element models, *J Anat* **210**: 41–53, 2007.
- Lanyon LE, Smith RN, Bone strain in the tibia during normal quadrupedal locomotion, *Acta Orthopaed Scand* **41**: 238–248, 1970.
- Moore WJ, *The Mammalian Skull*, Cambridge University Press, Cambridge, 1981.
- Murray PDF, *Bones: A Study of the Development and Structure of the Vertebrate Skeleton*, Cambridge University Press, London, 1934.
- Oxnard CE, Tensile forces in skeletal structures, *J Morphol* **134**: 425–436, 1972.
- Oxnard CE, *Form and Pattern in Human Evolution*, University of Chicago Press, Chicago, 1973.
- Oxnard CE, *The Order of Man*, Hong Kong University Press, Hong Kong, 1983, Yale University Press, Princeton, 1984.
- Oxnard CE, Mechanical stress and strain at a point: Implications for biometric and biomechanical studies of bone form and architecture, *Proc Austral Soc Human Biol* **3**: 57–109, 1991.
- Oxnard CE, Bone and bones, architecture and stress, fossils and osteoporosis, *J Biomech* **26**: 63–79, 1993.
- Oxnard CE, Lannigan F, O'Higgins P, The mechanism of bone adaptation: Tension and resorption in the human incus, *Recent Adv Human Biol* **2**: 105–125, 1995.

- Runnion CK, Oxnard CE, Robertson WV, Windsor CR, Biomechanical modelling of vertebrae using experimental stress analysis, *Proc Austral Soc Human Biol* **4**: 125–133, 1991.
- Strickler T, The functional morphology of the pectoral girdle muscles in the Chiroptera, Doctoral Thesis, University of Chicago, 1975.
- Thompson D'A, *On Growth and Form*, Cambridge University Press, Cambridge, 1917.
- Timoshenko S, *Strength of Materials. Part I: Elementary Theory and Problems*, 3rd ed., Van Nostrand, Princeton, 1955.
- Washburn SL, The relation of the temporal muscle to the form of the skull, *The Anatomical Record* **99**: 239–248, 1947.