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BIOMECHANICS OF THE HOMININE CRANIUM WITH SPECIAL REFERENCE TO HOMO ERECTUS AND THE ARCHAIC HOMO SAPIENS

by

Christopher John Knüsel

B.A.(Hon.) University of Wisconsin-Madison 1984
M.A. University of York, York, England 1986

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

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Abstract:

The adult cranium has traditionally been used to construct hominine phylogenies. This approach, however, disregards the acquired, functional components resulting from cranial growth and development. Such phylogenies are thus open to questions of validity. In order to remedy this situation a biomechanical analysis of the cranial first-class lever system was performed to interpret cranial shape, and a series of osteological observations made which identify anterior dental loading as an habitual behaviour of the earliest hominines.

A quantitative analysis employed craniometric measurements of the size, shape, and lengths of the load and lever arms of a series of crania drawn from a mixed hominine cast collection, a very robust Northwest Amerindian sample, and a gracile Calcuttan sample. Statistical comparisons of the attachment area of M. semispinalis capitis demonstrated strong correlations between cranial thickness and the lengths of the load and lever arms.

A photoelastic analysis, which allowed recording of both the magnitude and direction of strains, was carried out to determine how differing cranial shapes influence the transmission of applied forces. The results indicate that the cranial vault of each specimen experiences differential deformation in response to loads of identical magnitude. The Homo erectus cranium demonstrates a unique directional strain pattern different from that of the Cro-Magnon and Skhul crania, whose strain patterns were more similar. The magnitude recordings reveal that the Skhul cranium is most well-designed to perform anterior dental loading and Cro-Magnon, the least. The *torus occipitalis transversus* and occipital bun (chignon) act to prevent transmission of forces to the interparietal portion of the occipital.

It is concluded that the shape of these early hominine crania may be interpreted to result from the commencement of strenuous anterior dental loading at an early age when the greatest impact is made on bone morphology. It is suggested that some of the assumed diagnostic occipital structures used to identify palaeospecies in the hominine fossil record may not be of genetic origin, but rather of an acquired nature, resulting from anterior dental loading and likely other behaviours involving strenuous head movement. This suggests that a re-appraisal of the palaeospecies may be in order.

"Morphology is not only a study of material things and of the forms of material things, but has its dynamical aspect, under which we deal with the interpretation, in terms of force, of the operations of Energy" (p.19).- D'Arcy Wentworth Thompson in On Growth and Form

"But, Parmenides, said Socrates, may it not be that each of these forms is thought, which cannot properly exist anywhere but in the mind. In that way each of them can be one and the statements that have just been made would no longer be true of it." Plato in Parmenides 132b

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Chapter 1: The Research Problem and Theoretical Considerations

Rassenkunde, the study of races, their origins, and their spread has occupied the efforts of several generations of physical anthropologists and archaeologists. Most recent research has demonstrated that questions of the relatedness of human groups cannot be answered from measuring the skulls of our ancestors, largely, it appears, because of the presence of factors that do not obey strictly genetic rules (see, for example, Hiernaux 1963, Howells 1973). Unfortunately, the attempts to identify "types", varieties, or races within modern humans and their ultimate failure have left a lasting mark on studies of our less numerous and less well-known earlier ancestors, the early hominines.

Many studies, and particularly those employing a cladistic method, attempt to group widely spaced and temporally sparse hominines upon supposed shared genetically controlled morphological structures. That these few individuals are representative of any previously existing species or even a population of a species is doubtful (Williams 1987). Moreover, that these crania should reveal genetic relationships is even less likely than those more recent attempts made with modern human geographic variants since they do not sample the same biological population. In truth, we do not even know which cranial traits will reveal genetic relationships. It seems, then, that fruitful research may lie not in the possibility that these relationships will be revealed, but in attempting to understand the factors which confound such attempts. This dissertation aims to identify the biomechanical significance of some size and shape parameters of the cranium that likely possess an acquired component greater than that previously considered. These are some of the potential non-genetic or epigenetic factors (those relating to growth sensu Herring n.d.) that contribute to cranial morphology and that likely derive from the function the cranium must perform in the course of growth and development. The present research employs statistical and photoelastic studies to expose some of the functional constraints that influence cranial configuration. Before embarking on a discussion of these studies, a review of the manner in which we study morphology, and specifically cranial morphology, of our hominine ancestors is in order.

1.1 The Study of Variable Morphology

Perhaps the first realisation one encounters in attempting to understand cranial morphology is that palaeoanthropologists have difficulty partitioning the observed variation in fossil hominine specimens into those of an acquired as opposed to those of phylogenetic significance. Even isolation of taxonomically valent traits by cladistic analysis may suffer from the same problem. Variably shaped crania identified within hominine populations have caused Day (1982b), for example, to suggest that stratigraphic and dating problems have contributed to the occurrence of two morphologically disparate individuals in close proximity at the Omo site; one, Omo 1, anatomically modern in appearance and a second, Omo 2, more similar to *Homo erectus* in morphology. This sort of perplexing situation may, in fact, be explained by taphonomic factors, but they may also be true associations and warrant consideration as such. Cladistic analysis has served well in providing a method for ordering hominine remains in relation to one another, but it is not equipped to answer how and why such changes occurred in the past. Several researchers have attempted to make sense of this variation through invoking "local" hominine populations (Pilbeam 1975; Howells 1980; Stringer 1982, 1985, 1989; Trinkaus 1986), "polycentric" or multi-regional evolution (de Lumley 1975, 1985; Genet-Varcin 1980; Coon 1962, Wolpoff *et al.* 1984), population isolates (Trinkaus and Howells 1979; Trinkaus 1984, 1986; Trinkaus and Smith 1985), hybrid populations (Bräuer 1984, Hublin 1983) or even "cranial races" (Howells 1973) based on general regional differences observed in skeletal remains. These notions surfaced after linear models of evolutionary change failed to accommodate the diversity of hominine morphologies in the Upper Pleistocene, after the presumed radiation of *Homo erectus* outside of Africa (Wolpoff 1980, Kennedy 1980). The Upper Pleistocene came, in time, to be recognized as a pivotal period in hominine evolution, characterised by increasingly polytypic hominines, climatic change (Turner 1975, de Lumley 1975), alterations in stone tool technology (Binford and Binford

1969, Brose and Wolpoff 1971, Bordes 1972, White 1982, Harrold 1986, Mellars 1988), and novel cultural behaviours (Harrold 1980; Shipman 1983; Binford 1985; Bunn and Kroll 1986; Potts 1984, 1988; Chase and Dibble 1987; Gargett 1989; Lindly and Clark 1990; Marshack 1989). In light of these major evolutionary changes in both the cultural and biological domains, linear evolution and concepts of evolutionary stasis have had to be emended by the concepts of theoretical population biology, specifically because of their usefulness in describing and explaining differential evolutionary changes and rates within and between populations of organisms. Consequently, the emphasis in research has shifted to a concentration on short-term evolutionary changes brought about through interactions with a variable environment as in the regional approach employed in The Origin of Modern Humans (Smith and Spencer 1984) and in Smith et al.'s recent (1990) article in the Yearbook of Physical Anthropology, "Modern Human Origins". The emphasis is on attempting to understand the processes involved in and influencing evolutionary change on a regional level. The taxonomy of processes (Gould 1977) which incorporates an appreciation of the several types of adaptation (Gould 1971) and phenotypic plasticity (Hughes 1968, Kennedy 1989) are replacing the older taxonomy of morphological end-results and static morphospecies.

Recent researchers (Bilsborough 1972, Trinkaus 1983a, Rightmire 1979, Pope and Cronin 1984, Wolpoff et al. 1984) have incorporated morphological allowances in drawing distinctions between proposed species. Each, through close scrutiny of morphology, has discerned a mosaic evolution of morphological traits that links hominine populations with succeeding populations in a geographical area; Bilsborough in Europe with Neanderthals, Trinkaus in the Middle Eastern branch of that group, Rightmire in South African Archaic Homo sapiens and Pope and Cronin and Wolpoff et al. in Asian hominines. Each has characterised these hominine groups as comprising a coherent adaptive pattern in relation to regional environments. With accumulating specimens of Homo erectus similar arguments should be forthcoming from many regions of the world. That "Pithecanthropines" and "Sinanthropines" are included in the taxon Homo erectus attests to the recognition of geographic variation in morphology (Santa Luca 1980). In response to these developments palaeoanthropologists have begun to question species recognition, specifically how and why certain features came to be and were altered in the past (Trinkaus 1983b; Stringer and Trinkaus 1981; Stringer et al. 1984; Smith 1982, 1983; Frayer 1984).

Biomechanical studies provide a method of investigating the relationship between function and form during development. As an organism grows, its skeleton must adapt to the ever-increasing and strenuous adult behaviours to which it is subjected. Bock and von Wahlert (1965) intimate this concept when they write:

> ...our understanding of biological adaptation contains certain serious limitations which may be traced back to the prevailing philosophy accepted by anatomists during the last century.

> The most pertinent element of this philosophy is the postulate that morphology should be a study of pure form divorced from function. Morphological features were treated as geometrical units that changed during ontogeny and phylogeny according to rigid and often rather 'biologically abstract' mathematical laws. Structures were not regarded, as they should be, as biological features functioning together as integral parts of the whole organism. Nor were the changes in these structures during ontogeny and phylogeny regarded as modifications in response to alterations in relationships between the form-function complex and the environment (pp. 269-270).

This type of theoretical perspective seems to have been anticipated first among critics of Darwinian adaptation, as early as the beginning of the present century. Authorities such as D'Arcy Wentworth Thompson (1961) contended that shape and form of living creatures depend more on biochemical and physical constraints than on genetic adaptability. In fact, the question of evolutionary relatedness ultimately becomes one of understanding the relationship of shape and form to the function of morphological structures, what has been called the form/function complex.

1.2 The Form and Shape of Bone

Although the words "shape" and "form" are used interchangeably in everyday speech, they would be better used in hominid palaeontology if considered two separate concepts. It seems that Platonic philosophical notions have greatly influenced the way in which hominid palaeontologists understand these two concepts and from a confusion of them come many difficulties. Most researchers refer to a type specimen when comparing hominine remains and especially crania, thus invoking Plato's concept of the perfect Form (the abstract or perfect image of an object that one holds in one's mind) and compare it to a new specimen which represents the "imperfect particular" (the various shapes that a class or group of objects may take) (see Plato's Parmenides for a discussion of Form). This approach allows some appreciation of morphological change through time and aids in developing phylogenetic trees. Such an approach does not, however, allow for any appreciation of the variation of the individual parts that a particular cranium may have and certainly does not allow for an accounting of acquired morphological alterations brought about through growth and development. What this view accomplishes in terms of simplification is more than offset by what it loses in the appreciation of growth and development and the variation that inevitably arises from the process of becoming an adult. It fails to recognise the contribution of shape or epigenetic changes to the adult configuration. In truth there is no optimum shape, only a sufficient one for each individual which allows it to perform a suite of behaviours. Form, on the other hand, can be thought of as at an optimum since, in considering it, one need not consider morphological variation. In order to draw accurate phylogenies, however, shape must be separated from form.

Even when variation in the development of features is identified, it is often the cause of considerable dismay. This dismay comes from a confusion of shape and form. As an example of a scholar having to grapple with such confusion, Tillier (1989) writes of Neanderthal morphology: "Une precocité de l'ossification pour l'occipital et le temporal a été suggérée.... L' analyse des caractères retenus par cet auteur ne permet pas de maintenir cette hypothèse. De plus, il semble qu'une variation individuelle puisse exister chez les Néandertaliens" (p.324). In fact, if these morphological changes are observed to vary from individual to individual, it is possible that they are shape changes due to maturation differences that result from variation in the behaviours of individuals. This type of observation makes perfect sense since not all individuals in a group would be expected to behave in identical fashion just as they would not be expected to be genetically identical. Gould and Lewontin (1979) describe the approach which identifies morphological change in a feature with genetic predisposition as the "sign" theory of morphology. Proponents of the sign theory see structures only as a means of tracing of lineages, but they do not consider them as useful designs for existence. In other words, there is only a genetic cause for a particular morphological feature. This approach stands in contrast to a second understanding of morphology that harkens back to Thompson (1961), who attempted to understand structures through a multi-facetted consideration of causes, which included those of a mechanical nature, not only those which may have a genetic basis. In other words some structures owe their shape to mechanical causes that are not related to the genotype. Thompson (1961) writes:

> In the biological aspect of the case, we must always remember that our bone is not only living, but a highly plastic structure, the little trabeculae are constantly being formed and deformed, demolished and formed anew. Here, for once, it is safe to say that 'heredity' need not and cannot be invoked to account for the configuration and arrangement of the trabeculae: for we can see them at any time of life in the making, under the direct action and control of the forces to which the system is exposed. If a bone be broken and so repaired that its parts lie somewhat out of their former place, so that the pressure and tension lines have now a new distribution, before many weeks are over the trabecular system will be found to have been entirely remodelled, so as to fall into line with the new system of force (p. 237-238).

The importance of this viewpoint is that it introduces a measure of doubt in the drawing of phylogenetic trees without due consideration of those features which are a part of the functional shape of an element- those features which can be accounted for through a functional cause. Gould (1971), following Thompson, reminds us that no explanation of form is complete without reference to the physical forces that contribute to the appearance of anatomical elements. The shape of bone reflects its function and is the intermediary between the function and the form. The form of a bone, its proportions, are those which are likely under genetic control, but its surface morphology and its dimensions are those which are susceptible to shape changes caused during the functioning of the particular morphological structure. The view here, then, interprets the form as an heritable component of bone, but that the shape and, moreover, the mass of bone is environmentally determined.

This conclusion derives from several empirical sources. Lanyon (1980) has commented that "... the general shape [i.e. their form] of bones is predetermined but that many of their dimensions and characteristic features, particularly the size and position of their crests and tuberosities, are dependent upon the presence and activity of an associated musculature both during growth and development" (p. 457). Lanyon based this appraisal upon observations of the effect of neurectomy of tibiae of young rats where the normal weight, thickness, cross-sectional shape and longitudinal curvature were affected by the loss of nervous control to the affected limb. "Normal" bones, then, would result from an environment which was mechanically and physiologically normal for any particular geographic area or period of time. Bone is thus seen to adapt its shape sufficiently to the mechanical and physiological environment in which it finds itself. Similarly, in protein malnutrition the dimensions of the child's growing bones are affected, but not the proportions of those bones (Himes 1978). Himes writes, " Although growth in length, and growth in diameter of tubular bones are both inhibited by PCM [protein-calorie malnutrition], the proportions of the bones, as determined by width-length ratios, generally remain unaltered..." (p.160). Such variation would suggest that dimensions- the lengths and widths of skeletal elements- are not genetic, but part of the phenotype, shape not form. The proportions of bones, that is their relative proportions, are likely genetic and are thus less susceptible to environmental disturbances.

A more useful viewpoint, then, separates shape from form in the study of morphology. Form is understood to represent simply the class of objects (e.g. tibiae); whereas, shape would be more usefully seen as the variation that makes a particular tibia unique or that belonging to a particular animal or even individual. Actually, this relationship is intimated in Wolff's Law, which states that, " The form of bone being given, the bone elements place or displace themselves in the direction of the functional pressure and increase or decrease their mass to reflect the amount of functional pressure" (quoted in Bassett 1968). The shape is a result of the action of the environment during growth and development. When applied to individual skeletal elements, one would equate the form with the genetic programming which dictates the presence of a skeletal element in a particular location, and the shape with the phenotypic expression of the genotype to a particular suite of behavioural circumstances. Therefore, even if the shape of a particular bone is quite abnormal, by its location in reference to other bones we can identify it as a particular element. Shape, on the other hand, is understood to represent that configuration of an element which is the result of environmental effects on the process of growth (the enlargement of skeletal elements) and development (the replacement (remodelling) and movement (modelling) of bone) (Burr and Martin 1989). No genetic change need be posited in changes in the shape of a particular skeletal element. Shape is intimately bound to the function of the element in the host of behaviours in which an individual engages throughout its lifetime. Young individuals experience both growth and development; whereas, adults likely experience reduced levels of both processes (ibid.).

Often in hominid palaeontology, a discipline focused largely on the study of cranial morphology, individual areas of the cranium which change through time are seen to be under "selective pressure". When these changes include some areas and not others 'mosaic evolution' is invoked, largely because some areas have 'proceeded' to become more 'modern' in appearance while others have remained more 'primitive'- that is, more like those of the putative ancestor. In these instances evolution is observed to act on some structures and apparently not on others at particular moments in the past. Gould and Lewontin (1979) remind us, however, that organisms are integrated entities and not collections of competing and discrete objects. There is, therefore, no quest for modernity- no quest to attain to the perfect modern Form as implied in Platonic philosophy. By extension, this writer contends that morphological features whose shape is associated with a particular function should not be used in cladistical analyses as the shape does not arise from genetic propensity, but from repetitive and habitual behaviour.

When these notions are applied to a complex set of elements like those which contribute to the cranium, we must first realise that the cranium functions as a single entity and not as a competing series of elements. A change in one part will likely cause alterations to other parts, but no part gains or loses adaptiveness to another. Morphological change must be anchored in and seen as a consequence of adaptive behaviour, which precedes all morphological change. Behaviour is more plastic than morphology, so it is the most likely cause of speciation. Selection works upon the population variation to sort out those individuals most adept at the new behaviour (Bock and von Wahlert 1965). Due to the inherent plasticity of bone, however, not all behavioural changes will lead to a new morphospecies. Not all changes in shape need be related to genetic alterations of any type. Gould (1971) describes one such example of this phenomenon in the following manner, " No adaptation and no selection on the part at issue; form of the part is a correlated consequence of selection directed elsewhere. Under this important category, Darwin ranked his 'mysterious' laws of the 'correlation of growth'. Today, we speak of pleiotropy, allometry, 'material compensation'.... and mechanically forced correlations in D'Arcy Thompson's sense.... Here we come face to face with organisms as integrated wholes, fundamentally not decomposable into independent and separately optimized parts" (p. 157). This approach is echoed in recent thinking concerning the workings of bone in its adaptive process in response to activity. Burr and Martin (1989) have identified a functional unit, a group of cells working together, that is responsible for skeletal adaptation. Furthermore, they note that genetic or metabolic regulation of the functional unit operates on the entire process of bone adaptation and not on any one part of it. Thus a single change to the regulation of the functional unit can affect the entire process of bone adaptation. The study of these epigenetic mechanisms is thus seen as the link between molecular genetics and functioning organisms (Herring 1990). If we apply this understanding to cranial morphology, we can suggest that a single change to one part of the cranium can cause changes throughout the entire structure.

Since bones change in response to particular environmental vicissitudes (Saville and Whyte 1969), a clear understanding of adaptation is essential to understanding shape and form. How do organisms adapt? Gould (1971) has called attention to a confusion that exists in understandings of adaptation, which is understood as the process by which organisms achieve a harmony with or "fit" to their immediate environment. Thomas Henry Huxley, although a firm supporter of Darwin's notions of adaptation, questioned whether natural selection could account for physiological species, as well as morphological species (Clark 1984). Darwinian adaptation is a heritable form of adaptation which involves selection upon genetic variation. Gould (ibid.), however, identifies three types of adaptation, only one of which can be called

Darwinian adaptation. The other two, often confused with Darwinian adaptation are physiological adaptation, encompassing plastic changes which accommodate the organism to a particular environmental extreme located within its range; and cultural adaptation, which is heritable in that it is learned and passed from one generation to another. Bock and von Wahlert (1965) discuss physiological adaptation in the following manner: "We regard physiological adaptation as a special case of the general principle that the phenotype is an expression of the genotype in a particular environment" (p.284). Although physiological and cultural evolution may have their roots in genetics, they must be activated by certain types of environmental stimuli. Moreover, they can arise at any point in time when the environmental stimulus reaches a particular threshold. Although the capacity or the potential for physiological adaptation is genetic, in order to be expressed in the phenotype, a particular environmental stimulus must be present.

1.3 Hominines and Adaptation:

The forms of adaptation outlined above, Darwinian, physiological, and cultural, may occur together and it is likely that all played their role in the evolution of the hominine lineage. All three forms of adaptation may contribute to the cranial configurations observed in the fossil record. Wolpoff (1980) has demonstrated that the hominine cranial vault assumes a modern morphology before the craniofacial skeleton. He has described this pattern as mosaic evolution progressing from posterior to the anterior of the cranium in the hominine lineage. Keeping in mind Gould's dictum regarding the integrated nature of morphological structures these changes must be understood in conjunction, especially in this instance, because they occur in single individuals who are representatives of past populations. Populations evolve and individuals adapt, but parts of individuals can only change their shapes to better accommodate the particular adaptive behaviour upon which the individual has embarked. In order to understand the processes behind particular adaptations we must attempt to separate shape changes from formal changes through the reconstruction of the behaviour or behaviours that may have caused shape changes to occur. In order to do so, however, we must first characterise the important parts of the cranium which will help to reveal its functional aspects. It is likely that in these we will isolate its shape, its non-genetic features. These features are discussed in Chapter 3.

The present problems which hinder our ability to sort hominines into species, then, appears ultimately to lie in our inability to differentiate between physiological and cultural adaptation and Darwinian adaptation and to identify them in the fossil record. Our present state of knowledge places us in the frustrating position which allows us to identify changes in morphology but not to understand whether particular groups of hominines represent separate species; whether or not, for example, Homo erectus and the Archaic Homo sapiens simply differ in their physiological solution to particular environmental conditions or cultural behaviours or in more fundamental and more specifically significant ways. These questions eventually influence our notions of extinction and speciation of these hominines. Therefore, to suggest that Neanderthals (Trinkaus and Howells 1979, Trinkaus and Smith 1985) or Asian Homo erectus (Stringer and Andrews 1988) became extinct, or moreover that Homo erectus (Howells 1980) represents an extinct species is certainly premature. That all form need not relate to phylogenetic relations has been echoed in recent treatments of the question of evolutionary change among hominids. Turner and Chamberlain (1989) contend that only alterations to the "fertilisation system", characteristics relating specifically to mate recognition, will necessarily correlate with speciation. They comment quite succinctly on this question: " There is no consistent correlation between speciation and morphological change" (p. 127).

In their studies of the form/function complex, Preuschoft et al. (1986) have noted that there is a "gap" between the function and the biological role of morphological features. The biological role is the range of activities in which any particular structure could serve but needn't necessarily serve in the course of an individual's lifetime. The function then relates to the capacity in which the structure normally serves during the lifetime of the organism. The range of purposes to which a particular feature might be put are thus not equivalent to the capacity in which the feature is presently serving. Any structural entity is capable, then, of much more than that to which it is exposed in the course of day to day habitual behaviours. Any given animal can cope with much more than it encounters under normal circumstances and conditions. A loose relationship then exists between form and biological roles, and in this realization, lies our dilemma of attributing particular functions to certain morphological configurations.

Animals can adapt phenotypically, producing morphological change, without the necessity of speciation events. Bock and von Wahlert (1965) discuss form and function as each relates to speciation and suggest that speciation actually proceeds from a change in the biological role that a morphological feature serves. A speciation event, then, might be precipitated by a shift in the frequency of certain behaviours. Only after the population has embarked on an altered behaviour does selection act on individuals within populations to sort out those which best perform the new biological role. This viewpoint stands in contrast to the concept that morphological features are the subject of evolution and speciation events. The behaviours and their frequency within populations of organisms are the subject of evolution and the individual performing these behaviours is the object of selection.

Another question relating specifically to human behaviour concerns how cultural adaptation influences morphology. Human populations live in a wide range of habitats, and each group survives and thrives in very different environments, but they have not speciated- presumably because of adaptations to their cultural assemblages. The cultural behaviours of Homo erectus populations may thus have prevented speciation from occurring. Similarly, the technological changes identified between the Upper and Middle Palaeolithic need not have been commensurate with biological change as White (1982) has previously suggested. Culture then may act to maintain a certain morphology, perhaps more often than it provides the necessary impetus for speciation, which has been the more often cited function of changing tool assemblages (Trinkaus and Howells 1979, Kennedy 1980, Wolpoff 1980 among others). Fundamentally, the problem centres on the influence of behaviour on morphological features. The biomechanical approach to morphology is the subject of the next section.

In summary, this section has emphasised the potential importance of physiological and cultural adaptation, as opposed to Darwinian adaptation, in the morphological alterations noted in the hominine lineage. Culture, a series of highly plastic and mutable behaviours that define human groups, has been forwarded as the mechanism which acts to prevent speciation. That is, culture buffers environmental stimuli that would enforce extreme shifts in the behaviours of non-culture bearing animals. Both cultural and physiological adaptation, however, can and usually do produce morphological changes of soft tissue and bone, but they may not have a genetic basis. Morphological changes noted in the cranial morphology of the hominines thus need not relate to speciation, but may in fact be shape changes related to changing cultural behaviours. To confound cultural or physiological adaptation with

Darwinian adaptation is to confuse shape changes acquired over the lifetime of the individual with speciation.

1.4 Biomechanical Perspectives on the Interaction of Muscle and Bone

Gould (1970) makes the point that biologists employ functional and quantitative approaches to the study of bone shape. These approaches rely upon a mechanical view of osseous structures similar to the mechanical models employed by engineers in the study of machines. The human body is a machine whose movable parts consist of muscle and bone, and therefore any discussion of this approach must begin with a review of the literature on muscle and bone interaction. Since muscles and bones behave differently throughout life, any consideration of their interaction must see them as a result of development. Washburn's (1947) early work concerning muscular activity and its effect on skeletal morphology suggested a relationship between muscle function and the development of bone. Washburn (ibid.) demonstrated that the temporalis muscle in rats functions to stimulate the formation of the coronoid process of the mandible and that muscular excision resulted in the absence of this portion of the mandible and influenced the development of the processes and articulation areas of the cranium and mandible. He found, for example, that with the excision of temporalis and nuchal muscles, the shape of the nuchal area was altered. When the temporalis muscle was removed the nuchal crest became reduced in size and more anteriorly positioned. With the excision of the nuchal musculature entirely, the nuchal crest failed to develop altogether. The results of this research provide strong evidence that the configuration of the associated musculature plays a role in bone configuration at the posterior of the cranium.

Other researchers eventually came to concentrate on the basicranium and its synchondroses, the epiphyses on the basicranium, as the site that seems to contribute a great deal to final cranial shape and size. The basal synchondrosis has been demonstrated to fuse quite late in growth, after adulthood has been attained between 20 and 25 years (Krogman and Iscan 1986, Gray's Anatomy 1977). Dubrul and Laskin (1961) excised the sphenoccipital synchondrosis in rats and report "man-like" changes as the result, including increased shortness and roundness of the cranium, curvature of the cranial roof, more forward placement of the occipital condyles, and ventral and forward rotation of the plane of the foramen magnum. These researchers were led to believe that the mechanical cause of these alterations was a shortening of the cranial base. Moore (1965), again in experiments using rats, achieved similar results with rats fed on soft diets (a diet similar to that of modern humans). The animals developed smaller, more rounded skulls than those sustained on a hard diet and this change was consequent upon a greater reduction in muscular function. Moore reports, however, that very little change occurred in overall cranial shape, only minor differences being found in cranial indices. Moore's data suggest that marked changes in the timing of growth in the braincase and facial skeleton of his sample did occur. Cranial growth, then, appears to be influenced by masticatory muscle function.

Since this work, the biomechanical literature has been replete with further evidence to substantiate the essential and fundamental role of the musculature in the development and alteration of bone and how this process works on a microscopic level through the piezoelectric effect (Bassett and Becker 1962, Bassett *et al.* 1964, Tschantz and Rutishauser 1967, Currey 1968, Doyle *et al.* 1970, Lanyon and Baggot 1976, Lanyon *et al.* 1982, Lanyon and Rubin 1984, Shaw *et al.* 1987, Carter 1987, Lanyon 1987). Much of this work has as an ultimate goal the understanding of osseous disorders such as osteoporosis (excessive osteoclastic activity) and osteoarthritis (excessive osteoblastic activity), but it also has the potential to provide insight into the skeletal morphology of earlier hominines.

There are two types of bone remodelling: that which is associated with skeletal ageing in certain vertebrates (Haversian remodelling), and a second which concerns the process of bone growth (Enlow 1976). This second type of remodelling is sometimes referred to as modelling, but both processes result in osseous changes. Bone growth (modelling) involves the sequential conversion of a particular part of bone directly into another portion as the bone enlarges during growth. During growth, then, the bone experiences continuous modelling until adult size is attained. Modelling maintains the generalised form of the bone, but does not alter the shape of the bone. The effects of traumatic injury preventing this process can be observed in the mandible and cranium of an 18-year-old from an old Slavonic burial ground dating from the 9th century (Horejs and Stloukal 1985). In this example the bilateral fusion of the temporomandibular joint has prevented bone growth remodelling and resulted in a noticeably immature appearance of the mandible and cranium, although those changes influencing the latter structure are not described.

Haversian remodelling is of utmost concern here in that it occurs in response to the strain situation in a particular area of a bone (Carter 1984, Evans and LeBow 1951, Lanyon et al. 1982). Bone remodelling is adaptive in that the strains in the bone are less than before the remodelling event occurred as demonstrated by Lanyon et al. (ibid.). The aim of such a process is to repair bone microdamage through an increase in bone mass while attempting to maintain a structure of least weight at the least metabolic cost (Currey 1984a and b, Chamay and Tschantz 1972). Remodelling occurs in response to dynamic loading and not static loading (Lanyon and Rubin 1984, Chamay and Tschantz 1972). Growing bone demonstrates a net accumulation of bone mass in response to dynamic loading and microdamage and can result in bone hypertrophy as seen in osteoarthritis (Radin et al. 1972) or, more importantly for this study, in the case of increased physical activity in immature animals (Chvapil et al. 1973, Kiiskinen 1977, Woo et al. 1981, Carter 1984). Chvapil et al. (1973) found significantly increased density of collagen in the femora of exercised adult rats, while juvenile rats possessed both heart hypertrophy with a 28% increase in the weight of the heart and 51% more collagen present. Results such as these demonstrate the high potential for plastic alteration in the body's systems in sub-adult individuals. These researchers do not firmly establish the cause for these differential responses in juvenile and adult rats, although they posit that the most reasonable cause would appear to be that physical conditioning shifts the equilibrium between collagen synthesis and its degradation in the direction of greater collagen accumulation. This process is greatest in intermittent loading of the skeletal element (Goodship et al. 1979). Static loading of bone, unlike intermittent loading, is seen to cause curvature changes, but does not appear to alter the thickness or the width of bone (Hert et al. 1969).

Subsequent research has clarified this supposition. Kiiskinen (1977) found that intensive physical training increased the density and decreased the volume and length of bones, often at the same time thus increasing the breaking load of the femur. Doyle et al. (1970) hypothesize that " the weight of a muscle reflects the forces that it exerts on bones to which it is attached, and a reduction or increase in muscle weight results in a corresponding loss or increase of bone" (p. 393). Kiiskinen concludes his study with the interpretation that physical training in growing mice accelerates the maturation process. Here, then, if we can assume that all homeothermic animals will respond in a similar fashion, and this analogy seems likely in that bone appears to respond similarly in all mammals (Gordon 1978, McNeil-Alexander 1983, Lanyon et al. 1975), then these observations can be applied to provide an hypothesis applicable to Neanderthal morphology.

Trinkaus (1981) has suggested that Neanderthal limb proportions are those associated with cold adaptation and are reflective of the operation of Allen's and Bergman's Rules. Although this explanation accounts for the shortened condition of Neanderthal distal limb segments living in Western Europe, it does not explain the thickened cortices which have a distribution throughout individuals found in other climates such as those living in Pleistocene Africa. It would seem that heightened activity levels might prove a more likely reason for the thickened cortical bone observed in Neanderthals and Homo erectus. A more likely explanation would be that through the onset of adult activities at younger ages, these individuals developed bone hypertrophy in many areas of the body, including the long bones and cranium (cf. suggestion of Lovejoy and Trinkaus 1980). In support of this hypothesis, Kiiskinen (1977) and Saville and Whyte (1969) found significant age-related differences in the responses of animals in their study with mature animals characterised by simply increasing muscular hypertrophy, while immature animals experienced osseous changes presumably due to the heightened sensitivity of connective tissues during growth in immature animals. Buskirk et al. (1956) corroborate these findings in a study of tennis players who had played tennis since early in their teens and who possessed lengthened arm bones in their dominant arms. They concluded that the activity stimulated growth and that length changes cease at maturity.

Dalén and Olsson (1974) found in a comparative study of veteran cross-country runners and newly active adult runners that the former group possessed high bone mineral content, but that after three months of intensive training the novices demonstrated no such similar skeletal change, although an 11% increase in lung maximum oxygen capacity was achieved. These findings would seem to support those made by Kiiskinen from animal subjects. Once skeletal maturity is attained, bone is not as sensitive to environmentally produced stimuli, although muscle tissue remains much more sensitive far into adulthood. Thus, in this scenario, the increased thickness of Neanderthal and Homo erectus cortical bone, a systemic phenomenon, must be interpreted to represent at least in part high activity levels commenced early in life, before the onset of skeletal maturity. Unlike mature cortical bone, similar bone from immature individuals is very sensitive to environmental insult. Further support for this suggestion comes from the work of Himes (1978), who reports a reduction in cranial and cortical thickness and reduced dimensions of both the cranial and post-cranial skeletons of children and foetuses of mothers undergoing short-term protein-calorie nutritional stress. Evidence such as this suggests that the reduced thickness of these elements results from a systemic response to environmental changes that can occur very rapidly. Goodship et al. (1979), for example, found that within three months after ostectomy of the ulnae in a sample of young pigs the radius had increased its cross-sectional area so that it became equal to the combined areas of both bones.

Therefore, it would seem that the increased cortical and cranial thickness in evidence in our earlier ancestors should not be considered as two separate attributes, but together as a result of muscle activity. Himes (1978) does not comment on the effects of malnutrition on muscle development, but a plausible association between the skeleton and adhering musculature might be that muscle atrophy represents the proximate cause of the osseous changes noted in growing children. This hypothesis is in keeping with the clinical observations of Rális et al. (1976) who note that the paralysis associated with spina bifida in infants is accompanied by a diminution of the total area of cortical bone, its thickness, the number of Haversian systems, and the number of large remodelling areas in tibiae (i.e. areas undergoing replacement of bone). Interestingly, the shape of these tibiae is also affected, instead of assuming a normal triangular cross-sectional shape, they remain a round shape, likely as a result of lacking muscle activity. A similar suggestion has been levelled by Uhthoff and Jaworski (1978) who tentatively associate bone loss with the lack of muscular activity in immobilised individuals. The reduced activity of these muscles would have a similar, though less drastic, effect as that noted in disuse atrophy in limb bones as reported by Krolner and Toft (1983) and Uhthoff and Jaworski

(1978) in immobilised patients and by Smith et al. (1981) in inactive, osteoporotic women. One offshoot of this line of reasoning suggests that Neanderthal and Homo erectus infants who lived to adulthood must have had access to a protein and calcium rich diet in order to build up the muscle mass necessary to stimulate such thickened cortical bone.

Further to this research has been that of Woo et al. (1981), who found that there was no change in the mechanical properties of femoral cortical bone with increased exercise in an experimental group of swine. There was, however, a significant alteration in cross-sectional properties of the cortical bone; a 17% increase in cortical thickness, 23% increase in cortical cross-sectional area, and 21 and 27% increase in minimal and maximal area moments of inertia, respectively- that is in bending strength. These alterations are accompanied by medullary stenosis or reduction in the diameter of the medullary canal. These changes effectively strengthen the femur in vertical compression by increasing the external area of the bone. Rális et al. (1981) have suggested that thickening of the cortical bone can come from endoseal deposition unaccompanied by periosteal resorption. Such seems to describe the situation in Neanderthal and Homo erectus postcranial morphology. These results compare quite favourably to those observations reported by Lovejoy (1975) and Lovejoy and Trinkaus (1980) for thickened Neanderthal cortices. These researchers, however, determined that "... Neanderthal specimens were strikingly stronger than the comparative [modern] human sample, ... [in fact]... twice as strong as the modern human sample" (p.467). Studies on physically active modern individuals record similar results of bone hypertrophy for various areas of the body, including the scapula in some adults (Doyle 1977), the clavicle in fruit-pickers (Wienker and Wood 1988), the ulna in rodeo riders (Claussen 1982), the elbow joint in tennis players (Lewis 1971, Jones *et al.* 1977) and baseball pitchers (King *et al.* 1969), and the distal humerus in baseball players (Watson 1973). These alterations, then, seem to represent stress-related phenomena. Woo *et al.* (*ibid.*) contend that "Exercise training increases the internal stresses in bone, and the bone responds by increasing its cortical thickness and narrowing the medullary cavity" (p.786). The same researchers note that very intensive training may inhibit growth, especially in immature animals. All of these cases of bone hypertrophy are accompanied by muscular hypertrophy in the particular area, so it is surmised that a similar type of muscular hypertrophy would have been present in Neanderthals, but that many more anatomical areas were affected. This type of hypertrophy would indicate sustained involvement in adult activities from a young age in both Archaic *Homo sapiens* and *Homo erectus*. It is quite likely that the cranium will have been similarly affected. That extreme amounts of exercise can inhibit growth might explain the angled, "infantile" occipital of Neanderthals and *Homo erectus* as identified by Tobias (1959a) as a result of hypertrophied nuchal muscles.

1.5 Muscle and Bone Interaction in the Cranium

A similar biomechanical interpretation has not yet been suggested to account for increased cranial thickness, perhaps as a result of previously propounded opinions about cranial development. Lanyon (1987), for example, contends that "In locations where shape or protection are of prime importance the bone's architecture is achieved during growth under direct genetic control. In locations where resistance to repetitive loading is important only the general form of the bone will be achieved as a result of growth alone, the remaining characteristics result from functional adaptation" (p. 1083). Currey (1984a), writes the following in regard to the mechanical situation in the cranium:

> The situation for the skull vault bones is very different. In humans, unlike many mammals, in which the vault has to provide a firm origin for the biting and masticatory muscles, the main function of much of the skull is merely (if one can call it merely) to protect the brain from blows. How can the modeling system of the bones of the skull produce a skull that is not very heavy yet which has a fairly small chance of fracturing in the average lifetime?...To achieve an adaptively strong skull vault the cells would need to remodel when the strains imposed in day-to day living reached say one-twentieth of the yield strain (p.s122).

Currey (ibid.) notes, however, that "It is always risky to assert that structures are effectively unloaded" (p.122). Lanyon (1987) citing Currey (ibid.) suggests that the cranium is "over-designed in relation to functional loading" since functional strains are so small as to have little or no influence on cranial vault remodelling and thus make no contribution to cranial architecture. Additionally, although not explicitly stating so, such pronouncements may, in part, derive from the early work of Benninghoff (1925) who interpreted the anomalous lack of split-line pattern noted in the cranial vault as indicating that the cranium was unmodified by mechanical stresses. These results came from split-line observations which have since been demonstrated to reveal only the organisation of bone, but not its strain situation (Evans 1957).

Misunderstandings of cranial function appear also to stem from Lanyon and Rubin's (1984) research in which they demonstrated that dynamic loading is essential to commence remodelling in long bones and that static loading has no such influence. Since the cranium is not seen to be dynamically loaded, it cannot, by definition, remodel, which is interpreted to mean that cranial shape must be entirely genetically determined. Unfortunately, these associations have until the present study gone untested. There are, moreover, at least three problems with these notions. First among these is a confusion between individual cranial elements and the cranium as a whole. Evans and Lissner (1957), Robbins and Wood (1969), and McElhaney et al. (1970) have performed studies of the relative strengths of cranial elements and plugs taken from cranial elements. These researchers revealed the basic mechanical properties of cranial bone, finding it to be of a highly mechanically sound construction with the amount of strength in compression, tension, and shear correlated with the amount and orientation of the trabecular diploë which is responsible for the bone's strength. These researchers determined that there was a very large range of mechanical strengths between elements and between individuals. Information such as this would seem to suggest that cranial bone demonstrates such variability due to the different strains exerted by the musculature of particular individuals with varying cranial shapes. Although the stated intent of these studies was "to develop a structural model of the skull" (Robbins and Wood 1969: 236), the eventual outcome of the research was in fact to enhance our appreciation of the effectiveness of the cranium in withstanding the rigours of various accidents. No model of the entire cranium was ever made, which comes as no surprise since the intent of the research was only to ascertain where the cranium needed artificial re-enforcement. Cranial shape, then, would appear not to be adapted to a protective role, but to one perhaps having more to do with the transmission and dissipation of muscularly generated forces.

A second, and perhaps more fundamental problem, derives from the fact that the bone was treated simply as a material without any consideration for growth effects on morphology. Moreover, the previously stated interpretation is in disagreement with the results obtained from the study of Oyen and Russell (1982). These researchers write, " Woven bone tissue organized into fine cancellous bone tends to be especially prevalent in the supraorbital region and in the cortex of the maxilla. Woven bone also contributes to the formation of the zygomatic process and has been identified on the pterygoid plates and the occipital bone in the region of the nuchal lines and ridges" (p. 366). Woven bone such as that noted is associated by these researchers with areas undergoing active modelling and remodelling both of which occur during growth. Since this type of bone is found in the cranium, it follows that the cranium models and remodels much like other skeletal elements.

The final problem concerns the implication that the cranium, especially the human cranium, is not loaded in the course of movement. Dynamic loading has been characterised not as a gradual progression or a continuum of loading conditions, but rather more consistent with a series of discrete events during which the bone is deformed from a particular direction, partially released, and then loaded from another direction (Lanyon et al. 1975). Although the modern human cranium possesses reduced muscular attachments and is not required to withstand high forces exerted in the average modern lifestyle, the biomechanical studies, theoretical or otherwise, do not attempt to account for possible non-modern habitual human behaviours that affected morphology in our earlier ancestors. Although this writer would not expect that these behaviours be assimilated in the previously cited studies, they must certainly be of import in understanding the modern appearance of the human skull and the requisite demands placed upon it by modern behaviours. In order to assess whether or not the cranium is a dynamic entity one must determine the potential stresses to which the cranium is exposed.

Yamada (1970) has demonstrated that the greatest ultimate strength of elastic ligamentous tissue is found in the restiform portion of the *ligamentum nuchae*. It is this ligament which allows humans to hold their heads erect and quadrupeds their heads in a horizontal orientation without great muscular exertion. Such would suggest that the suboccipital portion of the cranium, to which this ligament attaches, is under constant stress from the nuchal muscles and from this elastic ligament, even in young individuals. Any activity that necessitates a shift in the position of the head requires muscular exertion and causes strain within the occipital area. The *ligamentum nuchae* and *M. semispinalis capitis* also form a bridge between the cranial and post-cranial skeletons. Thus motions which affect the upper torso would also affect the occipital bone. Therefore, it seems that these muscles, along with the masticatory muscles, would be those responsible for placing stresses on the cranial vault. The interpretation that can be drawn from this evidence is that the occipital must be an area uniquely affected by so many muscle attachments. This view suggests a certain dynamism lacking in the interpretation of Lanyon and Currey above. Indeed, Hoyte and Enlow (1966) observe that " Muscle pull is regarded as the primary force directly responsible for the formation of elevated tuberosities, tubercles, and crests upon which the muscles are attached" (p. 205). The modern cranium possesses many of these morphological features in the form of identifiable nuchal lines, occipital tori, and linear tuberculae on the occipital of some modern people (see Appendix 4). Earlier members of the Homininae, and especially *Homo erectus*, are noted for a series of "buttresses" which are similar, though accentuated, morphological features. Therefore, those areas which act as muscle attachments, including the occipital area, provide evidence to refute the assertions that the cranium and its vault is an unstressed and undynamic entity.

There are studies that suggest that the cranial vault does experience stress. Hoyt and Enlow (1966) contend that " There is no evidence that differences in principle exist between muscle attachments to those bones which form walls to enclose an organ whose growth and form materially contribute to the shape of those walls (such as the skull enclosing the brain), and the tubular bones enclosing only bone marrow. The complex relocations of the surfaces of growing long bones provide direct analogies to the remodelling surfaces of the cranial bones" (p.211). Citing evidence from guinea pig studies where patterns of morphological change occur in conjunction with those of the musculature, these researchers note that there is a harmonious relationship between brain and muscular growth in the cranium. To date no experimental evidence has been presented to reject the notion that the cranium experiences strain in response to muscular stress. Dempster (1967) suggests that the human cranial vault is subjected to three types of applied stress, including that exerted by the growing brain, middle ear, and tongue mass; those associated with the muscles, joints, and teeth; and those of an extrinsic nature such as the static loads created by binding of the head. Dempster, using a split-line technique and citing evidence that human bone is stronger under compression than it is under tension (cf. Evans and Lissner 1957, McElhaney et al. 1970) goes on to conclude that all of the form-texture relationships demonstrated by grain direction in the cranium and its various features accord with the best mechanical use of the material of which they are made. The modern human cranial vault is particularly revealing in this regard since it demonstrates a diffuse pattern of random lines across its entire surface. Dempster (ibid.) cites Coleman's work (1961) as demonstrating that plates of human bone subjected to bending force are stronger in the lengthwise direction of the grain as opposed to the crosswise direction across the grain (cf. Yamada 1970, Evans 1973, Currey 1984). He expands this understanding to the unusual, random pattern of the cranial vault and remarks that "... a randomly oriented braincase texture should be stronger in all directions under tensile and compressive loads than is bone in the cross grain direction. The skull vault, like the egg, gains strength through its form and through the use of a structural material that is equally strong in all directions" (p.31). Bone from the cranial vault, then, is anisotropic.

Evans (1973) elaborates on Dempster's observations by noting that the Haversian systems align themselves longitudinally in the bone, a position which would seem to explain why bone possesses these anisotropic properties. Haversian systems are characteristic of remodelled bone and thus their placement would seem to be dependent on the forces exerted on the bone most frequently (Carter 1987, Lanyon 1987). Benninghoff (1925) and Evans (1965) have demonstrated that the split-lines are related to the organisation of bone or other materials. Evans (ibid.) comments that "Stresscoat cracks only arise from *tensile strain* [his italics] in the underlying material and always lie transverse to the direction of the strain" (p. 189). Studies of individual specimens of cranial bone showed it to be much stronger in compression longitudinally along the bone (parallel to the grain) than in a radial direction (ectocranially to endocranially) (Dempster and Liddicoat 1952). Fractures of the cranium thus radiate outward from a compressive blow (Gurdjian et al. 1950). It would appear, then, that the human braincase responds to externally applied stresses because of the way its adhering musculature influences cranial growth, not because of any innate ability to protect the brain. If the latter were the case, then one would expect the cranial bone to be anisotropic for compressive forces. It is not since the thickness of the bone seems to have the most effect on resisting compressive forces and the cranium is not uniformly thick. The more usual force which the cranium experiences comes from microfracture caused by strong muscular contractions. Microfracture, which is interpreted to be the controlling factor in the remodelling of bone, is best resisted by bone that forms perpendicular to applied forces (Treharne 1981). The diffuse pattern of cranial bone would thus be interpreted to be the best form of resistance to microfracture created by forces directed from all around the cranium by the adhering musculature.

These assertions are supported by impact assessments made on whole crania by Gurdjian and Lissner (1945, 1946, 1947), Lissner and Gurdjian (1946), Gurdjian et al. (1947). These researchers observed several particularly relevant phenomena in their experiments, including the following:

1) The sutures of the cranium do not appear to hinder the transmission of forces across the ectocranial surface.

2) That notches and foramina represent areas of stress concentration. This reaction holds true for blows directed at the occipital squama, the force of which concentrates in the area of the foramen magnum.

3) Fractures of the skull are due to tensile stress at some distance from the point of impact.

4) Strain propagation characteristics are dependent upon the shape and variations in thickness: hence some variation may be expected in the strain paths in different skulls.

5) Contrecoup deformations of the fronto-sphenoidal juncture following midoccipital blows were obtained in one of six tested skulls.

6) Strain patterns indicate some difference in the behaviour of different skulls, but the direction of the forces was the same.

7) Following a deceleration impact there is an area of inbending, which is of irregular outline due to the presence of thickness irregularities and buttresses.

That fractures should result at the fronto-sphenoidal juncture from a blow directed at the occipital would seem to indicate that the cranium responds as a structural entity, transmitting forces across its surface. The fact that the sutures do not hinder the transmission of these forces comes as no surprise since, if such were not the case, the cranium's mechanically sound spherical shape would be compromised. Midline features such as sagittal crests or keels, occipital tori, and supraorbital tori suggest that the cranium does not respond as a series of elements, but as a unified whole since these features cross suture lines. Muscle force, though being less traumatic than those tested by Gurdjian and Lissner, and especially those exerted at the occipital, must have a similar influence on the cranium. These forces must be of a tensile variety based on the situation of the nuchal and masticatory muscles. That the cranium transmits compressive forces across its surface and fractures result from tensile forces some distance from the point of impact suggests that the cranium transmits forces in a tensile fashion, more similar to the applied muscular stress than to an external compressive force. Since osseous structures are designed to withstand those forces most commonly experienced (Lanyon and Baggot 1976, Lanyon et al. 1979), it would appear that the cranium is most often exposed to tensile forces. Moreover, that the various buttresses of the modern human cranium should influence the transmission of these tensile forces would indicate that they might perform a similar function in the transmission of muscular forces in the crania of earlier hominines. The changing positions and extent of these morphological features noted in the hominine lineage would suggest that the forces generated were different to some extent in our earlier ancestors, even those of more recent prehistoric populations like those represented by the prehistoric Northwest Coast sample examined later. The suggestion that cranial buttresses influence the transmission of forces across the ectocranium form a portion of those ideas tested below.

Chapter 2: The Functional Approach to Hominine Cranial Morphology:

Trinkaus (1984) advises in the following manner:

> It may ... be more profitable to set aside the ultimate phylogenetic question and concentrate efforts on functional evaluations of the discernible morphology and its patterns of change during the Late Pleistocene. Such a concentration of efforts may eventually hold the key to the phylogenetic question, since functional studies should ultimately allow us to evaluate whether, for example, supposed Neanderthal autapomorphies were clearly functionally based and likely to change rapidly in response to specific behavioral shifts (p.330).

An emphasis on functional studies and, specifically, on biomechanical explanations of morphological structures has characterised much recent research on the distinctive morphology of the Neanderthals and their immediate predecessors, Homo erectus (McHenry 1975; Molnar and Ward 1977; Trinkaus 1975, 1976a and b, 1977, 1978,1983a,1983b, 1986,1987; Ward and Molnar 1980; Lovejoy 1980; Trinkaus and LeMay 1982; Smith 1983; Maier and Nkini 1984; Russell 1985; Rak 1986; Demes 1985 a and b, 1986; Tompkins and Trinkaus 1987; Franciscus and Trinkaus 1988; Rosenberg 1988). The cranial vault is among the most studied anatomical structures. Although the morphological differences of the cranial vault are repeatedly cited in drawing distinctions between hominines (Howell 1951, Bilsborough 1976;

Stringer 1974, 1982, 1984; Hublin 1978; Santa Luca 1978,1980; Skelton et al. 1986; Stringer and Trinkaus 1981; and Bräuer 1981, 1984 among others), comparatively few studies of vault function have been undertaken- certainly far fewer than portions of the postcranium have received (Evans and Goff 1957; Napier 1967; Sigmon 1975; Tuttle and Basmajian 1975; Lovejoy 1975, 1978; Lovejoy and Trinkaus 1980; Stringer and Trinkaus 1981; Trinkaus 1976a and b,1978,1983; Kennedy 1985; Ruff and Hayes 1983; Tuttle 1987; Trinkaus and Churchill 1988; and Bridges 1989). The result of this uneven treatment is a confusing situation that recognizes the potential value of the cranium for developing phylogenies, but has failed to account for the processes by which cranial shape is attained. Part of the reason for such neglect is the inherent difficulty involved in studying the cranium's three dimensional shape and accounting for the wide range of muscular forces that the cranium must resist, including most notably those involved in mastication and head movement. Previous studies of cranial function (Moss and Young 1960; Endo1965, 1966a, 1966b, 1967, 1969, 1970; Molnar and Ward 1977; Hinton and Carlson 1979; Rak 1986; Russell 1985; Hylander 1975, 1979; Sakka 1984; Preuschoft et al., 1986; Trinkaus 1987; Demes 1981, 1982, 1984,1985, 1986a and b, 1987; Demes and Creel 1988; Picq and Hylander 1989 among others) have suggested, however, that cranial morphology like that of the postcranium may be described and explained in functional terms. A review of the work previously done on the mechanics of the cranium provides a means by which to initiate an investigation of its function.

Studies of the Homo erectus and Neanderthal viscerocranium like those undertaken by Russell (1985) and Rak (1986) have been strengthened by evidence derived from studies of modern human crania (Hylander 1975, Weijs and Hillen 1986, Hilloowala and Trent 1988a and b, Endo 1965-1970, Hannam and Wood 1989). These studies rely heavily on the effect muscles have on skeletal configuration and concentrate on the masticatory apparatus and its effect on facial proportions and contours. Hylander (ibid.) suggests that craniofacial morphology is heavily influenced by the functioning of the jaws in various masticatory and industrial activities (paramastication). Weijs and Hillen (ibid.) discuss the correlation between the cross-sectional area of the jaw musculature and a number of facial angles and dimensions, while Hilloowala and Trent (ibid.) have shown a similar correlation between browridge development and that of the anterior portion of the temporalis muscle.

These recent studies are based on the insights provided by Endo (1965, 1966a and b, 1967, 1969, 1970) who demonstrated that facial contours are shaped in order to dissipate and redistribute the forces generated during mastication, including all types usually associated with rigid frame structures. Thus one may measure the strain incurred by the facial skeleton by loading the dentition in a manner analogous to that experienced during life. Endo (1966b) concludes that "... the mechanical factors relative to the masticatory action may modify the form and structure of the facial skeleton to a considerable extent .... The modification may be made according to some principle to make the lightest structure, and the principle may resemble closely that of the 'uniform strength'" (pp.99-100). Rak (1985) applied Endo's findings to Neanderthal craniofacial configuration, finding in the process that Neanderthal facial morphology, though differing from the modern situation, was not mechanically unsound. Neanderthal facial morphology is designed to resist the stresses generated during anterior dental loading by the large and prognathic jaws. The more sagittally oriented infra-orbital plates of the Neanderthal facial skeleton are positioned to effectively resist bending and rotation in the nasal region during powerful anterior dental loading.

Russell (1985) in her study of the supraorbital torus found that this bony excrescence was located in an area subject to bending moments created by the jaws and thus could be interpreted as a response to increased stress in that area. Similarly, Hylander (1975) quite convincingly demonstrated that the mandible is more than a simple link between the adductor muscles and the bite force as Gingerich (1971) originally proposed. It is, in fact, a biomechanically determined lever, subject to environmentally and culturally induced stress in the form of bite force along the tooth row and a reactive force at the condyles as suggested by Hillen and Carlson (1979) for the temporomandibular joint in relation to masticatory activity.

There is the suggestion in these results that at least a portion of the morphological configurations observed derives from epigenetic growth phenomena, and cannot be equated directly with genetic causes. Many of the studies of hominine morphology suffer from affirmation of the consequent, namely that since a particular morphology is observed in a series of specimens it is considered to be adaptive and, therefore, ultimately genetic in origin, which accounts for the structure's existence. It is suitable to consider the morphology of the cranial vault from an epigenetic perspective before its configurations are attributed undue phylogenetic significance.

2.1 A Biomechanical Model of the Cranium:

The cranium has been observed to be a first-class lever with its fulcrum at the foramen magnum, its resistance (moment arm) at the anterior portion of the mouth, and its effort (lever arm) located at the posterior of the cranium in the form of the nuchal musculature (Fig. 1). This biomechanical perspective of the human cranium is generally that derived from the work of Adams and Moore (1975), Schultz (1955), and Wolpoff (1980). These researchers contend that the head is not just "dead weight" balanced on the spine at the foramen magnum, but that it is a dynamic skeletal element. Its position on the foramen magnum is maintained and its tendency toward face heaviness is offset by the nuchal musculature. Thus any activity performed at the anterior dentition must affect and influence the development of not only the facial skeleton but also the occipital and nuchal areas (Preuschoft et al. 1986; Demes 1982, 1985; Nanda and Goldin 1980, Goldstein et al. 1984). The model presented here would prefer to interpret the entire cranial vault as a dynamic entity whose function and shape is biomechanically determined. Preuschoft et al. (1986) favour such an interpretation while observing that "... our results show the existence of a causal relation between shape and mechanical function for the skull not less than for extremity bones" (p. 216). It is this perspective of the cranium that will be developed in this dissertation.

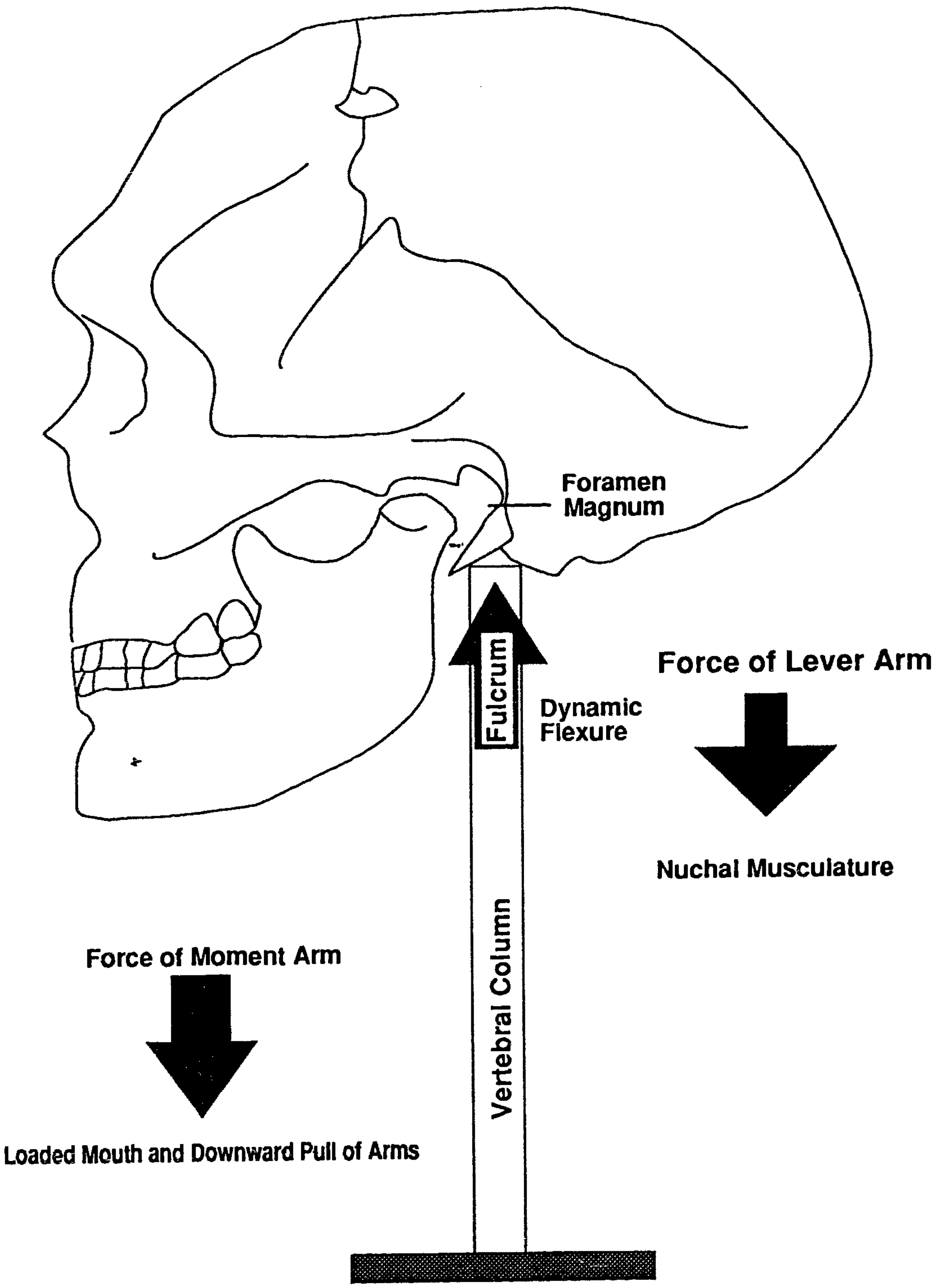


Figure 1: The cranium modelled as a first-class lever with the direction of the forces experienced in anterior dental loading.

2.2 The Biomechanical Significance of the Occipital:

Although Yamada (1973) has demonstrated that models of bent beams are sufficient to explain the distribution of stress and strain in the long bones, Demes (1984, 1985) and Preuschoft et al. (1986) have discussed the inability of such models to describe and explain the mechanics of the primate cranium. When the cranial base is loaded in compression a shell model seems more suited to such a task (Demes 1986). Demes (ibid.) describes the cranial shape of Homo erectus as "aberrant" in that such a shape requires "uneconomic reinforcement" (p. 45), referring to the buttressing originally identified by Weidenreich (1943) in the "Sinanthropines" (Asian Homo erectus). Demes (1984) goes on to remark: "The shell with the greatest curvature- therefore, one similar in shape to that of a modern human- in the investigation showed lower stress values than the less curved semiovoid shell when both were subjected to the same [compressive] load" (pp.46-47). However, the same researcher notes that the stresses evoked by the nuchal muscles are absorbed exclusively by the basicranium and are not transferred to the cranial vault. Thus the bent occiput of Homo erectus does not result in greater stress. This realisation, she says, weakens the interpretation which argues that the occipital torus acts as a buttress. It suggests, however, that the shape of the Homo erectus cranium is functionally significant. Demes' experiments support the interpretation that the occipital torus is an enlarged muscle enthesis, yet her tests fail to account for the dynamic, downward, tensile pull of the nuchal musculature and the influence this stress has on the cranial vault. Demes has loaded replicas of hominine basicrania in compression, which although a useful study in its own right is not, in fact, biologically meaningful because the action of the nuchal muscles is not compressive but tensile when the entire cranium is considered as an entity. These experiments, then, test only the strength of specific geometric shapes, and do not recreate the forces produced in the hominid cranium. If the occipital torus is an enlarged muscle attachment, then a test of this function is in order. What is needed, then, is a means by which to test the effect of the occipital torus on stress distribution in the cranium. It is this researcher's contention that the shape of the *Homo erectus* cranium is not uneconomic, but that is is designed to resist the increased muscular forces generated in the lifeway of the individual hominine in question. The function of the occipital torus is investigated below.

The occipital and nuchal areas of all hominines are scarred by bony muscular markings. These muscle markings relate to the following: supreme nuchal lines to the *M. trapezius*; the area between the superior and inferior nuchal lines to the *M. semispinalis capitis* and *M. obliquus superior*; and the inferior nuchal lines to the *M. rectus capitis posterior major* and *minor* (Sakka 1985, Hublin 1978, McMinn and Hutchings 1985). All of these muscles are attached to the cranium through entheses of variable development. These muscles act in conjunction to model the outer table of the cranium (Moss and Young 1960), leaving the inner table to respond to brain growth (Moss and Young 1960, LeMay and Trinkaus 1982). That these tables are separate functional entities is suggested by the discontinuities observed in the curvature of the two in relation to one another, especially pronounced in the nuchal area (Weidenreich 1943, Hublin 1982) (refer to Figs. 2-7). The entheses of the suboccipital muscles are characterised by a resorptive surface surrounded by an osseous thickening and what appears to be endosteal deposition of cortical bone (Hoyte and Enlow 1966), which gives them their well-excavated appearance.

That the nuchal muscles, *M. semispinalis capitis*, *M. trapezius*, and *M. rectus capitis major* and *minor* and *M. obliquus superior*, appear to influence occipital configuration is intimated by Bräuer and Leakey (1986) and Dempster (1967) and questioned by Hublin (*ibid.*). Hublin (*ibid.*) observes that the placement of the occipital torus relates not to buttressing but to the muscle insertions found in its vicinity and, specifically, to the *galea aponeurotica*. Hublin (1978) remarks that he cannot deny the influence of the musculature in the development of the occipital torus, but stresses that its prime cause is hyperossification that seems to be found in certain populations and certain individuals. It seems that Hublin would attribute this aspect of cranial morphology to a genetically-related predisposition. Such an observation, however, does not account for the distribution of the torus across what must have been several widely separated populations of Homo erectus. Indeed, the occipital torus has been included in the definition of the palaeospecies, specimens of which have been found throughout Eurasia and Africa (Howells 1980, Day 1986). The occurrence of this feature in Homo erectus and the Archaic Homo sapiens is far from static and does not demonstrate a uniform morphology in its placement or development. Vandermeersch (1989) has recently noted, in fact, that the occipital torus is much more weakly developed in the Near Eastern branch of the Neanderthal group and that it is accompanied by a suite of characters that separate Near Eastern from European Neanderthals, including a more rounded, less angled occipital; a less well-marked bun; and a supra-iniac depression that is less deeply excavated and smaller in its extent; in addition to a face which is not as prognathic.

The variability of the position and size of the torus among individuals suggests a functional cause. Thus its presence should be explained in functional terms relating specifically to developmental processes. The process of its formation is likely to relate to the appositional growth of bone and muscle. Bone becomes electrically polarised when it experiences deformation and the degree of polarisation is proportional to the amount of strain, its size, its direction, and the rate at which it is applied or released (Lanyon and Baggot 1976). A functional cause is also suggested by its proximity to M. semispinalis capitis, which inserts onto the superior nuchal line at the torus creating a large enthesis on the occipital. This observation has also been made by

Plhak (1986) who noted a close connection between torus development and the lateral expansion of M. semispinalis capitis. The action of this muscle provides dynamic forces through its enthesis as the cranium performs as a first-class lever. This muscle resists the downward thrust of the arms as the jaws act to hold the object and extends the head in shearing motions. The occipital, then, forms the lever arm of the cranium with its adhering musculature, and furnishes the effort in anterior dental loading. In order to firmly demonstrate the functional relationship between the cranial vault and jaws, one must identify those areas which are likely to monitor and gauge behavioural shifts. These factors are discussed in the following section.

Chapter 3: Osteological Indicators of Habitual Behaviours

Osteological indicators of habitual behaviours are those morphological shape changes acquired by bone in response to heightened muscular activity. These indicators include, but are not limited to, occupational markers of stress as identified by Kennedy (1989). Other indicators of habitual behaviour would include alterations in thickness, cross-sectional shape, asymmetrical development of limbs, and increased or diminished density of bone. Markers of occupational stress are among those osseous shape alterations to attachment sites for muscles- that is, the enthesis or insertion of the muscle, that allow the identification of particular behaviours. Enlow (1976) notes that such entheses are associated with remodelling activity that allows growth while maintaining fibrous attachment for the muscle. Behaviours, then, that commence early in life are those which would be expected to have the greatest impact on enthesis development.

3.1 The Entheses of the Occipital

Niepel and Sit'aj (1979) relate that the enthesis consists of the following:

1.) The attachment portion of the tendon.
2.) The attachment portion of the bone which is not covered by the periosteum.

3.) Interposed hyaline cartilage.

4.) Peritenon which passes into the perichondrium and periosteum.

5.) Additional structures such as bursae, fibrous tissue, adipose tissue cushions and sesamoid bones.

In order to reconstruct behaviours one must concentrate on the entheses for the various muscles recruited in the performance of a particular task. Distinctive entheses develop in response to the repetitive use of particular body parts and muscles in certain strenuous activities that stress the enthesis to the limits of its capacity (Niepel and Sit'aj 1979, Kennedy 1989). Bony rugosity results from the ossification of collagen fibres, producing enthesosites, the functional analogue of osteophytes in osteoarthritis (Niepel and Sit'aj ibid.). Therefore, a decrease in the relative size of an enthesis between individuals bespeaks of a functional difference and a large enthesis must be associated with a certain amount of powerful and repetitive movement. Entheses, then, do not simply transmit muscular forces to the bone but are, in themselves, dynamic entities (Niepel and Sit'aj ibid.). They are able to absorb a portion of the forces that they experience, but like bone they have a fatigue level and a failure point.

The insertion for M. semispinalis capitis appears to be one of, if not the largest, entheses in the human body. A very well-marked and relatively easily identified depression forms the enthesis for M. semispinalis capitis on the suboccipital bone (Figs. 8-11). The enthesis in this place is tendinous (Sakka 1985). It is this area which provides insight into the relative development of this muscle as it responds in the performance of particular strenuous behaviours. Some of these strenuous and repetitive uses result in enthesopathy, a pathological enthesis, and bear common names like "tennis elbow" (epicondylitis radialis) (ibid.). Niepel and Sit'aj (ibid.) identify two enthesopathies associated with the posterior of the cranium: enthesopathia occipitis, which affects M. trapezius and an accompanying disorder calcar occipitis anterius and posterius, which is ossification of ligamentum nuchae. This condition can be seen in a ct-scan (Fig. 7) in the cranium of a prehistoric Northwest Amerindian (Fig. 41). From Sakka's (1985) description of the nuchal musculature, however, and from an EMG study of the superficial musculature performed by this researcher, M. trapezius does not contribute to any great extent to resisting anterior dental loading.

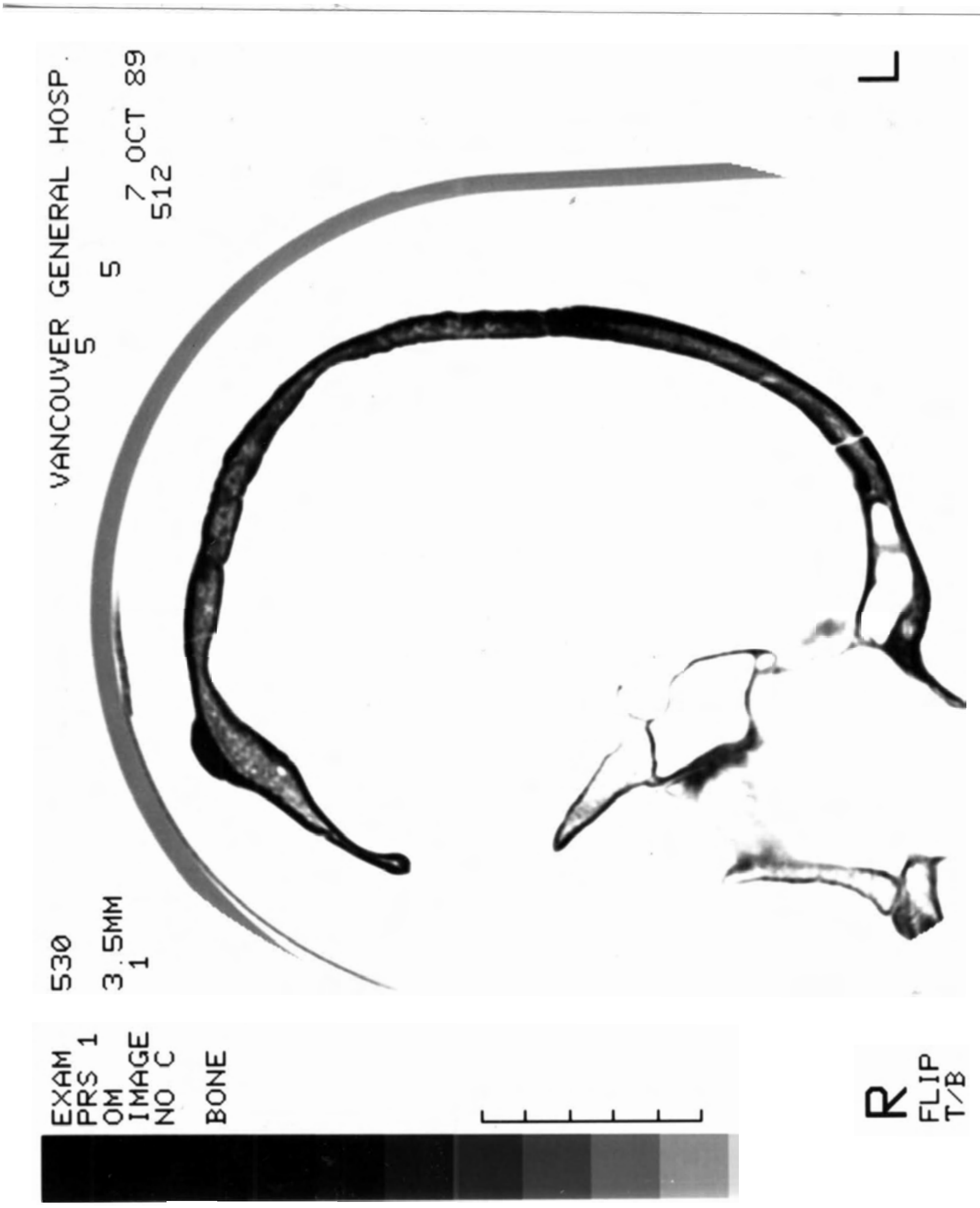


Figure 2: Ct-scan of Calcuttan 5, showing that the occipital torus in this individual is a response of the outer table of the cranium alone.

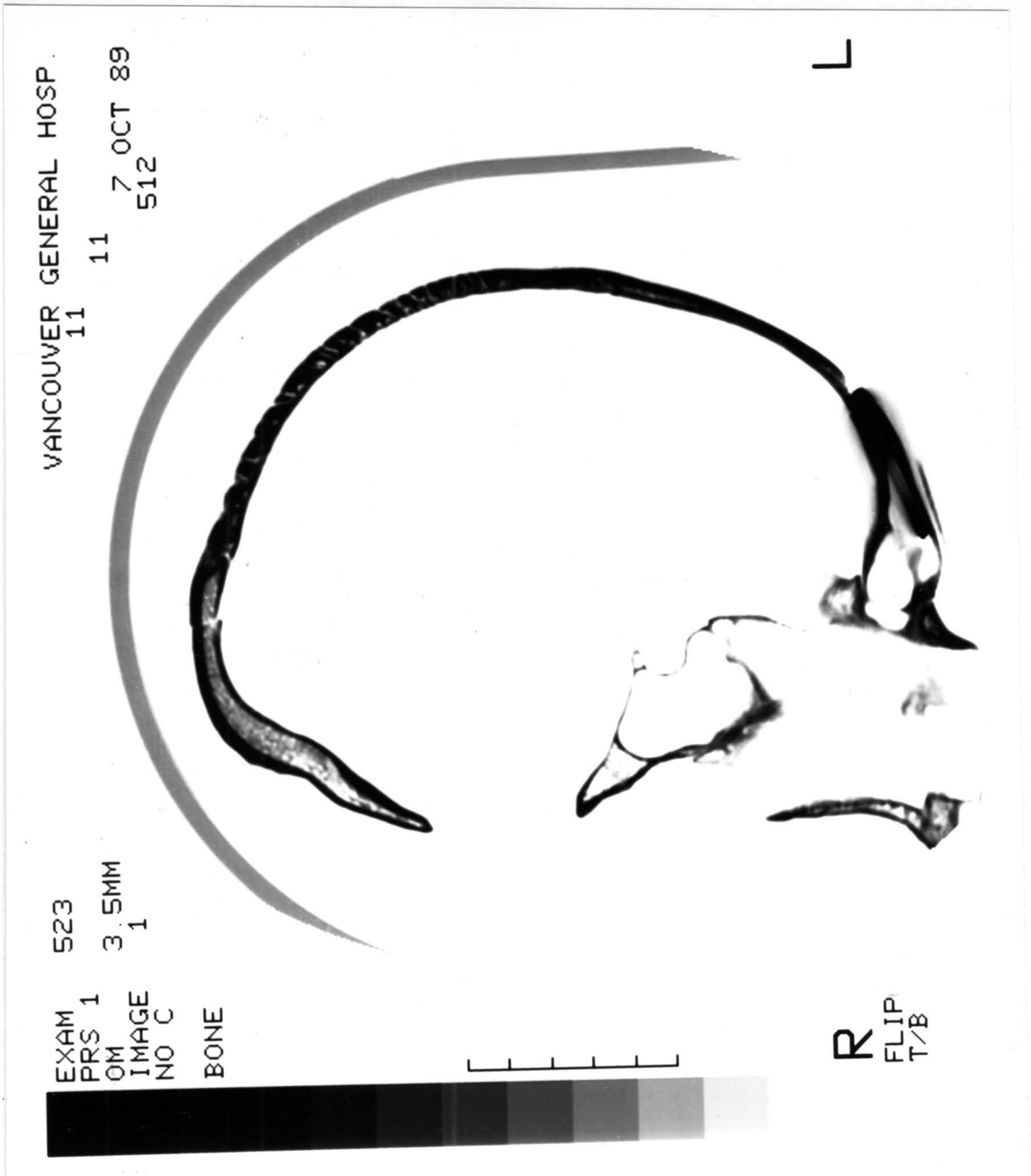


Figure 3: Ct-scan of Calcuttan 11, which exhibits a much expanded torus and bun. Note that the inner table and outer table do not mirror each other in thickness.

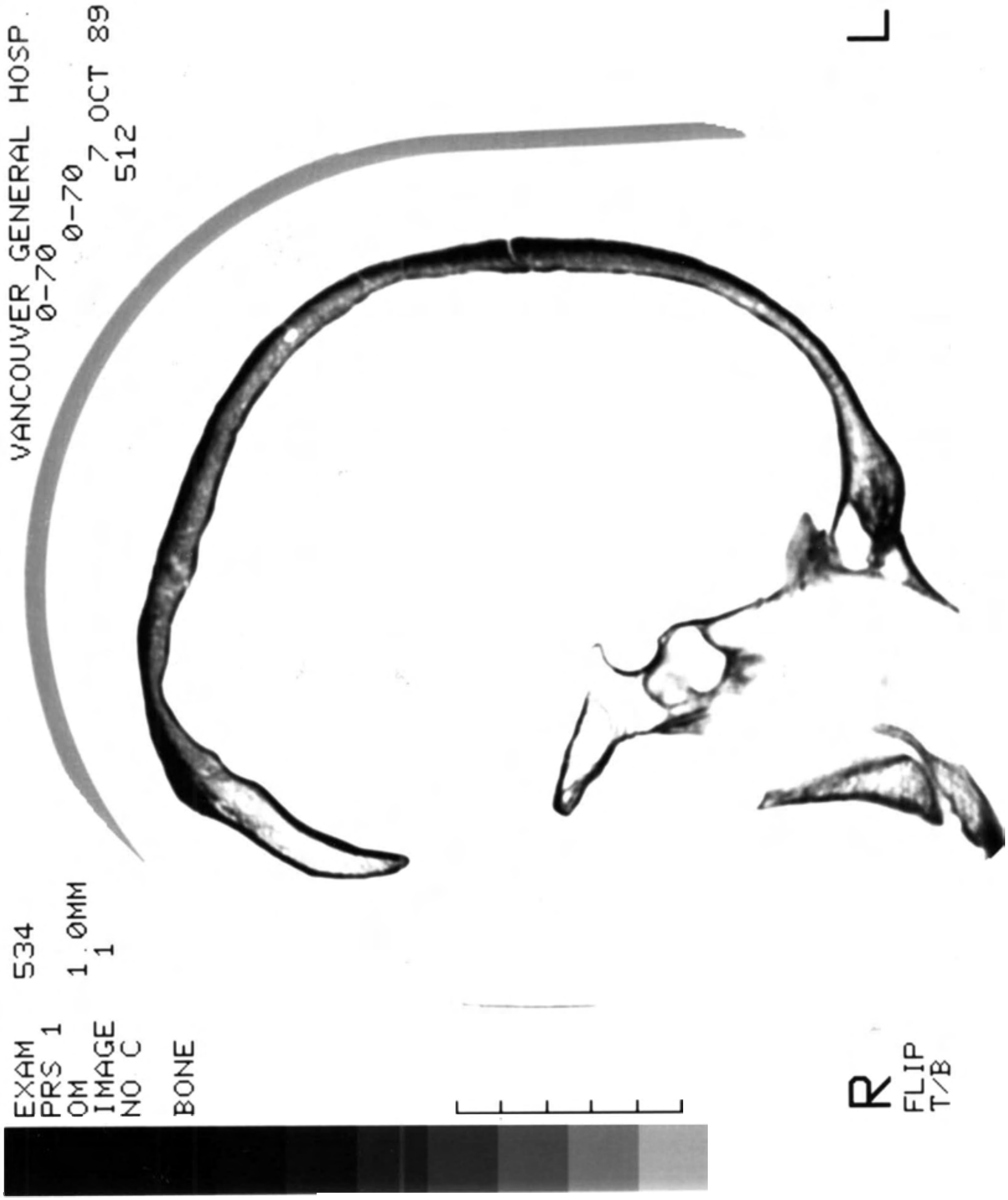


Figure 4: Ct-scan of Murray site prehistoric Amerindian from Lillooet, British Columbia. This individual is one of the two individuals possessing an extremely flat basicranium and well-excavated enthesis for M. semispinalis capitis.

Figure 5: Ct-scan of very robust prehistoric male Amerindian from the Namu site, British Columbia. Note the extent of the cranial thickness in this individual and the thickness of the outer table.

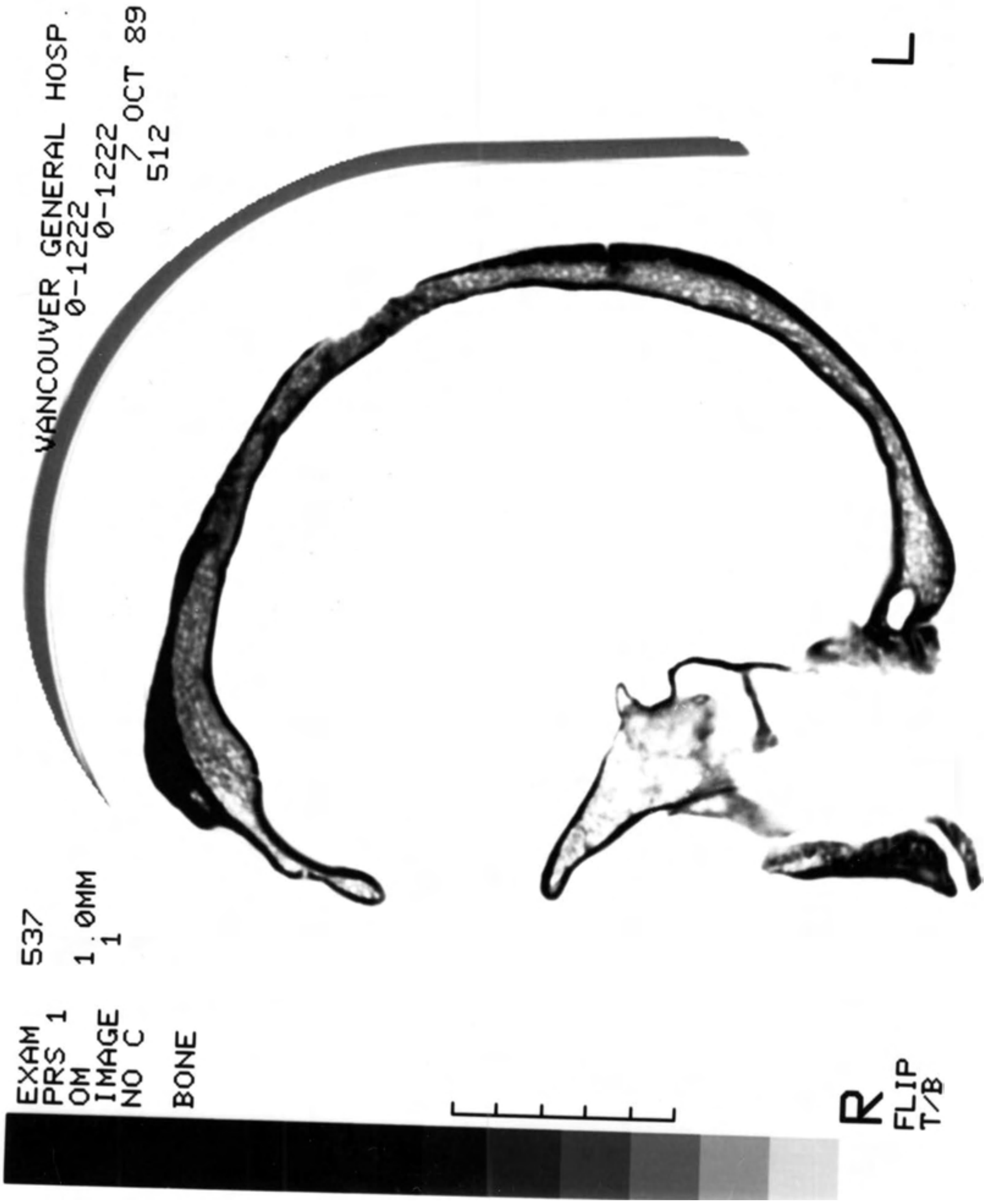
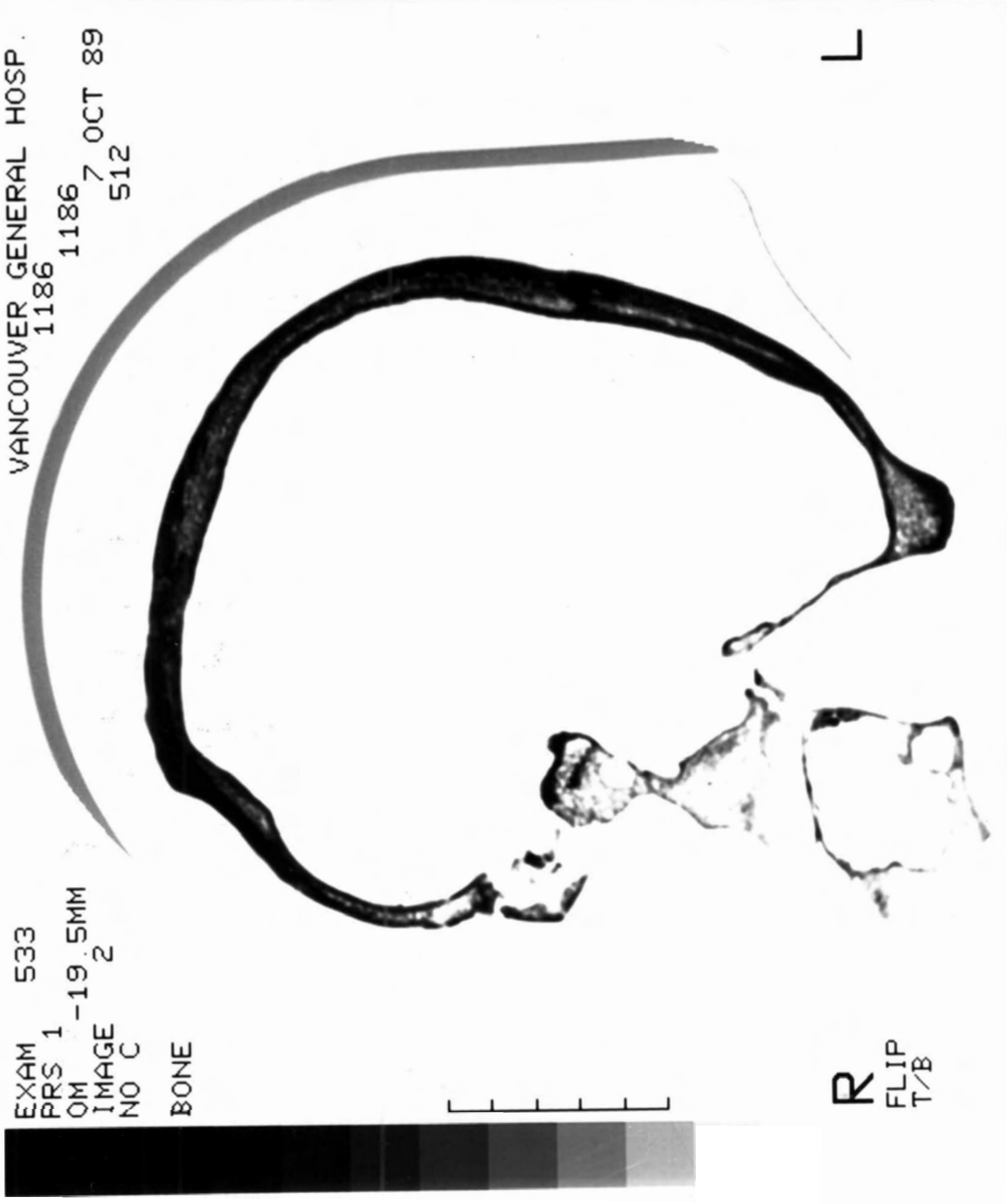


Figure 6: Ct-scan of Anthony Island male.



- Figure 7: Ct-scan of Crescent Beach burial 10.

Sakka (1985) describes *M. semispinalis capitis* in the following informative way: "Situé à la partie interne de la nuque.... il constitue une masse musculaire allongée, épaisse, puissante, étendue verticalement dans les gouttières vertébrales, du rachis à caille de l'occipital.... C'est le m. le plus puissant, le plus épais, celui qui a les insertions les plus étendues. Il joue un grand rôle dans la physiologie et la biomécanique cervico-céphalique et le port de tête..." (p. 54). This muscle, with its origins on the transverse processes of the first six to seven thoracic vertebrae and on the posterior aspect of the apophyses of the transverse processes of the fourth to seventh cervical vertebrae, inserts between the inferior and superior nuchal lines of the *os occipitalis* in humans (Sakka 1985, Crouch 1982). Based upon the different definitions provided by authorities, it would appear that considerable variation exists in the origin and insertion of this muscle, so all allowances have been included in this description. Gray (1977) notes, for example, that this muscle, identified as the *complexus* or *grand complexus* in his treatment, can apparently also have origins from the transverse processes the fourth, fifth, and sixth cervical vertebrae, and that a tendinous band, the *Biventer cervicis*, is sometimes considered a part of the *complexus*, which separates the muscle into two halves, one on either side of the cranium. One of the observations noted in measuring the cross-sectional areas of this muscle of the study sample (discussed below) is that its halves may be of slightly different sizes, perhaps indicating a preference for certain kinds of movement in some individuals. Kennedy (1989) suggests that variable muscular attachments may relate to differences in behaviour, although many of these variable muscular attachments in other parts of the body have been considered to be discrete traits and, therefore, an expression of the genotype (Saunders 1978, 1989).

From its size, position, and the well-excavated appearance of its enthesis, M. semispinalis capitis would appear to be that which is most active in the performance of tasks involving strenuous movements of the head. No empirical proof of this assertion can be offered here as the test of such an hypothesis involves embedding a probe in the muscle. This procedure was thus not possible in the present research. Moreover, Sakka (1985) reports that most knowledge of the function of the suboccipital musculature is based upon intuitive understandings of the orientation and directions of contracture of the muscles. However, it is this muscle which is responsible for the head extension (Crouch 1982), a movement related to anterior dental loading and is interpreted to be that muscle which resists the downward pull of the arms in this behaviour. A rugose and large M. semispinalis capitis enthesis, then, is one osteological indicator of habitual behaviours involving the head in anterior dental loading.

3.2 Toothwear and Anterior Dental Loading

Perhaps the most obvious indicator of anterior dental loading comes in the form of the heavily worn anterior dentition associated with the hominines prior to the advent of certain food and material processing activities (Trinkaus 1983, Hinton and Carlson 1979, Wolpoff 1971, Day 1986, Hylander 1975). Since the use to which the teeth are put influences the morphology of the craniofacial skeleton and since this researcher will argue below that the masticatory apparatus should include the occipital bone, the evidence provided by the wear observed on the dentition is of particular interest. Tooth wear has been demonstrated to be extreme in both early prehistoric and more recent prehistoric peoples (Molnar 1971; Molnar and Ward 1977; Richards and Brown 1981; Wallace 1975; Puech 1982, Puech et al. 1980; Brothwell 1981; Trinkaus 1983a; Tappen 1985; Richards and Brown 1986; Smith 1984, 1986; Bermùdez de Castro et al.1988; Formicola et al.1988; Brown and Molnar 1990). This extreme wear reflects the masticatory and paramasticatory uses to which the teeth were put. Each of the hominines examined in the photoelastic portion of this document is characterised by heavily worn dentition (McCown and Keith 1939, Weidenreich 1940, Vallois and Billy 1965, Tappen 1985). While observing this dental wear in the Cro-Magnon, Vallois and Billy (1965) comment upon its prevalence in prehistoric populations: "... l'extrême usure de la partie de dent subsistante ne peut être interprétée comme un signe de vieillesse, une telle usure étant normalement précoce chez les Hommes du Paléolithique..." (p.59). This tooth wear, which becomes extreme long before advanced old age commences (30-40 years old), becomes especially important in view of the biomechanical model proposed. Hylander (1975) notes the significance and importance of such habitual lifeways among the Eskimo, who use their teeth in the performance of numerous tasks associated with their lifeway. Hominines, unlike the Genus Australopithecus, are characterised by large anterior dentition and smaller posterior dentition (Brace 1967, Brace and Mahler 1971, Walker 1981, Wolpoff 1971, 1979, Frayer 1984). Therefore, the connection between these large anterior teeth, their wear, and the dietary shift they represent has been a much studied and considered area of research in hominid palaeontology (Molnar 1971; Wallace 1975; Hatley and Kappelman 1980; Puech et al. 1980; Tobias 1980; Walker 1981; Grine 1984, 1986; Smith 1984; Kay 1985; among others). The teeth reveal a tremendous amount of information about the adaptation of various animals to particular environments and food sources. Much of this work has aimed not only to reconstruct the diet and the environment which characterised fossil hominids, but also to gauge the evolutionary changes within the craniofacial skeleton.

The hominine lineage provides substantial evidence of jaw reduction in response to cultural change and increasing sophistication in the use of tools and extra-oral preparation of food (Wolpoff 1971, Brace 1967, Brace and Mahler 1971, Frayer

1984). Krogman (1931) notes in this regard that in apes one of the areas of greatest cranial growth is the craniofacial skeleton. These animals show no reduction of the craniofacial region because of their heavy reliance on intra-oral preparation of food which requires a great deal of grinding and, therefore, a large occlusal surface area. Dental reduction in humans is thus accompanied by a prolonged trend toward the reduction of the prognathism and size of the jaws and masticatory musculature in general, from the earliest hominids to the present day (Brace 1967; Smith 1983; Rak 1983, 1986; Preuschoft et al. 1986; Trinkaus 1987; Demes 1987, 1988). This trend, coupled with the evolutionary trend for increasing brain size, is one of the longest lasting trends and perhaps the only easily identifiable one still operative today. Before the full importance of this trend can be appreciated, it is essential to understand the biomechanical workings of the jaws. Many of these important realisations were made and developed by Hylander (1975, 1977, 1979a and b) and subsequently supported, refined, and defended by Molnar and Ward (1977), Bouvier and Hylander (1981), Corruccini and Beecher (1984), Rangel et al. (1985), and Armelagos et al. (1989), among others. This research has seen the interpretations of mandibular function transformed from those of a static link to a much more dynamic third-class lever.

Corruccini and Beecher (1984) have noted the association between occlusofacial dimensions and proper occlusal relations with high-demand mastication in an experimental sample of baboons. They conclude that the facial disharmonies in modern humans come about through the lack of high-demand masticatory behaviours like those more characteristic of prehistoric humans. The lack of high demand mastication may be that factor behind Hannam and Wood's (1989) results which revealed no correlation between the development and orientation of the masseter and medial pterygoid muscles and bite force. Brace and Mahler (1971) believe that occlusal problems appear even more recently with the advent of certain eating utensils such as the fork among Late Medieval peoples and are less prevalent among earlier humans. That the trend toward reduced jaws has continued in more recent historical periods has been demonstrated by Lysell (1958) who notes that medieval forebears are differentiated from modern people in regard to the comparatively large size of their dental arcades. The results obtained in a study by Bouvier and Hylander (1981) confirm this association in tests involving monkeys fed on hard and soft diets. They found that the monkeys maintained on a hard food diet, therefore one analogous to unprepared food, demonstrated an increased amount of remodelled bone in their mandibles and that this element was also deeper than those of the soft food group. The soft diet group ate a diet not unlike that of modern humans, consisting of flour, applesauce, powdered milk, and lard- all highly prepared foods. The authors concluded from this data that there is a relationship between in vivo bone strain conditions and secondary Haversian remodelling in bone. These researchers go on to comment that growth at the mandibular condyle is in compensation to alterations in function and occlusal relations.

A similar relationship between high demand mastication and powerful jaws has also been suggested for certain groups of modern humans. Hinton and Carlson (1979) indicate that the bite force generated by Australian Aboriginal populations is greater than that of several other groups of a more gracile morphology. Hylander (1975) has demonstrated this same phenomenon in Eskimos. These peoples engage in much more paramasticatory behaviour than do most other modern humans (ibid.). In fact, during the performance of anterior dental loading in an EMG experiment performed in conjunction with the present research the researcher found that the greatest limiting factor in lifting weight with the mouth was the weakness of the gomphoses of the teeth and not the strength of the superficial masticatory muscles, masseter and temporalis, and trapezius. The need for increased bite force, then, requires larger and rearranged jaws to maintain the required force for masticatory and paramasticatory tasks. Therefore, it appears that heightened muscular activity influences the growth of the jaws. These heavier jaws, in turn, would require more extensive nuchal musculature as these muscles are recruited in the performance of anterior dental loading and produce alterations in the entheses for these muscles.

Brace and Mahler (1971), Brose and Wolpoff (1971), and Hylander (1977) have connected heavy tooth wear with evolutionary alterations to the craniofacial skeleton, especially in

Neanderthals. Models of the morphological alteration differ between an infra-orbital plate theory proposed by Rak (1986) and supported by Demes (1987), although opposed by Trinkaus' (1987) zygomatic retreat model, the over-all conclusion reached is one that explains Neanderthal morphology as a consequence of biomechanical alterations to better resist bending and torsion presumably encountered during the performance of habitual masticatory and paramasticatory behaviours of these individuals. The end-result of these alterations was a shift to less powerful mastication through a reduction of the mechanical advantage of the primary masticatory muscles by the retention of a considerable amount of facial prognathism in Neanderthals when compared to *Homo erectus*. Demes (1987) contends that these behaviours represent a "deviant usage of the masticatory apparatus in the front teeth region" (p. 302), perhaps in reference to some masticatory and/or paramasticatory use. Neanderthal jaws, then, were highly stressed entities in the performance of habitual loading behaviours. Since the occipital area interacts with the jaws in anterior dental loading, its variable shape and topography likely relates to behavioural differences in successive members of the *Homo* lineage. The unusual morphology of the occipital area in Neanderthals and *Homo erectus* may thus be in some way related to the alterations noted in the jaws. That the anterior teeth are often more worn in Neanderthals and *Homo erectus* than the cheek teeth would support the view that these anterior teeth are functioning in loading behaviours and thus the length of this load arm of the cranium, which is increased by these structures, is of great significance (e.g. Brace et al. 1982, Wallace 1975, Trinkaus 1983a).

3.3 The Human Occipital Bone

Olivier (1975) reminds us that the occipital is perceived as a single entity. In fact, these erroneous perceptions are based in part on that element's being separated from the temporal and parietal bones by sutures in the adult state. It is not, in point of fact, a single cranial element. It forms from seven separate ossification centres, including two supranuchal centres (the interparietals), a basilar, two exoccipital, and two infranuchal centres (Sperber 1989). Moore and Lavelle (1974) identify the cranial base as of utmost importance in any discussion of the cranium because it lies in a position to affect both the cranium and the viscerocranium. The occipital is actually the only cranial bone other than the sphenoid which forms a portion of both the cranial vault and of the basicranium. Unlike the sphenoid, however, the nuchal plane of the occipital acts as a major site of attachment for the nuchal muscles and this relationship may be that which prompted Boule to call the basicranium the "veritable clé de voute de l'édifice crânien" (cited in Heim 1978). The occipital reflects this dual role in that it forms intramembranously like the other cranial vault elements in its supranuchal portion from two ossification centres, but also in cartilage more posteriorly and inferiorly in its suboccipital or infranuchal portions from five additional ossification centres. Ontogenetically, it shares much more in common with the infracranial skeleton than it does with the cranial vault (see developmental sequence illustrated in Gilbert 1989). Sperber (1989) suggests its development is in a modified vertebral pattern, with portions homologous to the centrum (the squamous portion of the occipital), neural arches (the occipital condyles and basioccipital), and the transverse processes (the exoccipitals) of several successive occipital vertebrae. Significantly, the squamous portion of the occipital above the superior nuchal line ossifies from two intramembranous ossification centres before the more inferior nuchal portion does so endochondrally about two weeks later. It is at the juncture between the intramembranous and endochondral portions that we observe the later formation of the occipital torus in certain hominines, both ancient and modern (Weidenreich 1940). Hublin (1983, 1986) notes that this distinctive feature is found only in members of the Homininae, and its first appearance within this sub-family is with KNM-ER 1813, a presumed Homo habilis. Weidenreich (1940) defines the occipital torus with the dual nature of the occipital in mind: "It is a restricted thickening of the occipital bone following the horizontal contour between the lambdoid sutures and coinciding with the occipital flexional angle which marks the boundary between the cranial base and the vault, its individual appearance depending mainly upon the degree to which the cervical muscles are developed" (p.491). Here, then, we have both a defined and limited location of the torus and a potential cause for its variable morphology.

It appears that the ontogenetic origin of the two portions of the occipital may play a role in the manner in which each responds to appositional growth in the cranium as a whole (Baer 1954, Ruff 1980). While most of the cranial bones are a single entity, even at birth the occipital is made up of four or five separate elements. It is likely, therefore, that the appositional growth of these centres will influence the configuration of the entire bone. One might say that the occipital's very unique ontogenetic growth pattern makes it an area of growth pressure since the infra-nuchal portion, deriving from two ossification centres itself, must respond to growth of the cranial vault and basicranium. Enlow (1976) notes that cartilage can be specially adapted to surface pressure and in fact can grow under high pressure, unlike bone that requires a periosteal membrane and vascularisation. Cartilage does not possess a perisoteal membrane since it is non-vascular and as a consequence is not susceptible to occlusion of its blood supply. For these reasons cartilage makes up the epiphyses of the long bones which are under compression. Thus the cartilagenous origin of the nuchal area would seem to suggest that there exists pressure in the region during growth, both of the ontogenetic variety and subsequently. Oyen and Russell (1981) note that woven bone has been identified in many regions of the cranium, including much of the craniofacial skeleton and, interestingly, the occipital. These researchers associate woven bone with quickly growing regions of juvenile individuals. The different ontogenies of the neurocranium and cranial base have drawn considerable interest. Babler and Persing (1982), for example, report that "The relative time delay between the onset of neurocranial and basicranial deformation and alterations in growth of the posterior cranium is of great interest. One possible explanation is that the cartilaginous growth centers of the basicranium respond at a slower rate to mechanical forces, in this case flattening of the cranial base, than the sutures" (p. 343). Baer (1954) identifies two basic and distinctly separate systems of growth in the skull characterised by an early expansion of the cranial vault in conjunction with and dependent upon cerebral expansion; and a second, later and more long-lasting growth of the cranial base and face, which tends to result in an unbending and flattening of the cranial base. This flattening of the cranial base is accompanied by extreme occipital curvature in fossil hominids- a retention of an infantile state of the occipital, causing the occipital to be angled even in its adult configuration (Tobias 1959b). Another interpretation of this combination of basicranial flattening and extreme occipital curvature might be that the basicranium appears to respond more slowly because the development and action of the nuchal musculature prevents the occipital from rapid vertical growth. Such would account for the "stability" of the occipital bone noted early on by Krogman (1931) in his cross-sectional study of cranial shape changes in growing apes. The curved occipital of infants, then, would seem to result from the lack of opposing and anchoring cranial bone to the development of the nuchal muscles. Heim (1989) notes, in this regard, that the occipital of infant Neanderthals tends to be more elevated than that noted in adults of the same group. The angled adult configuration, then, results from the interaction of the nuchal muscles with the growth of the brain and the occipital bone. Such an interpretation seems to accord with the following statement by Heim (1981): " La comparaison des dimensions des jeunes occipitaux montre que la principale différence existant entre les deux types repose sur la précocité relative du développement de l'os néandertalien dans le sens de la hauteur et sur le retard de sa croissance dans le sens transversal par rapport à l'enfant moderne" (p.196). The topic of differing ontogenies among fossil hominines will be addressed in a section below.

3.4 The Occipital Bun (chignon) and the Occipital Torus (*Torus occipitalis transversus*):

The two major alterations to the occipital that have drawn the attention of hominid palaeontologists, and which have also been cited repeatedly as distinctive features separating *Homo erectus* from the Archaic *Homo sapiens*, and particularly from Neanderthals, are the occipital torus (*Torus occipitalis transversus*) and the occipital bun, respectively (Howells 1980, Wolpoff 1980, Kennedy 1980). Trinkaus and LeMay (*ibid.*) provide a useful working definition of the occipital bun in the following manner:

> An occipital bun may be described as a posterior projection of the occipital squama, which is evenly rounded in *norma lateralis* and slightly compressed in a craniocaudal direction. The superior border of the occipital bun is along the lambdoid suture, and its inferior margin is in the region of the attachment of the 'tentorium cerebelli' to the inner table of the vault, where a groove is commonly formed by the transverse sinuses. The bun therefore encloses the occipital portions of the cerebral hemispheres (p.27).

Trinkaus (1983) contrasts the occipital torus and bun of Shanidar 2 and contends that, although similarly placed, these two structures are probably of quite different origin and perhaps different function as well:

> The transverse occipital torus is well developed between asterion and inion, forming a distinct inferior lip. It is divided into two inferiorly convex sections by a notch in the middle of the torus. This notch may indicate the division of the torus into a medial section for *M. semispinalis capitis* and a lateral section for *M. obliquus superior*. The surface between the inferior nuchal line and the transverse occipital torus is quite rugose, suggesting that these muscles were powerfully developed (p.97).

This researcher would see these alterations to the occipital as a consequence of the same biomechanical alterations that appear to have influenced the jaws. This particular view is a slight modification of Tobias' (1955) earlier contention that regulatory genes which control the developmental processes influencing jaw size and proportion are those under selective pressure. Crown morphology and dental dimensions may be under the control of these regulatory genes, but the shape and degree of expression of certain cranial traits may, it seems, be under non-genetic, environmental control. Smith (1983) sums up these hypotheses on a theoretical level in the following scenario:

> Since the cranium can be viewed as a first-order lever ...with the load arm represented by the pre-occipital condylar portion, any extension of the load (like a larger, more projecting face) would need to be compensated for by either increasing the lever arm (the post-occipital condylar portion) or the efficiency of the nuchal muscles (which provide the force) or both. Additionally, loading of the anterior dentition requires that the nuchal muscles exert considerable force in producing tension and torsion. On the basis of these factors, I see Neandertal occipital bunning as a compensatory phenomenon, not so much because it adds mass to the postcondylar cranium, but because it provides a more horizontal orientation for the nuchal plane and expands its area. Biomechanically, the former would substantially improve the physiological efficiency of the nuchal musculature by maintaining a greater cross-section of the muscle roughly parallel to the axis of contraction and by shortening the contractional lever arm (i.e. decreasing the distance between the origin and insertion of the nuchal muscles). The relatively horizontal positioning and expanded breadth of the nuchal plane is provided by the occipital bunning (p.154).

Tobias (1958a and b, 1959b) and, more recently, Trinkaus and LeMay (ibid.) have suggested that the rate and timing of growth and fusion may, at least in part, be responsible for the configuration termed the occipital bun or chignon of the os occipitalis in Neanderthals. Trinkaus and LeMay (1982) proffer an explanation involving growth which occurs in normal development at the lambdoid suture rather than muscular function as the cause for the occipital bun. These researchers suggest that increased vault size comes from osteogenesis along the cranial sutures, spurred by intracranial pressure. Osteogenesis of the cranial sutures proceeds from the metopic suture to the sagittal, coronal, and finally to the lambdoid suture. Trinkaus and LeMay (ibid.) thus reason that it is brain growth late in ontogeny that produces the bun. Differentiated timing of osteogenesis of the occipital and other cranial vault bones makes the occipital the site that must accommodate late brain growth. The only significant feature of the Neanderthal occipital, Trinkaus and LeMay (ibid.) emphasise, is the high frequency with which the bun occurs. This increased frequency, according to these researchers, relates to the characteristic platycephally of the Neanderthals. This interpretation compares favourably with that posited by Russell (1985) in her work with the supraorbital torus, which appears to represent an alteration of the os frontalis to accommodate the reduction of the stress distribution capacity of a receding forehead.

Although Trinkaus and LeMay (1982) have identified occipital bunning as related to late brain growth, Smith (1983) believes that the two causes, growth and muscular function, may be in some manner complementary. Smith's theoretical interpretation of the functioning of the cranium in earlier members of this sub-family is the focus of a portion of the conclusions derived from this research (see below). To determine whether or not these two structures are of the same or separate development it is necessary to determine the function of each. If each functions similarly, then they are likely shape changes relating to an increase or decrease in a particular behaviour, perhaps anterior dental loading. They may be analogous structures whose function is to accommodate the stresses emitted by the nuchal musculature.

3.5 Cortical and Cranial Thickness

Bone thickness has received a substantial amount of treatment in the literature, largely in response to the observation that earlier members of Homininae possess unusually thick cortical bone in the infra-cranial skeleton, as well as in the bones of the cranium, and that the thickness of cortical bone relates to functional variation between groups and individuals within the same group (Weidenreich 1940; Twiesselmann 1941; Getz 1959; Trinkaus 1976; Ferembach 1978; Ivanhoe 1970, 1979; Brown et al. 1979; Ruff and Hayes 1983; Kennedy 1984, 1985; Frayer 1984;

Smith et al. 1985; Jacobs 1985a and b; Bridges 1989). Thus thickened cortical bone whether located in the cranium or infra-cranium warrants consideration as another osteological indicator of activity. Weidenreich (1940) noted the thickened cranial bones of fossil hominines and was one of the first to formally describe and measure vault thickness, although he did not address its function, though intimating that it played a role in the buttressing system he identified in the tori found in the cranium. Thickened cranial vault bones are unique to the Homininae and distinguish these and modern human cranial bones from those of the Hominoidea, who possess comparatively very thin cranial bone (Weidenreich 1940, Twiesselmann 1941). The greater cranial thickness of some early hominines such as the Neanderthals (Trinkaus 1983), Homo erectus (Weidenreich 1943) and of individuals such as the Kow Swamp group of southeastern Australia (Thorne 1971), a group represented by individuals of a similar morphology to that of the Cossack Australian Aboriginal cranium (Freedman and Lofgren 1979a and b), an Eskimo sample (Hylander 1975) and a Northwest Coast Amerindian sample measured by this writer and discussed below all present thickened cranial bone. All of these groups are also characterised by extremes of anterior dental wear. Importantly, cranial bone thickness is also found to distinguish Pleistocene Australians from their modern descendants (Brown et al. 1979), so this thickness does not seem to be related to a genetic predisposition of a single human population as Hublin (1989) has suggested in relation to fossil specimens.

Hublin (1989) has demonstrated that cranial thickness and several other cranial traits obtain together in the same crania such that they should not be considered separately in phylogenetic reconstructions. Among these traits are localised phenomena like the occipital torus, the angular torus, and cranial thickness. Hublin (ibid.) attributes these features to hormonally mediated growth, a potential which has also been acknowledged in the biomechanical literature (i.e. Lanyon 1984) and, even more so, in the theoretical literature (Gould 1977, Alberich 1980, Smith-Gill 1983, Gould and Lewontin 1979). Kennedy (1985) suggests two hypotheses to account for cortical thickness which also involve physiological causes: one, a dietary shift to meat consumption, producing cyclical hypocalcemia; and the other, a genetic predisposition for endosteal deposition of bone. Ferembach (1985) has also made similar suggestions in regard to human populations making the transition from the Magdalenian to the Mesolithic periods. Riessenfeld (1967) also cites a dietary element in the production of brachycephalic individuals in nutritional deficiency in rats. This literature predicates itself upon not only selection and selective pressures, which have dominated most phylogenetic thinking recently, but also upon environmentally mediated adaptation through hormonal and physiological activity. The difficulty in understanding the cause of thickened cortical bone is summed up best by Trinkaus (1983a) when he writes:

> If one may assume that some increase in 'cultural adaptive efficiency', however marked in the archaeological record, corresponds to the Neandertal-Upper Paleolithic hominid transition, one may then postulate a decrease in the level of selection for robust individuals. If the femoral morphology of the Neandertals was largely determined by the genotype (a reasonable assumption, since it occurs continuously from *H. erectus* (e.g., Olduvai Hominid 28 and the Choukoutien sample through the Neandertals) the transition would have required a shift in selective pressure and possibly an influx of new genetic variation to have occurred *in situ*. If, on the other hand, the Neanderthal femoral morphology was developed each generation through biomechanical alteration of the skeleton in response to habitual stresses, it is not necessary to invoke high levels of selection or massive migrations. Since the pattern would arise anew each generation, a generation would be sufficient for the transition. Unfortunately it is not possible to determine which process contributed to the Neandertal and Upper Paleolithic femoral morphologies. Undoubtedly some combination was responsible (p.313).

Although Trinkaus (1981) implicates cold climate adaptation in the form of Bergman's and Allen's rules as having been responsible for the shortened distal limbs segments of Neanderthals, he does not claim that climate plays a significant role in the thickened cortical bone of these Middle Palaeolithic peoples. Kennedy (1984) describes thickened cortical bone in the African Kabwe individual, who lived in a much more balmy climate (Laporte and Zihlman 1983), although others within this group do not possess thickened post-cranial cortical bone (Kennedy 1990 cited in Smith *et al.*1990, Trinkaus 1976). Thickened cortical bone, then, may have a distribution like that noted in more recent human populations. This evidence suggests an acquired, rather than a genetic cause. Climatic effects do not seem to account for the distribution of thickened cortical bone among *Homo erectus* and archaic *Homo sapiens* populations either. Inuit populations, for example, do not demonstrate thickened cortical bone despite the fact that they appear to be a cold-adapted population (Gessain, cited in Tillier 1989).

There are other reasons posited in the literature to explain differing amounts of cortical thickness in various bones in various populations. Lanyon *et al.* (1979) associate thickened cortical bone on the cranial aspect of sheep radii with remodelling in response to tension. Bridges (1989) has investigated differences in cortical thickness in the femora and humeri of a population of prehistoric Amerindians from the southeastern United States and has offered evidence to suggest that activity differences over time account for significant differences noted in males and females in her sample. Trinkaus (1976, 1983a) has posited high activity levels produced by a robust morphology to account for Neanderthal thickened femoral cortices. Interestingly, although the Kabwe and Omo individuals possess thickened cranial and post-cranial bone (Day and Stringer 1982, Kennedy 1984), as do both the Neanderthal groups sampled by Trinkaus (1983) and the Cro-Magnon individual (Valois and Billy 1965), the now near contemporary Skhul V individual does not (McCown and Keith 1939, Trinkaus 1976). It would appear that some mechanical or perhaps behavioural difference based on either size, proportion, or shape must be responsible for this difference. Trinkaus (1976) suggests that part of the reason for the relatively thin cortical bone of the Skhul femora may lie in the increase in mean neck-shaft angle of the Skhul specimens, for example. Previously, Smith et al. (1985) determined that cranial thickness was related to cranial length, but not cranial breadth. Reference to the greatest length and breadth measurements of a sample studied as a part of this research reveal the same relationship between cranial length and four separate measurements of cranial thickness, but also correlation between these measurements and cranial breadth and with the size of the cranium (see below). Brown et al. (1979) report that differing shapes of morphological features on the cranium can influence cranial thickness. From Figures 2-7, one can see that cranial thickness increases at certain points along the cranial vault. This relationship between cranial features and cranial thickness will be examined below in the experimental portion of this document. As with anterior tooth wear and occipital morphology, it appears that thickened cortical bone may be more properly associated with activity than with any innate genetic propensity, which accounts for its inclusion as an osteological indicator.

Chapter 4: Growth and Development

Questions concerning the manner in which Neanderthal and other hominine infants and children grow and develop in comparison to the australopithecines and modern humans has become an important and contested topic in the recent literature. Growth and development are easily influenced by environmental stimuli and, therefore, warrant treatment in any consideration involving the onset of particular behaviours. Bromage (1989) has demonstrated that the facial area in at least early members of the genus *Homo*, that is those Plio-Pleistocene in age, mature in a manner more similar to that of the gracile australopithecines than they do like modern humans. From his results, Bromage has suggested that remodelling differences between members of individual palaeospecies may aid in developing phylogenies of fossil hominids. Moreover, however, although not an osteological indictor in its own right, if certain hominines can be shown to develop at different rates, then we may be able to infer from these differences that precocious growth results from the early assumption of adult behaviours as has been discussed by Woo *et al.* (1981) who noted precocious development in immature animals in response to increased activity (see above). Although he presents no data, Heim (1983) remarks in the following manner about the La Ferrassie 8 Neanderthal: "...les caractères particuliers de l'occipital néandertalien concernant ses dimensions, ses proportions relatives et ses traits anatomiques semblent résulter d'une ossification différente de la nôtre, qui est essentiellement dominé par une ostéogenèse et une croissance plus rapides. Une telle constatation rejoint d'autres observations de même ordre sur l'ensemble du squelette des Hommes de Néandertal" (p. 198). Others have also commented upon the precocious development that characterises Neanderthal infants (Tillier 1983, Dean et al. 1986), as well as older Neanderthal children and adults (Brothwell 1975, Wolpoff 1979, Thompkins and Trinkaus 1987). Recently, however, Tillier (1988) has denied that Neanderthals mature at a rate different from the modern human norm. Minugh-Purvis (1988) has noted that Neanderthals grew slowly at the modern human rate. The tooth eruption sequence and skeletal maturation were similar to those of modern humans. She writes, "If we look at the Neanderthal skeletal as compared to dental maturation, we see that Neanderthals clearly grew at the modern rate- which can only mean that they had a period of childhood dependency ostensibly the same as our own" (quoted in Marshack 1989, p. 24).

Those differences which Heim notes may, it appears, relate not to skeletal maturation differences but instead to different muscular development commencing early in the post-natal life of the infant and likely intensifying as the individual matures and takes on more and more adult behaviours associated with a particular lifeway. This interpretation is supported by Wolpoff's (1979) suggestion that the increased size of the deciduous dentition is in response to earlier weaning. Skinner (1989) presents evidence which seems to cast some doubt on the validity of this association in that he found that Upper Palaeolithic children appear to have been weaned somewhat earlier than similarly aged children in a Middle Palaeolithic sample. Skinner also notes, however, that Neanderthal children's permanent teeth were more quickly worn than their Upper Palaeolithic comparison sample. In other words, Neanderthal children appear to perform adult activities and behaviours, including dental loading, at an earlier age than do modern children. Hyper-muscularity in Neanderthals and their forebears might then be postulated as the cause for the distinctive occipital morphology of Neanderthals as identified by Hublin (1978, 1980, 1986), including most importantly the angulation and rugose occipital morphology that often produces an occipital torus. The evidence derived from the study of the infra-cranial skeleton of these earlier members of the Homininae would then seem to agree with this interpretation of the Neanderthal occipital morphology, especially in view of the close ontogenetic relationship between the occipital and the vertebral column outlined above.

The close functional relationship between the musculature and the jaws suggests that the two must be intimately related in growth and development and, furthermore, that these dental and masticatory changes are not the consequence of biological evolution, but rather the result of environmental stresses that impinge on the jaws during growth (Brace and Mahler 1971). Both

Oyen et al. (1979) and Tobias (1959a, 1958b) have noted that appositional growth in the cranium at the browridges and in the occipital region is correlated with dental development and eruption sequences. Oyen et al. (1979) "... infer that browridges in Neanderthals and other large-browed hominids were produced by growth processes that were developmentally and functionally very closely attuned to changes in the masticatory system" (p.86). Since the occipital has been argued to be a part of the masticatory system any changes in the rate of growth of the jaws would have a potential influence upon the shape the occipital takes throughout life, but especially from those influences experienced early in life when the morphology of bone is most influenced by muscular development (Chvapil et al. 1973; Kiiskinen 1977; Carter 1984, Carter et al. 1986 and Carter et al. 1986; Shaw et al. 1987). Carter et al. (1987) have, in fact, shown that metaphyseal cartilage in the femur is extremely susceptible to extrinsic factors from the immediate environment, including importantly muscular contracture, and they note that the first contractile elements of the muscular system appear in the embryo simultaneously with the primary ossification sites.

It seems likely that these realisations may apply to the early stages of the cartilagenous occipital bone as well. That the occipital bone has been used to determine the age of fetal and early post-natal infants seems to be much influenced by the growth of the cranium even early in development. Mechanical stimulation appears to be responsible for the appearance of both bone and secondary cartilage (Herring n.d.). This early growth can also be associated with muscular development even pre-natally. Fetal movements would be those made to develop coordination and promote differentiation and growth of tissues (Herring and Lakars 1981). In this regard, Redfield (1970) observes that the external features of the occipital appear as "ripple" marks and a slight development of the crista occipitalis externa by between six months to two years. It seems likely, then, that the shape bone takes begins with the first appearance of the muscle anlagen pre-natally and continues to change post-natally as the infant matures.

The appearance of these distinctive occipital features, then, is an important portion of the scenario laid out above in that their appearance would act to indicate important behavioural transitions in the lives of our ancestors, and moreover, the age at which individuals began to perform adult behaviours. It is not enough simply to compare adult and juvenile remains to ascertain whether or not the pattern is the same as Trinkaus (1988) has recently done with Neanderthal radial tuberosities. Since individuals may enter into adult activities during a range of ages, the exact physiological cohorts must be isolated and compared individually to ascertain if certain morphological features appear at a specific time in a disproportionately high frequency. If one does not do so, one cannot consider how much developmental plasticity is involved in the particular morphological configuration. Similarly, the linear growth observed by Brown et al. (1979) in the cranial thickness in an aboriginal population is likely an artefact of their not having accounted for the age of their subjects and not employing a prescribed time interval for measurement of cranial thickness. Even so, these researchers identified a growth trend that bore witness to growth from ages 8 to 18 that eventually discontinued during late adolescence, likely when growth and development of the craniofacial skeleton ceased.

The association between the craniofacial skeleton and the occipital in both growth and in development is one that is quite important to the scenario laid out above. Head posture, which is maintained by the nuchal musculature (Moore 1965, Schultz 1959), has been previously shown to affect occlusal morphology of the jaws and dentition and has been of interest for the clinical treatment of occlusion problems (Nanda and Goldin 1980, Winneberg and Pancherz 1983, Solow et al. 1982, Goldstein et al. 1984). It appears, then, that the two areas, the jaws and occipital, are related in both growth and development. In this regard, Oyen and Enlow (1981) have provided evidence that as the face grows and the masticatory system develops, the nuchal musculature must counterbalance the increased mechanical stresses exerted by the jaws and that this compensation produces more pronounced nuchal lines and crests in a varied group of primates. Krogman (1931) and Baer (1954) note that the eruption of the first molar and the time between the eruption of this tooth and the eruption of the third molar coincided with the greatest movement in the craniofacial skeleton. These researchers contend that growth is, in fact, completed by the time the second molar erupts. These two events occur when teeth erupt between the ages of six and eight years for the former and 12 and 18 years for the latter in archaeological Native American children (Ubelaker 1978). This time would coincide with the appearance of various adult cranial features. Both Tobias (1955, 1958b) and, more recently, Tillier (1983) have implicated the eruption of the dentition with alterations in the parietal and occipital bones and the maxilla, which would suggest that the onset of adult masticatory and paramasticatory functioning might be implicated in adult cranial shape and morphology as Weidenreich (1940) intimated in his mention of the cervical muscles in relation to the surface morphology of the occipital discussed above. As the dentition erupts, new patterns of jaw movements are required which cause muscles to move in an altered pattern, unlike that required during early infancy before the eruption of the dentition. The altered cranial morphology noted in successive members of the Homininae may be viewed, then, as an interaction between the growth of cranial elements and behaviour in response to the erupting deciduous and permanent dentition.

Oddly in view of the foregoing discussion, the nuchal muscles have not been firmly implicated in the eventual shape that the occipital takes in sub-adult and adult Neanderthal remains. McCown and Keith (1939) mention that the occipital torus represents a wave of bone which precedes the expanding attachment of the semispinalis muscles and that the torus "moves upwards" in growing youths (p. 248-cf. Krogman 1931), although they cite no empirical evidence to support these associations. In fact, many researchers have denied that these muscles influence occipital morphology in infants or adults (Patte 1955; Heim 1981, 1989; Trinkaus and LeMay 1982; Hublin 1986). Heim (1981) comments upon this phenomenon when he writes:

> La portion sus-iniacque de l'écaille occipitale surplomb la région nuchale en formant un <<bourrelet>> horizontal visible au niveau de la partie moyenne de l'os au-dessus de la zone rugueuse.... Ce futur torus occipitalis des Néandertaliens adultes est donc déja présent à ce stade précoce du développement. Il semble être la conséquence d'une disposition normale chez le foetus plutôt que le résultat d'une action musculaire comme on l'a souvent écrit. En effet, la dissection de foetus moderne nous confirme qu'une éminence transversale à ce niveau, située nettement au-dessus des insertions des muscles de la nuque, est déja présent bien avant la naissance (p. 198).

Heim (1989) thus contends that the torus found in infants and retained in adult Neanderthals results from differential growth of the interparietal and infranuchal portions of the occipital, but because he observes the same development in modern infants he does not admit the muscles as having any influence on the amount of straightening of the occipital in modern adults, but suggests what must be an implicit genetic cause. Although Heim implicates hormonal control in this altered growth pattern, he does not address the process or medium through which this occurs. He does not answer how or why the infantile shape is retained in the adults. Such an assertion and observation would seem to support, rather than deny the influence of the musculature on the shape of the occipital, even intra-uterine.

Contrary to Heim's argument, however, Brothwell (1975) observes that many distinctive Neanderthal features do not appear until puberty, noting that although Neanderthal traits are present in the Teshik-Tash 10 or 11 year-old juvenile, they appear to be absent in his opinion from younger Neanderthal children. Trinkaus and LeMay (1982) note the appearance of the occipital bun quite early in the developmental sequence of the Neanderthals and their immediate predecessors. Two immature Neanderthals from the last glacial, Engis 2 (age 5-6 years) and Teshik-Tash 1 (age 8-10 years), exhibit prominent occipital buns, and Le Moustier (age 15-16 years) may have had a small occipital bun. In addition, the Krapina B posterior cranium (5-6 years?) from the last Riss-Würm interglacial has a large occipital bun.

Weidenreich (1943) intimates a similar relationship between age and the appearance of the occipital torus in the Zhoukoudian specimens when he writes, "The more fragmentary Skull III was of about the same size as Skull I but belonged to a juvenile individual as is revealed by the conditions of the sagittal and lambdoid sutures which are preserved and *particularly* by the poor development of the occipital torus" (p. 183-emphasis mine). Brothwell (1975) suggests that this disparity derives from the activity of growth processes just before puberty, which are responsible for the appearance of the distinctive Neanderthal morphology. This researcher contends that it is conceivable based on the foregoing that these growth processes and the traits they produce are mediated through habitual strenuous activity.

Tillier (1984) notes that the Qafzeh 11 juvenile, aged 12-13 years with a nearly complete adult dentition, possesses an occipital morphology which"...s'intégre parfaitement dans le groupe [des adultes]... pour nombreux caractères archäiques qu'il possède" (p.23). At this age the morphology associated with adults is in place in the occipital region. Hublin (1980a and b), Heim (1981), and Tillier (1982, 1983a and b, 1984), on the other hand, note the appearance of distinctively Neanderthal morphology in the occipital of younger Neanderthal infants, including the development of a supra-iniac fossa, linear tubercle, superior nuchal lines, occipital curvature, and a weakly developed occipital torus. Tillier (1982, 1983b, 1984) notes the lack of a supra-orbital sulcus and distinctively Neanderthal traits in the craniofacial skeleton of these juvenile Neanderthals, however. She (1987) notes in the 6-year-old La Quina 18 individual the following morphological situation " La projection de la face vers l'avant, telle qu' elle s'observe chez l'adulte, n'est pas réalisé chez l'enfant comme en témoigne la position antérieur du pilier inféro-externe du maxillaire" (p. 204). Additionally, Tillier (ibid.) describes a supra-orbital torus "...tel qu'il a été défini chez l'adulte néandertalien *en voie de différenciation* " (p. 128 emphasis mine). The same researcher notes that " ... il est possible d'envisager une mise en place plus précoce des caractéres néanderthaliens pour les os de la voûte crânienne que pour ceux de la face" (p. 148). The facial skeletal development is observed to be "contemporains de l'entrée en fonction des dents permanentes" (Tillier 1989: p. 324). Tillier (1983b) describes a case of even less development in the slightly younger Engis 2 cranium, noting that many features are scarcely developed in the juvenile stage which later characterise the adult. Included among these are many of the crests which are found in the vicinity of the mastoid process, such as the mastoid and supramastoid crests, as well as certain features of the occipital, such as the linear tubercle and occipital torus, which is weakly developed in this individual. It appears, then, that the cranial vault of these juveniles assumes its adult form before the craniofacial skeleton follows suit sometime perhaps around adolescence when the permanent dentition erupts and that many of the distinctive features of the Neanderthal adult do not make their appearance until later.

Such an exegesis seems to accord with the description of the juvenile Homo erectus, WT-15000, described recently by Leakey and Walker (1989). This individual, possessing a nearly complete adult dentition, demonstrates occipital and frontal morphology commensurate with an adult. At puberty, then, these distinctive traits of the craniofacial skeleton appear, much like the secondary sexual characteristics that allow us to determine sex from partial cranial fragments. Therefore, just as Wolpoff (1980) identified a posterior to anterior progression of evolutionary changes in the crania of the Archaic Homo sapiens, it appears that development and growth of the juvenile cranium proceeds from cranial vault to craniofacial skeleton. This pattern fits the characteristics of the growing juvenile in that the occipital assumes an incipient adult morphology before a similar occurrence in the craniofacial skeleton sometime later in childhood.

These alterations to the occipital would seem to occur after weaning has been completed and the child has begun to participate, presumably, in dietary and cultural practices of the adults. In order to offset the heavy jaws and face necessary for successful participation, the nuchal area must provide the attachment areas for powerful nuchal musculature. The bun may thus develop in response to the development of large jaws and associated musculature necessary for pursuit of the lifeway. The cranium, presumed to be a dynamic entity under this scheme, must respond by dissipating potentially disruptive forces. It does that by increasing the strength of its sutures through increased cranial thickness. In support of this hypothesis, Washburn (1947) reports that the amount of growth at the sutures may indeed be influenced by mechanical factors independent of the bone matrix itself.

There is some experimental support for these assertions. Bennett (1965), in his study of cranial growth and wormian bone formation, has refuted the assumption that wormian bones are genetically determined and attributes their formation to genetic factors controlling growth at the posterior of the cranium, and especially to the attained length of the basi-occiput. He suggests that these ossicles are not under strict genetic control but, instead, result from growth stress at the cranial sutures. Herring (n.d.) cites instances where stress alone has produced more complex sutures as in the case of use of a cradleboard in Amerindians. The occurrence of wormian bones, dolichocephally, and occipital tori and buns may be connected in ontogenetic development. Krogman (cited in Washburn, 1947) notes that while the human brain has reached 90% of its adult size by the fifth year, the masticatory muscles have reached only 40% of theirs by that time. The slow development of the musculature of the cranium in relation to the attainment of full brain size leaves open the possibility that the nuchal musculature influences the final configuration of the cranium and, especially, the occiput. Interestingly, Trinkaus (1983) has noted a preponderance of wormian bones in his Shanidar and other Neanderthal samples, as indeed has Day (1986) in the Middle Pleistocene Dali cranium. Howells (1957) suggests that it is growth in the posterior part of the cranium that is responsible for ultimate length and not changes in the cranial base. It has also been noted that the ultimate length of the cranium is achieved later in development than that of the ultimate breadth of the cranium (Riesenfeld 1967).

4.1 Age-related Changes in the Development of Cortical and Cranial Thickness

If cranial and cortical thickness are reflections of the mechanics of the cranium and post-cranium and are due to heightened muscular activity, then we would expect to find this trait to differ among age cohorts with infants and children characterised by relatively thinner cortical bone than that of adults and between groups living different lifeways. Brown et al. (1979) make the following observation in their study of cranial thickness in Australian Aboriginals aged 8 to 18 years: "Compared with other populations, cranial thickness was greater in the Aboriginals from about age 12 years except for frontal thickness measured at nasion in males. This observation is explainable [sic] by the marked nasal depression which is a characteristic of the Aboriginal male adult" (p.70). These researchers note that the development of the adult cranial thickness proceeds at an almost linear increase until adult dimensions are attained, except in the frontal which experiences a growth spurt at adolescence. Moreover, and very importantly for this study, these changes are seen to be an important contributor to the length of the cranial base, head length and circumference.

Brown et al. (ibid.) observe that the cranial thickness values attained by modern Australian Aboriginals living non-traditional lifeways do not match the cranial thickness values recorded for late Pleistocene inhabitants of Australia (Throne 1971, Thorne and

Wilson 1977). One of the hypotheses proposed here is that cranial configurations monitor shifts in the activity patterns between groups of time-successive prehistoric peoples. Tweisselmann (1941) identifies several factors which he believes influence cranial thickness, including the size of the cranium, the age of the individual, and the chronological antiquity of the cranium (more ancient crania being thicker than those of more recent peoples). He notes that Amerindian crania are thicker than those of a modern European sample from a 17th century skeletal collection from Whitechapel, which according to the above hypothesis would relate to the prehistoric lifeways of the former and the reduced paramasticatory lifeways of the latter group.

Israel (1972, 1980) has noted changes in cranial thickness of adults associated with increasing age, producing an enlargement of 3.5% in overall thickness in both males and females. Tallgren (1974), however, has denied this relationship based on his study sample. Tallgren's sample, however, consists of edentulous orthodontic patients, which might account for his differing observations since the growth of the face in children is geared to dental development and likely dental attrition as well. It seems likely that the orthodontic devices altered the biomechanics of the craniofacial skeleton. From these data, it would appear that the craniofacial skeleton undergoes growth changes that are under biomechanical influences throughout life.

A review of the relevant literature substantiates this observation in Neanderthal infants and juveniles. Hublin (1980b) notes the presence of distinctive Neanderthal features in the occipital bone of the La Chaise Suard, Engis 2 and La Quina 18 children, all of whom are aged between 5 and 10 years. However, Hublin comments, " Il est intéressant de constater que ces caractères se manifestent alors même qu' aucune superstructure importante ne s'est encore développée. L'os est encore mince ou même très mince et, dans le cas de l'enfant de l'abri Suard en particulier, il semble modelé sur l'encephale" (p.671). Hublin reports, in fact, that the thickness of the latter specimen is only 2.8 mm at lambda and only 1.5 mm thick at the right portion of the occipital with little diploë expansion. Tillier (1982) concurs with this observation of relatively thin cranial bones in hominine children, although as expected there is quite a range of values from the relatively thick Skhul 1 at 5.0 mm at bregma to the very thin Engis 2 cranium at 2.5 mm at bregma. For the Qafzeh 11 12-13 year old, Tillier (1984) records values ranging from 2.0-6.0 mm depending upon the location with a thickness of 3.0 mm at bregma and 5.0 mm at lambda. These figures demonstrate that this anatomically modern individual had experienced some cranial thickening by this age. It is this researcher's contention that the thickening of the outer table and diploë layers of the cranium occurs in response to the biomechanical demands exerted by the developing masticatory apparatus, of which the nuchal area is a part, and furthermore, that this expansion occurs with the growth observed in juvenile dental and craniofacial growth. Although distinctive Neanderthal features appear already at 23 months, the increased thickness of the adult doesn't appear at this early developmental stage. A suggestion of hormonal activity allows another potentially more clear understanding of the thickened cortical bone possessed by some early members of the hominine lineage. It seems that cortical bone thickening affects both the outer table of the cranium and the cortical bone of the diaphyseal walls of long bones, the latter being affected by medullary stenosis as well. Since these influences are found in bones throughout the body and both males and females (Tweisselmann 1941, Brown et al. 1979, and this study), they add credence to the contention that a systemic cause is responsible. This understanding is made clear in the following passage from Burr and Martin (1989):

> Remodeling involves a net resorption of bone throughout life. According to the theory, its architectural effects are the opposite of the modeling effects: remodeling slows the normal age-related periosteal expansion but stimulates endocortical expansion....Modeling does not occur on Haversian surfaces; remodeling is responsible for all changes that occur intracortically. The architectural changes of activated modeling and inhibited remodeling are the same: periosteal apposition is stimulated but endocortical expansion is prevented. Conversely, when remodeling is increased, modeling is inhibited and expansion of the marrow cavity is accelerated" (p.191).

This researcher believes that this understanding of bone response allows an appreciation of what may have been metabolically regulated physiological conditions which accounted for the morphological situation observed in *Homo erectus* and some members of the Archaic *Homo sapiens*. These individuals demonstrate effects commensurate with active modelling and inhibited remodelling of cortical bone. This interpretation accounts for the stenosis observed in the long bones in some of these earlier hominines, as well as the thickened cortices that have been considered taxonomic markers of the identified morphospecies. This reading of the morphological situation in these individuals also allows an appreciation of the timing of these changes. Since modeling of bone is seen to be most active prior to skeletal maturity, it is in the younger individuals that heightened activity must have commenced. Thus we should expect to see the changes associated with adult activities at a specific range of age cohorts, perhaps those represented by childhood and adolescence. This interpretation is in keeping with the gradual appearance of adult features in the known juvenile Archaic *Homo sapiens*. The prediction would be that when we have a sufficient collection of immature *Homo erectus* individuals, a similar phenomenon, though one perhaps indicative of even earlier onset and the effects of more heightened modelling would be observed, especially if *Homo erectus* groups were less dependent on extra-oral food preparation than their Archaic descendants.

Chapter 5: Experimental Analysis

The experimental portion of this research consists of two parts. The first portion involves the use of photoelastic analysis to understand the manner in which cranial shape influences strain distribution and magnitude in crania experiencing anterior dental loading. Jones and Hungerford (1985,1987) and Post (1979) have successfully used this technique on various objects and recommend the technique for testing objects with no known strain pattern. Andonian and Tudor (1984) have, in fact, used the technique to study the strains experienced by a lion cranium during loading of the canine and achieved good results, but attempted no interpretation of the resulting strain pattern. Although Jones and Hungerford (1987) have demonstrated that strain-gauges are more sensitive than photoelastic coating, the latter was employed because of the absence of any studies of the strain direction in the cranium and none relating to magnitude of forces within the cranial vault. Traditional strain-guage methods require prior knowledge of strain direction. Therefore, the technique is most appropriate for unlocking the strain patterns of the cranium, an entity possessing both a complex geometric shape and a complicated arrangement of loading conditions through the action of the adhering musculature.

Oxnard (1971), who has used the photoelastic technique to better comprehend strain in the infra-cranial skeleton, has observed that the photoelastic method does not provide proofs for actual strain situations in objects, but rather provides analogous conditions to those observed to function in the living organism. The analogy employed here is that the cranial vault, whether of bone or modelled in epoxy plastic, will demonstrate similar surface properties due to the similar shapes of the material. The numerical values produced are not comparable between different materials of the same shape, nor do they reproduce the actual strains experienced in the bone of the cranial vault. However, they do provide a means by which to rank the responses of homologous areas in the cranial casts and within a single cranium.

5.1 Introduction: The PhotoStress® Technique

PhotoStress® is a technique which accurately measures surface strains, that is- the deformation, the lengthening or shortening, experienced at a point in a structure under either an applied static (long duration) or dynamic (short duration) stress (measured as the load per unit area). Strain is defined as the change in the length of a loaded specimen compared to the specimen's original length before loading. Strain is thus a dimensionless variable (the labels cancel each other). The method employs a strain-sensitive epoxy plastic coating which is bonded to the test specimen. The bonding agent contains a reflective constituent which allows the transmission of refracted light. The test specimen is illuminated by a reflection polariscope and, through the use of polarised filters, provides the viewer with a coloured display of the strain distribution and pinpoints areas under high, low, or no strain. These recordings are understood to result from the difference between the two principle strains, compressive and tensile, which cross each other at a 90° angle (Lanyon and Baggot 1976). Positive readings are tensile strains and negative readings are compressive strains.

As the photoelastic plastic coating retards the refracted light the magnitude (isochromatics) and direction (isoclinics) of strain are recorded as colour changes and banded lines, respectively (Dally and Riley 1978). In this study, the latter are enhanced in this case with a wax pencil for easier viewing. The numbers obtained are those produced by a compensator which acts to nullify or return the specimen to a its unloaded state while recording the number of revolutions of its knob needed to do so (Figs. 8a and b). The compensator nullifies the observed strain by altering the direction of the refracted light. The number of revolutions of the compensator are expressed as fringe values which in their turn can be converted to actual strain values, if so desired. The latter conversion was not performed in this experiment because the fringe values obtained are only in divisions of a fringe (a fraction of a fringe) due to the thinness of the plastic coating employed and high modulus of elasticity of the plastic crania and would have converted to very small strains.

5.2 Materials Required for the Photoelastic Analysis

The materials used in this research included several cranial cast specimens purchased from the Casting Program at the Museum of Anthropology, University of Pennsylvania, including the following cast specimens: Peking Lower Cave composite female (Weidenreich 1943), the anatomically modern Cro-Magnon male (Valois and Billy 1965), the La Chapelle-aux-Saints Neanderthal male (Boule 1908, Trinkaus 1983), and the early anatomically modern Skhul V male (McCown and Keith 1939). Each of these casts was made in an epoxy manufactured by the Hysol Corporation of Olean, New York, and is a faithful reconstruction of the cranium retaining all ectocranial contours but without reproducing the endocranial surface morphology. They are of a relatively uniform thickness throughout and are hollow as demonstrated by radiographs of the specimens.

The photoelastic portion of the research required a Model 031 Basic Reflection Polariscope (Fig. 8a and b) produced by the Measurements Group of Raleigh, North Carolina, and distributed by Intertechnology of Don Mills, Ontario, complete with a Model 232 Uniform-Field Digital Compensator calibrator, a 920-000281 Liquid Plastic Sheet Casting Kit, and 6 boxes of PL-1 General Purpose pre-measured liquid plastic, 3 boxes of PC-8 reflective adhesive, all produced and distributed by the same corporation, a small transite oven, and a balance.

Figure 8 a and b: The polariscope, showing the use of the compensator. The right hand of the researcher is on this device, the aperture of which is positioned in front of the polarised filters.

The testing apparatus consisted of a Tinius-Olsen testing machine produced in Willow Brook, Pennsylvania; two foam rubber pads; two lengths of string; a length of elastic band measuring about 100 cm; several lengths of steel wire measuring roughly 70 cm; a 50 cm piece of 2 x 4; one pair of small sharp-nosed pliers and one wire-cutting pliers; several black rubber pads; 12 aluminium discs measuring .5 cm high, 2 cm in diameter with a transverse hole drilled through and just wide enough to accommodate the wire as it is drawn through; two rolls of 1,000 ASA high-speed film; a Scotch-Weld Brand 2216 B/A Gray epoxy adhesive tube kit produced by 3M Canada Incorporated of London, Ontario; a dremel tool; and some emery paper.

5.3 Purpose of the Photoelastic Study

The purpose of the photoelastic study was to obtain data that could be used to observe the distribution and intensity of strain experienced by the cranium in response to applied stress. As discussed above, the craniofacial skeleton has received what today amounts to quite a considerable amount of research attention, but the cranial vault and occipital have received considerably less. These two related areas thus form the subject of this portion of the research. In part, this research is intended to test the assertions that cranial vault shape and occipital morphology are sound indicators of palaeospecific associations, and are not instead more likely the consequence of particular functional demands placed on the cranium by physical exertion. Many researchers have assumed that changes in cranial morphology have come about through speciation events and thus owe their presence to genetic causes. The experiment was designed to mimic, as closely as possible, the actual loading that the cranium experiences in the performance of everyday tasks, most importantly as indicated above, those which involve loading the anterior dentition, an activity which forms a component of many habitually performed tasks recorded ethnographically in groups characterised by traditional lifeways (as again recently demonstrated by Brown and Molnar 1990, and previously by Hylander 1977, Smith 1984, among others) and in prehistoric populations submitted to subsequent analysis (as, for example, that described by Molnar 1971, Wallace 1975, Puech et al. 1980, Trinkaus 1983, Tappen 1985, among others) as well as, to a lesser extent, those performed to this day by humans living in industrial societies (Schour and Sarnat 1942). This portion of the research was meant to test the strain responses to loading the first-class lever that represents the cranium (Fig. 1).

Since each of the experimental crania is made of the same material and is of uniform thickness, these two factors, the type of material and its distribution, is held to be constant. Intra-group comparison of the mechanical influence of the shape of the cranium is thus possible. Curve changes and orientation of morphological features are in this connection of interest since these phenomena are known to influence the mechanics of structures (Thompson 1984, Currey 1984) and, moreover, of the cranium (Demes 1985, Dempster 1967). The research is directed toward answering several related questions about cranial shape:

1) Whether or not the cranial vault experiences strain when placed under an applied load.

2) How the distribution of strain within the cranial vault is affected by the different cranial shapes.

3) How the occipital morphology influences strain concentrations at the posterior of the cranium.

4) Ultimately, which cranium is most mechanically well-designed under defined loading conditions.

A "well-designed or "economical" cranium for the purposes of this study will be understood to mean that configuration which deforms the least under applied load and thus records the lowest magnitude readings for any particular area. A cranium which is considered to have the most mechanically sound distribution of plastic is that which demonstrates the least deformation in homologous areas. For the strain direction portion, "well-designed" will be defined on the basis of whether or not areas of relatively high concentration of lines are found to develop in crania. Concentrations of directional lines are seen to relate to areas experiencing heightened deformation. An absence or unconcentrated pattern of such lines indicates a cranium of sounder mechanical design. Several expectations and hypotheses are thus suggested:

1) Strain will be exhibited under conditions which mimic anterior dental loading, which is an applied stress.

2) Transmission and distribution of strain across the cranial vault surface will vary according to the particular morphology of the cranium. If high magnitudes are recorded in any region, then that region will be under differential strain. Similarly, those areas which do not demonstrate high magnitudes will be considered to be relatively unstrained. Distinctive directional recordings located in a restricted area will be interpreted to be those created by a less efficient cranium. These concentrations result from relatively strong deformation.

3) The cranium with the most efficient shape will deform the least and that possessing the least efficient shape will deform most, deformation being measured by the magnitude and direction recordings. Crania that experience greater deformation will be considered to be less well-designed for anterior dental loading.

4) Since a sphere is one of the most sound of geometric shapes, those crania of a less spherical shape should reveal more easily identified directional patterns.

5) A test will be conducted of Demes' (1983, 1985) assertion that strain concentrates in the basicranium and that the walls of the cranial vault experience bending stress. It is hoped that this research will illuminate how the different surface morphologies of the chosen crania influence the distribution of strain across their ectocranial surfaces, and specifically how the occipital torus (torus occipitalis transversus) and occipital bun (chignon) influence strain patterns at the posterior of the cranium.

5.4 Photoelastic Procedure

The photoelastic portion of this research follows those procedures recommended by Intechnology Inc. These will be reviewed here in somewhat abbreviated form and will include any alterations or adjustments to that prescribed procedure determined to be applicable by the researchers. The process begins with the preparation of a sheet of photoelastic plastic, in this case a sheet measuring 9 X 6 in. (23 X 15 cm) in area and .08" (.036 cm) thick was prepared. The casting plate was levelled and covered with a thin coating of releasing agent, which as its name indicates inhibits the epoxy sheet from adhering to the plate once it is formed. The casting plate was heated to a temperature of between 90-110° F (32-43° C), one compatible with the PL-1 plastic, while the pre-measured resin and hardener were warmed in the small transite furnace to a similar temperature. The temperature of the resin was monitored with a thermometer that was periodically used to stir the plastic preparation so that the reading resulted from a uniformly heated liquid.

Once the optimal temperature of between 32-43° C was attained, the hardener was rapidly poured into the resin- all the while stirring the gradually mingling constituents with the thermometer. The exothermal reaction which characterises this mixture was allowed to proceed until a temperature of between 125-130° F (52-55° C) was achieved. Prior to pouring the liquid mixture, the plate was turned off to facilitate the curing process.

It is imperative to begin to pour the mixture onto the casting plate at a time when this range is first attained as the reaction commences very quickly once the mixture heats to 52° C. Pouring of the mixture should proceed from the centre of the plate outward in a rather deliberate fashion to develop a uniform coverage and hence a sheet of uniform thickness throughout. Curing time for the sheet thus prepared was somewhat in excess of the 1.5 hours prescribed in the manual. In order to determine whether or not the sheet has reached a contourable state, it is best to attempt to lift only a corner of the hardening material to ascertain whether or not the sheet stretches, thus requiring further curing, or maintains its shape, indicating that it is ready for application to the test object.

The test object must be cleaned thoroughly with isopropyl alcohol and gauze, as indeed should all instruments which make contact with the epoxy resin and sheet. This cleaning removes all surface grit and dust from the object. The presence of such impurities will prevent a firm, faithfully contoured bond to the test specimen. Before the sheet is removed from the casting plate, the researcher's hands, a scissors, and the surface of the test specimen must have a generous coating of mineral oil, which prevents the hands and instruments from sticking to the newly made sheet. The sheet is then contoured to the test specimen using the entire width of the fingers in a gently massaging fashion; one must not attempt to poke the sheet since such an action causes stretching of the material and finger prints in the plastic. Once the sheet is applied to the desired area it can be cut with the scissors so that no loose and extraneous ends remain. In the case of the crania the right side of the cranial vault of each specimen encompassing an area from the coronal and sagittal sutures posterior until the attachment area of M. semispinalis capitis was covered. Thirty-six hours or more later the hardened cast was ready for permanent application to the cranial cast. The cast was then re-fitted to the cranial vault and masking tape used to outline the contoured sheet's extent, leaving sufficient space so that the tape could be removed while yet providing a clean line of adhesion.

The adhesive for bonding contoured sheets consists of a resin and hardener. The reflective resin was mixed with its hardener in a ratio suggested by the manual (100 pph of hardener /1 gm of resin) using a balance and applied to the clean cranial vault surface with a clean wooden tongue depressor until the entire surface was sufficiently covered. The cast was then fitted into place again, pushing in places to release any air that may have become trapped beneath its surface and at the same time making certain that the boundary of the contoured sheet was well sealed. The now adhering contoured sheet was allowed to cure to the surface of the cranial vault for a period in excess of the 48 hours suggested, usually several days. Once the contoured sheet had cured, the masking tape was removed leaving a generally clean juncture between the margin of the sheet and the surface of the cranial cast.

Aluminium discs were prepared such that high tensile steel wire could be drawn through a transversely drilled hole. Before placement of the aluminium discs each was buffed with emery cloth to furnish greater surface area, affording a sounder bond. The areas on the crania for the placement of these discs were prepared with a dremel tool, providing a depression just large enough to accommodate the discs. During this procedure the researcher donned a filter mask as a great deal of plastic dust fills the air during the creation of a suitable depression. These discs were then attached- one to the hard palate and two near the muscle insertions of M. rectus posterior minor and M. semispinalis capitis, the placement depending on the cranial morphology of the particular specimen. A 3M special epoxy-based glue was used to ensure what proved to be a sufficient bond. The bond was allowed to cure under sustained weight, usually several rather hefty books, over a period of several days. Once the discs were ascertained to be firmly attached the wire was drawn through the discs and tied off with clips to avoid tangling.

5.5 The Procedure Relating to Tests of the Cranial Casts

Each cranium was loaded in a Tinius-Olsen testing machine. The cranium was attached to the upper horizontal frame of the machine with high-tensile steel wire and affixed with reef or square-knots (Figs. 9 and 10). A load-cell was attached to the movable beam of the machine and the cranium positioned such that the cell contacted the area of the foramen magnum, which had previously been covered with a rubber pad. In order to ensure that the crania would not be damaged if the wire or the discs failed, an elastic band was drawn through the zygoma, crossing the basicranium in the area of the basal synchondrosis, and tied off to the upper member of the testing machine. Additionally, so that the crania would not impact with the sides of the testing machine two foam pads were tied in place with a length of string. During all testing the researchers wore protective plastic face shields in case the wires failed. Since the machine was originally designed for compression testing, the cranium was by necessity positioned upside down in the device and load applied by the machine at the foramen magnum. This load was thus resisted by the wires attached at the palate and the occipital area. In this manner the requisite tension loading was achieved-that is, the cranium was loaded in tension as it would be in life in anterior dental loading. Each cranium was loaded to 150 lbs. (68 kg.). Measurements were attempted at higher loadings, but the bond between the cranium and the adhering discs failed at higher sustained loads. In order to facilitate the taking of readings from the occipital region, a 2 X 4 board was placed across the upper frame of the compression testing machine, the cranium rotated such that the area of interest was facing the polariscope, and the wires attached at opposite ends of the piece of wood.

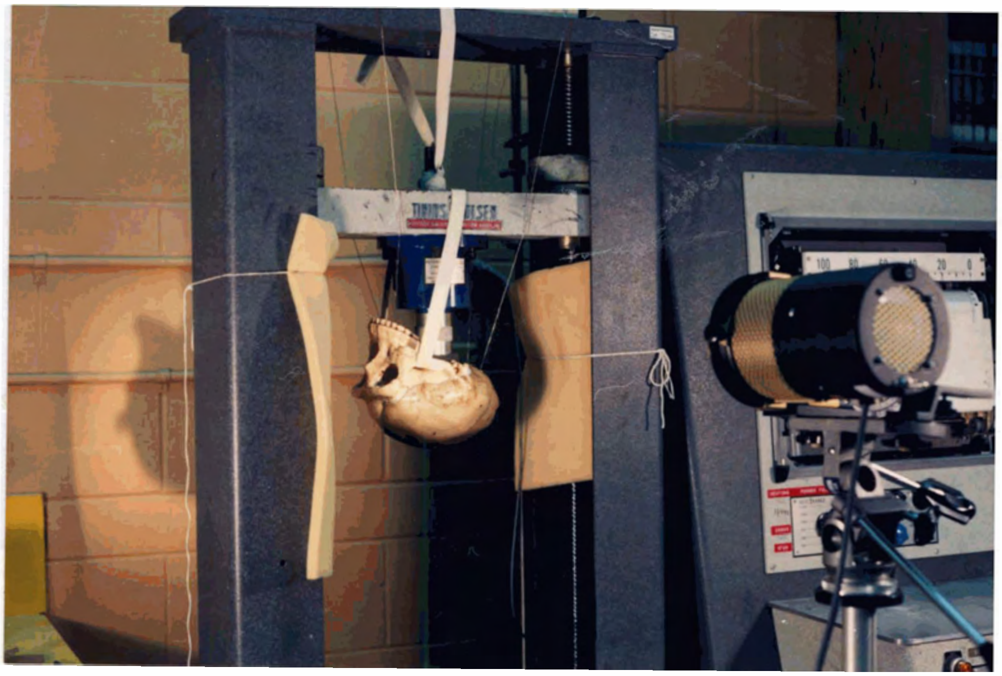


Figure 9: "Sinanthropus" (Homo erectus) loaded in the Tinius-Olsen mechanical press.

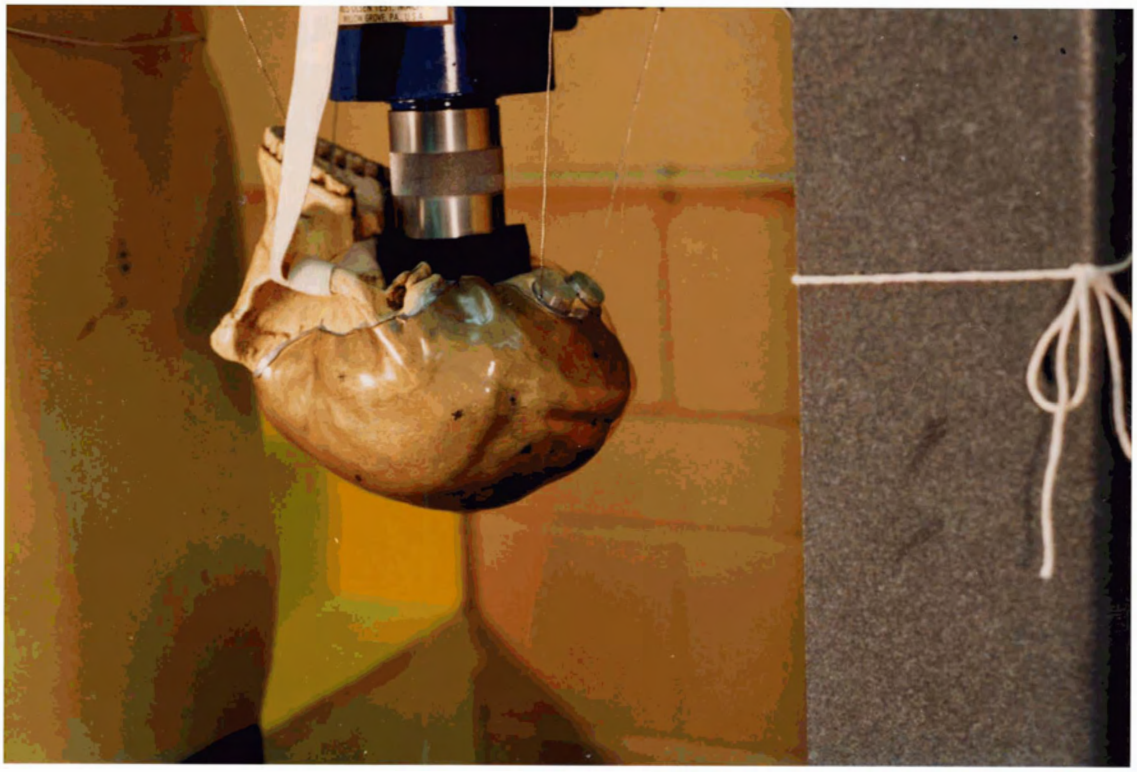


Figure 10: "Sinanthropus" (Homo erectus) loaded in the mechanical press close-up, showing the aluminium disc attachments and the extent of the photoelastic coating on the right side of the specimen.

Once the crania were loaded two types of data were collected, one to ascertain the magnitude of the strains in the crania (isochromatics), and a second to account for the direction of that strain (isoclinics). All of these data were collected through the use of the polariscope; the first data set retrieved by observing a colour change from silver to black in the photoelastic plastic coating at the indicated landmarks and reading the compensator calibrator, and the second through noting the movement of fuzzy black bands across the surface of the cranium as the polarising filter lens was rotated through 90° or until these bands were no longer easily discernible. The first of these measurements was recorded using the compensator calibrator to take readings at previously identified landmarks, including the following: apex, asterion, a point from the mid-parietal region of each cranium, a similar point from the mid-temporal region, a point from the middle portion of the interparietal area of the planum occipitalis, and another similarly positioned point on the planum nuchale. These points were chosen in order to standardise the position of the recordings on crania of very different morphologies and are interpreted to represent each cranial element, as well as each potentially separate structural entity nearest curves and angulations. Readings were taken by both researchers and blind comparisons made. In each case the magnitude measurements were recorded three times by each researcher and compared. Both researchers found that they agreed with each other's results within one division of a fringe in each case, so the lower of the two was recorded. No appreciable differences were noted between these trials.

The direction data were observed as black bands and a permanent record of these was made by tracing over them with the wax pencil. Additionally, these patterns were photographed with high-speed film, although the wax lines were much easier to see and were thus used in deference to those on the photographs. In order to assure that the crania were all uniformly positioned for the recording of isoclinics (direction readings), the 0° axis on the polariscope was oriented to the Frankfurt Horizontal. In those instances when recordings were required of the posterior of the cranium, the polariscope was oriented along the axis created by the superior nuchal lines or the occipital torus, whichever was most easily discerned by the researchers.

5.6 Discussion of the Results of the Photoelastic Experiments with the Cranial Casts:

5.6a The Cranium as a Whole

The results of the experiments upon cranial casts are collected in Table 1. The La Chapelle-aux-Saints Neanderthal was eliminated from the results because the aluminium discs broke away from their attachments carrying off a portion of the adhering ectocranial plastic surface in the event. The resulting numbers were recorded from the compensator calibrator as divisions of a fringe which, as mentioned above, are equivalent to the number of revolutions needed to return the specimen to its unstrained state (from a black colour to a silver one). These recordings indicate that each cranium responds slightly differently from others in the study sample in homologous areas. Moreover, the differences between crania extend to strain direction as well. Since all crania were loaded in a similar fashion, differences in strain magnitude and direction result from the variable shapes of the ectocranial surfaces of the hominines under study. These results are not in complete agreement with those of Demes, nor with the theoretical assertions of Lanyon (1987) and Currey (1984), who have contended that the human cranial vault is largely unstrained. Based on her compression experimental results, Demes writes, "It is of great importance for the strength of the skull base that the basic shape is oval. This assures that the stress caused by the reaction force at the head joint is transferred to the cranial vault mainly via the side walls. The mechanically less resistant region of the skull base located in front of the foramen magnum is thus subjected to less stress" (p. 45). The basicranium contains many voids and thin bones, which are points of potential weakness for strain distribution and, therefore, must be left unstrained. The results obtained in this research demonstrate that Demes is essentially correct, but that the differing shapes under tension influence the concentration and distribution of the strains in varying ways within each vault. For example, all vault shapes demonstrate a concentration in the area of the nuchal squama, the area posterior to the foramen magnum, and little or no strain concentration in the squamous portion of the occipital. These results, like those of Demes before, suggest that, in fact, the cranial vault does indeed experience strain even when loaded to only 150 lbs (68 kg.). These results contradict the theoretical viewpoints of Lanyon (*ibid.*) and Currey (*ibid.*), who may have been influenced by Benninghoff's (1925 and cited by Evans and Goff 1957, and Tappen 1954) split-line work (*contra* Dempster- see above), which demonstrated no crack pattern in the cranial vault, this despite the plethora of Haversian systems, which are interpreted to derive from remodelling of bone in response to stress. As Evans and Goff (*ibid.*) point out, however, split-lines do not record stress trajectories and they are only of use in revealing the structural arrangement of bone, but not its mechanical properties.

Hominine	Temporal Squama	Parietal Squama	Apex	Asterion	Occipital Squama	Nuchal Squama
Cro-Magnon	22.0**	12.0	8.0	8.0	-7.0*	5.5
Skhul V	7.0	5.0	4.5	1.0	1.0	9.0**
Sinanthropus	8.0	8.0	5.5	9.0**	0.0	8.0

* area recorded under compression
** highest value recorded in each cranium

Table 1: Strain indicated in divisions of a fringe in the 150 lb. test of the crania.

The implication is that the nuchal muscles produce stresses in the cranial vault to which the cranium must adapt and that this adaptation is made by the entire cranium as a functional unit and not through changes effected by individual cranial elements alone. Thus certain crania will respond differently and with more intensity than others when subjected to the same stress. The following sections shall concentrate on these adaptations.

All of the identified regions of the cranial vault experience strain when tensile loads are applied to the anterior dentition and to the nuchal area simultaneously, even at the relatively small load of 150 lbs. (68 kg.). The isochromatic fringe orders (magnitude recordings) reveal that the Cro-Magnon cranium differs from the other two crania, producing high values for vault landmarks and a lower value for the nuchal area. The other crania, Skhul and Homo erectus produce the reverse of this pattern with the nuchal area producing either an equivalent or higher value than the vault landmarks. Such results indicate that the configuration of the Cro-Magnon cranium is less well-adapted to anterior dental loading in that the cranial vault deforms to a greater extent in this individual than do the others under the same loading conditions. Why this should be the case doubtless relates to the shape and proportions of the Cro-Magnon ectocranium. When one compares the values of craniometric parameters to those of the other crania, some indications as to why such should be the case becomes apparent. Demes (1983, 1985) has demonstrated that the curvature of the parietal bone of the cranium influences the distribution of strains in the cranial vault of the human skull and that more curved parietals (i.e. like those of modern *Homo sapiens*) deform less than those that are more flat (i.e. like those of *Homo erectus*). The values obtained for parietal curvature for each cranium are recorded in Table 2.

Hominine	Parietal Curvature
Cro-Magnon	**91.5**
Skhul V	**94.0**
"Sinanthropus" (*Homo erectus*)	**94.2**

Table 2: Parietal curvature of the crania employed in this study as represented by the parietal arc/chord index. Data collected from Weidenreich (1943), McCown and Keith (193), Valois and Billy (1965).

Russell (1985) and Demes (1983,1985) have noted that the height of the cranium has an impact on strain distributions. The values attained for the basion height index (defined by Bass 1971) are as gathered in Table 3.

Hominine	Basion Height Index
Cro-Magnon	74.5
Skhul V	73.7
"Sinanthropus" (Homo erectus)	72.1

Table 3: The basion height index of the crania employed in this study. Data calculated from Appendix 4, to which the reader is referred.

Thus, the Cro-Magnon cranium is the most dolichocranic, the longest (see Appendix 4), and tallest of the crania with the least occipital curvature (see Table 4) but greatest parietal curvature of the specimens under study. These differences carry great mechanical significance.

Hominine	Occipital Curvature
Cro-Magnon	79.36
Skhul V	79.0
"Sinanthropus" (Homo erectus)	73.5

Table 4: Occipital curvature of the crania employed in this study, measured by the chord/arc index.

Sources for calculations: McCown and Keith (1939), Tobias (1959b), Weidenreich (1943).

The importance of curve changes and their effect on strain distribution has been suggested by Lanyon (1980), who has noted that curved bones are the engineering equivalent of a pre-buckled strut. The sole advantage of such a structure derives from the fact that it serves to attenuate and absorb, rather than transmit muscular forces. Demes (1983) has demonstrated that the walls of the cranial vault are subjected to bending stresses during loading and that these stresses increase with increased width and length of the braincase and decrease with the curvature of the cranial wall so that individuals who possess a flattened cranial base with a long, low, and broad cranium like Homo erectus develop higher bending stresses in the parietal region than those that are less so, like modern Homo sapiens morphology. This research corroborates Demes' findings with Homo erectus possessing strong directional lines in the temporal and parietal areas, unlike the other crania under consideration here (Fig. 11). Demes' work and the results of this research provide empirical support for Lanyon's observation regarding the importance of the pre-buckled strut for strain distribution.

Figure 11: "Sinanthropus" (Homo erectus) directional results during loading. Note the black banding which has been accentuated with a wax pencil.

The importance of curvature is that is it has the potential to influence and be influenced by other structural modifications within the cranial vault (Olivier 1974). For example, Tobias (1959a) has noted a negative correlation between occipital curvature and cranial length. Tobias (1959b) notes that all early fossil hominids have "ultra-strong" occipital curvature and that this morphology, which is similar to the morphology of infants, likely relates to genetically moderated growth differences. Furthermore, the extent of occipital curvature is negatively correlated with cranial length and vice versa (Tobias 1959a). Therefore, the greater the cranial length, the greater the occipital curvature (ibid.) (i.e. less angulated). The results of the present study support Tobias' findings, producing a negative correlation (-0.322, p= .0289) between occipital angulation and greatest cranial length (Fig. 12). Presumably, such a relationship reflects differences in growth and possibly in nuchal musculature development associated with individuals possessing long crania and thus requiring greater muscular development. Both Baer (1954) and Smith et al. (1985) have demonstrated that a number of cranial measurements correlate with skull length, thus demonstrating the effect of the timing of sutural fusion at the spheno-occipital synchondrosis. The lever arm of the first-class lever which characterises the mechanical functioning of the cranium is not correlated with the occipital angulation (Fig. 13). Therefore, long crania with long load arms require more occipital angulation due to the greater mechanical advantage required of the nuchal muscles. It would appear, then, that the length of the lever arm can only become so long before it loses its mechanical advantage. The nuchal muscles themselves must compensate for any lengthening of the load arm through increasing their cross-sectional area and, therefore, their muscular force (see below).

This researcher would contend that the developmental and growth differences within the occipital might well explain Tobias' (1959a) observation that the upper part of the occipital (from lambda to inion) is less correlated with the total occipital curve than is the curvature of the lower occipital arc (from inion to opisthion). The nuchal area would be immediately and locally influenced by adhering musculature; whereas, the interparietal or supranuchal portion of the occipital would not be expected to be influenced since it does not act as an area of muscle attachment. Therefore, as the cranium lengthens, the greater the occipital curvature (the more angled the occipital bone). All three crania under consideration here fit Tobias' statistical predictions in that they are dolichocranic and possess great occipital curvature when compared to the other crania in this study, with Homo erectus being most extreme in this regard. Demes (1986) has remarked that "The shell with the greatest curvature (therefore, one similar in shape to that of the modern human) in the investigation showed lower stress values than the less semiovoid shell when both were subjected to the same load" (p. 47). The present study does not demonstrate this relationship in that although Homo erectus experiences the more extreme concentration of deformation lines, it is the more modern

Cro-Magnon cranium which experiences the greater strain magnitudes in tension testing.

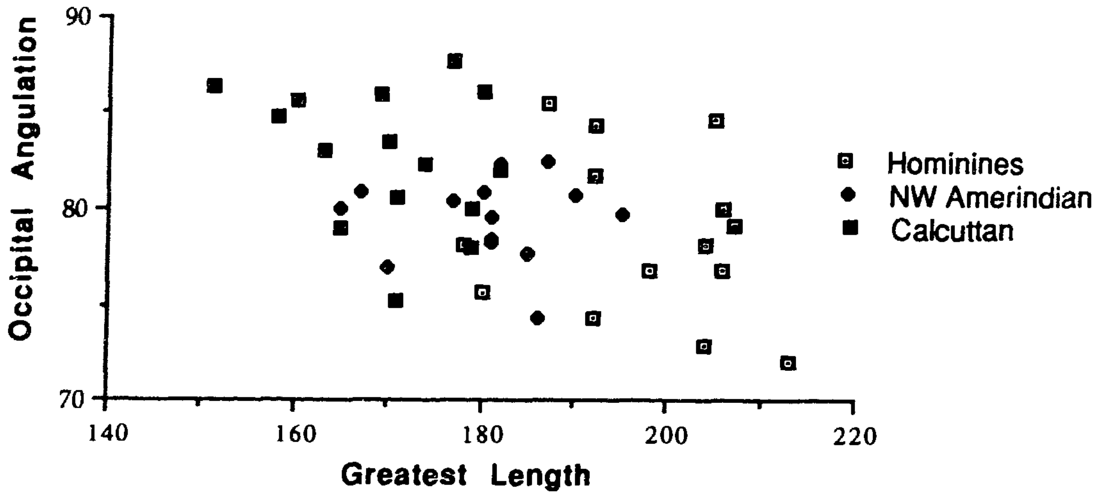


Figure 12: Regression resulting from a comparison of the occipital angle and cranial length (cm). The correlation coefficient (R) of -0.322 (p= .0286) provides a negative correlation. When using Tobias' Occipital Index a similar result was obtained. Thus the length of the cranium is negatively correlated to occipital angulation in this sample- the longer the cranium the greater the degree of occipital angulation (N= 45).

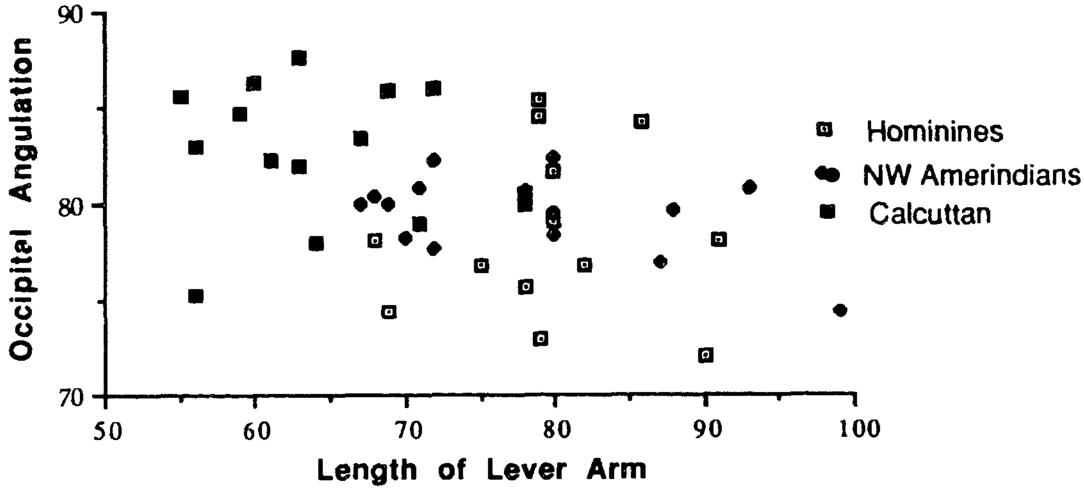


Figure 13: A regression plot of the length of the lever arm (mm) to occipital anglulation. The -0.117 (p= .02) correlation coefficient (R) suggests that the length of the lever arm does not appear to influence the degree of occipital angulation (N= 45).

The results obtained in the present study suggest that the situation is somewhat more complex than that envisioned in Demes' work. Under tension testing the Cro-Magnon cranium does not demonstrate strain concentrations like those noted in *Homo erectus*, but it records the highest magnitude readings achieved in the study for all of the cranial landmarks of the cranial vault with the exception of asterion, for which the value achieved by *Homo erectus* is marginally greater. This cranium is most like the modern human configuration (more spherical in shape) and its more curved vault distributes strains quite evenly across the ectocranium as indicted by the directional recordings. It does, however, experience higher strain values than the other crania included in the study. In other words, the Cro-Magnon cranium performs anterior dental loading less efficiently than the other crania in the study, although its geometric shape is most well-designed for the transmission of forces and distributes force quite evenly. It seems to resist force with its entire ectocranial surface. It is likely, however, that the less angled occipital of this specimen creates greater strain in the cranial vault and this relationship accounts for the magnitude readings noted. This information indicates two things: one, that this individual did not perform anterior dental loading as strenuously as the earlier hominines and, second, that it likely possesses lessened cranial thickness as a result of its more spherical shape.

The reverse situation obtains in the *Homo erectus* cranium. This cranium demonstrates great concentrations of strain in its temporal and parietal areas, but records vault values that are intermediate between those achieved in Cro-Magnon and Skhul. The *Homo erectus* cranium is the least spherical of the crania included in this study, it is the most platycranic, and possesses the greatest occipital angulation. The bending strains exhibited in the walls of the cranial vault suggest that it responds most uniquely among the crania studied. Curiously, it produces the highest magnitude reading for asterion, a high reading in its nuchal area, and no strain at all in its occipital squama. This information would seem to suggest that the basicranium of *Homo erectus* is under heightened strain.

The Skhul V cranium does not differ substantially from Cro-Magnon from the perspective of craniometrics. Both the Skhul and Cro-Magnon crania are quite efficient in the manner in which they dissipate or diffuse the same stresses, providing a situation in which no directional concentrations are noted (Figs. 14 and 15). This diffuse or dispersed pattern is similar to that noted by Dempster (1967) in his study of the texture of the cranial vault bone in modern humans. This pattern of bone orientation in the cranial vault would seem to be oriented to prevent the concentration of strains in any one area of the cranium and its diffuse pattern assures that strains are similarly transmitted across the vault surface. The prediction derived from this observation is that the cranial vault of *Homo erectus* should demonstrate a less diffused bone morphology and one that is more strongly oriented due to its more well-developed musculature.

Skhul V appears to be the most well-designed cranium tested in that it produces the lowest vault values for all landmarks except for apex. Thus similarly shaped vaults provide strikingly different responses under the same loading conditions. This seemingly contradictory information is likely explained through reference to the data received from the magnitude distributions. These reveal that the Cro-Magnon cranium responds very differently from the way in which the Skhul V cranium does. The Cro-Magnon cranium demonstrates deformation in the occipital squama greater than that in the nuchal squama. In fact, it is the only cranium which showed a negative or compression reading for the occipital squama. Conversely, the other crania demonstrate a greater magnitude recording in the nuchal plane but reduced or no strain concentration in the squamous portion of the occipital. Skhul shares a relatively high reading for the nuchal area with *Homo erectus*, which possesses the greatest occipital curvature and occupies an intermediate position for vault strain between Cro-Magnon and Skhul V. A plausible explanation for this relative functional difference which sees each cranium dissipating strains quite efficiently but with one, the Cro-Magnon cranium, producing higher magnitude readings than the Skhul V cranium is the presence of "buttressing" features present in the Skhul V cranium and reduced or lacking in the Cro-Magnon specimen. Both Skhul V and *Homo erectus* possess localised occipital thickenings which the Cro-Magnon individual lacks and both experience heightened strain readings in the nuchal area. The greatest difference between these two crania in terms of magnitude occurs at asterion. The strains affecting the basicranium are relegated to the nuchal area in Skhul V, while those noted in Homo erectus appear to influence the basicranium as a whole. The occipital thickenings and occipital angulation represent important curve changes in the cranial vault and will be addressed in the following section.

Figure 14: The Skhul V cranial cast under load, demonstrating the colour changes associated with a diffuse pattern of strain distribution.

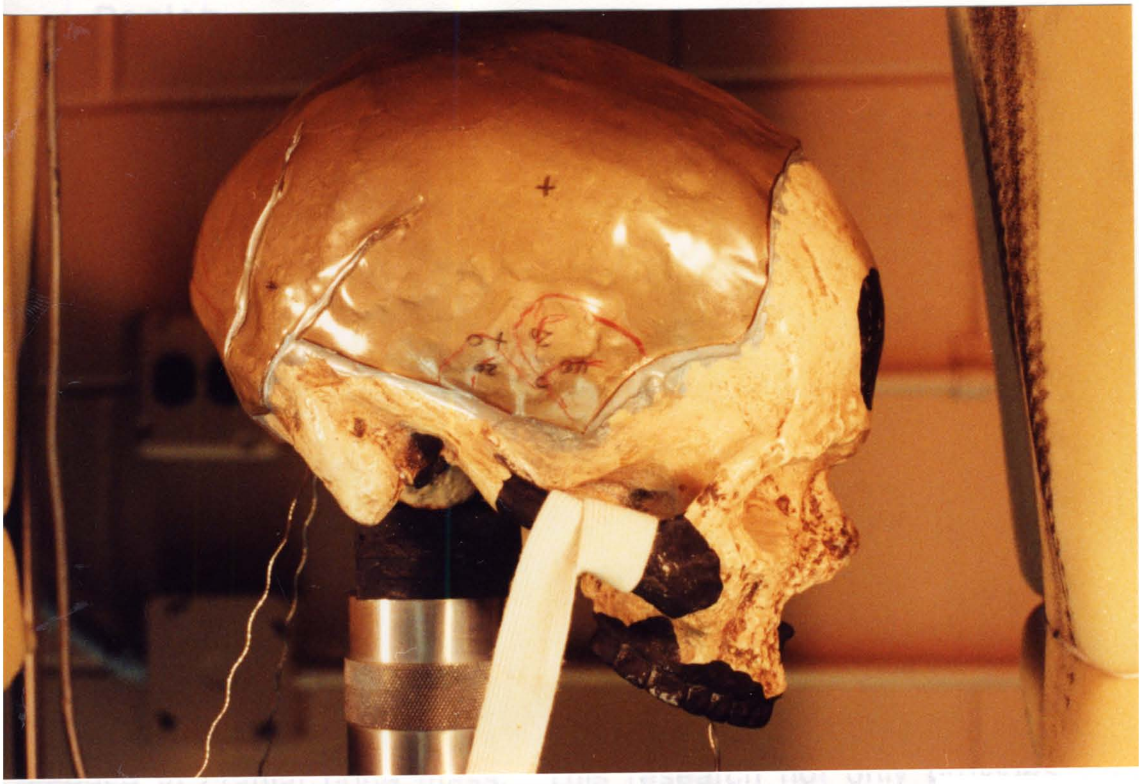


Figure 15: The Cro-Magnon cranial cast under load, demonstrating no concentration of strains. Those indicated by the red lines appear to be an incidental fringe effect.

5.6b The Strain Situation in the Occipital Region

Part of the goal of this research was to attempt to understand the function of the occipital torus (torus occipitalis transversus) and the occipital bun present in certain members of the Homininae and to ascertain what these structures' functions are in relation to the cranial vault. Demes (1983) has contended that the occipital torus acts as a muscular attachment area; whereas, Hublin (1989) sees it as a part of a systemically and physiologically dictated thickening of cortical bone evidenced throughout the skeleton of certain members of the Homininae. He thus interprets the occipital torus and the angular torus as an increase in cranial bone mass. This research not only provides further insight into these assertions, but allows an appraisal of Demes (1983, 1985) contention that forces concentrate in the basicranium and that the walls of the cranial vault experience bending stress. Demes performed her experimentation on semi-ovoid shells modelled upon geometric shapes, but she did not test actual cranial shapes like those found in earlier members of the Homininae. Additionally, her tests were made in compression and not under tension, the latter being more representative of the actual anatomical situation in human crania under applied stress.

Demes (1983) has denied any association between the occipital torus, one portion of the buttressing system originally identified by Weidenreich (1943), and influence on strain concentration and distribution, writing "The angled occipital profile of Homo erectus skulls doesn't create a stress concentration. The occipital torus of these fossil hominids isn't a reinforcing ridge but can be understood as a muscle insertion" (p. 283). This researcher has no qualms in accepting Demes' experimental results, although he would contend that the occipital torus of Homo erectus is more than an expanded muscle attachment. It is this structure which also contributes to the pronounced occipital curvature noted in Homo erectus and to a lesser extent in later members of the hominine lineage. Moreover, previous research results indicate that the various ridges and crests of the ectocranium do have an effect on the transmission of forces across the cranial surface (Gurdjian and Lissner 1945, 1946, 1947; Lissner and Gurdjian 1946; Gurdjian et al. 1947). Therefore, the buttressing system of Homo erectus may indeed relate to the influence such structures have on force distributions in the cranial vault. The largest of these ridges, the torus occipitalis transversus warrants closer scrutiny.

The least strained area for each cranium is the occipital squama (interparietal portion), which recorded the lowest values from among those areas recorded for each cranium, except in the case of Cro-Magnon. It would appear that the angled occipital that characterises all of these crania to a certain, though differing, extent influences the occipital squama, releasing it from a certain amount of strain. The Homo erectus cranium, the cranium constructed from partial fragments, but possessing the cranial vault of Weidenreich's (1943) Skull XI, demonstrates that this region of the occipital is completely unstrained at 150 lbs. (68 kg). Thus Demes' (1983, 1985) assertion concerning the unstrained occipital squama of the shell shaped like the basicranium of Homo erectus is borne out under tension testing. However, in every other cranium this region demonstrates a differing amount of strain. Therefore, it is the contention of this researcher that the occipital torus is more than a large muscle attachment and a means of lengthening the lever arm of the cranium. It is this structure which also contributes to the pronounced occipital curvature noted in Homo erectus and to a lessened extent in the later members of the hominine lineage.

When one considers the values recorded for the occipital region among crania, however, one notes that those with lessened curvature as revealed by the occipital index produce higher strain magnitudes. The crania, in fact, demonstrate a progression from Homo erectus to Skhul V to Cro-Magnon with the latter being the least curved of the specimens (Table 4, p.125). This ordering corresponds with the degree of "modern" morphology present in the individual crania. It would appear that the angled occipital that characterises all of these crania to some extent influences the occipital squama. It performs a very important role in retaining forces within the nuchal plane and releasing the occipital plane from strain concentrations in Homo erectus. Moreover, the bun development in the Skhul V cranium, which also contributes to a relatively more angled occipital, appears to reduce the amount of strain noted in the occipital plane relative to that experienced in the homologous area of the Cro-Magnon specimen. Torus and bun development, then, may be interpreted as compensation for the more flat cranial vault walls of Skhul V and the much flatter cranial vault walls of the Homo erectus cranium when compared to that of Cro-Magnon.

Mechanically these occipital structures behave very much like a pre-buckled strut. They serve to exaggerate the curvature of the occipital and diminish forces generated by the nuchal muscles. Torus and bun development appears to be correlated with the amount of occipital curvature in these specimens. The torus and bun, then, act to concentrate strain in the basicranium, which likely accounts for the thickened cranial bone noted in these two regions (McCown and Keith 1939; Weidenreich 1941, 1943).

Hominine	Length of Load Arm (cm)	Cranial Module	Ratio
Cro-Magnon	**122**	**163.33**	**0.75**
Skhul V	**120**	**151.00**	**0.79**
"Sinanthropus"	**118**	**140.00**	**0.84**

Table 5: The ratio of the length of the load arm to the cranial module (measurements by the author).

$$\frac{\text{Length of Load Arm}}{\text{Cranial Module}} = \text{Ratio}$$

Hominine	Cross-sectional Area (cm^2)	Cranial Module	Ratio
Cro-Magnon	1.79	163.33	1.10
Skhul V	2.87	151.00	1.90
"Sinanthropus"	2.48	140.00	1.77

Table 6: The ratio of cross-sectional area of M. semispinalis capitis to the cranial module (measurements by the author).

$$\frac{\text{Cross-sectional area of M. semispinalis capitis}}{\text{Cranial Module}} \times 100 = \text{Ratio}$$

The heavily angled occipital of Homo erectus in effect turns a shell with little or no strain concentration into a more beam-like or even tube-like structure as indicated by the directional strain pattern of "Sinanthropus" as compared to that of the other crania under study. Deformation in the region of the temporal and parietal bones is most evident in Homo erectus and much less so in the other crania. Homo erectus crania have been noted to have extremely flat cranial bases whether of Asian or African affiliation (Weidenreich 1943, Pilbeam 1975, Demes 1983, Maier and Nkini 1984). Maier and Nkini (ibid.) associate the flat basicranium with shortening of the face relative to other primates. Moreover, Riessenfeld (1967) associates greater facial protrusion with dolichocephalisation in some human populations. These features describe the morphological situation in Homo erectus: a relatively small cranium with flattened cranial vault walls, a lengthened lever arm (see Table 7), a proportionately longer load arm (increased prognathism)(Table 5), and large nuchal muscle attachment areas anchored on a highly angulated occipital region relative to modern human morphology would provide the jaws with powerful leverage (Table 6). The Skhul V cranium, which possesses the largest insertion area for *M. semispinalis capitis* demonstrates deformation (magnitude data) to the same extent as that noted in *Homo erectus*, but does not demonstrate the same concentration of forces in the temporal and parietal region (Table 1). This difference is likely due to the heightened cranial vault of the Skhul V cranium.

To compare the degree to which each cranium is capable of anterior dental loading, a force assessment was made to attempt to reconstruct the potential force exerted by the mouth in the specimens under study (Fig. 16). This calculation reconstructs the potential "bite pull" that each cranium was capable of when the anterior dentition were employed as a vice for holding food or objects. In this analysis a mixed hominine sample, a prehistoric Northwest sample, and a Calcuttan sample were employed for comparative purposes (see Appendix 2). The equation used is as follows:

> Force of Anterior Dental Loading x Length of Load Arm = Force of *M. semispinalis capitis* x Length of Lever Arm, where the force of Anterior dental loading is the unknown variable and the force of the muscle is calculated from its insertion area

The calculation demonstrates that the fossil hominine sample possesses the greatest reconstructed potential bite pull force, followed by the Northwest Amerindian sample, and then the Calcuttan sample, which produced the lowest overall figures. The implication here is that the Northwest sample was performing such a behaviour and the Calcuttan sample was not. Therefore, it would appear that the hominine and Northwest samples would be able to generate greater force in anterior dental loading with their relatively larger nuchal muscles. Indeed, in this regard the Skhul V and *Homo erectus* crania distinguish themselves in possessing among the largest anterior dental loading potentials, being surpassed greatly only by the Kabwe cranium. Skhul for its cranial size surpasses *Homo erectus* in nuchal musculature development as expressed as a ratio of *M. semispinalis capitis* standardised to the cranial module (see Table 6), but this specimen possesses a relatively reduced load arm length and heightened cranial vault relative to that of *Homo erectus*. The suggestion here is that the Skhul individual was still practicing anterior dental loading, but that it was more well-designed for this behaviour because of its shortened load arm, which ultimately allows the cranial vault to become more heightened. Skhul, then, presents a better morphological solution to the behaviour than does *Homo erectus*.

Hominine	Length of Load Arm	Length of Lever Arm	Index
Cro-Magnon	122	79	154.4
Skhul V	120	80	150.0
"Sinanthropus"	118	81	145.7

Table 7: The ratio of load arm length to lever arm length (measurements by the author).

$$\frac{\text{Length of Load Arm}}{\text{Length of Lever Arm}} \times 100 = \text{Index}$$

A consequence of this more powerful anterior dental loading, however, would be heightened bending like that recorded by the isochromatic fringes in the temporal and parietal areas of the Homo erectus cranium. The larger, more modern Cro-Magnon cranium with its more bent parietals, less angulated occiput, shortened lever arm, and less well-developed nuchal muscles (as revealed by cross-sectional area of its muscle attachments) allows for much less, if any, concentration of strains in any one region of the cranial vault. Thus it presents a diffuse pattern of directional strains when subjected to the applied stress of anterior dental loading. When this cranium is loaded to the same extent as the Homo erectus , however, it demonstrates more overall deformation in the identified areas (Table 1) than those of Skhul, which possesses buttressing accompanied by higher, more curved, more modern appearing cranial vaults. The Homo erectus cranium deforms less as a whole, but demonstrates greater concentration of bending forces (directional data) in the temporal and parietal region, therefore, requiring thickened cranial bone in those areas. Demes (1984) has shown that forces generated by the temporo-mandibular joint are resisted by a cranial construction which possesses cranial base flexure and has the effect of transferring stresses to the cranial vault walls. Thus the thickened cranial vault bones of *Homo erectus* are a reflection of the lack of cranial base flexure. The strength of cranial bone comes from its relative thickness so thickening the bone effectively strengthens the structure (Evans and Lissner 1957; McElhaney *et al.* 1970; Gurdjian *et al.* 1947). However, the relative decrease in overall strain in the occipital region of the *Homo erectus* cranium would seem to be a means by which to reduce the effect of the strains exerted by the nuchal muscles on a cranium already more strained because of its flat cranial base. The flattened cranial base, however, would seem to result from the large nuchal muscles which exert force on the nuchal plane.

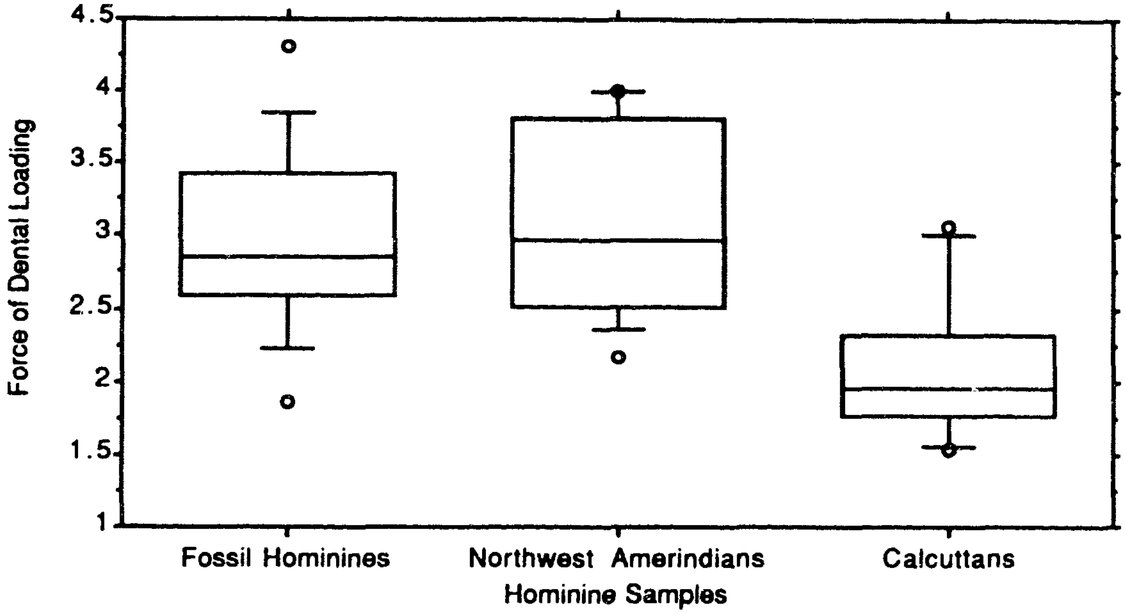


Figure 16: A graph of the mean and two standard deviations demonstrating the reconstructed force of anterior dental loading or "bite pull" for the study samples. The Northwest Amerindians and Fossil Hominines are very similar and are interpreted to have performed strenuous anterior dental loading in the course of their lifeway, while the Calcuttans did not. The Murray site female and Calcutta 5 are the outliers for their respective samples as identified by the small circles (°).

It is likely that the thickened cranial bone noted in *Homo erectus* specimens is the means by which the increased bending in the flattened cranial vault walls in *Homo erectus* is ameliorated. Average cranial vault thicknesses decrease from 14.1 mm in "Sinanthropus" (Weidenreich 1943) to 8.0 mm in Cro-Magnon (Vallois and Billy 1965) to only 4.5 mm in Skhul (McCown and Keith 1939). Skhul V presents a very interesting pattern in that it possesses the more spherically shaped cranial vault shared with modern human morphology, but also possesses the cranial buttressing, though somewhat diminished, as *Homo erectus*. It is, as noted previously, this cranium which records the lowest strain values for most regions of the cranium. That Skhul V should possess the lowest values and also relatively thinner cranial bone might account for the presence of cranial buttresses in this otherwise more modern appearing individual. The buttresses are pre-buckled struts which dissipate what must have been large forces generated by this individual's well-developed nuchal muscles as indicated in Fig. 16. Previous research results indicate that the various ridges and crests of the cranial vault do have an effect on the transmission of forces across the ectocranial surface (Gurdjian and Lissner 1945, 1946, 1947; Lissner and Gurdjian 1946; Gurdjian *et al.* 1947). Therefore, the buttressing system of *Homo erectus* relates to the influence such structures have on force distributions in the cranial vault. The flatness of the cranial base noted in *Homo erectus*, in fact, appears to result from a flat, "pulled down" nuchal plane in response to the powerful pull of the well-developed nuchal muscles. The *Homo erectus* cranium, then, presents a very powerful leverage system where the load and lever arms are almost of equal length (Table 7).

Demes' contention that the *Homo erectus* cranium is uneconomically designed is unsupported by these results. The *Homo erectus* and Skhul crania would seem to be much more functionally sound in anterior dental loading in the occipital region than the Cro-Magnon cranium. A force distribution such as that noted would be especially important in view of the fact that the occipital squama has been demonstrated to transfer forces to other parts of the cranial vault, and interestingly to the greater wing of sphenoid, when loaded (see Gurdjian and Lissner references and discussion above). When comparing this cranial element with that of modern individuals, Weidenreich (1943) comments "That the reduction of the greater wing of sphenoid is not confined to the height of the wing but involves the entire bone is evident from cross sections through the wing.... Compared with "Sinanthropus" the greater wing in modern man has shrunk to almost two-thirds of its original thickness" (p.171). Such an observation would again seem to indicate that there is a functional link between the presumably large muscular forces generated at the posterior of the *Homo erectus* cranium with the bone thickness and torus and bun developments in these individuals. Similar traits characterise the Northwest Coast sample employed in this study and are likely the consequences of heavy and strenuous muscle exertion in behaviours such as anterior dental loading.

5.6c The Strain Situation in the Anterior Portion of the Cranial Vault

When one shifts to the more anterior portions of the cranial vault, similar relationships exist to those noted in the posterior portion of the crania (Table 1). In each case the parietal squama is as strained or less so than the temporal squama. So, as one proceeds up the parietal its curvature reduces the strain experienced at the suture. Thus apex is less strained than the the previous two areas in each of the crania. The values achieved at asterion may be related to either the exertion of the applied stress or the bending produced in the cranial walls. The number of the rugose non-metric traits associated with this area may be a reflection of the considerable strain exerted upon the region during the lives of certain individuals. It is in this region that one finds the supra-mastoid crest and occipito-mastoid crest. Weidenreich (1943) identified these features as a part of the buttressing of the Homo erectus cranium. Their presence in the area might be quite plausibly related to the action of M. splenius capitis, M. sternocleidomastoideus, or the digastric muscles. The curvature which characterises all of the crania under consideration here aids to release the sagittal suture from strain. They, too, act as pre-buckled struts and diminish strain from an area which given straight walls would be under considerable strain. The sagittal keel of certain individuals would further strengthen the suture as it resists the pull of the masticatory muscles M. temporalis, specifically, in this regard.

Chapter 6: The Statistical Analysis

6.1 Purpose of the Statistical Study

A craniometric analysis was carried out upon a mixed group of hominines in order to test several expectations developed from the anterior dental loading hypothesis discussed previously. The samples employed in this study included 15 crania from a prehistoric Northwest Amerindian population, 15 crania derived from a Calcuttan population of East Indians, and a varied sample of 15 cast crania representing Homo erectus; Archaic Homo sapiens, including Neanderthals; early anatomically modern Homo sapiens; and anatomically modern Upper Palaeolithic Homo sapiens sapiens. The sample consists of individuals of a considerable morphological variety and of both males and females (see Appendices 1 and 2). The Northwest Coast sample is characterised by a robust and rugose cranial morphology; whereas, the Calcuttan population is of a very gracile morphology. The former population has been noted to possess extremely thick cranial bone and thickened post-cranial cortical bone as well (pers. obs.). These individuals also demonstrate a number of traits that Trinkaus (1983b) has associated with Neanderthal populations, including at least the following: squatting facets; retroversion of the proximal tibia; bowing of the ulna and radius; and large and rugose muscle attachments, especially of the brachial elements, and of the supinator crest of the ulna, the radial tuberosity of the radius, the deltoid tuberosity, and the crests of the greater and lesser tuberosities, which are accompanied by a deep bicipital groove of the humerus (pers. obs.). If these traits are related to an active and strenuous lifeway as Trinkaus (1983a and b) has suggested, then the Northwest Amerindian group of individuals derive from such a population.

The first expectation of this study derives from the fact that two of these populations, the Northwest sample and the mixed fossil hominines, are noted for anterior dental wear and generally robust skeletal morphology. The third group, the Calcuttan population, is a modern sample of very gracile individuals who are not known to engage in strenuous anterior dental loading. It was assumed, then, that one might be able to distinguish those individuals who performed such behaviours from those who did not through craniometric analysis.

Part of the purpose of the statistical study was to attempt to quantitatively identify the previously discussed osteological indicators in skeletal samples. Therefore, this portion of the study concentrated on nuchal muscle development and craniometric parameters, including not only those measurements associated with size, but those which account for the shape of the cranium and cranial thickness as well, size being held constant. In order to control for size effects each measurement was standardised to the cranial module and an adjusted value obtained. Perhaps key among these measurements are those interpreted on a theoretical footing to be of a specifically functional significance and are implicated in the use of the cranium as a first-class lever. Measurements included those of the moment (load) and lever arms of the cranium and muscular attachment areas that occur on the *os occipitalis* (refer to Figs. 1 and 17-20). Most important among these muscular measurements is that of the enthesis area of *M. semispinalis capitis*. As noted previously, *M. semispinalis capitis* acts both to extend and rotate the head and is thus implicated in anterior dental loading (Crouch 1982). The cranial module and cranial index and the length, breadth, and height measurements which make up these indices were also considered as these size measurements have the potential to influence the development of the nuchal muscles. Larger headed people can be expected to have larger muscles simply because of the greater force needed to move a larger head. Occipital angulation was also measured in hopes of further elucidating the relationship between this factor and cranial parameters as intimated by the photoelastic portion of this research.

Among the expected outcomes of this analysis one may number several based upon the model as presented above. One would expect that the size of the cross-sectional area of *M. semispinalis capitis* should correlate with cranial bone thickness since osseous mass is built up through strenuous and intermittent muscular activity (the piezoelectric effect). Larger enthesis areas are considered to be produced by larger muscles more capable of exerting strong muscular forces. Additionally, one might expect a longer load arm to correlate with greater *M. semispinalis capitis* development as it is this muscle which must lift the face in extension against the presumed downward pull of the arms in anterior dental loading. This muscular development should be demonstrated to be independent of the size of the cranium in individuals who habitually performed anterior dental loading in comparison to those individuals who did not. Since the cranium is not considered to be balanced atop the vertebral column by the load and lever arms, these two should be of disproportionate lengths. The proportionately shorter lever arm must offset the longer load arm through muscular and ligamentous exertion. The early hominines should demonstrate greater muscular development since these individuals are likely to have possessed fewer means of extra-oral preparation of food compared to modern individuals. In other words, these earlier hominines more frequently and more strenuously performed anterior dental loading.

6.2 Materials Required for the Statistical Analysis

The craniometric statistical portion of the research required a standard Matui Manufacturing Company vernier scale stainless steel caliper; a combination square; a Gneupel spreading caliper calibrated to 30 cm; a tape measure; a StatWorks™ Macintosh software statistical package; a zero setting device polar compensation planimeter with optical tracer produced by the

Enduro Company of Tokyo, Japan; several blank tranparency sheets and water soluble markers; and a Canon AE-1 camera with a zoom lens, several roles of 100 ASA film, a piece of black velvet, a cork flask-holder, and two studio lights. The data analyses and creation of graphs was done using the Macintosh programmes StatWorks™, StatView 512™, and Cricket Graph™.

6.3 Methods and Procedures:

Measurements of potential functional significance were taken of the cranium and compared using linear regression equations and analyses of variance to determine what, if any, relationship exists between cranial size and shape and cross-sectional area of the musculature. These measurements were standardised to the cranial module to remove the effect of size and to allow in this way comparison of adjusted variables and unadjusted variables. These values are collected in Table 8. All measurements were obtained through the use of spreading calipers, sliding calipers, and a tape measure and rely in most instances on previously identified craniometric points (Howells 1973, Brothwell 1981). Cross-sectional area of the nuchal muscles (cm^2), a measurement not previously defined, was determined from planimeter measurements of life-size photographs of the basicranium taken at a uniform angle ensured through the use of a combination square. Moreover, the lever arm (effort), also previously undefined, has been defined here as the distance (mm) from the superior nuchal line at the external occipital protuberance (inion) to a point most inferior on the occipital condyles; whereas, the load arm or resistance is defined as the distance from incision between the upper central incisors to the same point on the condyles. It is assumed that this point on the condyles represents the fulcrum of the first-class lever of the cranium as it sits upon the superior articular facets of the atlas.

Cranial thickness measurements were obtained through the use of a General Electric computer tomographic scanner housed and operated by Vancouver General Hospital, Vancouver, British Columbia. Scans were taken through both the coronal and sagittal sutures and then 2 cm to the side of each. Cranial thickness measurements were obtained from the area of the suture and then roughly 2 cm off the suture, producing two measurements for each of the four slices. One hundred and twenty scans were in this way produced. Those measurements derived from the same area of the two slices were used to generate an average thickness for that particular orientation and thus account for irregularly distributed bone mass. No cranial thickness measurements could be obtained from the mixed hominine sample as these casts do not faithfully record the cranial thicknesses of the original specimens. Statistical manipulations were then performed in an attempt to understand the significance of cranial thickness.

Figure 17: Norma basalis view of the os occipitalis of the Skhul individual, which possesses the greatest proportion of muscular attachment size for its cranial size as accounted for by the cranial module.

Figure 18: *Norma basalis* view of the *os occipitalis* of Calcuttan 5, one of the two individuals whose cranium is "over-muscled" for its size. Note the flattened nature of the occipital condyles, the mediolaterally rotated mastoid process, and the accessory facets posterior to the condyles.

Figure 19: Norma basalis view of the os occipitalis of Calcuttan 11, which possesses a wide occipital bun. Note the relationship between the bun and the muscular attachment areas for M. semispinalis capitis.

Figure 20: The Murray site female in norma basalis, showing the double condylar facetting, accessory facets, and arthritic lipping of the occipital condyles, and anteriorly directed mastoid processes.

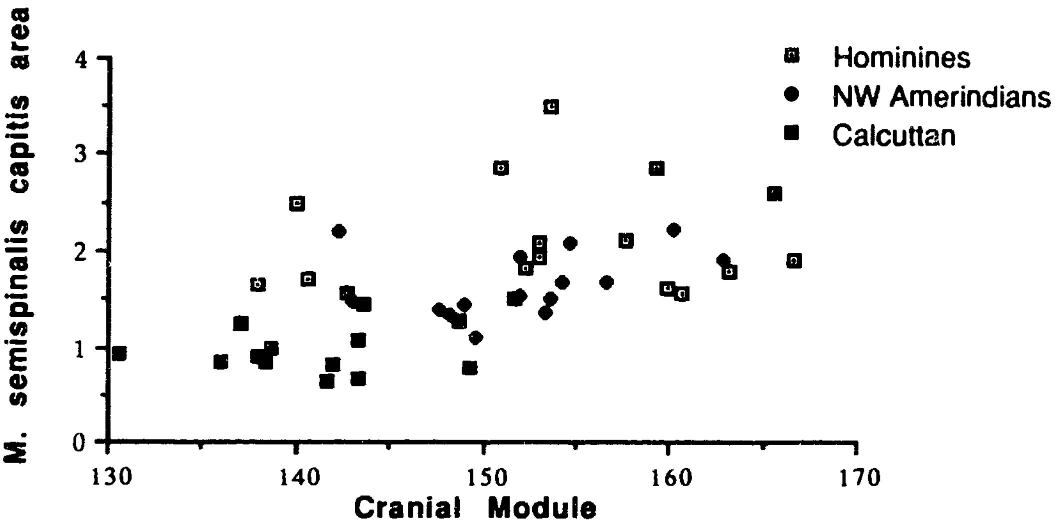


Figure 21: Regression of the cranial module (mm) when compared to the cross-sectional area of M. semispinalis capitis enthesis (cm^2). The correlation of 0.502 (R) (p= .0001) although establishing some relationship between head size and muscle development, demonstrates that there are other factors influencing the development of this muscle and not size of the cranium alone (N= 45).

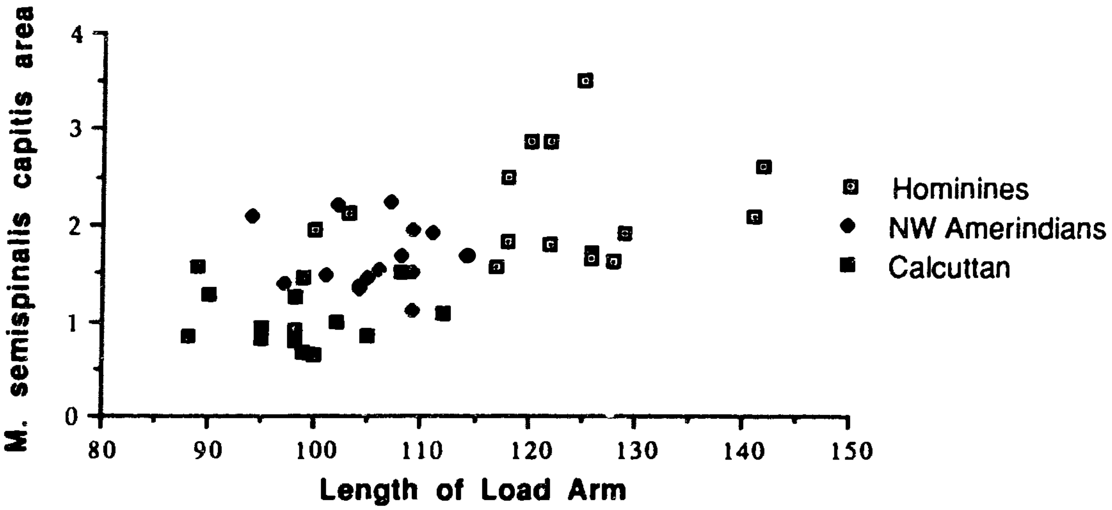


Figure 22: This regression resulted from the comparison of the length of the load arm (mm) and the cross-sectional area of M. semispinalis capitis (cm^2). The two measurements are correlated relatively strongly with an R-value of .589 (p= .0001) and when adjusted for size at .425 (p= .0033) which posits that a longer load arm requires greater muscle development at the posterior of the cranium (N= 45).

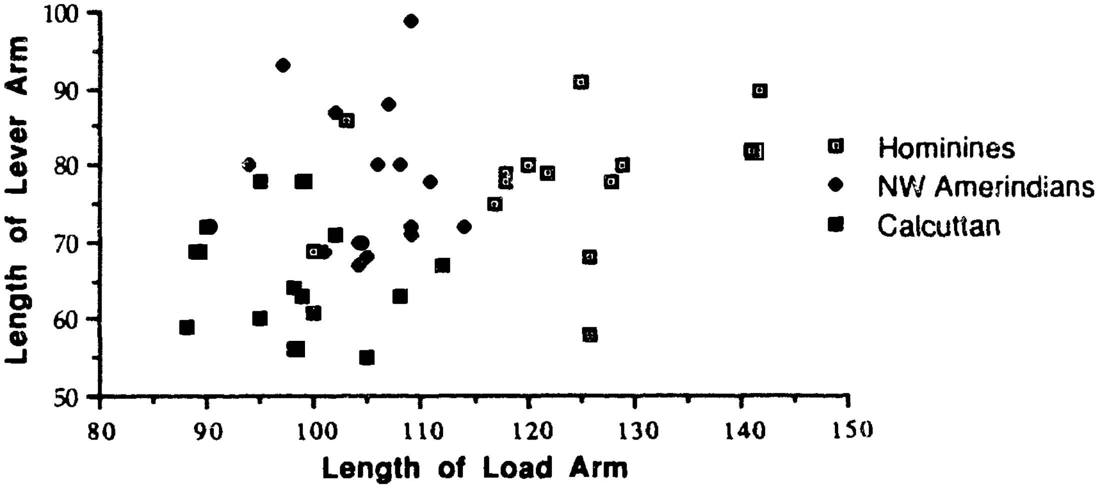


Figure 23: The regression produced through a comparison of the length of the load arm (mm) of the cranium with that of the lever arm (mm). An R-value of .358 (p= .0136) and an adjusted score of .061 (p= .6830) demonstrates that these two lengths are not highly correlated. Therefore, these two lengths do not act to balance the cranium atop the vertebral column (N= 45).

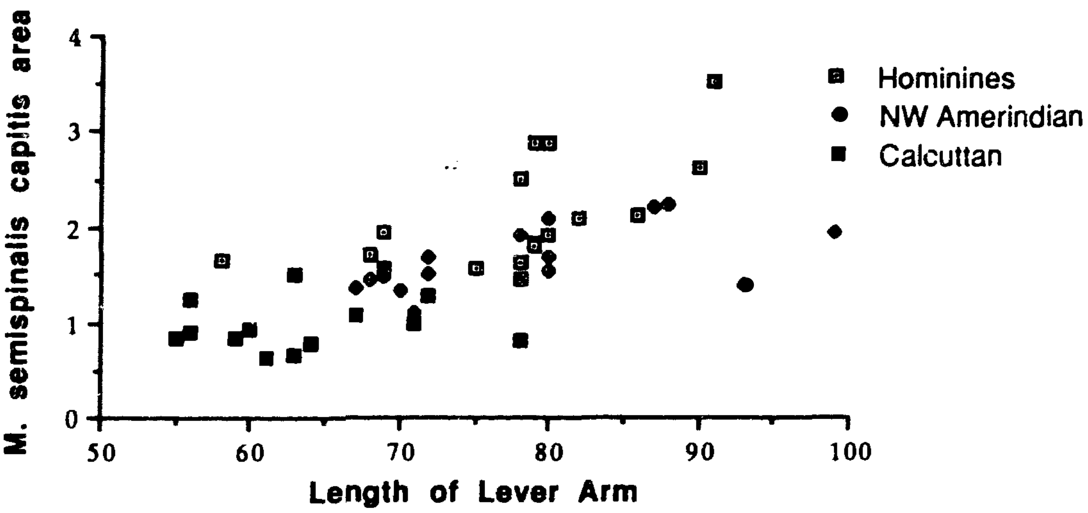


Figure 24: The regression received from a comparison between the length of the lever arm (mm) of the cranium and the cross-sectional area of the enthesis for M. semispinalis capitis (cm^2) which produced a correlation coefficient (R) of .692 (p= .0001) and an adjusted score of .567 (p= .0001) for the entire sample of crania (N= 45).

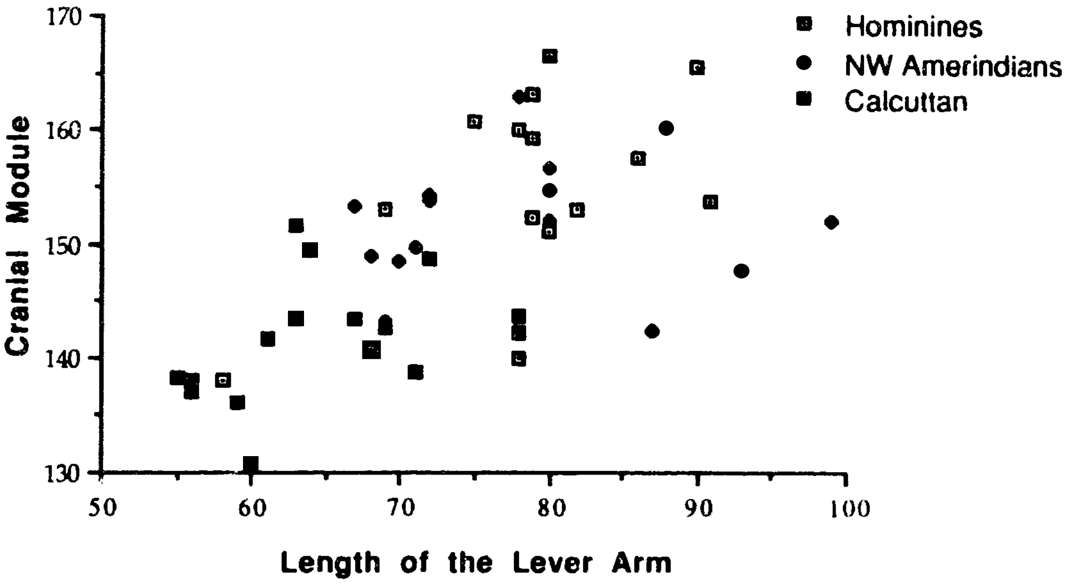


Figure 25: The regression resulting from a comparison of the cranial module, which measures size of the cranium and lever arm length. The correlation coefficient (R) of .680 (p= .0001) suggests that large crania possess longer lever arms (N= 45).

6.4 Results of the Statistical Study:

There is a relatively strong correlation (.589) between the length of the load arm and the cross-sectional area of M. semispinalis capitis (Fig. 22). This relationship holds only when the hominines are pooled with the two more recent samples. Therefore, it would appear that among the hominines the head is acting as a first-class lever, but this use is not as strongly indicated for the more recent samples. Moreover, when the size of crania is held constant the correlation drops to .425, but is significant (p= .003), indicating that although large crania do have larger entheses areas, size does not account for all of the enthesis development noted. This result indicates that the longer the load arm is, the greater the area of attachment for the musculature. This association meets expectations in that the hominines in general, and earlier hominines especially, are noted for their prognathic jaws. An even stronger correlation exists between the length of the lever arm and the cross-sectional area of this muscle (Fig. 24) and this correlation remains strong even after size is taken into consideration (.567). This result seems to indicate, as expected, that the development of M. semispinalis capitis exerts a strong influence on cranial shape in the occipital region. Furthermore, when the lengths of the lever and load arms are compared, they are demonstrated to be independent of each other, producing no strong correlation (Fig. 23). This result provides strong support for the rejection of a model of the cranium which suggests that the head is somehow balanced atop the vertebral column. If such were the case, then one would expect these two lengths to be dependent and equal in length. That they are not shown to be independent suggests that the nuchal muscles do offset the comparatively shorter lever arm length when compared to the longer load arm.

Correlated	Raw						Size Adjusted					
Variables	all			recent			all			recent		
X:Y	r	p	r^2	r	p	r^2	r	p	r^2	r	p	r^2
Lever: Load	.358	.0136	.128	.213	.2429	.045	.061	.6830	.004	-.170	.3534	.029
Lever: Occ. Ang.	.302	.0411	.191	.423	.0159	.179	.393	.0610	.154	.234	.1170	.055
Load: Occ. Ang.	-.322	.0289	.104	-.367	.0386	.135	-.234	.1170	.005	-.075	.6847	.006
Lever: SemiSpSqRt	.692	.0001	.480	.698	.0001	.487	.567	.0001	.322	.579	.0005	.335
Load: SemiSpSqRt	.589	.0001	.347	.322	.0721	.104	.425	.0033	.176	.108	.5574	.012
Lever:SubOccSqRt	.616	.0001	.379	.604	.0003	.365	.356	.0141	.356	.386	.0290	.149
Load: SubOccSqRt	.191	.1995	.036	.374	.0347	.140	.290	.0481	.084	.177	.3333	.031
SemiSp:SubOcc	.576	.0001	.332	.737	.0001	.543	.465	.0010	.465	.671	.0001	.451
SemiSqRt: SubSqRt	.580	.0001	.336	.740	.0001	.547	.321	.0277	.103	.582	.0005	.339
SagThk:SemiSqRt	-	-	-	.638	.0001	.408	-	-	-	.478	.0076	.228
CorThk:SemiSqRt	-	-	-	.679	.0001	.461	-	-	-	.548	.0017	.228
SagOff:SemiSqRt	-	-	-	.546	.0011	.299	-	-	-	.357	.0529	.127
CorOff: SemiSqRt	-	-	-	.596	.0005	.355	-	-	-	.437	.0156	.191
CorThk:SubSqRt	-	-	-	.671	.0004	.435	-	-	-	.381	.0370	.145
SagThk:SubSqRt	-	-	-	.671	.0001	.450	-	-	-	.323	.0800	.104
SagOff:SubSqRt	-	-	-	.580	.0008	.336	-	-	-	.210	.0440	.260
CorOff:SubSqRt	-	-	-	.655	.0001	.429	-	-	-	.352	.0930	.124
Bite Pull:SagThk	-	-	-	.643	.0001	.413	-	-	-	.619	.0003	.383
Bite Pull: SagOff	-	-	-	.535	.0023	.286	-	-	-	.475	.0079	.226
Bite Pull: CorThk	-	-	-	.675	.0001	.456	-	-	-	.649	.0001	.421
Bite Pull:CorOff	-	-	-	.601	.0004	.361	-	-	-	.558	.0014	.311

Table 8: Correlated variables, size adjusted and unadjusted, between hominine and more recent samples. "SqRt" represents the square root of a linear variable for comparison purposes with areas.

The length of the lever arm forms a strong correlation (r= .680) with the cranial module (Fig. 25). Since the lever arm determines the length of the posterior of the cranium to some extent the relationship between this measurement and cranial module is to be expected. The strong correlations between the cross-sectional area of the musculature and the suboccipital area in most cases (see Table 8) again suggests a size related factor. That the size adjusted complete sample should produce a relatively weaker correlation suggests that the more recent samples' muscular area is more a reflection of size of the suboccipital area than those correlations noted in the hominine sample. That the Northwest Amerindian sample does not demonstrate a strong correlation suggets that although these individuals were loading their anterior dentition, they were not doing such an activity as strenuously. The correlation drops off to being relatively weak in the more recent human samples when corrected for size (Table 8). This observation would seem to suggest that the development of the nuchal musculature is largely dependent on the length of the load arm, specifically in individuals employing their heads as first-class levers, in this case the hominine group. Although the cross-sectional area of this nuchal musculature correlates to size dimensions of the cranium, when that cross-sectional area is standardised to the area of the suboccipital, producing a ratio which accounts for the amount of the suboccipital taken up by the muscular attachment, and then compared to the cranial module, there is no strong correlation between the size of the cranium and the relative size of the muscular attachment area (Fig. 26). Thus, the association of load arm length with muscular development is not simply a reflection of cranial dimensions, especially in the hominine sample.. This conclusion is in keeping with the results of Taylor and DiBennardo (1980) who statistically demonstrated that the shape of the cranial vault is not correlated to facial length (identified by these researchers as prosthion-basion length). These results indicate that the nuchal muscles are correlated with load arm length and that this relationship is at least partially independent of the size of the cranial vault. In fact, there is a consistently stronger relationship between the enthesis area of *M. semispinalis capitis* and lever and load arm lengths and vault thickness than between these measurements and suboccipital area (compare Figures 31-34 and 35-38 and Table 8). This result supports the contention that the cross-sectional area of the enthesis for *M. semispinalis capitis* is a sound osteological indicator of anterior dental loading.

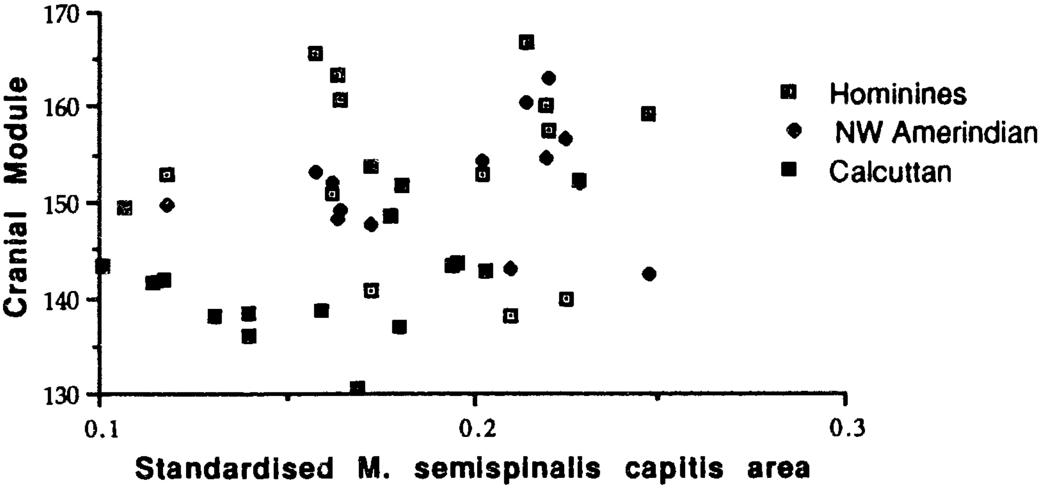


Figure 26: The regression resulting from the standardisation of the cross-sectional area of the attachment for M. semispinalis capitis to the suboccipital area and compared to the cranial module. The size of the cranium is thus shown not to contribute to the relative development of the muscle, producing a correlation coefficient (R) of .217 (N= 45).

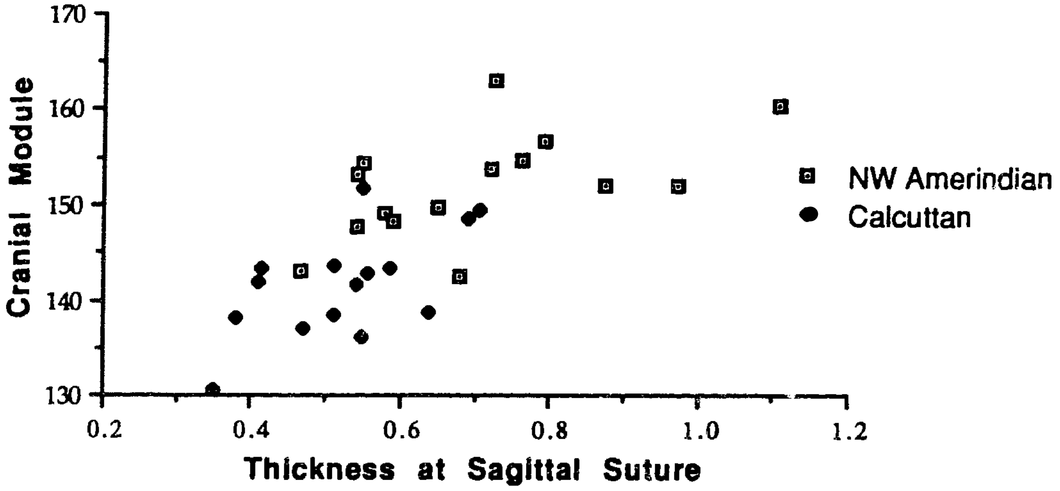


Figure 27: Regression of cranial thickness at the sagittal suture as compared to the cranial module. A correlation coefficient (R) of 0.71 (p= .0001 R^2 = .487) demonstrates a strong correlation between large crania and cranial thickness as measured at the sagittal suture (N= 30).

Cranial thickness measurements correlate very strongly with the cranial module and with the three measurements that compose this index: length, width, and height of the cranium. Thus larger crania appear to have thicker cranial bone. In fact, the highest correlations in the study were achieved between the cranial module and cranial thickness (Figs. 27-30). Cranial thickness measurements also correlate very strongly with muscle attachment area even when these measurements are standardised for cranial size, and especially so with the thickness measurements obtained at the sagittal and coronal sutures (refer to Table 8). The lower correlations for the size adjusted variables, however, suggest that the size of the cranium affects cranial thickness. This size factor, though, might relate to the larger muscles needed to move a larger head which in turn contributes to increase the thickness of the cranial bone through the heightened piezoelectric activity of these larger muscles. The highest correlations achieved in this regard occur between the attachment area of the M. semispinalis capitis and the thickness of the coronal suture recording an unadjusted size correlation of 0.679, or when size of the cranium is controlled, 0.548 (Figures 31-34). These correlations drop off as one moves away from the sutures. It appears that an increase in sutural thickness is effected by the tensile forces exerted by M. semispinalis capitis, and especially so in large-headed individuals. The appositional growth at the sutures would thus appear to be affected by the tensile forces exerted by the nuchal musculature. Since the correlations drop off away from the sutures suggests very strongly that these sutures represent areas of potential weakness within the cranium and thus are disproportionately thickened in comparison to areas off of the sutures. The force of M. semispinalis capitis acts at a right angle to the coronal suture and this orientation doubtless accounts for this suture's being most highly correlated with enthesis area. That the correlations are not perfect likely relates to the muscular forces exerted by other nuchal muscles not accounted for in this study and perhaps also those exerted by the craniofacial masticatory musculature. The same likelihood may also explain the reduced R^2's in these and other correlations. The muscular forces that influence cranial parameters are so many that any one cannot account for any more than a portion of the causes. A strong indication that this may indeed be the case comes from the strong correlation between reconstructed bite pull and sagittal sutural thickness (Table 8), for it is this suture which one would suspect is most influenced by the action of the temporalis muscles located on the sides of the cranial vault.

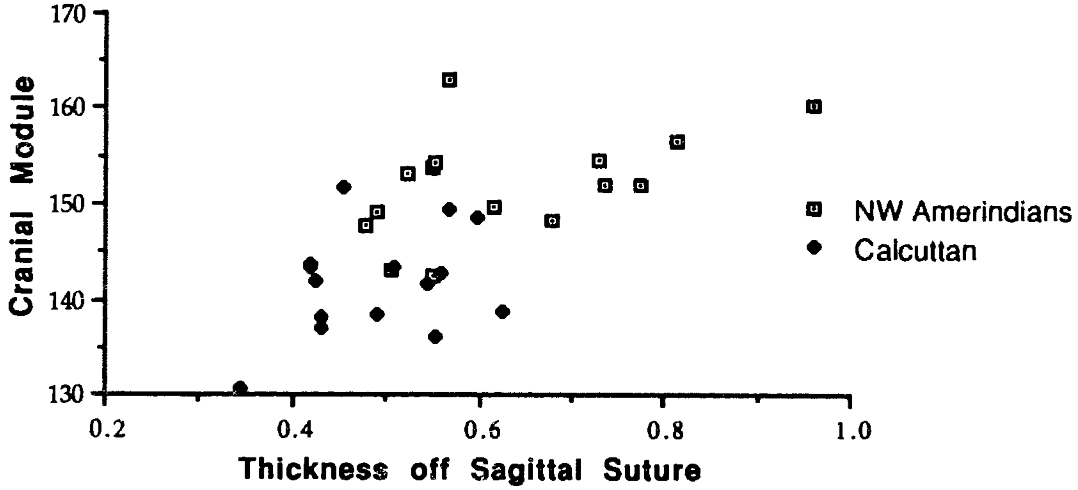


Figure 28: Regression of cranial thickness 5 cm. from the sagittal suture as compared to the cranial module. A correlation coefficient (R) of 0.649 (p= .0001, R^2= .421) demonstrates a good correlation between large crania and cranial thickness as measured near the sagittal suture (N= 30).

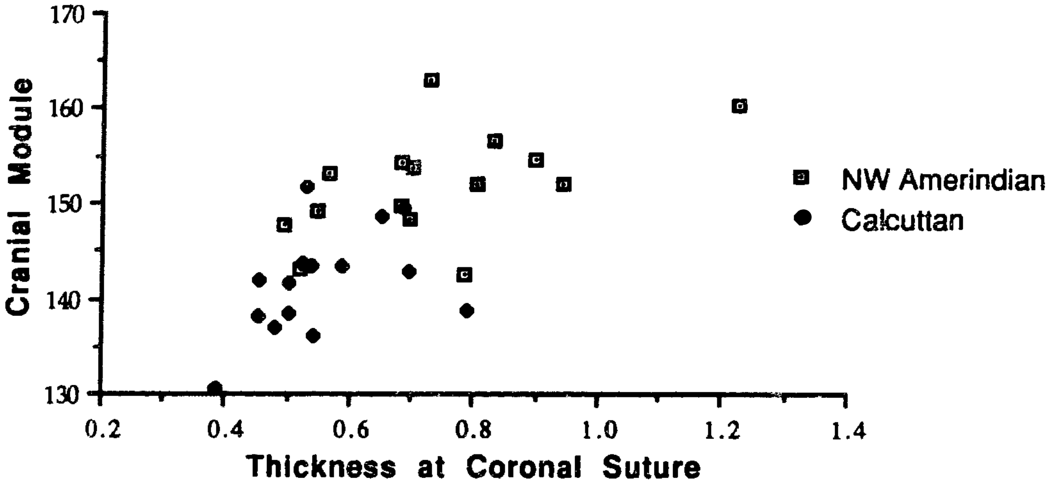


Figure 29: Regression of cranial thickness at the coronal suture as compared to the cranial module. A correlation coefficient (R) of 0.658 (p= .0001, R^2= .433) demonstrates a strong correlation between large crania and cranial thickness as measured at the coronal suture (N= 30). When this regression is log-transformed, no appreciably better correlation results (R= .686, p= .0004).

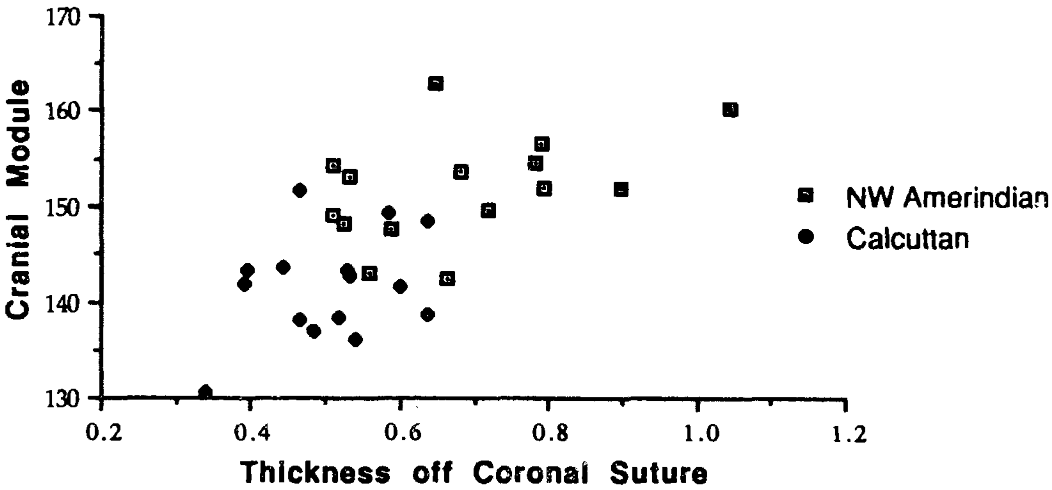


Figure 30: Regression of cranial thickness 5 cm. from the coronal suture as compared to the cranial module. A correlation coefficient (R) of 0.643 (p= .0001, R^2= .414) demonstrates a strong correlation between large crania and cranial thickness as measured near the coronal suture (N= 30).

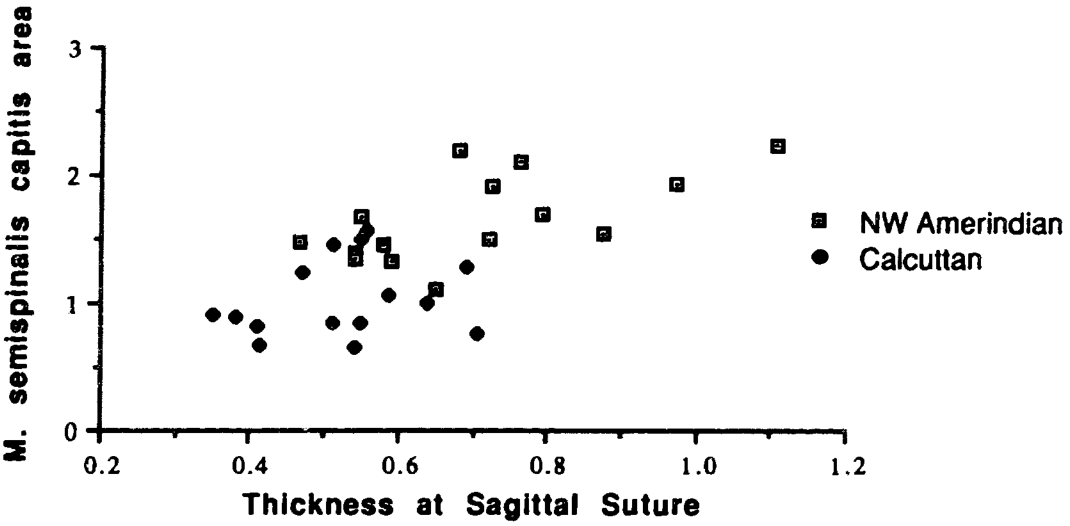


Figure 31: Regression of cranial thickness at the sagittal suture against cross-sectional area of the insertion for M. semispinalis capitis. An unadjusted correlation coefficient (R) of .638 (p= .0001, R^2= .408) and an adjusted score of .478 (p=.0076, R^2= .228) suggests that these measurements are strongly correlated and that the extent of muscle action has an influence on the thickness of the cranial bone at the suture (N= 30).

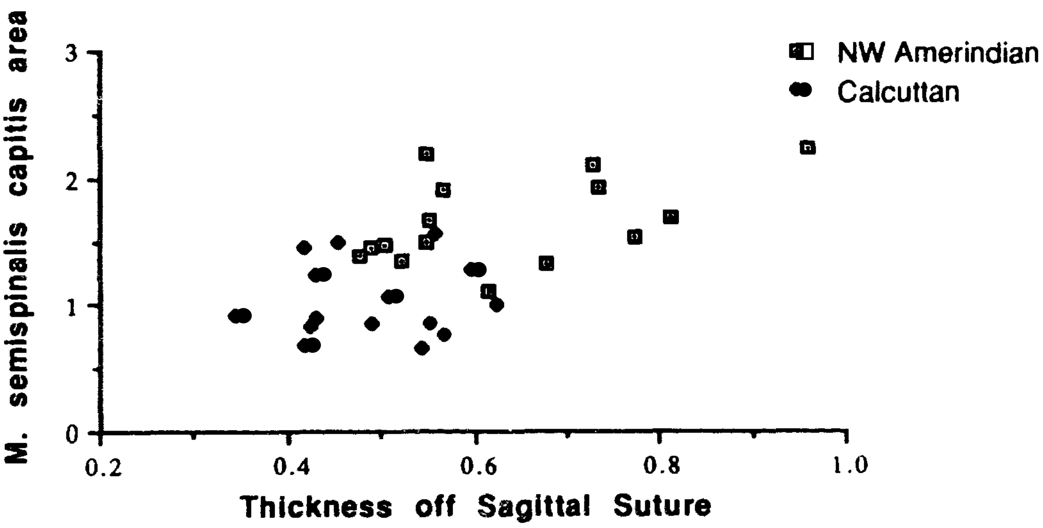


Figure 32: Regression of cranial thickness 5 cm from the sagittal suture as compared to the cross-sectional attachment area of M. semispinalis capitis. A correlation coefficient (R) of .546 ($p= .0001$, $R^2= .299$) and an adjusted score of .357 ($p= .0529$, $R^2= .127$) suggests a less strong correlation than that noted between cranial thickness at the sagittal suture and the extent of the attachment ($N= 30$).

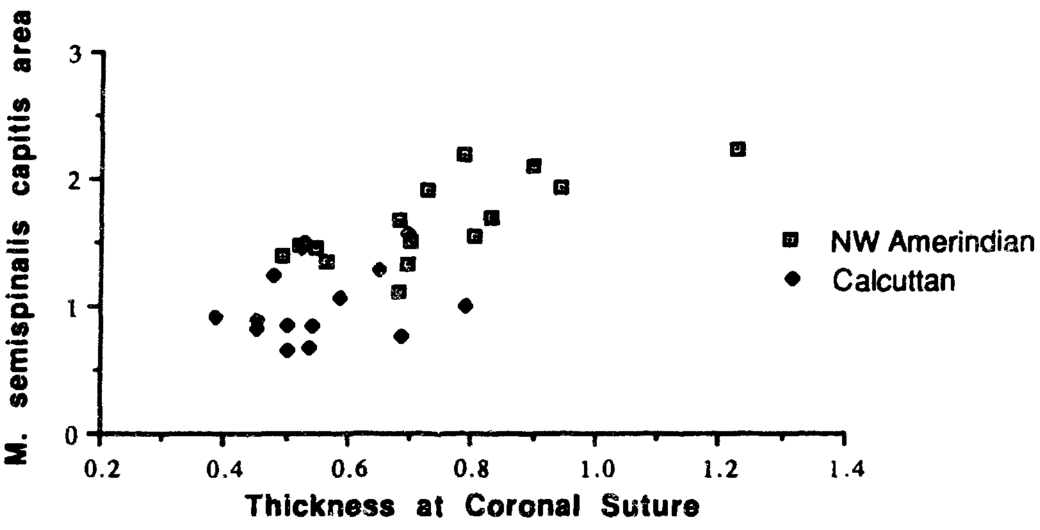


Figure 33: Regression of cranial thickness at the coronal suture as compared to the cross-sectional attachment area of M. semispinalis capitis. A correlation coefficient (R) of .679 (p= .0001, R^2= .461) and an adjusted score of .548 (p= .0017, R^2= .228) provides the strongest correlation between cranial thickness and muscular attachment development. A log-transfromation did not improve the correlation (R= .514, R^2= .264, p= .0037) (N= 30).

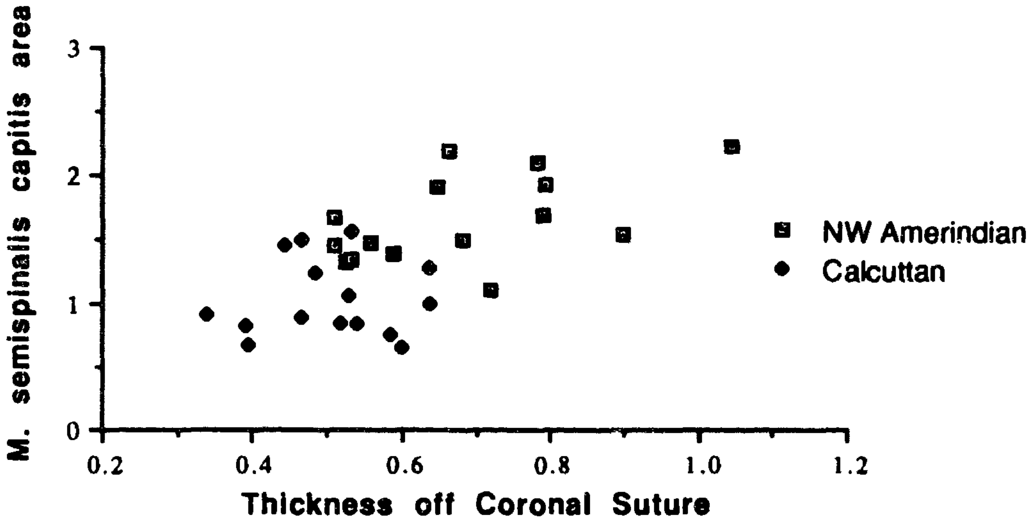


Figure 34: Regression of cranial thickness 5 cm from the coronal suture as compared to the cross-sectional attachment area of M. semispinalis capitis. A correlation coefficient (R) of .596 (p= 0005, R^2= .355) and an adjusted score of .437 (p= .0156, R^2= .145) suggests a less strong correlation than that noted between cranial thickness at the coronal suture and the extent of the attachment, but this correlation provides evidence that muscle action has its greatest influence in the coronal plane which lies perpendicular to the direction of the muscular force (N= 30).

The area of the suboccipital region (the nuchal portion of the occipital) also correlates quite strongly with cranial thickness measurements, but not as strongly as that noted between the cross-sectional area of M. semispinalis capitis and thickness measurements, however, ranging from .671 at the coronal suture to .580 off the sagittal suture (refer to Figures 35-38). This reduced correlation appears to be a reflection of the percentage of the suboccipital area occupied by the attachment area for M. semispinalis capitis. Such evidence supports even more strongly the association between the size of this muscle and and its influence on cranial proportion. A similar picture is obtained by comparing both the unadjusted and size adjusted suboccipital areas for the three samples:

	Raw (cm^2)	**Size Adjusted**
Hominines	79.8	5.2
NW Amerindian	86.6	5.7
Calcuttan	67.6	4.8

Table 9: Mean suboccipital area by sample absolute and size adjusted data.

Here one notes that the Northwest sample has both absolutely and relatively larger suboccipital areas. As previously noted, however, this group has a reconstructed bite pull which is inferior to that of the hominines. It seems that the cross-sectional area of this muscle in relation to its extent on the suboccipital is the most important factor governing cranial shape and configuration. In other words, the extent of this muscle's development appears to be the most important element in the correlation and not the size of the suboccipital area. Interestingly, it appears that individuals with rounder crania possess smaller attachment areas than those possessing long crania (Figure 39). Here again, there is the suggestion that the development of this muscle has some influence in producing dolichocranic individuals with long load arms (prognathism).

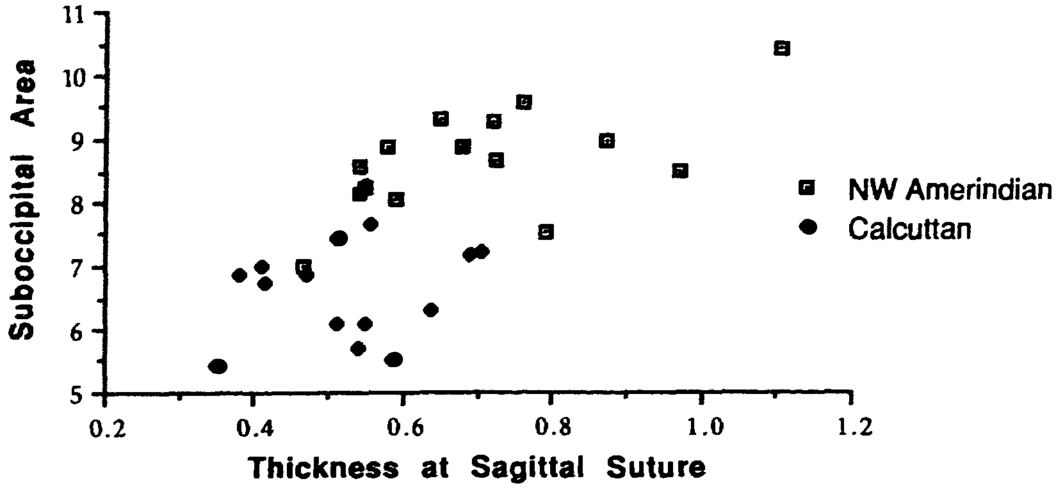


Figure 35: Regression of cranial thickness at the sagittal suture as compared to the area of the suboccipital region. A correlation coefficient (R) of .671 (p= .0001) suggests that this area and its adhering musculature plays a role in the thickness noted at the suture (N= 30).

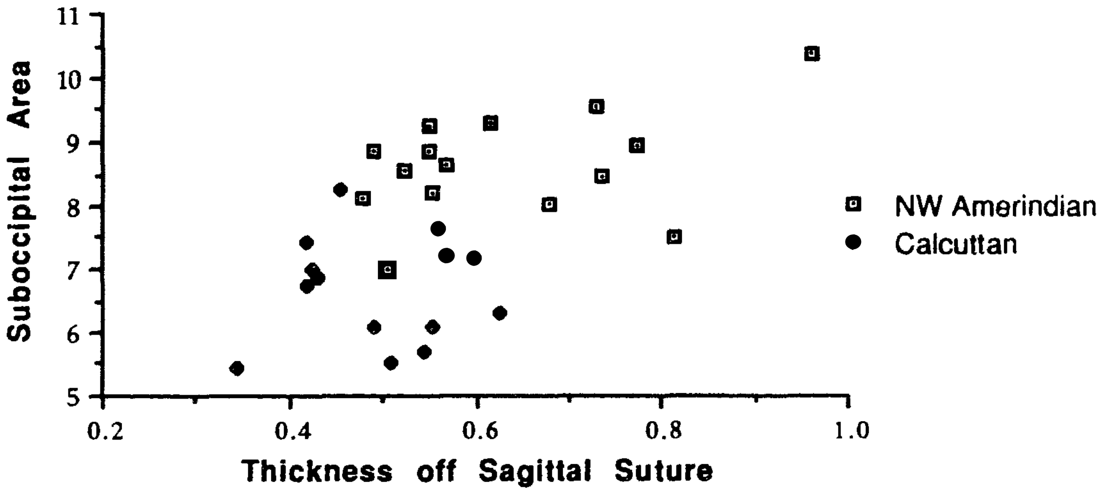


Figure 36: Regression of cranial thickness 5 cm from the sagittal suture as compared to the area of the suboccipital region. A correlation coefficient (R) of .580 (p= .0008) suggests a less strong correlation than that noted between cranial thickness at the sagittal suture and the extent of this area. This relationship mirrors the one for the attachment area of M. semispinalis capitis which provides evidence that the basicranium has an influence on cranial dimensions (N= 30).

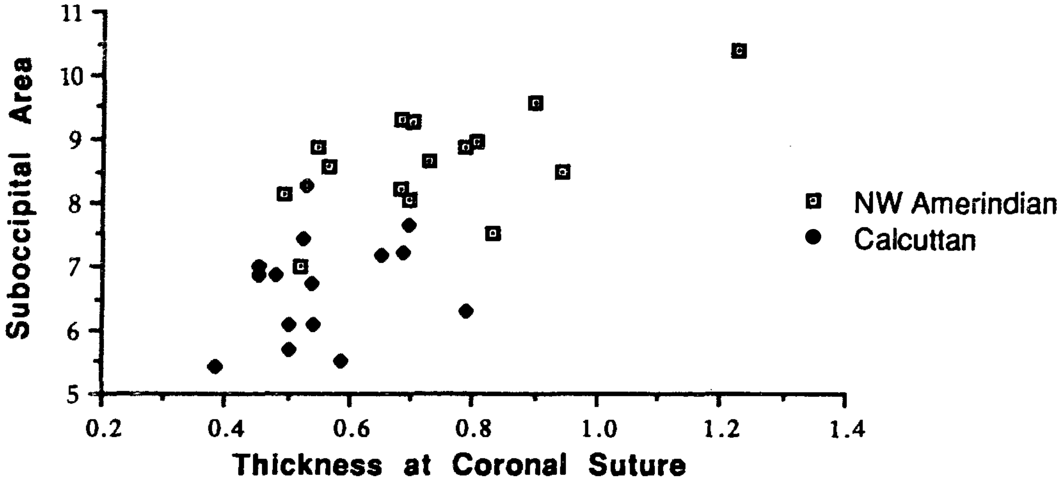


Figure 37: Regression of cranial thickness at the coronal suture as compared to the area of the suboccipital region. A correlation coefficient (R) of .671 (p= .0001) provides the strongest correlation of any other between cranial thickness and the area of the suboccipital, again very much like the pattern noted for the muscle.

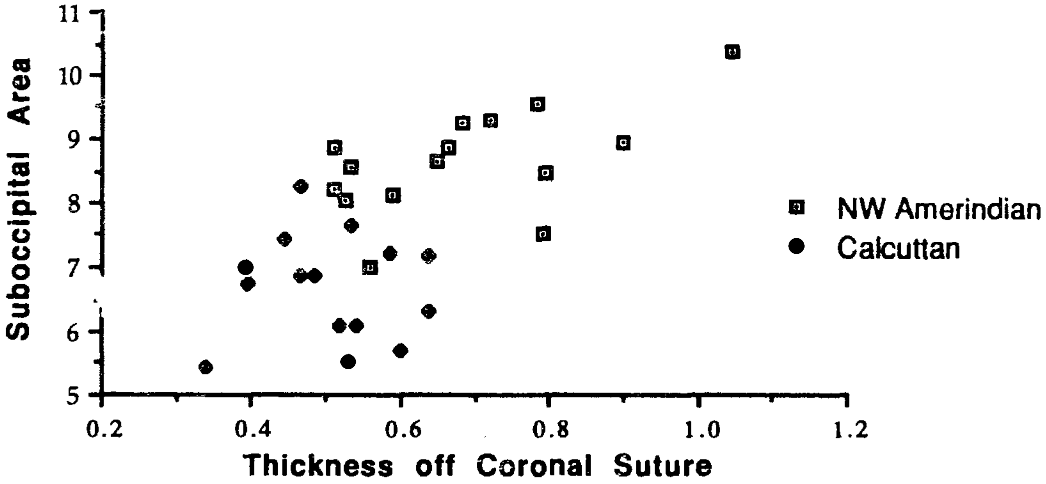


Figure 38: Regression of cranial thickness 5 cm from the coronal suture as compared to the area of the suboccipital region. A correlation coefficient (R) of .655 (p= .0001) suggests a less strong correlation than that noted between cranial thickness at the coronal suture and the extent of this area, a pattern like that noted for the muscle attachment. This relationship suggests that the muscle has an effect on the extent of the suboccipital region and upon cranial thickness (N= 30).

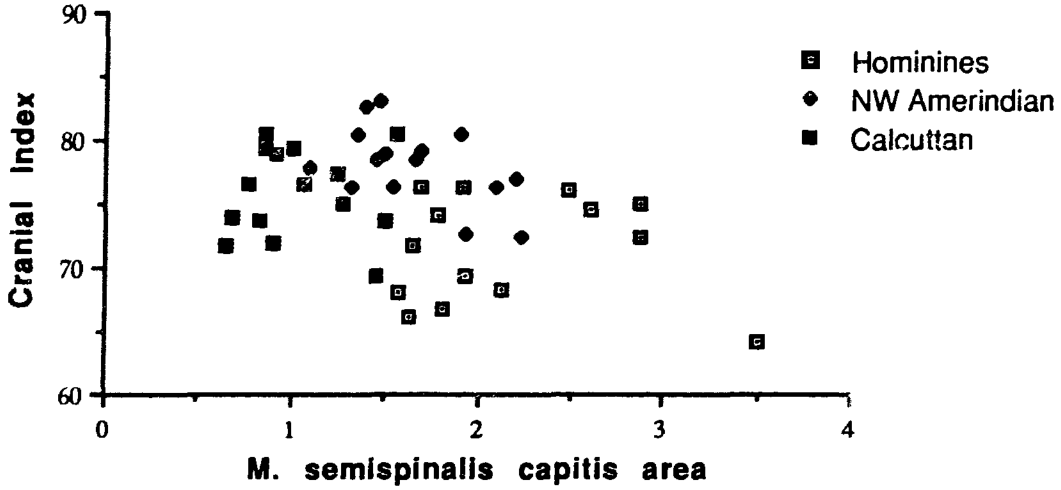


Figure 39: Regression resulting from the comparison of the cranial index and cross-sectional area of M. semispinalis capitis. The cranial index is not correlated with the degree of muscle development, producing an R-value of -.347 (p= .0001). The distribution obtained, however, suggests that in general individuals possessing a more rounded (brachycranic) crania have smaller entheses for this muscle and that long crania (dolichocranic) have more well-developed muscles, leaving larger enthesis areas.

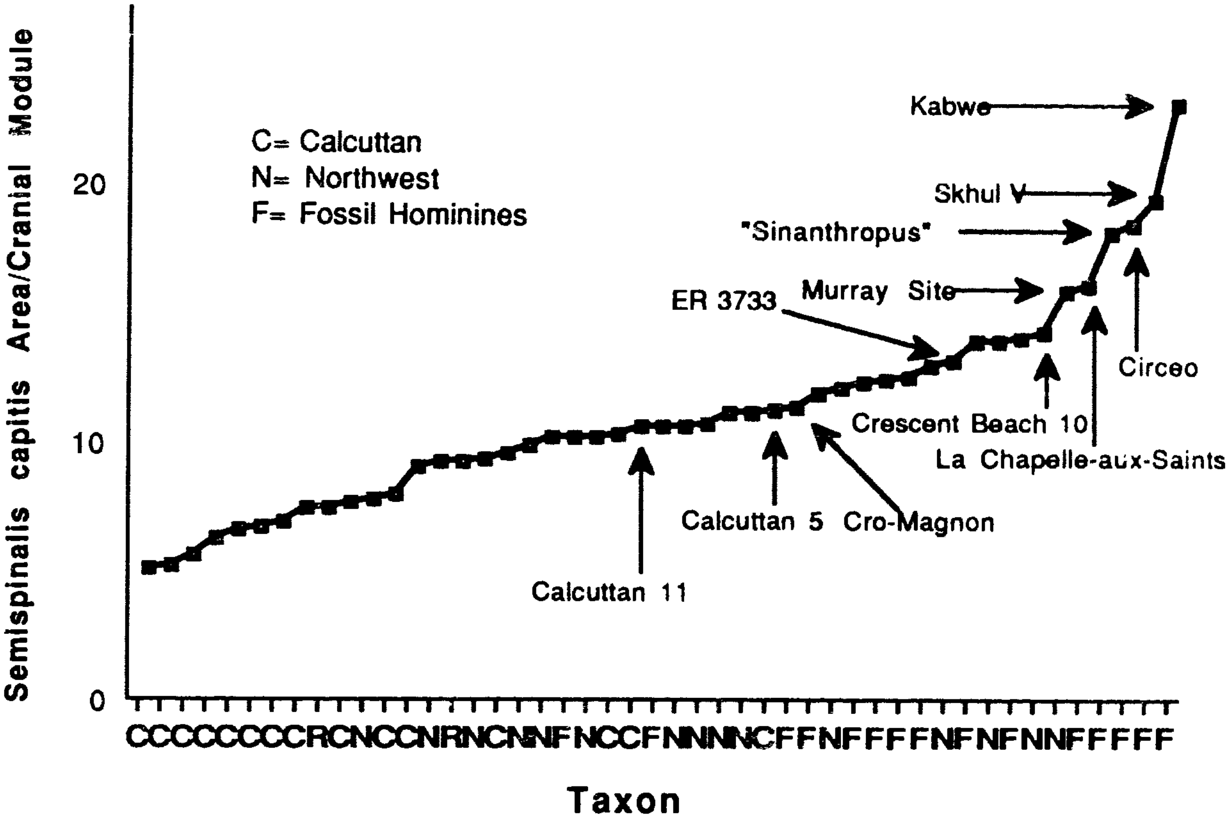


Figure 40: The trend produced from a comparison of the cross-sectional area of M. semispinalis capitis standardised to the cranial module among specimens. Certain individuals possess much greater muscular development than would be determined from the size of their crania. Calcutta 5, 11, and the Murray Site individuals appear to be over-muscled for their head size, which likely relates to behavioural differences in the use of their heads. C= Calcuttan, F= fossil hominines, N= Northwest Amerindian, R= recent Bushman and the Hotu Neolithic cranium for comparative purposes.

When relative bite pull is calculated for the samples a clear division occurs between the hominines and the Northwest Amerindians on one hand and the Calcuttans on the other. The latter group clearly possesses a much reduced bite pull. This observation is interpreted to mean that the Calcuttans did not anteriorly load their dentition as heavily. The mean relative bite pulls are as follows: Hominines 2.99 ± .166, Northwest Amerindian 3.04 ± .171 and Calcuttans 2.12 ± .13. A t-test of these means yielded a t-value of 4.204 (p= .0003). Cranial thickness measurements are also significantly different between the two more recent groups as determined from two-tailed Student t-tests (unpaired t-scores range from 3.275-3.351 with significance values ranging from .001-.003). This result suggests a functional cause linking bite pull and cranial thickness. Furthermore, there is a good correlation between

	Size Adjusted			
	Northwest		Calcuttan	
	r	p	r	p
Lever: SemiSpSqRt	.593	.0198	.247	.3742
Load: SemiSpSqRt	.210	.4521	.108	.7014
SagThk:SemiSqRt	.453	.0896	.061	.8300
CorThk:SemiSqRt	.592	.0202	.143	.6118
BitePull:SagThk	.588	.0213	.237	.3959

Table 10: Correlated variables among recent humans only. "SqRt" represents the square root of a linear variable for comparison with areal measurements.

this bite pull and cranial thickness at the sutures as previously demonstrated, which have been identified as potential areas of weakness in the cranium (see Table 10). An index which standardises the muscular attachment area to the cranial module (to control for size) produces a very tight curve, which suggests that certain crania in the sample, those which are somewhat removed from the smooth curve possess larger entheses than would be dictated by the size of their crania (Figure 40). This trend demonstrates that the size of the muscular attachment is not a function of head size- some of these individuals possess much larger attachment areas than would be dictated by their cranial size. In fact, this index continuously sorts out a group consisting of early hominines, including the uniquely modified Kabwe specimen (the most rugose individual), the *Homo erectus*, Archaic *Homo sapiens* and Neanderthal, as well as Upper Palaeolithic individuals and male Northwest coast crania, from the gracile Calcuttan sample, and the Northwest Amerindian females (Appendix 2 and Column 28).

The relatively small *Homo erectus* crania included in this study, those of "Sinanthropus" (Asian *Homo erectus*) and ER 3733 find themselves in a group of much larger headed individuals. From these data and assessments one would describe *Homo erectus* as overly muscled for its cranial size. The attachment area for *M. semispinalis capitis* makes up some 39% of the basi-occipital area of the Kabwe specimen, the highest value attained, and 33% and 29% for "Sinanthropus" and ER-3733 crania. It would seem, then, that the thickened cranial bone is essential to withstand the force of these large nuchal muscles on a relatively diminutive head.

Interestingly, two Calcuttan males are also included in this group, numbers 5 and 11. Both of these individuals possess crania similar in size to those of the Homo erectus included in this study. They are unusual in that they possess large muscular attachment areas compared to the size of their crania. Calcuttan 5 is also that individual who as previously noted possesses a thin, but salient occipital torus similar in breadth proportions to those of Homo erectus (Figs. 7 and 43).

The highest percentage of the suboccipital area occupied by the attachment area of M. semispinalis capitis for the Northwest Coast series is that of an individual from the Murray site in the Interior of British Columbia near Lillooet (Figs. 4 and 42), some 25%, and for the Calcuttan population, 20% in Individual 5. These two individuals are extremes among their respective series. Like Homo erectus these individuals are over-muscled for their particular head size as measured by the cranial module. Individual 5 possesses an unsual occipital, several features of which it shares with the Murray individual. Chief among these is not only the rugose occipital morphology (Figs. 18 and 20) with the attendant tori and crest development (see Appendix 4, Columns 11-22), but also a flattened basi-occipital, a low cranial vault (compare this variation in Figs. 41-48), and a cranial thickness which is in all but one case above the mean for its group. Both crania are above (Murray site) or well above (Calcutta 5) the means for their samples as a whole.

The occipital morphology and the occipital angulation of these crania is strikingly similar in several cases between fossil hominids and modern individuals (Figs. 41-48). These crania with increased angulation also possess quite low cranial vaults, falling below the means for their samples and at the bottom of the range (Murray site) or near it (Calcutta 5). Since the coronal suture lies in a plane perpendicular to the nuchal musculature and it is at the sutures that the cranial bones grow, alterations in this region would be interpreted to strongly contribute to cranial height. It would appear that the action of these muscles has influenced the growth of the cranium in these two individuals, producing thickened cranial bone, a cranial vault of reduced height, and a flattened basioccipital. Another similarity noted in creating ct-scans of the crania is that the Northwest sample is characterised by a coronal suture drift (Figs. 41 and 42), which is a trait also possessed by many of the individuals in the hominine sample, including members of *Homo erectus* and the Archaic *Homo sapiens* and to a lessened degree in Calcuttans 5 and 11 (Figs. 44 and 47), but not in the more " normal" Calcuttan 7 (Fig. 48). This coronal drift is in the direction of the pull of *M. semispinalis capitis* and could be interpreted as a consequence of this muscle's heightened functioning in these individuals.

Figure 41: The robust Crescent Beach burial 10 male in norma lateralis, demonstrating a more flattened nuchal area and an ossified ligamentum nuchae, which lends a beak-like appearance to the occipital and can be observed as an enthesophyte formation on the planum nuchae.

Figure 42: The Murray site female in norma lateralis, showing the extent of the flattening and "pulled down" appearance of the cranial vault, which is reminiscent of Homo erectus cranial morphology.

Figure 43: The Skhul cranium in norma lateralis, demonstrating a nuchal morphology very similar to the Murray site female.

Figure 44: Calcuttan 5 in norma lateralis, demonstrating the great nuchal flattening and occipital torus present in this individual.

Figure 45: The nuchal morphology of "Sinanthropus" (*Homo erectus*) as seen in *norma lateralis*. Note the similarity between this morphology and that of Calcuttan 5 and 11.

Figure 46: The extremely flat nuchal area of the Kabwe cranium in *norma lateralis*. This individual possesses the greatest occipital curvature noted in this study.

Figure 47: Calcuttan 11 in norma lateralis, which shows the contribution the bun makes to lengthening the cranium and to the occipital curvature of this individual.

Figure 48: Calcuttan 7 in norma lateralis, demonstrating a more common cranial morphology with a rounded nuchal area.

In addition to possessing unusually large cross-sectional areas of the enthesis for M. semispinalis capitis, both of these individuals possess unusual occipital condyle morphology. The Lillooet Native female demonstrates a curious double facetting of each condyle with evidence for accessory facets and osteoarthritic changes with the left condyle of a noticeably different shape from that on the right (Fig. 20). These changes are similar to those described by Hedges (1984) in a Neolithic Orkney Islands population where Chesterman (cited in Hedges 1984) noted the existence of expanded nuchal muscles in women associated with a post-bregmatic or saddle-shaped depression near the coronal suture. He hypothesized that these osteological alterations are those associated with using a band slung across the head and shoulder in order to carry loads. This individual also possesses anteriorly directed mastoid processes. In support of this interpretation is Chesterman's identification of osseous alterations in the occipital condyles of the population, where doubling or even tripling of the occipital condyles were noted in a third of the available crania. Calcuttan 5 also possesses altered occipital condyles with accessory facetting bilaterally and a noticeably flattened left condyle with a medially expanded right mastoid process (Fig. 18). It would seem that some particular behaviour involving the head and neck is indicated, a behaviour which would have produced what must have been hypertrophied M. semispinalis capitis muscles. It may be that the individual from

Calcutta was a Coolie, a porter. Lapierre (1985) describes the occupation of one of these men in Calcutta in the following manner: "Coolies, their faces distorted with strain, trotted along with baskets and packages piled on their heads" (p.23). Scher (1978) describes similar osteoarthritic changes in Black South Africans who habitually carry loads upon their heads, although through radiological analyses these lesions occur lower in the cervical portion of the vertebral column.

A review of the ethnographic literature of the Northwest reveals not only instances of anterior dental loading but also that Native populations regularly used tump-lines or head-straps to transport goods, including the Thompson Indians who live in the area from whence the cranium in question derives (Teit 1975). The tump-line, unlike the Neolithic strap, extended across the forehead and extended down the back (Eells 1985). The tump-line would require strong flexion of the head against the posterior pull of the strap. The more anteriorly directed mastoid processes suggest that this position may relate to the creation of a more powerful lever arm to resist the backward pull of this strap. In describing the use of this device in the Puget Sound, Waterman (1973) writes: "The burden-strap made in this region is of the type commonly used throughout western North America, having a broad part which fits the forehead, and two lines which are passed around the load which is to be carried. Most of the burden-straps which I obtained were already made fast to berrying baskets by means of deerskin loops....The pack strap or 'tumpline' enables a woman to carry an extraordinary load. In the old days a burden of a hundred and fifty pounds, with a baby on top of that, was not unheard of. This is considered nowadays a pretty full pack for a horse " (pp.37-38). Although these changes are noted in a high frequency in the entire Prehistoric Amerindian sample (pers. obs.), the prediction based upon the foregoing would suggest that this particular woman performed this carrying task from a very young age. Such could also be suggested to explain the unusual morphology of the Calcuttan male in the study sample. Although no similar argument for tump-line use could at this time be levelled to explain Homo erectus nuchal plane morphology, this evidence demonstrates that hypertrophied nuchal muscles appear to influence cranial morphology.

Chapter 7: Discussion and Conclusions

Two repeated statements in the literature have been demonstrated to be incorrect as a result of this research. One of these is the theoretical viewpoint which holds that the cranial vault is unstressed during loading of the cranium. The results of the photoelastic trials do not corroborate this viewpoint, and in fact, provide evidence which demonstrates that the way in which the cranium experiences strain is dependent upon its shape and configuration. It distributes forces across its ectocranial surface as it functions as a first-class lever in anterior dental loading. A more indirect, but equally informative, result derives from the associations revealed by the statistical study. This study provides evidence which strongly connotes a relationship between muscular development, head size, cranial thickness and the lever and load arms of the cranium. An outgrowth of this perspective is that the shape of the hominine cranial vault can only be explained in reference to more than genetic causes. Additionally, more than a single model is required to explain the responses of cranial vaults of differing morphologies. It is in some cases modelled most faithfully by a shell in Archaic and modern *Homo sapiens sapiens*, and in the case of *Homo erectus*, by a beam or tube.

The second of these repeated, though until now unverified, assertions is that the nuchal musculature does not influence cranial shape and configuration. It appears that part of the consternation regarding the relationship between the nuchal musculature and its relationship with vault shape and configuration involves a general confusion over the function of the occipital torus and accompanying occipital angulation. The magnitude recordings revealed by the photoelastic coating indicate that the occipital torus acts not only as a muscle attachment but contributes to strain reduction in the interparietal portion of the occipital squama. This realisation hinges upon the contribution made by the torus to increasing the angulation of the occipital. Much of this increased curvature in *Homo erectus* represents a protrusion of the occipital torus, whose function is most closely modelled as a pre-buckled strut in that it diminishes or absorbs strain. The correlation between the lever arm length and the nuchal musculature confirms even more strongly that a part of the occipital torus' function is to supply increased muscular attachment upon an otherwise relatively small cranium as Demes (1983, 1985) has suggested, especially since the inferior portion of the torus is largely given over to the enthesis for *M. semispinalis capitis*. The increased enthesis size in earlier hominines and in the prehistoric Northwest group, and certain members of other human groups (e.g. Calcuttan 5 and 11) would require the additional angulation because of its ability to absorb or diminish potentially disruptive muscular force. It also seems that the occipital bun acts in a manner similar to that of the torus, which suggests that the two structures may be of one ontogeny and not two separate ones.

The posterior extension of the occipital created by the occipital torus predisposes the cranium to tensile bending strains concentrated in the temporal and parietal region, thus requiring thickened cranial bone in *Homo erectus*. Basically, this structure acts to concentrate forces in an area low on the vault in the vicinity of the many various crests and buttresses noted in the cranium of *Homo erectus*. This research confirms Demes' *(ibid.)* previous assertion concerning the relationship of bending forces with cranial thickness.

Hannam and Wood (1989) have recently questioned the relationship between the cross-sectional areas of the jaw musculature and a number of facial angles and dimensions as proposed by Hillen and Weijs (1986) who have documented that the size of the masticatory musculature correlates strongly with cranial dimensions. As previously noted, Hilloowala and Trent (1988a and b) have also determined that the extent of browridge development and the anterior portion of the temporalis muscle are highly correlated. Hannam and Wood have revealed similar correlations between the cross-sectional areas of the masseter and medial pterygoid muscles with each other and with bizygomatic arch width, but they found that they could not predict bite force efficiency from the orientation of these muscles, and concluded that there is no clear-cut and easily identifiable relationship between muscular strength as represented by cross-sectional area of muscles and biomechanical efficiency as predicted by the positioning of the muscles. They found that similar bite forces can be generated by more than one particular facial arrangement. One can only conclude that there may be more than one morphological solution to a particular functional necessity in modern humans. A portion of this disparity may relate to the reduced demands made upon the modern masticatory system and a variation in the types of masticatory behaviours in which modern people engage. In other words, it may be that physiological and cultural factors are blurring the relationship posited to exist between muscular development and bite force.

The results of this study would seem to suggest that many modern people will not demonstrate correlation of cross-sectional area of muscle insertion with cranial dimensions, but the same incongruity does not characterise earlier human populations who engaged in behaviours such as anterior dental loading. The Calcuttan sample employed in this research revealed no strong relationship between reconstructed bite pull and cranial thickness; whereas, the prehistoric Northwest Amerindian sample did. Processing of materials has been taken over entirely by machines in most modern societies; whereas, in the prehistoric past the Northwest Amerindians employed their anterior dentition to a considerable extent in such processing behaviours (Teit 1975).

The present study also demonstrates a relationship between the length of the load arm and M. semispinalis capitis, this musculature and cranial thickness, and cranial thickness and reconstructed anterior bite pull. The strongest correlation was found between the cross-sectional attachment area of M.

semispinalis capitis, the largest muscle that draws its insertion from the cranium, and the thickness of the coronal suture. This relationship derives from the direction of the force which this muscle exerts-that being through the coronal plane of the cranium, that structure lying perpendicular to the applied stress. *M. semispinalis capitis*, then, is linked to the construction and shape of the cranium. This muscle furnishes the necessary force to actively resist loading of the load arm of the cranium. Therefore, cranial features such as cranial thickness, expanded muscle insertion areas and a lengthened load arm have been identified as osteological indicators of anterior dental loading. Their functional association is more clear as a result of this research. The cranium appears to consist of two functional zones: that associated with the masticatory musculature and the craniofacial skeleton and that of the nuchal musculature and cranial vault. This finding supports the anatomical separation of the cranium into the viscerocranium and the neurocranium. These two functional zones, however, influence each other through shared members, most notably the *os occipitalis*, the nuchal portion of which is more accurately associated with the jaws and their development.

These findings contradict Lanyon's contention that the cranium, the size and shape of its constituents, are under complete genetic control. As recently as 1987 Lanyon has commented in the following way about cranial dimensions and morphology:

> ... [Such is] the situation in locations such as the vault of the human skull where normal functional

> loads are slight and yet there is obvious survival value in providing a strong protection for the brain (Curry 1984). In such locations direct genetic control alone produces a structure which is sufficiently robust for its primarily protective purpose. As a result it is over-designed in relation to functional loading. Functional strains will therefore be so small as to have little or no influence on its remodelling, and will thus make no contribution to its architecture (p.1085).

It may well be that the modern cranium is over-designed in relation to modern functional loading, but this relationship must not be construed to exist for all morphologically modern hominine crania, and especially those from the more ancient past. In fact, the cranium does appear to respond to the biomechanical demands placed upon it and is not simply a product of genetic design. Differently shaped crania respond differently to similar loads, loads that mimic those exerted by the nuchal musculature in anterior dental loading. The modelling of the hominine skull obeys a strain distribution like that expected of a single functional entity. All crania are of a coherent functional design. Each responds according to models of their various constituents- a beam or tube in the case of *Homo erectus* cranial morphology and a shell in the case of more recent hominids.

M. semispinalis capitis is observed to draw its insertion from the area of the *torus occipitalis transversus* in *Homo erectus*, leaving a well-developed enthesis scar beneath this structure. In early hominines and in individuals of more modern appearing morphology, the analogous area is often characterised by thickenings of the cortical bone (refer to Figs. 2-7). These ct-scans demonstrate that only the outer table of the cranium (the ectocranial portion) contributes to the torus and bun morphologies associated with the occipital. This observation is in accordance with the findings of Brown _et al._ (1979) who noted a divergence in the growth of the inner and outer tables about the age of puberty. The entire curvature of the cranium, then, does not appear to respond to muscular stress in the same manner. Such would seem to suggest quite strongly that the three layers of osseous tissue that characterise the cranium perform as three separate functional entities and each area of the vault performs in a slightly different way in response to applied stress with the sutures and areas characterised by curve changes seeming to be among those areas most affected. The inner table responds to brain growth recording the convolutions of the _dura mater_, the diploë whose function in red blood cell production is well-known, also apparently acts to separate the function of this table from that of the outer table, which responds to the forces generated by the adhering musculature and has been shown to lend a certain amount of strength to the cranium. Therefore, the occipital torus and increased cranial thickness is not buttressing as found in a Gothic cathedral, but is more similar to a Romanesque basilica with its thick walls and lack of windows (the biomechanical equivalent of foramina and apertures). The cranium of these individuals has compensated for the hypertrophy of the nuchal musculature through an increase in the thickness of the substrate that these muscles immediately act upon. To what might one attribute this thickening?

The two major evolutionary trends in human evolution include a general reduction of the masticatory complex and a heightening of the braincase. Wolpoff (1980) has characterised these changes as indicative of mosaic evolution. This notion of evolutionary change comes from the realisation that portions of the cranium seem to follow different rates of change through time. It has been noted, for example, that the posterior of the cranium appears to assume a more modern configuration before similar changes occur in the anterior portion of the cranium and affect the supra-orbital region and the jaws. The cranium has thus been interpreted to "evolve" from the posterior to the anterior. Another reading of this information would see mosaic evolution as the consequence of physical changes caused by changing behaviour.

Modern cranial morphology is posited to result from a reduced demand on the masticatory apparatus, producing the high-domed vault, thin cranial walls, reduced muscle attachment area, and diminished jaws of modern humans as represented in this study by the gracile Calcuttan sample. Taylor and DiBennardo (1980) and Moore and Lavelle (1974) have postulated that cranial vault form results from growth changes in the chondrocranium, which includes the basal portions of the occipital bone. Muscular forces resulting from strenuous muscular exertion would then be an integral influence on the shape and dimensions of the cranium.

It would appear that the long-term trend towards decreasing alveolar prognathism (shortening of the load arm) in the hominines is itself a consequence of the reduction in the size of the jaws and that their reduction is a plastic alteration in response to changed behaviours. That modern occipital morphology seems to appear prior to the modern facial morphology would suggest that at least part of the facial morphology is formal (of the genotype). Thus the craniofacial morphology changes more slowly in response to relaxed selection than the occipital morphology (cf. Brace 1967), which is a shape or epigenetic change. The only genomic change that need be posited to explain changing hominine morphology may involve strong positive selection in the early portion of the lineage for large anterior teeth (cf. Trinkaus 1987). These teeth were selected for in our earlier ancestors because of their utility in behaviours involving heavy and repetitive anterior dental loading that caused the teeth to wear quickly. The increased size of these teeth required a more spacious and prognathic dental arcade. This larger arcade coupled with the heightened strength of the masticatory and nuchal muscles necessary for the performance of habitual loading behaviours required certain structural changes in the cranium. These changes occurred throughout growth and development as the permanent dentition erupted and came into use. As the importance of the behaviours requiring anterior dental loading reduced in importance, the plastic changes which accomodated the behaviour appeared in a less and less well-developed form. This accounts for the apparent "rapid disappearance" of Homo erectus populations and the equally "rapid appearance" of anatomically modern human morphology in the fossil record.

That the teeth of the earlier members of the Homininae differ from our own in proportion as well as dimension (Brace 1967, Wolpoff 1971) has recently been questioned by Tillier (1989) who has claimed that there is no appreciable change in dental dimensions noted between earlier hominines and later ones. Such would seem to suggest that the large teeth are genetically determined. Presumably, the reduction of the face would result from a behavioural change that required less forceful mastication and paramastication. Large anterior teeth are retained as morphological reminiscences of a time before the advent of completely modern, culturally mediated, behaviour, early in the lineage. The less strenuous use of the jaws resulted in alterations in the chondrocranium and ushered in a host of cranial shape changes in the latter portions of the lineage. Gould and Lewontin (1979) make reference to a single genetic change which can produce several epigenetic changes. Hominid cranial morphology may represent a prime example of the operation of such an event. The single genetic change may very likely be that which sets hominine dentition off from that of the australopithecines, namely the large anterior dentition of the hominines when compared to the relatively smaller anterior teeth of the australopithecines.

The reduction in cranial rugosity noted in anatomically modern humans relates either to the use of more sophisticated tool assemblages, which seems unsupported by the archaeological record (Frayer 1984), or more likely to new uses being applied to old tool assemblages or, in other words, to some new behaviours in the Middle Palaeolithic. Alternatively, the cranial changes noted might relate to the later commencement of adult activities in the Archaic Homo sapiens and early anatomically modern humans when compared to that of Homo erectus. Anterior dental loading in the performance of masticatory and paramasticatory behaviour would have a profound influence upon the growing cranium, ultimately altering adult cranial shape and dimensions. An early initiation into adult behaviours would have significantly increased the number and extent of the osseous thickenings that characterise early hominine cranial morphology.

One notes osseous alterations throughout the cranium of Homo erectus. The crania of Skhul V, Archaic Homo sapiens, and the Northwest sample, who have been demonstrated to be capable of exerting as powerful or even more powerful relative bite pulls than Homo erectus, exhibit less osseous response and a greater muscular response (they have greater or equal muscular cross-sectional areas). These individuals, then, do not possess the low vault associated with Homo erectus, whose adult morphology is that of an individual who experienced greater muscular exertion during growth and development. Skhul V, Archaic Homo sapiens, the Northwest group, and modern humans possess the morphology of individuals who commenced adult activities somewhat later in life as characterised by greater alterations to the musculature. These physiological responses are those associated with modern immature athletes, who demonstrate osseous responses to strenuous exertion, as opposed to the muscular hypertrophy experienced by skeletally mature athletes in the performance of the same behaviours. Such an understanding might explain the very "modern" appearance of Skhul V, an early anatomically modern human, and the gracilisation which affects the Archaic *Homo sapiens* as a whole. The unique shape of the *Homo erectus* cranium and its eventual disappearance, then, may actually demarcate not a speciation event, but the advent of new behaviours with new biomechanical requisites demanding a lesser emphasis on the early commencement of adult activities.

Whether or not a presumed behavioural change from *Homo erectus* to the Archaic *Homo sapiens* to anatomically modern humans is representative of a speciation event would depend on the advent of an entirely new behavioural repertoire, perhaps though not exclusively, involving a dietary shift of kind rather than frequency. This researcher finds no evidence for the occurrence of this type of dietary shift from at least 2.0 mya with the advent of *Homo erectus*. The plastic changes which originally accomodated anterior dental loading disappear from the fossil record very quickly because they are acquired characteristics- part of the shape (phenotype) of the hominine cranium- not a genetic or formal part of the hominine morphological pattern. They owe their origin and disappearance to a physiologically mediated response to changes in the intensity and frequency of certain behavioural activities involving the cranium.

This reading of the evidence is not meant to diminish the importance or sophistication of *Homo erectus*' behavioural repertoire. On the contrary, these behaviours must have been quite successful as the shape of the hominine cranium appears to undergo little change for a period in excess of 1 million years during the tenure of *Homo erectus*. The unique shape of the *Homo erectus* cranium, its long duration, as well as the extended duration of the Acheulian assemblages of Europe and Africa and Chopper-Chopping tool tradition of Asia suggest *Homo erectus* to be both an efficient and viable member of the Homininae. The long duration of these tool traditions and cranial morphology thus suggest unique and long-lasting behavioural characteristics. Indeed, the "uneconomical re-enforcement" posited by Demes (1986) to characterise the cranial morphology of *Homo erectus* is in fact quite indicative of a structure adapted mechanically to a different behavioural repertoire, including what must have been intensive loading of the anterior dentition from a very young age, effectively altering the lever arm, the occipital bone, in the process.

This view appears to find concordance with that of the emerging archaeological picture of *Homo erectus* subsistence adaptation (Shipman 1983; Binford 1981, 1985; Binford and Ho 1985; Binford and Stone 1986; Bunn and Kroll 1986; Potts 1984, 1988; Gowlett *et al.* 1981, Brain and Sillen 1988; Blumenshine 1988; James 1989). These studies have questioned the association of early hominids with behaviours such as big-game hunting, certain tool uses, and habitual use of controlled fire, as well as the attendant social behaviours implied. Potts (1984) has suggested, in fact, that early hominines did not employ home bases that characterise modern hunter-gatherer groups, but instead relied upon a stone cache strategy whereby the food was transported to the requisite stone cache for quick preparation and consumption to avoid contact with the carnivores inevitably attracted to the sites of such activities. Potts (*ibid.*) writes, "... because this foraging system may not have a modern analog, it is difficult to choose a modern primate or hunter-gatherer from which to reconstruct further the social behaviour and demography of these early hominids. The idea of resource transport emphasizes that there are differences between early hominids and chimpanzees- and between early hominids and ourselves" (pp. 346-347). It appears that with early hominines we are dealing with uniquely adapted ancestors who experienced different constraints upon behaviour and required the performance of activities that may not have been present to the same degree in descendant populations- and which, therefore, no longer influence the descendant populations' behaviour or biology. These behaviours, however, may have had a profound influence on the biology of the earlier hominines, including *Homo erectus*.

Of the factors responsible for necessitating this type of behaviour we must look to the manner in which food and materials were processed. Perhaps chief among these processing behaviours is the habitual use of controlled fire. Recently, the earliest date for the habitual and controlled use of fire has been rigorously questioned by James (1989), who has suggested a relatively late date for its advent, perhaps as late as the Middle Palaeolithic. Gowlett et al. (1981), however, has proposed an earlier date for the use of controlled fire, providing 1.42 million-year-old evidence for fire use at Chesowanja, Kenya. Brain and Sillen (1988) have found evidence that would place the advent of fire at about 1.5-1.0 million years ago. All of these researchers recognise the need for further evidence from other sites to show when habitual and controlled use of fire first made its appearance. If it is demonstrated that the later date is a more accurate reflection of the advent of this behaviour, then the preparation and consumption of raw meat and vegetable foods, in addition to certain paramasticatory behaviours, may have greatly contributed to the need of large anterior teeth and powerful nuchal musculature of these earlier hominines. Their subsequent reduction, then, can be interpreted as a result of the appearance of more sophisticated food preparation techniques, including the habitual use of controlled fire to prepare more easily masticated foods and perhaps even more easily worked materials. The highly angulated occipital with its accompanying bun or torus and thick cranial bone would then be seen to be a type of physiological adaptation made early in development to coincide with the commencement of adult behaviours at an appreciably younger age. The disagreements surrounding the age at death of early hominine infants as reviewed above may, in fact, relate to the more rapid development of the skeleton of these infants, suggesting an older age at death than that attested by their dentition.

This type of reasoning also has interpretive value for addressing the Middle to Upper Palaeolithic transition. The assumption throughout the debate on the Upper to Middle Palaeolithic transition is that the observed cranial morphology is the result of innate genetic differences between the hominines in question, anatomically modern humans and the preceding populations in various regions of Africa and Eurasia. The foregoing research suggests that functional factors may influence cranial shape, especially it seems, in younger individuals, producing significantly altered adult shapes. This research provides indications that some of the "taxonomic markers" of Homo erectus and the Archaic Homo sapiens may be the result of altered behaviours and reduced muscular demands upon a generalised hominine skeleton.

The regional continuity model of modern human origins relies heavily on the evidence that many modern populations share features with previous hominines found in the same geographical areas today and in the more recent past (Smith et. al. 1989 and above discussion). White (1982) contends that no biological change need be posited to explain the shift from Middle to Upper

Palaeolithic tool assemblages- only that social change be required. This social change might be the one that allowed a more gradual and less strenuous introduction to adult behaviours. Additionally, Trinkaus (1983b) discusses the possibility that Neanderthal infra-cranial morphology was no less capable than our own, only that it was more robust- slightly different in degree. These phenomena would be part of the continuing trend which sees culture emphasised as opposed to brawn in the hominine lineage. Perhaps the morphological pattern noted in Neanderthals results from the relatively early development of the nuchal musculature, which, it seems, may also account for the great length of Neanderthal cranium, the greater occipital angulation accounting for a longer cranium. All of these alterations, then, would derive from the effect muscles have on growth of the basicranium. The rapid and regional appearance of modern humans would thus relate to the advent of new social behaviours that allowed a later initiation into adult behaviours and activities.

These new behaviours produced modern cranial morphology very quickly in geological terms, resulting in the rapid appearance of the high-domed vault, diminished jaws, and more rounded occiput characteristic of many modern humans, but retaining the well-developed nuchal musculature needed in the performance of processing behaviours. This is evidence that these individuals were still practising anterior dental loading as least as much as that demonstrated by the Northwest Amerindian sample. The transition from childhood to adult activities was likely a more gradual one in these individuals than that retrodicted to exist in Homo erectus populations. That Neanderthals have been demonstrated to possess jaws of a diminished mechanical efficiency suggests that the trend to less powerful and strenuous use of the jaws was already apparent in this branch of the Archaic Homo sapiens (Demes 1987).

Can morphological change of a phenotypic variety occur as quickly as required in this scenario? Carlson and Van Gerven (1977) present evidence that behavioural changes can produce cranial morphological changes in less than 10,000 years in response to a dietary shift to agriculture, probably a shift no more radical than that which occurred at the Middle to Upper Palaeolithic transition. Trinkaus (1983a) observes a reduction of masticatory and nuchal robusticity within his Shanidar sample, which seems to derive from a period probably greater than 10,000 years in duration. Therefore, morphological change can be expected to be more extensive over a much longer time and could account for the transition from Homo erectus to the Archaic Homo sapiens. In fact, in comparison to the long tenure of Homo erectus morphology that of the Archaic Homo sapiens is fleeting, perhaps some 80,000 years. This scenario would posit them to be a group in transition-a group experiencing the advent of new behaviours influencing growth and development. In short, like Sir John Myres' Greeks (cited in Renfrew 1987), the Archaic Homo sapiens "...were ever in the process of becoming" (p.177).

7.1 Research Prospectus

Future research would most profitably be concentrated upon the following endeavours:

1) An electromyographic analysis of the deep nuchal muscles to ascertain which are most active in anterior dental loading and other behaviours.

2) A longitudinal study of cranial thickness in a series of growing immature humans in order to ascertain a more exact correlation between the eruption of the dentition and changes in cranial shape and configuration. Such research would also by necessity have to concentrate on the first incidence of certain behaviours involving the muscles of mastication and the nuchal muscles. Herring (1985) is presently involved in such research with pigs.

3) We are in need of more and more thoroughly described infant and juvenile early hominine remains- both pre-natal and post-natal individuals. There is an especially important paucity of individuals in the first two years of life (Tillier 1989) and few occipital remains covering the immature age cohorts (Heim 1989). Such remains would allow us to gauge the appearance of various cranial traits with changes in the

dentition and craniofacial skeleton as the individual attains adult behaviours. These remains must be studied in restricted physiological age cohorts as "juvenile" or "infant" categories are not precise enough to allow faithful determinations of when these traits make their appearance.

4) A more thorough and well-dated understanding of when controlled and habitual use of fire entered the hominine behavioural repertoire in various regions would also be helpful. The use of fire is suspected of being the prime impetus behind the reduction of the cranial and facial skeletons, including the more correctly associated nuchal musculature within the masticatory musculature.

5) A more detailed micro-morphological study of the human occipital area is needed to ascertain how that area remodels with growth and development. One of the assertions suggested by this research is that the occipital is an area under growth stress as the nuchal muscles develop and the lambdoid suture synostoses. Remodelling changes should be observed in the crania of an archaeological sample consisting of all age cohorts, but especially those containing the requisite juvenile remains. Bouvier and Hylander (1981) have, in fact, suggested that through micromorphological examination of Haversian remodelling and cortical thickness, one should be able to determine which portions of the

skeleton are experiencing fatigue stress through repetitive loading. Nilsson and Westlin (1971) found greater bone density in the lower limbs of athletes than in non-athletes, for example. The prediction would be that the nuchal plane of the occipital would show evidence of remodelled bone and increased density; whereas, the interparietal portion of the occipital squama should not demonstrate the same alterations. This difference would be due to the effect a strongly angulated occipital would have on strain distributions in well-muscled, active individuals.

6) A detailed study of the skeletal changes noted in individuals who perform activities requiring heightened muscular exertion from a young age, especially those involving the nuchal musculature. Some of the requisite information can be gleaned from the radiology and sports medicine literature, but what is most needed in this regard is a study of enthesis development in non-pathological individuals for any part of the body.

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Appendix 1: Justification of Cranial Measurements

Measurements: These measurements describe the size and shape of the neurocranium and for the dimensions of various features located on the basicranium. This area is largely the focus of the study as its growth seems to be largely responsible for adult cranial dimensions (Howells 1957, Moore and Lavelle 1974, Taylor and DiBennardo 1980).

Neurocranium: These are measurements designed to record the size, shape, and dimensions of the neurocranium.

Greatest Length (Glabello- occipital length- glabella to opisthocranion): A measurement of the length of the neurocranium, which may have some bearing on the muscularity of the nuchal muscles, since they are responsible for maintaining head posture and initiating head movements.

Basion-Bregma Height: A measurement of the height of the cranial vault. Presumably, individuals with a higher neurocranium may develop larger muscles and muscle attachment areas to provide necessary movement.

Bi-Euryon Breadth: A measurement of the width of the neurocranium.

Length of Lever Arm (from most inferior point on occipital condyles to superior nuchal line at the external occipital protuberance): A measure of nuchal muscle function in the first-class lever which characterises the cranium.

Length of Load Arm (distance from incision to most inferior point on occipital condyles): Another functional measurement which accounts for the resistance (length of the moment arm) to movement initiated by the nuchal muscles. A measurement that is somewhat similar to the prosthion-basion length.

Cranial Features:

Computed:

Occipital Angulation: A ratio of the occipital chord (linear measurement from lambda to opisthion) to the occipital arc (curvilinear distance from lambda to opisthion), a means by which to account for angulation in the occipital. Formula: chord/arc X 100= angulation ratio

Cranial Module: A measurement of cranial size
Length+Breadth+Height/3= cranial module

Tobias' (1959b) Occipital Index: Derived from Pearson's Occipital Index, this measurement comprises both the sagittal cord (S 3) and the arc (S'3) between lambda and opisthion.

$$\text{Oc.I.} = \frac{S3}{S'3} \quad \frac{S3}{24(S3-S'3)}$$

Basion-Height Index: A measurement of the height of the cranium.

$$\text{Ba-Height} = \frac{\text{Basion-Bregma Height X 100}}{\frac{\text{Cranial Length+Breadth}}{2}}$$

Cranial Index: A ratio of the breadth of the cranium to its length and used to identify the shape of the cranium (dolichocrany or brachycrany).

$$\frac{\text{Breadth X 100}}{\text{Length}}$$

Planimeter Measurements: The following measurements are meant to account for the muscle size in the measured crania. Large attachment areas will be interpreted to relate to hypertrophy of the adhering musculature.

Suboccipital Area: A measurement of the nuchal area defined as that posterior to the occipital condyles, medial of the digastric fossae, and anterior to the superior nuchal line.

Area of attachment of *M. semispinalis capitis*: A measurement of the cross-sectional area of the enthesis for the muscle.

Area of attachment of *M. rectus capitis minor*: A measurement of the cross-sectional area of the entheses for this pair of muscles.

Observations, including those of the *planum nuchae* and *planum occipitalis* (Present/Absent and Degree: 1=slight, 2=moderate, 3=heavy): The following traits have been used to identify a system of buttressing, as well as cranial robusticity, that characterises hominine crania, both recent and ancient.

angular torus (*torus angularis*)- related to the origin of *M. temporalis* and muscular development

external occipital protuberance (*protuberantia occipitalis externa*)- related to ligamentum nuchae

linear tubercle or occipital crest (*tuberculum linearum*)- related to the attachment of ligamentum nuchae (Hublin 1978, Gray's Anatomy)

nuchal lines (*lineae nuchae*)
linea nuchae suprema- related to the insertion for *M. trapezius*
linea nuchae superior- related to the insertion for *M. semispinalis capitis*

linea nuchae inferior- related to the insertion for *M. rectus capitis major* and *minor*

occipital torus (*torus occipitalis transversus*)- interpreted as a portion of the buttressing associated with early members of the Homininae and likely the result of hypertrophy of *M. semispinalis capitis*

occipito-mastoid crest (*crista occipitomastoidea*)- related to the origin of *M. digastricus*

sagittal keeling- a strengthening of the sagittal suture

supra-iniac fossa (*fossa supratoralis*)- observed by Hublin (1978, p.26) to be found in a man with a large external occipital protuberance and in Neanderthals likely related to muscular development

supra-mastoid crest (*crista supramastoidea*)- related to the development of *M. sternocleidomastoideus*, *M. splenius capitis*, and/or *M. longissimus capitis*

supra-orbital torus (*torus supra-orbitalis*)- related to bending moments in mastication

The two expressions of this torus, continuous or discontinuous, may relate to the biomechanical alterations in successive members of the Homininae.

Appendix 2: List of Hominine Specimens

Sample 1: Mixed Group of Hominines

1-Skhul V
2-ER-3733
3-Steinheim
4-Choukoutien Upper Cave Male
5-Predmosti Male
6-La Chapelle-aux-Saints
7-Kabwe
8-La Ferrassie Male
9-Cro-Magnon
10-Choukoutien Upper Cave Female
11-Gambles Cave
12-Circeo
13-"Sinanthropus" composite cast
14-Arago XLIV
15-Chancelade Female

Sample 2: Northwest Amerindians

16- ElSx-1 1/77/1 Namu Male
17- CC-82 Kamloops, B.C. Male
18- "F" Female
19- EiRm 71-1 Clinton, B.C. Male
20- DgRr1-M75 Crescent Beach Male
21- "J" West Trail Island Female
22- ElSx-1 FS2.12.E.1 73-6 Namu Female
23- 0-1186-1 Burial 10 Crescent Beach Male
24- 81-26 Brilliant, B.C. Female
25- 0-1222 Anthony Island Male
26- "E" Kamloops, B.C. Area? Male
27- EeRl 18 0-70 Murray Site Female
28- DgRr1-21 Crescent Beach Male
29- ElSx-1 77/5/01 Namu Female
30- ElSx-1/77/7/1 Namu Male

Sample 3: East Indians (Calcuttan Population)

31- Male 4
32- Male 5

33- Male 6
34- Male 7
35- Male 9
36- Male 11
37- Male 16
38- Male 17
39- Male 18
40- Male 20
41- Male 21
42- Female 24
43- Male 26
44- Male 27
45- Male 30

Appendix 3: List of Measurements

1- Greatest Length (Glabello-occipital Length)
2- Basion-Bregma Height
3- Bi-euryon Breadth
4- Length of Lever Arm
5- Length of Load Arm
6- Occipital Angulation
7- Cranial Module
8- cross-sectional area of M. semispinalis capitis
9- cross-sectional area of M. rectus capitis posterior minor
10- area of the suboccipital
11- angular torus
12- external occipital protuberance
13- linear tubercle
14- supreme nuchal line
15- superior nuchal line
16- inferior nuchal line
17- occipital torus
18- occipito-mastoid crest
19- sagittal keeling
20- supra-iniac fossa
21- supra-mastoid crest
22- supra-orbital torus
23- Thickness at Sagittal Suture
24- Thickness off Sagittal Suture
25- Thickness at Coronal Suture
26- Thickness off Coronal Suture
27- Cranial Index
28- area of M. semispinalis capitis/cranial module X 100
29- area of M. semispinalis capitis/area of suboccipital
30- Basion Height Index
31- Load Arm X area of M. semispinalis capitis
32- Tobias' Occipital Index
33- Anterior Bite Pull of Hominines
34- Anterior Bite Pull of Northwest Amerindians
35- Anterior Bite Pull of Calcuttans

Appendix 4: Raw Data

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	Gl-Op	Ba-Br Height	Bi-euryon	Lever Arm	Load Arm	Occipital Ang.	Cranial Module
1	192	122	139	80	120	81.74	151.00
2	178	120	136	68	126	78.18	140.67
3	181	139	130	58	126	-	138.00
4	206	122	140	75	117	76.80	160.67
5	206	128	136	78	128	80.00	160.00
6	213	122	159	90	142	72.00	165.67
7	204	130	131	91	125	78.18	153.67
8	207	120	158	80	129	79.16	166.67
9	205	128	152	79	122	84.62	163.33
10	187	126	125	79	118	85.45	152.33
11	192	123	133	69	100	74.40	153.00
12	204	129	153	79	122	72.93	159.33
13	180	123	137	78	118	75.65	140.00
14	198	146	138	82	141	76.80	153.00
15	192	129	131	86	103	84.35	157.67
16	181	133	143	80	106	79.51	152.00
17	182	126	139	72	109	82.31	153.67
18	165	135	137	69	101	80.00	143.00
19	177	126	139	68	105	80.47	149.00
20	181	145	138	80	94	78.46	154.67
21	179	138	144	67	104	80.00	153.33
22	167	137	138	93	97	80.90	147.67
23	195	145	141	88	107	79.69	160.30
24	181	131	138	70	104	78.33	148.33
25	186	127	135	99	109	74.40	152.00
26	185	132	145	72	114	77.69	154.33
27	170	140	131	87	102	76.99	142.33
28	187	150	148	80	108	82.40	156.67
29	180	145	140	71	109	80.80	149.67
30	190	143	153	78	111	80.74	163.00
31	179	138	137	64	98	77.93	149.33
32	169	136	136	69	89	86.00	142.67
33	171	135	126	78	95	80.51	142.00
34	158	134	127	59	88	84.76	136.00
35	174	133	125	61	100	82.30	141.67
36	179	126	124	78	99	80.00	143.67
37	165	125	131	71	102	79.00	138.67
38	170	123	130	67	112	83.48	143.33
39	180	122	135	72	90	86.09	148.67
40	163	121	126	56	98	83.05	137.00
41	160	116	127	55	105	85.71	138.33
42	151	108	119	60	95	86.32	130.67
43	182	103	134	63	108	81.97	151.67
44	171	103	123	56	98	75.20	138.00
45	177	100	131	63	99	87.74	143.33

	M. semi	M. rec cap	Area of Sub	AngularTorus	Ex. Occ. Pro.	Linear Tub.	Supr. Nuc. Line
1	2.87	-	9.63	2	2	1	1
2	1.70	.27	5.96	3	2	2	2
3	1.65	-	4.47	2	1	1	2
4	1.57	.93	8.28	1	1	2	2
5	1.63	1.23	7.57	2	3	3	A
6	2.60	.60	8.70	2	1	A	3
7	3.50	.70	9.09	3	3	3	A
8	1.92	.45	7.82	1	1	1	A
9	1.79	1.14	9.45	1	2	2	3
10	1.82	.46	7.76	A	1	1	A
11	1.93	.82	8.28	2	1	1	A
12	2.88	-	9.78	1	A	A	A
13	2.48	.77	7.57	3	1	1	A
14	2.10	.62	8.08	3	1	2	1
15	2.13	.50	7.30	1	2	1	A
16	1.55	.69	8.96	A	1	3	1
17	1.50	.64	9.26	A	3	2	A
18	1.47	.38	7.00	A	1	1	1
19	1.46	.29	8.89	A	1	A	1
20	2.10	1.18	9.55	2	2	2	2
21	1.35	.80	8.57	A	1	2	1
22	1.40	.50	8.12	A	1	1	1
23	2.23	.72	10.40	2	3	1	2
24	1.32	.64	8.06	A	2	1	A
25	1.94	.37	8.47	1	3	1	1
26	1.67	.41	8.23	1	2	1	A
27	2.20	.68	8.88	A	1	2	1
28	1.69	.68	7.50	3	2	2	3
29	1.10	.52	9.30	1	3	1	A
30	1.91	.76	8.65	A	2	2	1
31	0.77	.71	7.22	2	2	1	2
32	1.56	1.02	7.66	2	2	1	3
33	0.82	.54	6.98	1	1	1	1
34	0.85	.65	6.10	1	1	1	1
35	0.65	.45	5.68	2	1	1	A
36	1.46	.30	7.45	1	1	A	2
37	1.00	.60	6.29	2	1	1	2
38	1.07	.42	5.50	2	1	1	2
39	1.28	.60	7.19	1	1	A	1
40	1.24	.38	6.88	2	2	1	3
41	0.85	.56	6.07	2	1	1	1
42	0.92	.38	5.44	2	A	A	1
43	1.50	.71	8.28	2	1	3	3
44	0.90	.66	6.87	2	1	2	2
45	0.68	.50	6.75	2	1	2	A

	Sup. Nuc Line	Inf. Nuc. Line	Occ. Torus	Occipito-mast.	Sagittal Keel	Supra-iniac Fo	Supra-mastoid
1	3	2	1	2	2	2	2
2	3	2	3	3	2	A	3
3	2	1	1	A	2	1	1
4	3	2	1	1	2	1	2
5	2	2	1	1	2	1	2
6	3	2	2	3	2	1	1
7	3	3	2	3	3	A	3
8	3	2	2	3	2	A	3
9	3	2	1	A	3	A	3
10	2	2	1	A	1	A	A
11	3	2	1	2	1	A	1
12	3	A	A	3	2	1	3
13	3	3	3	3	3	A	3
14	2	2	3	3	3	A	3
15	3	3	A	1	2	1	1
16	2	2	1	2	1	A	2
17	3	3	2	3	2	A	1
18	2	2	1	2	A	A	2
19	1	1	A	2	1	A	1
20	3	3	1	1	2	2	1
21	2	2	2	1	A	A	2
22	2	1	1	2	A	A	1
23	3	2	1	1	3	1	3
24	2	2	2	1	A	A	1
25	3	3	1	2	3	1	2
26	2	3	1	1	2	A	2
27	2	2	1	2	2	A	1
28	3	3	2	3	3	1	3
29	2	1	1	3	1	A	2
30	2	2	1	2	A	1	3
31	2	2	1	1	1	A	1
32	3	1	3	A	3	2	3
33	1	2	1	1	1	A	1
34	1	1	1	1	A	A	A
35	2	2	1	A	A	A	2
36	1	2	2	1	1	A	2
37	2	1	A	1	1	A	1
38	2	2	1	1	1	A	1
39	1	1	1	1	2	A	2
40	3	2	1	2	1	A	2
41	1	1	A	A	A	A	1
42	1	1	A	1	A	A	1
43	3	3	1	1	1	A	2
44	2	2	A	1	1	1	1
45	1	2	A	1	1	A	A

	Supra-orb.	Sagittal Thick	Sagittal Thick	Coronal Thick	Coronal Thick	Cranial Index	M. semi/C.M.
1	2	-	-	-	-	72.40	19.0
2	3	-	-	-	-	76.40	12.1
3	3	-	-	-	-	71.82	12.0
4	2	-	-	-	-	67.96	9.8
5	1	-	-	-	-	66.02	10.2
6	3	-	-	-	-	74.65	15.7
7	3	-	-	-	-	64.22	22.8
8	2	-	-	-	-	76.33	11.5
9	1	-	-	-	-	74.15	11.0
10	A	-	-	-	-	66.84	11.9
11	1	-	-	-	-	69.27	12.6
12	2	-	-	-	-	75.00	18.1
13	3	-	-	-	-	76.11	17.7
14	3	-	-	-	-	0.01	13.7
15	A	-	-	-	-	68.23	13.5
16	2	0.875	.775	.800	.900	76.37	9.8
17	2	0.720	.550	.700	.685	79.01	10.2
18	A	0.465	.505	.520	.560	83.03	10.3
19	1	0.580	.490	.545	.510	78.53	9.8
20	2	0.760	.730	.895	.785	76.24	13.6
21	1	0.540	.525	.565	.535	80.45	8.8
22	A	0.540	.480	.490	.590	82.63	9.5
23	2	1.105	.960	1.225	1.045	72.31	13.9
24	1	0.590	.680	.695	.525	76.24	8.9
25	1	0.970	.735	.940	.795	72.58	12.8
26	1	0.550	.555	.680	.510	78.38	10.8
27	1	0.680	.550	.785	.665	77.06	15.5
28	2	0.790	.815	.830	.790	79.14	10.8
29	1	0.650	.615	.680	.720	77.78	7.3
30	1	0.725	.570	.725	.650	80.53	11.7
31	1	0.705	.570	.685	.585	76.54	5.2
32	2	0.555	.560	.695	.535	80.47	10.9
33	A	0.410	.425	.450	.390	73.68	5.8
34	1	0.550	.555	.540	.540	80.38	6.2
35	A	0.540	.545	.500	.600	71.84	4.6
36	1	0.510	.420	.525	.445	69.27	10.2
37	A	0.640	.625	.790	.640	79.39	7.2
38	A	0.585	.510	.585	.530	76.47	7.5
39	1	0.690	.600	.650	.640	75.00	8.6
40	2	0.470	.430	.480	.485	77.30	9.1
41	A	0.510	.490	.500	.520	79.38	6.1
42	A	0.350	.345	.385	.340	78.81	7.0
43	2	0.550	.455	.530	.465	73.63	9.9
44	1	0.380	.430	.450	.465	71.93	6.5
45	A	0.412	.420	.535	.395	74.01	4.7

	M. semi/SuOc	Ba Height Ind.	L.A.X M.semi	Tobias' Occ. In.	F. Hom.	F. NW	F. Cal
1	0.298	79.2	229.600	0.584	1.913	1.170	0.503
2	0.285	81.6	115.600	0.545	0.917	0.991	1.209
3	0.369	88.0	95.700	0.586	0.760	1.004	0.673
4	0.190	90.4	117.750	0.640	1.006	0.946	0.570
5	0.215	89.2	127.140	0.630	0.993	1.787	0.396
6	0.299	84.4	234.000	0.597	1.648	0.870	1.150
7	0.385	86.7	318.500	0.602	2.548	1.342	0.696
8	0.246	81.1	153.600	0.591	1.191	1.834	0.640
9	0.189	84.5	141.410	0.571	1.159	0.888	1.024
10	0.235	84.3	143.780	0.590	1.218	1.762	0.709
11	0.233	86.3	133.170	0.617	1.332	1.055	0.445
12	0.294	86.9	227.520	0.551	1.865	1.876	0.581
13	0.328	80.7	193.440	0.634	1.639	1.252	0.875
14	0.260	85.1	172.200	0.622	1.221	0.717	0.514
15	0.292	80.6	183.180	0.576	1.778	1.342	0.433
16	0.162	83.7	124.000	0.553			
17	0.173	80.6	108.000	0.556			
18	0.210	84.1	101.430	0.542			
19	0.164	79.0	99.280	0.560			
20	0.220	86.3	168.000	0.568			
21	0.158	90.5	90.450	0.577			
22	0.172	84.8	130.200	0.526			
23	0.214	90.9	196.240	0.561			
24	0.164	82.9	92.400	0.574			
25	0.229	84.1	192.060	0.571			
26	0.203	81.5	120.240	0.567			
27	0.248	87.2	191.400	0.590			
28	0.225	92.9	135.200	0.611			
29	0.118	92.9	78.100	0.626			
30	0.221	90.2	148.980	0.615			
31	0.107	80.7	49.280	0.571			
32	0.204	78.6	107.640	0.552			
33	0.117	74.0	63.960	0.565			
34	0.139	82.5	50.150	0.542			
35	0.114	74.5	39.650	0.615			
36	0.196	75.2	113.880	0.559			
37	0.159	67.2	71.000	0.536			
38	0.195	73.2	71.690	0.552			
39	0.178	73.7	92.160	0.584			
40	0.180	67.8	69.440	0.538			
41	0.140	73.4	46.750	0.546			
42	0.169	68.8	55.200	0.559			
43	0.181	65.0	94.500	0.547			
44	0.131	66.2	50.400	0.547			
45	0.101	61.2	42.840	0.531			