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Scanning electron microscopy of human lumbar vertebral trabecular bone surfaces

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Summary. Trabecular bone from fourth lumbar vertebral bodies of 30 autopsy subjects (18 male and 12 females, 30–91 years of age) was investigated using surface mode scanning electron microscopy. In the younger individuals, proper coupling of formation and resorption appeared to have maintained both the bone mass and the shape and structural integrity of the trabecular elements. In elderly individuals, including osteoporotics, irregularities and uncoupling of these activities brought about a loss of bone and a disruption of trabecular structure. Distinct resorption patterns (lateral and vertical) are responsible for trabecular thinning and removal of structural elements. Irregularities in the formative process in old age may account for the compensatory thickening and changes in shape and texture of trabecular elements. The mechanisms involved in the occurrence of microfractures and the fate of disconnected elements were also identified. An increased proportion of arrested mineralizing fronts is found in older individuals and in frank osteoporotics. Resorption may occur through osteoid and arrested mineralizing fronts, as well as through resting, fully mineralized surfaces.

Key words: Trabecular bone – Lumbar vertebrae – Collagen – Resorption – Mineralization

Introduction

Scanning electron microscopy (SEM) of bone matrix and bone mineral surfaces has contributed significantly to our understanding of bone structure and function. Using SEM, morphological appearances of free surfaces can be characterized: microscopic structure can be studied, and the nature of in vivo cellular activities and mineralization mechanisms can be deduced (Boyde 1968, 1972; Boyde and Hobdell 1969a, b). Some well-documented studies include the description of lamellar bone and primary membrane bone and their mineralizing fronts (Boyde and Hobdell 1969a, b; Boyde 1980; Boyde et al. 1982), osteocyte lacunae (Marotti 1981), osteocyte orientation and canaliculi (Marotti et al. 1985a, b), bone endosteal surfaces (Krempien 1979; Reid 1987), cell matrix interface (review by Jones et al. 1986), resorbing surfaces (Krempien and Klimpel 1981; review by Boyde and Jones 1987), and a study of fossil bone (Bromage 1987).

Many pathological conditions of bone have also been studied using the SEM [reviews by Sela 1977 and Boyde et al. 1986; Paget's disease of bone (Munzenberg et al. 1971; Chappard et al. 1984); osteoporosis (Dempster et al. 1986); renal osteodystrophy (Krempien et al. 1977); hyperparathyroidism (Krempien et al. 1975); familial hypophosphataemia (Steendijk and Boyde 1973); osteogenesis imperfecta (Lindenfelser et al. 1972; Reid and Boyde 1983)].

Whitehouse et al. (1971) described the structural arrangement of trabecula within a vertebral body using low-power SEM micrographs. However, the detailed morphology of trabecular bone surfaces in lumbar vertebral bodies has rarely been subjected to SEM study. Trabecular bone at this site undergoes considerable changes during ageing. The structure changes from one with prominent plate-like trabecula – a honeycomb in three dimensions – to one dominated by rods or needle-like features. Perforations and the removal of trabecular elements are commonly seen with ageing (Parfitt 1987), but the mechanisms responsible for such changes are not well understood. Microfractures have also been frequently observed in old and osteoporotic patients, but have not been adequately investigated. The occurrence of vertebral crush fractures in old age also emphasises the importance of micromorphological studies of trabecular bone surfaces.

In the present study, SEM was employed to characterize trabecular bone surfaces of fourth lumbar vertebral bodies derived from young adult, old and osteoporotic subjects. The objective of the study was to understand the micromorphology of these surfaces and relate

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them to already described changes that occur during ageing and in osteoporosis.

Materials and methods

At the time of routine autopsies, fourth lumbar vertebral bodies were removed from 30 subjects (18 male and 12 females) aged from 30 to 91 years. Cleaned samples were stored in 70% ethanol until required.

Using a low-speed diamond saw (Buehler Isomet-11-1180), 4-mm-thick plane parallel mid-sagittal sections were cut from each vertebral body and cleaned with a fine jet of water to remove marrow and soft tissues. They were then treated with a solution of 2% hydrogen peroxide at 37° C for 24 h to remove residual soft tissue and superficial non-mineralized bone matrix (osteoid), defatted in room temperature 50:50 chloroform:methanol for a few hours and air-dried.

A Cambridge Stereoscan S4–10 SEM was used for the study. The samples were coated with gold by sputtering and examined in the SEM operated at 10 kV for both secondary electron imaging (SE) and backscattered electron imaging (BSE), using an annular, four-segment, solid-state BSE detector. Stereopair micrographs were recorded with a tilt angle difference of 10°.

Results

The three main morphologies which characterize the different activity states of bone surfaces – forming, resting and resorbed – (Boyde and Hobdell 1969a, b; Boyde 1972; Boyde and Jones 1972) could readily be identified on various components of the human trabecular bone (Figs. 1, 2) but there were marked differences in the amount, morphology and the distribution of these activities in different age groups.

Fully mineralized collagen bundles characterizing resting surfaces in the peroxide-treated samples were evident mainly in young adult samples. In old samples, the proportion of such intact-collagen-bundle resting surfaces was reduced, especially in osteoporotics. "Prolonged resting surfaces" identified by the extension of mineralization into the ground substance outside the most superficial layer of collagen at the matrix surface, thus obscuring collagen fibre detail, were only a characteristic of younger adult samples (Fig. 2).

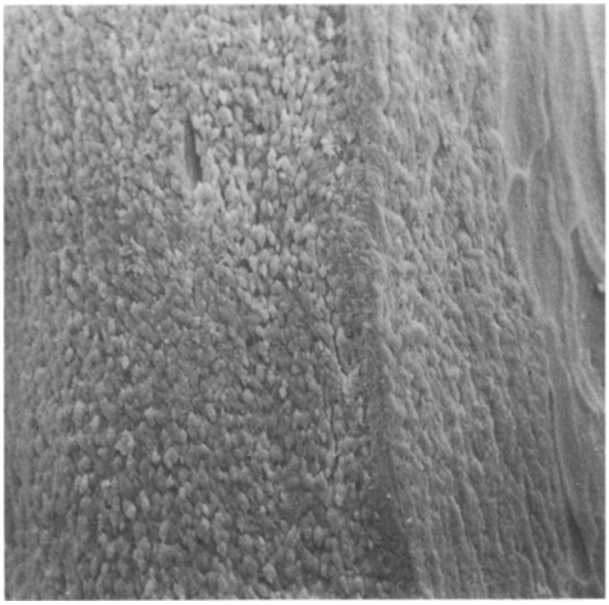


Fig. 1. Female, 30 years. Mineralizing front and a resorbing surface (*far right*) on a rod-shaped trabeculum. The resorption bays are aligned along the long axis of the rod. Field width 95 μm

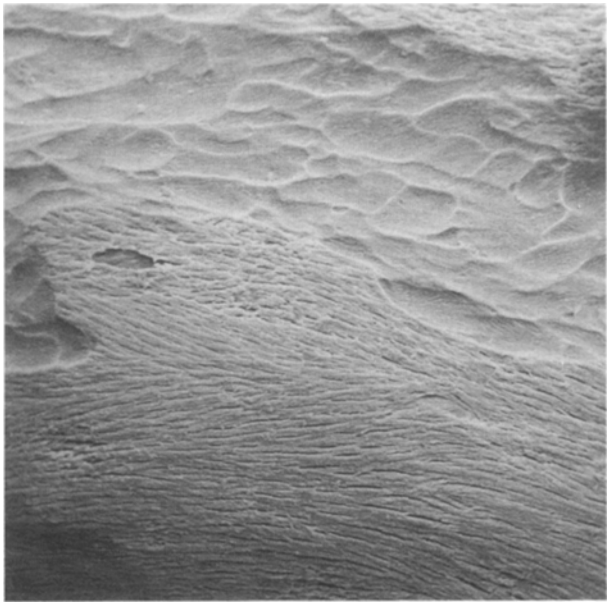


Fig. 2. Male, 35 years. Superficial resorption of the surface of a rod (*top*) and resting surface (*bottom*) showing arrangement of collagen bundles into overlapping domains with distinctive collagen orientations. The half-formed osteocyte lacuna back wall was completely mineralized. Field width 185 μm

In osteoporotics, the majority of the surfaces exhibited either osteoclastic resorption lacunae or incomplete collagen bundles after peroxide treatment. The morphology of such surfaces was not equivalent to those in which evidence of active mineralization can be adduced (such as is possible from simple knowledge of the location of constantly growing fronts in young human and young non-human material, and where double tetracycline labelling can be shown). These regions, where the mineralization of the collagen fibres is incomplete but apparently not progressing, we have termed arrested mineralizing fronts.

The greatest diversity in activity with age was observed in resorbing surfaces (Boyde and Jones 1979). In younger samples, it was usually possible to see evidence for resorption-repair "coupling" activity in any one trabecular element, with formation infilling resorbed regions. However, in old and osteoporotic samples, one type of activity mostly dominated over an extensive area or sometimes in one trabecular element. These changes in the balance of surface activity were related to structural changes, such as perforations, thinning and removal of trabecular elements, or in some cases the thickening of the remaining vertical structures, that take place with age and in osteoporosis.

The organization of collagen in trabecular bone relates to the morphology of the elements in which it is

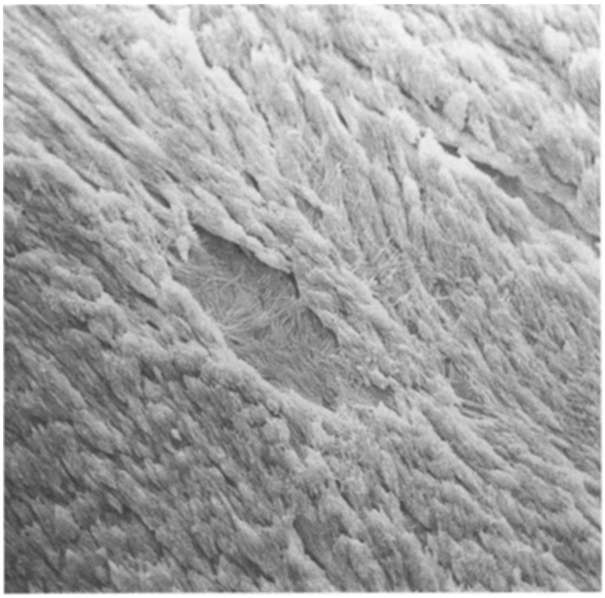


Fig. 3. Female, 30 years. Nearly fully mineralized, but still mineralizing surface on a rod. Discrete collagen fibrils are evident in the mineralized parts of the collagen bundles: complete mineralization in the osteocyte lacunar back wall. Field with 50 μm

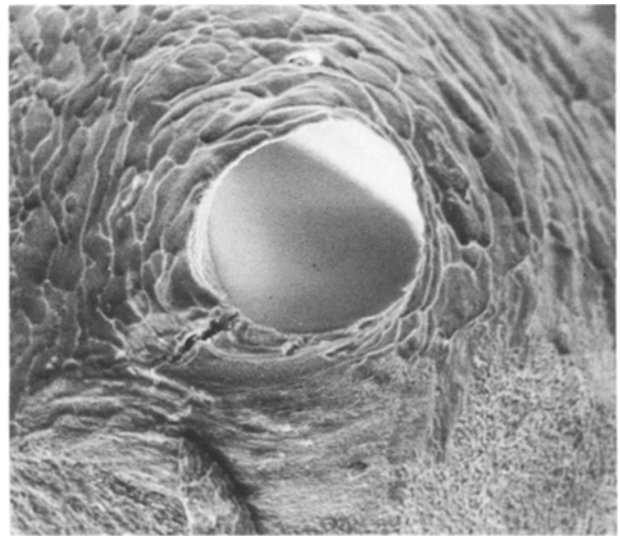


Fig. 5. Male, 41 years. A round opening from a plate showing "snail track" type resorption bays tracking collagen orientation around the circumference of the opening. Field width 180 μm

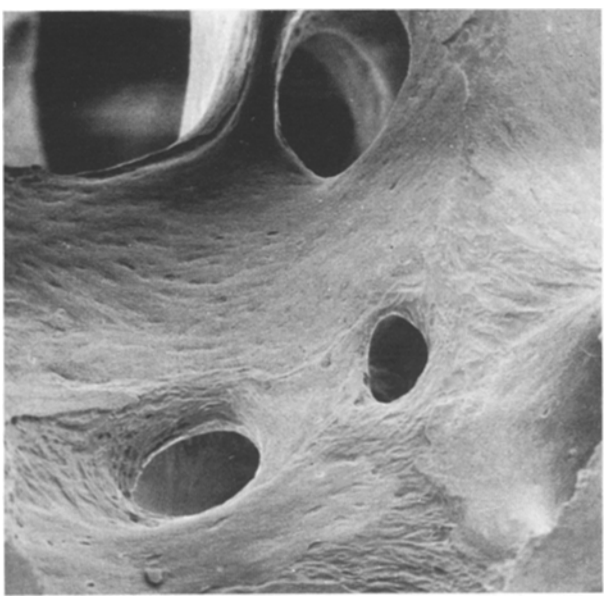


Fig. 4. Female, 30 years. An area dominated by plates from the middle region of a mid-sagittal section of a 4th lumbar vertebral body, showing the usual round or oval openings found in such plates. Field width 955 μm

Fig. 6. Female, 30 years. Resorption of trabeculum has been followed by formation (*top*), suggesting normal "coupling" between these two processes in this younger specimen. Field width 470 μm

found. In rod-shaped trabecula, the collagen fibre bundles are mainly aligned along the long axis. Overlapping "domains" (Boyde and Hobdell 1969a, b) at angles to each other are still more parallel than perpendicular to the rod (Fig. 2).

The plates usually encountered in the middle zone of mid-sagittal sections of the vertebrae contain several round or oval openings (Figs. 4, 5). The alignment of the collagen fibre bundles apparent on the surface of the plates tended to follow the contours of the bone surface. At the margins of the plates they were aligned approximately parallel to the margins. At the junction between a plate and a rod, the bundles converged to form the rod (Fig. 6). At the boundary of the openings, the exposed, visible portions of the domains were very narrow and each was partially overlapped by a differently oriented domain in accordance with the smooth boundary.

At surfaces where recent resorption had occurred, prominent collagen fibre bundles could be observed in the floors of resorption bays and the different orientations within successive lamellae were evident at the various depths revealed. The organization exposed by resorption sometimes suggested a change over time in the

Fig. 7. Female, 75 years. Junction between a plate and a rod showing superficial resorption (*top*) and less regular orientation pattern of collagen bundles (*bottom*). Field width 205 μm

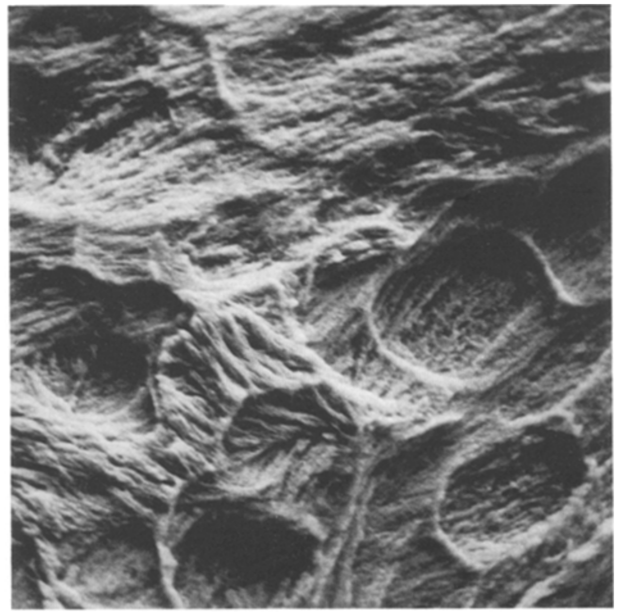


Fig. 9. Female, 75 years. Detail from field shown in Fig. 7: deep, round resorption bays with contrasting orientations of collagen bundles at various depths exposed by osteoclastic resorption, indicating that only the most superficial bone showed the less regular collagen orientation pattern. Field width 105 μm

Fig. 8. Female, 75 years. Enlargement of field shown in Fig. 7, showing fully mineralized surface. Field width 50 μm

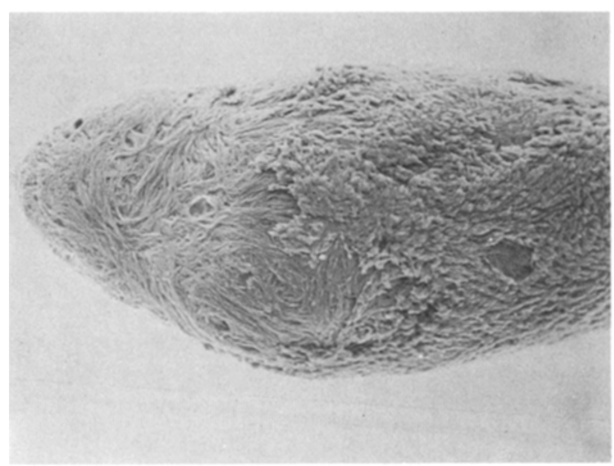


Fig. 10. Male, 71 years, osteoporotic. Tip of a disconnected rod swathed in new collagen bundles. The collagen at the tip is completely mineralized. Further back, more superficial matrix layer shows characteristics of a mineralizing front. Field width 190 μm

structural role of the bone tissue comprising the trabecular element.

At forming surfaces, parts of incompletely mineralized collagen bundles presented as aligned mineral residues representing the mineralized lengths of individual collagen fibrils (Fig. 3). In young adult specimens, the structural organization of collagen indicated by these segments was similar to that previously reported for cortical bone (Boyde 1972, Reid 1987). However, in some old and osteoporotic samples, a less regular collagen organization was evident on trabecular surfaces (Figs. 7, 8) and even though not organized into extensive domains, these collagen bundles were completely mineralized (Fig. 8). However, such irregular collagen orientation seems to be a surface phenomenon, since normal lamellar organization could be observed in deeper layers revealed by resorption (Fig. 9). Atypical collagen patches were sometimes related to micro-cracks or mineral discontinuities between increments of bone. A different organization of collagen bundles was also seen in areas of healing microfractures (Fig. 10) and in regions where microcallus was forming.

The characteristics of the resorbing surfaces showed considerable variability both within the same age group

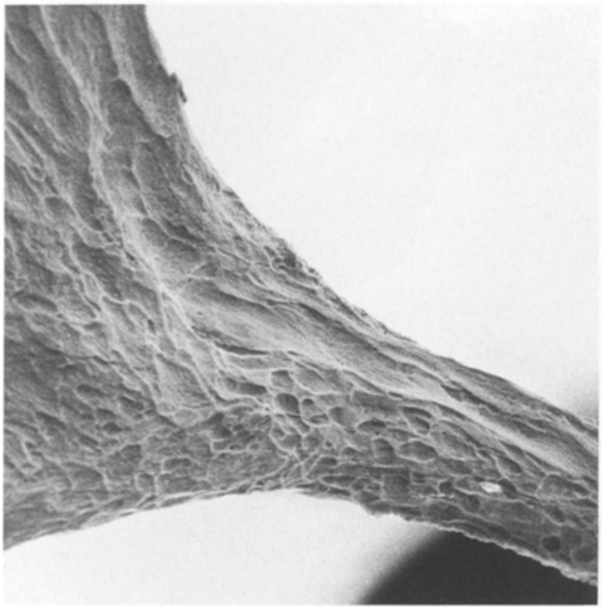


Fig. 11. Male, 69 years. A trabeculum showing different morphological types of resorption bays. An elongated resorption track is evident on the upper part of the trabeculum: the lower part shows smaller, more equidiametrical pits. Field width 215 μm

Fig. 13. Female, 75 years. Most of the surface of this area has been superficially resorbed. A patch of resting surface (*left*) and a forming front can be seen on the far left side, with deeper resorption appearing at the centre. Field width 470 μm

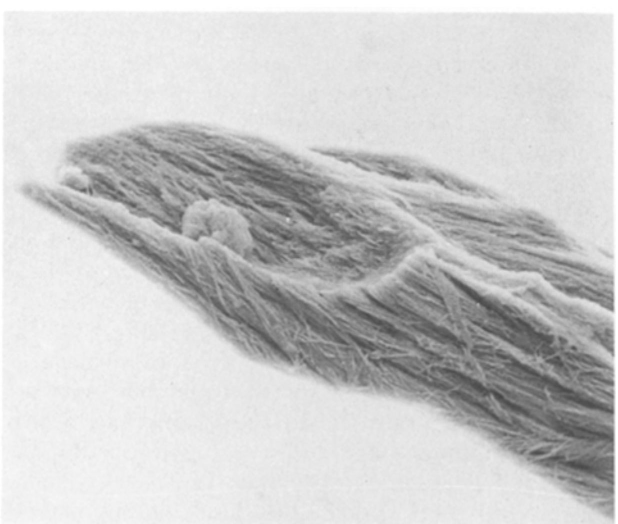


Fig. 12. Male, 71 years, osteoporotic. Tip of a rod which has been completely cut through by osteoclasis. Field width 50 μm

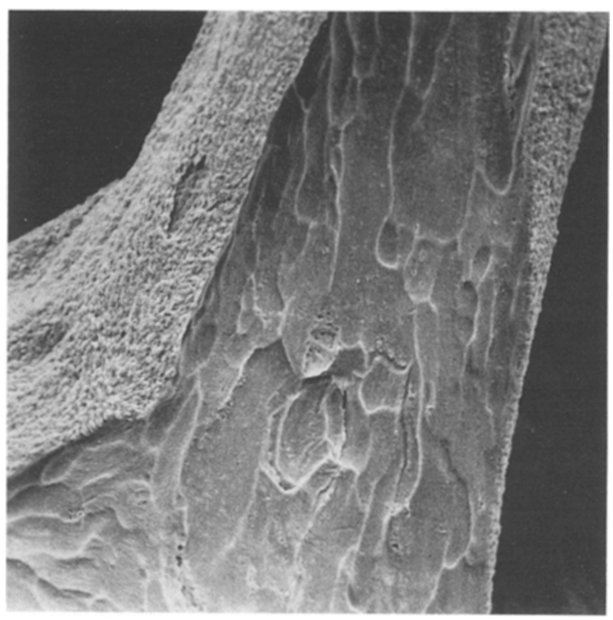


Fig. 14. Female, 91 years. Trabeculum very deeply grooved by resorption. The mineralized collagen in the back wall of the lacuna exposed by resorption was intact, presumably protected by an osteocyte. Field width 190 μm

and at different ages. These variations were related to the structural changes of trabecular bone that occur with age, such as thinning, perforation and removal of structural entities. The size and shape of resorption bays varied from very long, shallow, elongated furrows ("snail track" resorption bays: Boyde and Jones 1979) to rounded deep lacunae (Fig. 11). The elongated tracks were usually aligned with their neighbours and followed the orientation of collagen in adjacent areas (Fig. 1; Reid 1987). Around openings on the plates, resorption bays followed the circumference of the opening, suggesting that they also track the collagen orientation here (Fig. 5). The amount of bone removed by resorption varied from superficial skimming of surfaces to complete perforation or disconnection of trabecular elements (Fig. 12).

In young specimens, resorption was dominantly superficial (Fig. 2) and involved extensive areas over the trabecular surface. Such resorption was followed by formation to cover up the area resorbed (Fig. 6). In most instances, resorption seemed to have been initiated at a node and had advanced towards surrounding rods and

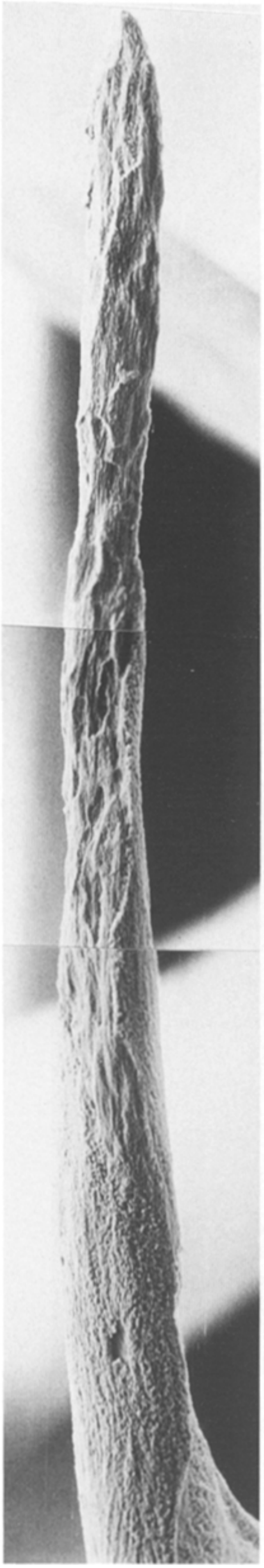


Fig. 15. Male, 69 years. Trabeculum terminated by osteoclastic resorption. Montage ×475

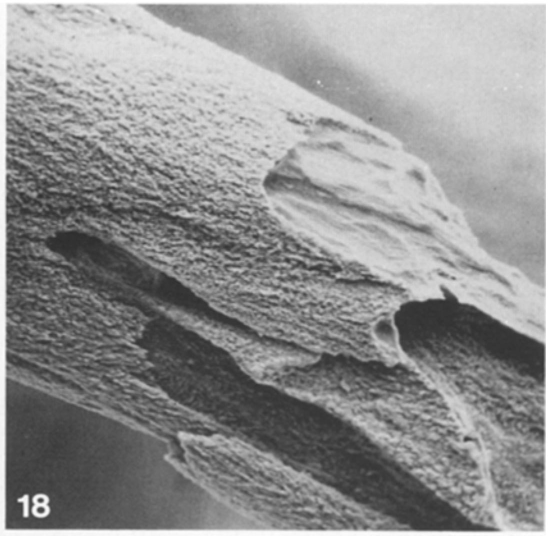
Fig. 16. Female, 89 years, osteoporotic. A rod-shaped trabeculum cut away by deep resorption (final disconnection of the rod may have occurred during specimen preparation). No superficial resorption can be seen on surrounding mineralizing front surface. In the upper part of the figure, a trabeculum has been completely surrounded by newly formed tissue. Field width 470 μm

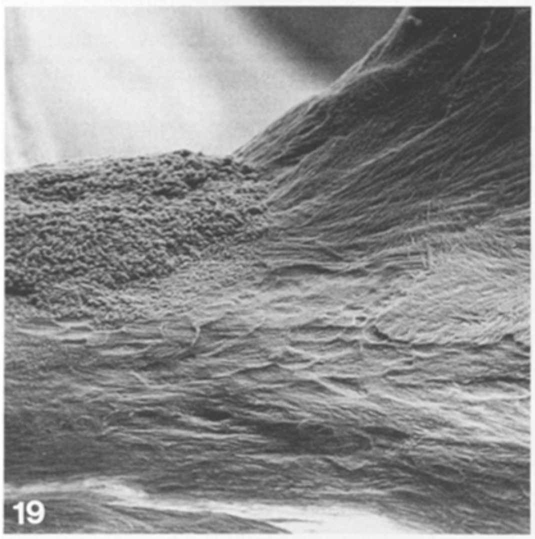
plates. This type of resorption can be considered as a part of the normal remodelling process where bone mass is maintained through coupling of the two processes.

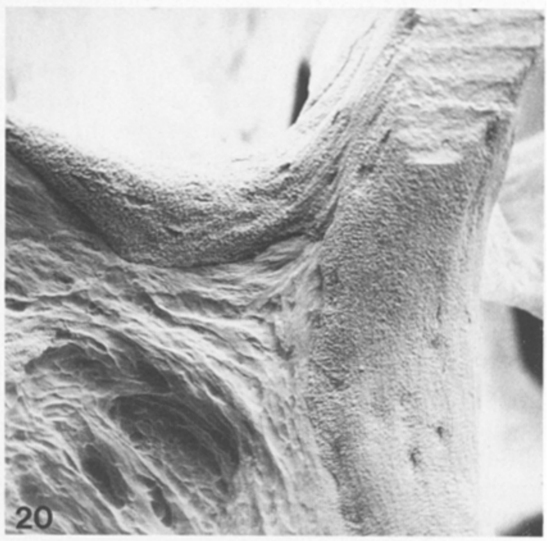
The removal of trabecula seemed to be initiated by the appearance of perforations on different elements simultaneously and was most often seen in old and osteoporotic specimens, although occasional perforations were also observed in younger specimens. They frequently appeared to be initiated at a node or at the centre of a plate (Fig. 13) where superficial resorption had occurred previously. Perforations sometimes commenced from the base of a previously formed groove, most commonly during resorption of rods (Fig. 14).

Many different types of resorption pattern were observed in rods. The thinning of rods seemed to have been brought about by successive episodes of osteoclastic resorption from one node to the other (Fig. 15). The elongated, shallow, narrow track type of resorption, with parts of remaining tracks from previous episodes, was frequently seen on such surfaces. Sometimes a mixture of both skimming and deep types of resorption bay was evident on the same trabeculum (Fig. 11).

When removal of a rod rather than thinning had resulted, three distinct resorption types were observed. Firstly, without any evidence of prior superficial resorption, short but deep excavations were present, cutting right across a trabeculum. In some specimens it appeared that the trabeculum may have broken away before a complete separation, perhaps by a minimal load in vivo or during the preparation of the specimen (Fig. 16). This type of resorption was usually observed at the end of a rod where it was connected to a node or a plate. Secondly, after superficial resorption characterized by the snail track type of bays, some rods were deeply grooved by what appeared to be a more aggressive type of osteoclastic activity, making an extensive concave surface to the trabeculum (Fig. 17). Perforations or rod severing sometimes appeared to have commenced on the floors of these grooves. Thirdly, osteoclasts grooving a rod may have "tunnelled in", undercutting the surface (Fig. 18). Sometimes several such tunnels could be seen around one trabeculum, with some showing evidence







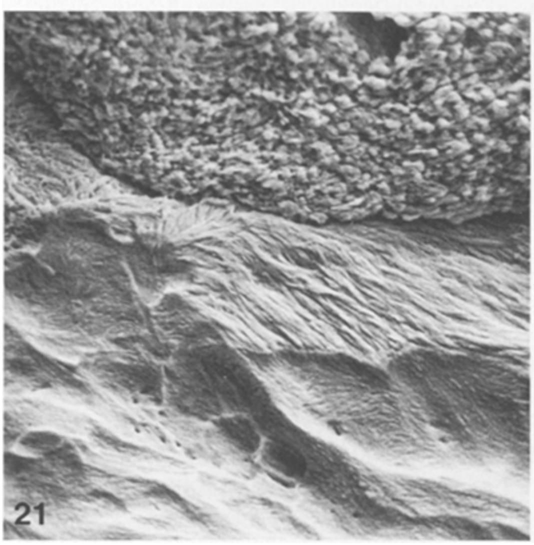


Fig. 17. Female, 89 years, osteoporotic. Both superficially and deeply resorbed rod. Field width 470 μm

Fig. 18. Female, 91 years. Three undercut grooves on a single rod: evidence of repair is seen in the mineralizing front morphology in the floors of these grooves. The unresorbed surface of the rod also has a mineralizing front morphology. Field width 190 μm

Fig. 19. Female, 75 years. A superficially resorbed trabecular surface (*below*) being covered by a thick formative (mineralizing) front (*left*), resting surface right. Field width 190 μm

Fig. 20. Female, 75 years. Two large formative, mineralizing fronts (forming new bone packets or parts of the same packet) approaching each other from two sides to cover resting surface and several generations of resorption bays. A deep pit at the centre of the plate might indicate an early step towards perforation. Field width 470 μm

Fig. 21. Female, 75 years. Higher magnification showing detail of mineralizing front from **Fig. 20.** New formation has partially covered fully mineralized collagen bundles at the upper part of the surface, with resorption in the lower part of the field. Field width 85 μm

Fig. 22. Male, 74 years. Disconnected end of a trabeculum. Field width 540 μm

of repair in the base. Excavation by the osteoclasts had obviously continued in some instances until or after the rod was disconnected, especially with the deeper types of resorption.

The floors of resorption bays showed a variety of microscopic textures. Smooth floors were evident where the surface was resting after an initial resorption event (resting resorbed: Figs. 2, 15). The "snail tracks" frequently displayed this texture. In areas of active resorption, collagen fibre bundles with various orientations were observed in the exposed lamellae at different depths (Fig. 9), while mineral nodules of varying sizes were apparent on the floors where active bone formation had begun (Fig. 18). Osteocytic lacunar profiles of different sizes were also frequently observed within resorption bays (Fig. 14).

Another feature consistently observed in both young and old trabecular bone during the present study was the resorption of osteoid (non-mineralized matrix, whether or not still mineralizable) by osteoclasts (Boyde 1968; Boyde and Hobdell 1969a, b), indicating that osteoclasts do not confine their activity to fully mineralized bone surfaces.

The specimens used during this study were made superficially anorganic by treating them with hydrogen peroxide to remove the unmineralized organic matrix. This treatment regime is preferred to the more aggressive preparation with, for example, cold sodium hypochlorite or hot 1,2-ethane diamine that was used in prior studies because it leaves delicate trabecular structures strong enough to withstand minor shocks in handling.

As in cortical bone, different stages of mineralization could be recognized from the texture of mineralized surfaces, even though mineral clusters in osteoid may be lost during the preparation. These ranged from stages with less elongated mineral nodules in which it was more difficult to see the direction of the collagen fibres (Figs. 1, 19), to those where the nodules were well aligned, which may represent a later stage in the completion of mineralization. The finding of mineralized lengths of individual collagen fibrils may indicate a looser packing of fibrils or a surface reaching a resting phase (Fig. 3).

In the young adult specimens, the amount of bone formed was more or less equivalent to the amount resorbed (Fig. 6), with local restoration of smoothly convex surfaces. This would result in a maintenance of bone mass, with little change in size and shape of the individual trabecular elements. Contrary to this, in old and osteoporotic specimens, extensive areas of mineralizing front were observed, spreading over resting and resorbed surfaces (Figs. 19, 20 and 21). In plates, such fronts appeared to have advanced as steeply thickening coats from two sides towards each other (Fig. 19), while in rods, signs of mineralization (indicating new formation) sometimes surrounded a trabeculum (Fig. 16). This process would undoubtedly change the size and shape of trabecular elements and account for the compensatory thickening and structural changes of some trabecula seen in old age. The morphological type of mineralization was not constant in the old: this may explain the rugged appearance of trabecula seen especially in osteoporotic specimens.

Mineralization, indicating repair, was observed not only in shallow resorption bays but even in deep tunnelling grooves (Fig. 18). The surrounding surface was often still incompletely mineralized when deep resorption had disconnected a trabeculum, and new mineralization was also observed on disconnected trabecula. The extent, siting and character of resorption and repair often appeared to be quite independent of each other in the older specimens, indicating an uncoupling of these processes.

Osteocyte lacunae showed several morphological differences depending on the activity status of the surface, irrespective of age. Generally, they were elongated with their long axes aligned with the surrounding collagen fibre bundles, as previously described (Jones 1973). Examples of half-formed lacunae in resting or forming surfaces can be seen in Figs. 2–4. Resorption also had exposed lacunae at different depths, forming profiles of various shapes on the surface (Fig. 21). The walls of the osteocyte lacunae were sometimes proud of the resorbed surface (Fig. 14) indicating a degree of protection offered by the surviving osteocyte in vivo (Boyde 1980).

The collagen of the walls of osteocyte lacunae was completely mineralized in resting and resorbed surfaces at all ages. Sometimes, the thick, mineralized collagen bundles of the underlying lamellae were evident (Fig. 14); and in some forming surfaces, the lacunar wall showed a pattern of randomly oriented fine fibrils (Fig. 3). The mineralizing lacunar floor showed the same characteristics as the surrounding surface in very actively forming surfaces.

The lacunar walls were penetrated by a variable number of canalicular openings, and their frequency in lacunae or on resorbed surfaces, where they were sometimes crowded together, indicating the whereabouts of underlying or previously overlying osteocyte lacunae, could not be used to assess age.

In most of the old, and especially in the osteoporotic specimens, trabecular disconnections were widely observed. These disconnected trabecula were usually rod shaped, but were thin, long and frail compared with the thick, sturdy rods of young specimens. The disconnections had occurred at any distance along the rods, and were not always microfractures, having also resulted from the resorption of the whole thickness of the trabecula by osteoclasts (Figs. 12, 15).

Microfractures were usually noted at the centre, or the thinnest and therefore weakest part of a trabeculum. They were always associated with some degree of resorption on the surface, ranging from a minimum of resorption on one side only to unequal degrees of resorption round the entire trabecular surface (Fig. 16), presumably depending on the local strain experienced.

It was evident from the gap separating the ends that once a trabeculum had become disconnected, and was therefore no longer subjected to mechanical force, both resorption and formation had continued, later ceasing and leaving the broken ends as tags (Fig. 22). Occasionally, the tips of these ends were rounded by the laying down of collagen bundles (Fig. 10).

Discussion

The results of this study show that the basic micro-organization of vertebral trabecular bone is not significantly different from that previously described for other sites (Boyde and Hobdell 1969a, b; Boyde 1972; Reid 1987). The differences noted reflected the structural variations in trabecular architecture. Thus, in rods the main alignment of the collagen bundles is along the main axis, whilst in plates various collagen orientations are possible, depending on their shapes. Superficial, skimming resorption follows collagen orientation. Accordingly, in oval or round openings of the plates, resorption bays are arranged around their circumference.

The most interesting results of the present study concern the incidence of the different surface activity states. In the young age group, a normal remodelling process with a morphological coupling of resorption and formation was inferred. However, in the older age group, and especially in the osteoporotic subjects, many changes were evident in conformity with the known structural changes in trabecular elements that occur with advancing age.

It is well known that the rate of mineralization in adult trabecular bone tissue (at around 0.9 μm per day) is considerably less than the values found in young growing individuals. The indifferent morphology of the fronts here regarded as arrested mineralizing fronts could possibly reflect the lesser mineralization rate and disorganization of the superficial collagen. However, the amount of the surface with this topography was clearly greater than any reported estimate of the proportion of surfaces at which double tetracycline labels – indicating active, measurable progression of the mineralizing front – have yet been found. Thus it seems that elderly and osteoporotic individuals have, to an extent increasing with age, non-mineralized matrix present at free bone surfaces, and our unpublished data suggests that thin layers of non-mineralized matrix may also be included within bone. The question arises as to whether this non-mineralized matrix can validly be called osteoid, as at present there is no evidence to suggest that such layers can or do mineralize. Rather, the reverse must be true for much of the surface, because osteoclastic resorption occurs in and through the layer without an interim stage of full mineralization of the collagen.

Arrested mineralization fronts are a common finding in pathological conditions bracketed under the term histological osteomalacia, here underlying thick layers of non-mineralized and, we contend, non-mineralizable matrix. Again, resorption can and does occur through the defective "osteoid", and masses of such non-mineralized matrix are removed in healing "adult rickets" not by mineralization, but by resorption during remodelling-replacement (Boyde et al. 1986).

The trabecular bone structure consists of a complex three-dimensional network of plates and rods (Whitehouse et al. 1971). During age-related bone loss, thinning and perforation of trabecula leads to a conversion of plates to rods, with the end result of removal of entire structural elements (Parfitt et al. 1983). In describing the mechanisms involved in this process, a quantum concept has been proposed (Parfitt 1979), according to which bone loss occurs either because osteoclasts erode cavities that are too deep, or because osteoblasts deposit new layers of bone that are too thin. The former process has been attributed to the rapid loss of trabecular bone resulting from complete removal of structural elements, and the latter to a slow loss with progressive trabecular thinning (Parfitt 1984).

Such conclusions have been reached from studies made on thin histological sections and by measurements of quantities such as mean trabecular wall thickness. Arnold (1970, 1981), using macrophotographs of trabecular bone specimens, first proposed the occurrence of perforations due to focal excessive resorption which led to thinning and loss of structural elements. During the present study with the SEM, it was possible to study the initiation of such perforations, usually at the centre of a node or a plate. The fact that their appearance is preceded by superficial resorption underlines the presence of two types of osteoclastic activity. Similar differences were also observed in rods, where successive episodes of superficial resorption led to thinning, while deep grooving, tunnelling or perforation was responsible for their disconnection. The two patterns of resorption can be interpreted as indicating different movement patterns of the osteoclasts (Jones et al. 1986). The superficial planing of the surface suggests lateral movements during resorptive phases, a co-ordinated wave of resorption passing over the surface. The deep or vertical resorption evidently involves little lateral movement during resorption.

Although new bone formation was observed on most of the surfaces and even on the floors of deep excavations made by osteoclasts, the resorption bays were rarely filled, particularly in the older bone. The results of this study therefore confirm the quantum concept of bone loss, but also emphasize the importance of the location of aggressive resorptive activity.

Two aspects of uncoupling between formation and resorption were seen in the present study, one explainable by a delay in the recruitment of osteoblasts until several episodes of resorption, or even perforation, of the trabeculum had occurred, and the other where arrested or active mineralizing fronts were disproportionately common when compared with younger age group, evidence for a compensatory increase in trabecular thickness unrelated to microcallus formation (Atkinson 1967; Siffert 1967; Pesch et al. 1977).

The observation that fractured trabecula were frequently partially resorbed confirms that microfractures may occur when resorption weakens the trabecula to such an extent that they are no longer able to withstand the mechanical stress. However, if they do not break, the resorption may continue until complete trabecular cleavage. The dramatic reduction in the number of trabecular elements with age indicates that such disconnected elements are ultimately removed by complete resorption. However, some evidence for a degree of repair of disconnected elements was also observed during the present study.

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