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Issues related to mineralized tissue biology in human evolutionary research

This communication has two primary aims concerned with mineralized tissue biology (e.g. hard tissue biology of bone and tooth) research in human evolutionary studies: First, to introduce the literature and the methods (at the time of this symposium) so that one has an idea of the nature of this research and where one can go for details of the methodologies, etc; Second — and of primary concern here — to discuss issues that have come to light as a result of these studies mainly because of its recent beginnings as a subfield within paleoanthropology.

Issues related to skeletal studies include: 1) whether different cortical surface patterns and bone tissue types influence the appearance and interpretation of bone growth activity states; 2) if SEM analyses of cortical surfaces in fossil hominids allow one to construct meaningful representations of remodeling patterns; 3) whether these representations can be used in phylogenetic arguments; and 4) how intraspecific variability would affect these issues. Issues related to dental studies include: 1) the relationship between the rate and pattern of early hominid dental development; 2) experimental support for the calibration of early hominid dental developmental rates; and 3) whether replica techniques are suitable for microanatomical studies of these sorts.

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**Introduction**

Researches on the mineralized tissue biology of early hominids have been progressing rapidly in America and England these last few years. Thus I think that now is a particularly good time to summarize the recent history of this endeavor, while the science is still fresh so-to-speak.

However, the following is not a review per se. The pioneering studies in this field are only 5 years past, and most of the subsequent papers include what is still a manageable literature review. The intention here is then twofold. First, rather to simply introduce the literature and the methods so that one has an idea of the nature of this research and where one can go for details of the methodologies, etc. Second — and of primary concern here — many new issues have come to focus as a result of these studies mainly because of its recent beginnings as a subfield within paleoanthropology and because of a general unfamiliarity amongst the anthropological community with the concepts and techniques, etc. Most of these issues are unpublished, being criticisms brought up frequently at scientific meetings. This is of course healthy but little tangible criticism has reached the science journals. To date there is no published treatment of these criticisms, nor is there a theoretical outline on which to assess some of these issues, and so much of this paper will be devoted to these matters.

In the main, developmental studies of early hominids have focused on mechanisms/processes of growth (i.e., the secretory activities of bone and tooth forming cells) and hence the developmental dynamics of fossil hominid teeth and bone. DAHLBERG (1965)
equipped that such studies were not amenable to alizarin injection techniques or longitudinal radiographic assessment of embedded bits of «Bjorkian metal». He noted:

In general, it must be admitted that fossils and skeletal materials have been well described, classified, and studied. Some have been the subject of cephalometric techniques for limited comparative studies. Measurements have been made, recorded, and processed but very little has been gleaned regarding the specific processes of growth and development...the actual mechanism that produces a specific face, tooth, or part has not received sufficient attention (p. 159).

Earlier approaches to fossil hominin skeletal and dental development concerned themselves with patterns of ontogenetic change. For instance, Rak & Howell (1978) compared a juvenile Paranthropus calvarium to that of an adult of the same species and inferred the growth necessary to accommodate the difference between them. Heintz (1966) plotted hominin cranial specimens over regressions of ontogenetic dimensional change in apes of various but unknown ages to demonstrate the vectors of their growth pattern. Skinner (1978) succeeded Heintz (1966) by introducing dental maturation criteria (biological age determinations) into studies of craniofacial ontogenetic change rendering a more complete portrayal of early hominin growth and development.

Until recently, radiodontological studies prevailed in descriptions of fossil hominin developing dentitions (ie., Skinner & Sperber, 1982; Sperber, 1985). Alan Mann (1975) compared the pattern of dental development, eruption and wear from four Paranthropus mandibular fragments to human and chimpanzee developing dentitions. From this he concluded that early hominids demonstrated a hominine pattern of growth and development.

However, more recently, established mineralized tissue biology theory and techniques, as for the study of enamel (e.g., Boyde, 1963) and bone (e.g., Boyde & Jones, 1972) formation, have been adopted by human paleontologists to study the processes of early hominin growth and development. For the most part these studies (below) are distinguished by their utilization of light and scanning electron microscopy to characterize the mineralizing fronts of fossil enamel, dentine and bone. Discussion pertinent to both skeletal and dental studies will be presented here.

Skeletal studies

I. Bone growth remodeling (versus remodeling associated with repair, mineral homeostasis, Haversian system development, etc.) refers to the coordination of bone deposition and resorption during the resizing and shaping of bone during growth. Broman (1984a) first conducted bone growth remodeling research on fossil hominids. It was shown that the microanatomy of both forming and resorbing surfaces, characteristic of the remodeling mechanism, could be examined by an integrative light and scanning electron microscopy approach. This study was balanced, of course, by research on the abrasion of depositional (forming) bone surfaces because these surfaces suffer most during the fossilization process.

Methods appropriate to the study of fossil hominin bone growth remodeling research have been described in detail elsewhere (Broman, 1984b, 1985a,b, 1987a) and are only briefly summarized here. Scanning electron microscopic (SEM) imaging of developing cortical bone surfaces reveals characteristic microscopic surface features of bone formation and resorption (Boyde, 1972, 1980; Boyde & Jones, 1972). Bone forming cells, osteoblasts, elaborate an organic matrix containing collagen which subsequently mineralizes. The
mineralizing front is characterized by incompletely mineralized collagen fiber bundles represented by spindle-shaped mineral clusters aligned in tandem along the lengths of the fiber bundles. Collagen fiber bundle orientations are often related to the associated vasculature and may be organized into a much larger feature called intervascular ridging bone (IVR). This cortical surface pattern is relatively resistant to abrasion and makes possible the identification of forming bone surfaces on abraded fossil hominid bone (Bromage, 1984b). Bone resorption is an integral part of the bone growth remodeling process that permits the resizing and reshaping of bone during growth. The coordinated activity of bone matrix resorbing cells, osteoclasts, results in fields of anisotropic resorption bays (Howship’s lacunae) visible by SEM on fossil hominid bone.

A high-resolution replication technique, using an addition-cured silicone-based dental impression material to form the negative, and an epoxy resin to form the positive, is most suitable for the imaging of fossil material by SEM (Bromage, 1985a, 1987a). These materials science researches have indicated that detail on the order of 0.1 to 0.3 microns is replicated, which is far smaller than required to image IVR bone and resorption lacunae (some thirty and more times smaller). The metalized replicas, prepared for SEM, lend themselves to the preliminary imaging of IVR bone by low magnification light binocular microscopy.

When all aspects of this methodology are employed it is possible to map immature fossil hominid bone growth remodeling fields and explain the respective morphogenetic consequences. There are two preliminary (Bromage, 1985b, 1987b) and one comprehensive account (Bromage, 1989) of early hominid facial remodeling.

These studies have revealed that specimens attributed to Australopithecus retained the primitive hominoid facial remodeling pattern (i.e., depositional on all anteriorly-facing surfaces), reflecting their relatively prognathic facial profiles compared to modern Homo. Paranthropus exhibited a unique facial remodeling pattern somewhat paralleling modern Homo (i.e., some resorptive fields on anteriorly-facing surfaces), accounting for the relative orthognathy of this taxon.

As I believe that phylogeny is defined as shifts in ontogeny through time, it is apparent that ontogenetic data may inform us about and test claimed morphological transformation series’ and synapomorphic and symplesiomorphic characters. For instance, Bromage (1989) has suggested that a morphological similarity of the midface between A. aferensis and Homo is the result of uniquely derived ontogenetic mechanisms in the latter. Thus what could be interpreted as a shared primitive condition might instead be interpreted as a homoplasy.

II. It is both important and relevant to address the problems and the potential of microscopic analyses of surface bone growth remodeling. In particular, four main issues have been identified. First, do different cortical surface patterns and bone tissue types influence the appearance and interpretation of bone growth activity states? Second, do SEM analyses of cortical surfaces in fossil hominids allow one to construct meaningful representations of remodeling patterns? Third, can these representations be used in phylogenetic arguments? Fourth, how would intraspecific variability affect these issues?

The first question can be approached by recounting the criteria employed in SEM interpretations of bone growth activity states. The forming bone surface of parallel fibered lamellar bone tissue types, prepared by making the most superficial layers anorganic, show a mineralizing front in which the collagen fiber bundles are incompletely mineralized as demonstrated by mineral clusters along their lengths (Boyde, 1980). These mineral clusters are not confined to the collagen in woven bone. Howship’s lacunae, resulting from the resorbing activities of osteoclasts over woven bone tissue surfaces are
essentially the same as that observed over adult lamellar bone (Boyd & Hobdell, 1969).
Resting bone surfaces also figure in the classification of bone growth activity states (Jones & Boyd, 1970).

These surfaces are characterized by a general smoothing and rounding of the edges of resorption lacunae and a gradual loss of collagen fiber definition, irrespective of the cortical surface type. Only by electron microscopy of the bone surface is it currently possible to make these kinds of distinctions (i.e., light microscope studies are currently unable to make these distinctions).

Bone growth activity states can thus be interpreted regardless of the bone tissue type, provided that incompletely mineralized collagen fiber bundles, sharp-edged resorption lacunae and/or evidences of resting-formed or resting-resorbed surface features are evident (e.g., Reid, 1987). It is also apparent that the related cortical surface patterns do not interact in any way with the bone growth activity states to prevent their correct interpretation.

Cortical surface patterns are generally described on the basis of the forming bone activity state and its associated vasculature. Developing fine cancellous, or woven bone tissue is characterized by a random network of collagen fibers deposited around a profuse network of vascular canals such that its surface appears very rough and porous. This tissue type grades into one which is less porous and yet again into one which is a parallel fibred lamellar bone characterized by a moderate network of vascular canals and an undulating cortical surface parallel with the orientation of the collagen fiber bundles and vasculature (TVR bone: cf. Bromage, 1984b).

This surface grades into one which is highly oriented, contains relatively few vascular canals and has a smooth surface. These cortical surface patterns reflect the rapidity of bone formation from relatively fast in the case of woven bone (4 or more microns per day) to relatively slow in the case of adult lamellar bone (0.9 microns per day) (cf. Boyd, 1980).

Given that cortical surface patterns are defined on the basis of the forming bone growth activity state, it can be generally deduced that the presence of these patterns determine bone formation and nothing else. By definition these patterns do not involve resorptive growth reversals, contrary to Oyen et al. (1979) who suggested this possibility in the formation of the «vermiculate» surface pattern. Rather, in the vicinity of a reversal the cortical surface pattern will either grade over a short distance into the resorptive field or it will abruptly meet the resorbing edge of the reversal.

In practice the relation between a particular cortical surface pattern and the forming activity state will not always be faithful simply because of the lag time between the onset of a resorptive reversal and the time that the surface pattern is obliterated. This lag time is bound to be relatively short, however. Stereopair SEM micrographs of resorbing woven bone surfaces appear to show that the elevations above the numerous vascular canals are resorbed away first, thereby leveling the surface relief (cf. Boyd & Hobdell, 1969). Subsequent interpretations of the bone growth activity state would have to be made by SEM, upon which the resorptive lacunae would be clearly visible. The low undulating relief of primary vascular bone would also reduce to a gross resorptive plane which would then have to be verified by SEM. Such would also be the case for the remaining parallel fibered surface patterns and, in addition, over the various consolidated, compacted and remodeled tissues that erode to the surface by cortical drift.

Second, it may justifiably be asked if one could determine representative patterns of facial remodeling on fossil hominids based on SEM analyses of cortical surface patterns. The TVR bone pattern described by Bromage (1984b) has been taken to represent
patterns, any differences in the size of a bony structure must be due to a discrete difference in the rates of remodeling.

Even still, one should continue to be aware of the potential taxonomic and phylogenetic significance of the shape, placement and extent of remodeling patterns as other possible sources of important differences between taxa.

Fourth, insofar as craniofacial bone remodeling is linked to craniofacial form, it must then also account for the normal biological variation observed within and between populations of a species. This variation will principally depend upon remodeling differences due to age related growth phenomena, sex, individual differences and other population differences arising from influences such as dietary consistency, habitual breathing patterns, etc.

To be sure, there are no studies that purport to examine population differences in facial remodeling although we would be strongly justified in believing that much of the variation observed in modern humans, for instance, is due to a remodeling difference. How much of this difference we could attribute to remodeling patterns or remodeling rates must still be investigated. In any case, no such control in studies of early hominid facial growth is possible at the present time particularly since the likelihood of recovering hominid specimens belonging to single populations is very remote.

Individual variation has been investigated by Kurihara et al. (1980) who noted that «variations in the distribution, configuration and size of these resorptive fields relate to the topographic characteristics of the different individual specimens» (p. 104). This variation could have been the result of genetic, epigenetic or environmental factors but it nevertheless reveals the possibility that, with further work, we may be able to develop criteria for the prediction of remodeling patterns from morphological variations. Until then it will not be possible to identify individual remodeling differences from general species specific remodeling states in early hominids.

There are no studies that examine remodeling differences between sexes of a species. Again we would be justified in suggesting that the size and shape differences we observe are due to differences in remodeling. We might predict, however, that the difference in size, especially in the case of modern humans, might not be due so much to remodeling rate differentials but due to the longer duration of growth in the female. Differences in form, however, can equally be accommodated by rate differentials as well as variations in the remodeling patterns.

Kurihara et al. (1980) examined the distribution of resorptive fields in modern human maxillas and mandibles from 36 individuals ranging from perinatal to 14 years in age. They noted an age related development and spread of resorptive fields which established themselves fully by the mixed dentition stage, beginning about 6 years of age. However, whereas maxillary reversals began to develop before or during the early primary dentition, mandibular reversals lagged behind until the later primary dentition. Thus there is a certain amount of age related change in modern humans. If this can be used as a model for the hominoids in general then we can be assured that the definitive growth remodeling state has been achieved by most hominids studied to date (Bromage, 1989).

There is one further point that should be made. the real and potential sources of variation noted above cannot exceed to any marked degree the basic species specific remodeling pattern. Indeed, this basic pattern underlies the most fundamental property of harmonious craniofacial growth and distinguishes species that we differentiate on the grounds of their craniofacial morphology. In theory, therefore, we must be able to differentiate unique patterns of facial growth and remodeling between these species which transcend the variations superimposed by age, sex, individual and population differences.
forming bone surfaces only when it occurs. The mapping of this surface pattern by low magnification stereo light binocular microscopy is a minimum estimate of the extent of forming bone surfaces on growing bone. Subsequent SEM imaging of the bone surfaces could help to verify the presence of the pattern, show an encroaching resorptive field, or illustrate the formative landscape of lamellar bone tissue which cannot be discriminated from other smooth surfaces by light microscopy.

One of the important benefits of the abrasion studies by Bromage (1984b) was the appreciation that a surface had actually been abraded, if even in some undefined manner. This makes it possible to avoid the possibility of classifying an abraded surface as a biological one. Thus abraded surfaces are not mapped by speculation and the results of microscopic analyses refer only to evidences of bone growth activity states. However, because of some surface abrasion on most fossils, it is not possible to discriminate resting bone surfaces from active ones. The remodeling interpretation explicitly states that a given surface is representative only of the last bone growth activity state. However, this latter problem is shared by all remodeling studies to date which have employed the histological technique. The histological studies of facial remodeling by Enlow and his coworkers classify all bone surfaces as either depositional or resorptive although we know that an increasing proportion of bone surfaces are resting during growth (Reid, 1987) and that this has been recognized as an important surface activity for some time (e.g., Hoyte, 1966).

Nevertheless, the remodeling interpretations provided by the histological data have been successfully applied to morphogenetic interpretations of facial growth for many years (e.g., Enlow, 1962, 1966a,b, 1968, 1975). This indicates that the relation between the last bone growth activity state and craniofacial morphogenesis is a close one and that it will have some validity in its application to facial growth and remodeling interpretations of fossil hominids. Thus, except for the limitations imposed on remodeling interpretations by surface abrasion, it may be concluded that analyses of cortical surface patterns combined with SEM observations of remodeling surface features, can provide meaningful representations of remodeling patterns (Saunders, 1985).

Third, it is my interest in the relation between ontogeny and phylogeny that makes me query the potential that remodeling patterns may have in phylogenetic arguments. However, if one accepts that phylogensis is the result of repeated shifts in ontogeny through time, then it is evident that a specific ontogenetic comparison between organisms may also be used in a phylogenetic argument. It should, of course, be understood that the same limitations apply to the validity of these arguments as apply to all phylogenetic comparisons (e.g., discriminating a parallelism from a shared derived trait).

It must also be acknowledged that many morphological features of the craniofacial skeleton are used to define early hominid taxa which we then link into some phylogenetic relationship. By recognizing the intimate relation between bone growth mechanisms and a resultant morphology, we can also recognize the taxonomic and, potentially, phylogenetic importance that differences in craniofacial remodeling have in phylogenetic arguments.

In practice this does not exclusively depend upon differences in remodeling patterns. The rate of a growth remodeling activity is also important. Just as the rate of bone formation is related to the size of a bone when measured against age (Sullivan, 1976), so is it related to taxonomic and phylogenetic differences, as are the remodeling patterns. Indeed, if one accepts that size differences apply in the characterization of taxa and phylogenetic change, then should the remodeling patterns be the same, remodeling rates will necessarily be invoked in descriptions of ontogenetic and phylogenetic differences. In other words, given similar growth and development periods and craniofacial remodeling
patterns, any differences in the size of a bony structure must be due to a discrete difference in the rates of remodeling.

Even still, one should continue to be aware of the potential taxonomic and phylogenetic significance of the shape, placement and extent of remodeling patterns as other possible sources of important differences between taxa.

Fourth, insofar as craniofacial bone remodeling is linked to craniofacial form, it must then also account for the normal biological variation observed within and between populations of a species. This variation will principally depend upon remodeling differences due to age related growth phenomena, sex, individual differences and other population differences arising from influences such as dietary consistency, habitual breathing patterns, etc.

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In practice our ability to differentiate species specific patterns amongst closely related species, and forms with a very similar craniofacial morphology, will depend upon our technical assay, especially when remodeling rate differences have to be identified.

**Dental studies**

I. We originally embarked on studies of early hominid dental development because the age in chronological years, at which bone growth remodeling and morphogenetic events actually occur, is the dependent base on which to assess, for instance, differences in rates of growth between modern humans, early hominids and the apes. Thus my colleague, Chris Dean, and I published the first of a generation of studies on early hominid developing dentitions that challenged the prevailing paradigm on which hominin studies were then based (Bromage & Dean, 1985).

We noted that coarse incremental growth markings in enamel, called striae of Retzius, could be seen passing obliquely from the enamel-dentine junction to the tooth surface where they became visible as perikymata (particularly on human and hominin permanent incisors).

Whereas the amount of enamel between striae of Retzius varies, there is an average of 7-8 cross-striations between adjacent stria of Retzius. Cross-striations occur along the lengths of enamel prisms and it has been generally accepted that they result from a circadian variation in the rate of matrix secretion by enamel forming cells. This suggests that, in turn, perikymata occur with the same near-7 day, weekly, or circa-septan periodicity.

We obtained high resolution replicas of incisor crowns for several early hominin species and observed them by SEM. Then, by counting the number of perikymata and adding a liberal 9 months for other estimated variables, a crown formation time could be obtained for incompletely formed lower incisor and upper central incisor crowns. This also represents age at death because these crowns begin to calcify around birth. We thus showed that surface manifestations of incremental growth features of enamel reflected a known periodicity and hence an absolute time-scale for dental development events.

Chronological ages at death for hominids were calculated that corresponded to a more ape-like than human pattern of growth and development (Bromage & Dean, 1985), contra Mann (1975).

II. Subsequent research expanded the scientific basis for this work and dealt with three primary issues. First, the difference between the rate and pattern of dental development. Second, the confirmation of enamel incremental periodicity. Third, the efficacy of replica techniques employed.

After the Bromage and Dean (1985) publication there was much public (i.e., unpublished) debate over the relation between pattern and rate of dental development.

Basically, our conclusion was that little could be said about the durations of dental developmental events from ‘pattern’ information alone, as Mann (1975) had done for Paranthropus (cf. Bromage, 1987c). For some it was confusing that we had obtained ages at death for hominids, which we likened to ape-like growth and development schedules, while crown formations times between some hominids and modern humans and apes were not so different. However, what was important was that many of those hominid specimens, aged at something like 3 to 3.5 years, also had first permanent molars coming into occlusion. In humans the central incisors erupt into the mouth in proximity to the eruption of the first permanent molars at around 6 years of age. In extant apes the central incisors erupt into closer proximity to the second permanent molar while the first permanent molars erupt at around 3 to 3.5 years of age.

In the case of Australopithecus, for instance, the pattern of incisor development and eruption was demonstrably like that of the extant apes. Importantly however, the rate of dental development was also demonstrably like that of the extant apes inasmuch as their first permanent molars had erupted at around 3 years of age. Paranthropus on the other hand was human-like in its pattern of incisor eruption (i.e., coincident with the first permanent molar) but their first permanent molars were erupting at such an early age (around 3 years instead of 6 years as in humans), illustrating the ape-like maturation period in which these events were taking place. «These results reflect a dramatic advance in our appreciation of the biology of these species which have, until now, been regarded in ‘human’ years» (Bromage & Dean, 1985, p. 526). Indeed, it represents a new paradigm on which to interpret aspects of early hominin biology and lifestyles.

Thus over the last three years more than a dozen contributions by Chris Dean, David Beynon, Glen Conroy, Holly Smith, myself and colleagues, employing a variety of independent methods (e.g., enamel incremental periodicity, rate of enamel formation, radiographic imaging, computerized tomography, dental developmental pattern, and life history correlation) have indicated that Plio-Pleistocene hominin growth and maturation periods were more like those of modern apes than humans.

Second, critics have noted that incremental features of enamel employed in a few of these studies, were assumed to represent daily and circa-septan rhythms (cf. Bower, 1985, 1987) (there being much circumstantial evidence collated over the last 3/4 of a century) (cf. Dear, 1987a). For instance, Boyde (1964) counted every cross-striation from the neonatal line through the developing dentition of a child and obtained an age at death consistent with conventional age determinations.

Thus I was drawn to the experimental study of enamel incremental periodicity to test this assumption. I was also drawn to such a study because at the most fundamental level of investigation, that is the enumeration of enamel circadian increments, it represents a method of determining the duration of life history periods over which enamel is formed that depends not on intra- or interspecific developmental variation.

Confirmation of enamel incremental periodicity was made possible using Macaca nemestrina developing teeth that were sequentially labeled at recorded intervals with three fluorescent substances chosen for their reported minimal interference with bone growth compared to other vital labels. Thus it was possible to confirm that indeed cross-striations represented daily incremental events (Bromage, 1991).

Third, recently Alan Mann and colleagues (1989) presented yet another important issue for those wishing to employ high-resolution replication techniques. These authors also tried to replicate human incisor crowns and count the numbers of perikymata.
However, something on the order of half the numbers of perikymata were obtained (this would push incisor crown formation times into the macaque range) compared to the numbers that Bromage and Dean (1985) had obtained for a comparative sample of human central incisor crowns with a continuous series of perikymata. This might make suspicious rugose replication techniques, accounting for the discrepant results. (The original data obtained by Bromage and Dean (1985) on modern human teeth were gleaned from SEM imaging of the actual specimens themselves, not replicas).

We know very well that anthropologists wishing to conduct mineralized tissue research must take to heart the relevance of many endeavors, not the least of which is a materials science approach to complement their microstructural research. Thus these problems are not a worry insofar as materials science investigations have indicated that detail on the order of 0.1 to 0.3 microns may be replicated (Bromage, 1985a, 1987a; Beynon, 1987).

Conclusions

There is much to be gleaned from mineralized tissue biology approaches to human evolutionary research. It is my hope that the summary of these developments and theoretical and practical issues provided here, will stimulate others to objectively pursue this new approach to address old problems.

It is clear that mineralized tissue biology has a great deal to contribute to our understanding of human evolution. Where fossils were once dead lumps of bone, teeth and morphology, they now exude the lives of their owners. We can translate the cellular behavior of these fossils' bone and tooth forming cells into ontogenetic and phylogenetic data, and even now begin to characterize many aspects of early hominid life history.

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