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Neandertal Craniofacial Growth: An Ontogenetic Model

Michael David Green

To the Graduate Council:

I am submitting herewith a thesis written by Michael David Green entitled "Neandertal Craniofacial Growth: An Ontogenetic Model." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Arts, with a major in Anthropology.

<div align="right">Fred H. Smith, Major Professor</div>

We have read this thesis and recommend its acceptance:

Richard Jantz, Allison Galloway, William Bass, Jim Heller

<div align="right">Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School</div>

(Original signatures are on file with official student records.)
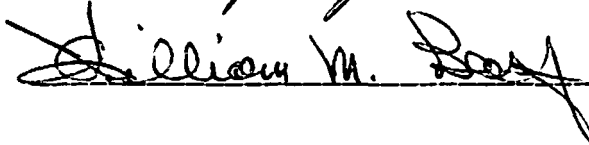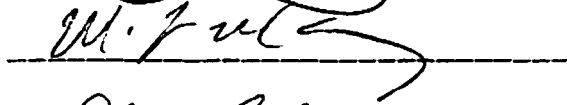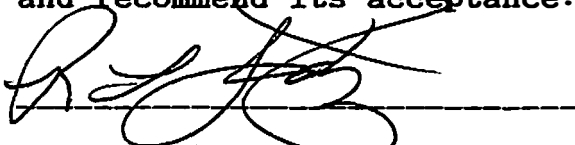
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NEANDERTAL CRANIOFACIAL GROWTH:

AN ONTOGENETIC MODEL

A Thesis

Presented for the

Master of Arts

Degree

The University of Tennessee, Knoxville

Michael David Green

August 1990

This work is dedicated to my mother and to the
memory of my father.

"The hour of departure has arrived, and we go

our ways - I to die and you to live. Which is

the better, God only knows."

<div align="right">Socrates</div>

ACKNOWLEDGEMENTS

ABSTRACT

This research seeks to develop a model, using
modern fetal crania, of Neandertal craniofacial growth.
An argument is made that the developmental approach
offers greater insight into Neandertal adaptive
morphology than the standard functional models.
Discussion of the relation between allometry and
heterochrony is followed by a general genetical overview
and a description of modern fetal craniofacial growth.
These patterns are then extrapolated to the Neandertal
condition.

Samples for this work consist of modern fetal
crania, three modern adult samples, one sample of early
modern humans and a sample of Neandertal adults.
Principle components analysis was utilized, as was least
squares and reduced major axis regressions. A technique
was devised where derivatives were taken from
polynomials generated from multiple regression.

The results would indicate that the posterior
cranial base, and not the anterior base, has the neural
like growth pattern. The anterior base has a growth
pattern similar to that of facial length and facial
height. Using patterns of morphogenesis and known

principles of cartilage kinetics, a model of Neandertal craniofacial growth was created. Emphasis was placed upon the effects of global growth acceleration on synchondrosal cartilage dynamics and the resulting relation of base flexure to facial projection. It was concluded that many features of the Neandertal cranium and face are the byproduct of selection for rapid growth rate. It is also concluded that these effects need not imply species level genetic differences. In fact, tests using least squares and reduced major axis regression imply that early modern Europeans had growth rates intermediate between Neandertals and modern blacks. This result is consistent with Assimilation models and inconsistent with the Total Replacement models.

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Since I was first inclin'd to the Contemplation
of Nature, and took pleasure to trace out the
Causes of Effects, and the dependance of one thing
upon another in the visible Creation, I had
always, methought, a particular curiosity to look
back into the first Sources and ORIGINAL of
Things; and to view in my mind, so far as I was
able, the Beginning and Progress of a RISING
WORLD.

The Sacred Theory of the Earth (1691)
Thomas Burnett

I prepared myself for a magnitude of reverses; my
operations might be incessantly baffled, and at
last my work may be imperfect, yet when I
considered the improvement which every day takes
place in science and mechanics, I was encouraged
to hope my present attempts would at least lay the
foundations of future success. Nor would I
consider the magnitude and complexity of my plan
as any argument of its impracticality. It was with
these feelings that I began the creation of a
human being.

Frankenstein (1818)
Mary Shelley

I believe there is a theory that men and women
emerge finer and stronger after suffering, and
that to advance in this or any world we must
endure ordeal by fire. This we have done in full
measure, ironic though it seems. We have both
known fear, and loneliness, and very great
distress. I suppose sooner or later in the life of
everyone comes a moment of trial. We all of us
have our particular devil who rides us and
torments us, and we must give battle in the end.

Rebecca
Daphne du Maurier

INTRODUCTION

The Neandertals were Upper Pleistocene humans with a temporal range that coincides with the Riss/Wurm Interglacial and the first stage of the Wurm glaciation and were distributed from Western Europe to Central Asia (Trinkaus and Howell 1979). The anatomical pattern of European Neandertals is quite distinctive. They can be distinguished from modern humans by their longer, wider and lower crania. Neandertals also possess a massive supraorbital torus coincident with a low sloping frontal. There is often a marked angulation in the occipital region, termed the occipital bun, that is usually accompanied by lambdoidal flattening. The face is massive with significantly longer vertical dimensions than in modern humans. Their characteristic nasomaxillary regions are inflated and with the zygomatics angled posteriorly. Prognathism is concentrated in the sagittal plane, giving their faces a keel-like appearance. Their mandibles are recognizable by their lack of a mental eminence and the presence of a retromolar space, a reflection of their facial prognathism. Neandertal nasal apertures are broader and higher than modern humans and their cranial bases are weakly flexed (Brose and Wolpoff

1971; Howell 1952; LeGros Clark 1978; Rak 1986;Smith
1983; Trinkaus and Howell 1979). The size and wear of
the Neandertal anterior dentition would lead some re-
searchers to believe that the Neandertal face was stuc-
turally adapted to quite strenuous paramasticatory be-
havior (Smith 1983; Smith and Paquett 1989).

The Functional Approach

Previous attempts to understand the dento-facial
morphology of Neandertals have focused upon such
functional aspects as force dissipation (Rak 1986, Smith
1983) and adaptation to cold (Coon 1973). Smith (1983)
argues that the verticality of the alveolar clivus, the
well developed browridges, and the size of the anterior
dentition indicate structural adaptations to
paramasticatory behavior. Rak (1986) concurs, arguing
that the distinct Neandertal facial topology is a
"specific architectural modification that...best opposes
the rotation of the snout in the sagittal plane about a
bilateral axis"(Rak 1986:153). Additionally, Brose and
Wolpoff(1971) argue that Neandertal occipital bunning is
a specific adaptation to counterbalance the projection
of the face. The effect is to reorient the lever arm for
the nuchal musculature thus increasing its leverage.

The Developmental Approach

In an evolutionary analysis, developmental data can
be utilized in a variety of ways (Langille and Hall
1989:74): (a) to uncover the evolution of developmental
systems, getting at those processes operative in the
past and how they may have changed during the course of
a lineage; (b) to analyze the importance of
developmental constraint on evolutionary change; (c) to
establish phylogenies. This study will focus on (a), by
focusing in on those developmental parameters necessary
to account for craniofacial differences in European
archaic Neandertals) and modern Europeans. In other
words,..." in what sense the patterns (homologous
structures) are transformable one into the other"
(Goodwin 1984:102).

Development is a vast reservoir of size/shape
variability. The one dimensional genome as translated
into three dimensional morphospace, exposes to the
rigors of selection a series of phenotypes that may
differ greatly in their size, shape, and physiological
function. Given constraints, selection can operate upon
variation in ontogenetic pathways to achieve or approach
some workable effect.

All phenotype characters, and especially those making up the cranium and face, are to some degree intercorrelated. Any developmental change in a feature will have correlated effects on others, the pattern of which will change since trait variance - covariance structures change during ontogeny (Atchley and Newman 1989). The possibility then for any feature is strong that its configuration is influenced considerably by changes in other features not necessarily functionally related to it. This is in contrast to selective scenerios that fragment the organism into parcels, explaining each as some specific, often independent adaptation, molded by natural selection. Gould and Lewontin (1979), in their campaign against panselectionist scenerios were not arguing against the power of natural selection to guide the construction of environmentally conducive morphologies so much as they were defending its credibility in the face of functional/adaptational provincialism. A particularly critical point made many times in the writings of Lewontin and Gould is that present function is not a necessary indication of processes involved in the origin of a feature or constellation of features (Lewontin 1985).

The importance of this reminder resides not in simply pointing out contrary possibilities or its representiveness of a growing disquiet regarding the power of natural selection. Its importance is that traits, in singular or in configuration, are constructed by numerous processes and that throughout life, perform a multitude of functions. How, in fossil materials, is one to know if a feature is specifically "adapted" to any one of its functions? In vertebrates, a case is at best difficult to make. For instance, Emerson (1985) undertook a detailed study of biomechanical jumpers and leapers, with special emphasis on frogs. Figure 1 (Emerson Fig. 4-10:72) illustrates the structural/functional relationship between components that reflect upon performance. Clearly, there are numerous "solutions" to performance "problems" in this interaction scheme. For example, the hindlimb - body length ratio is a feature with numerous biomechanical and behavior implications (especially leaping distance) any one of which could be argued to be the focus of natural selection. Frogs are characterized among vertebrates by their high hindlimb-body length ratio. There is a large degree of variability in this ratio, with closely related groups having more proximate ratios than more distantly related
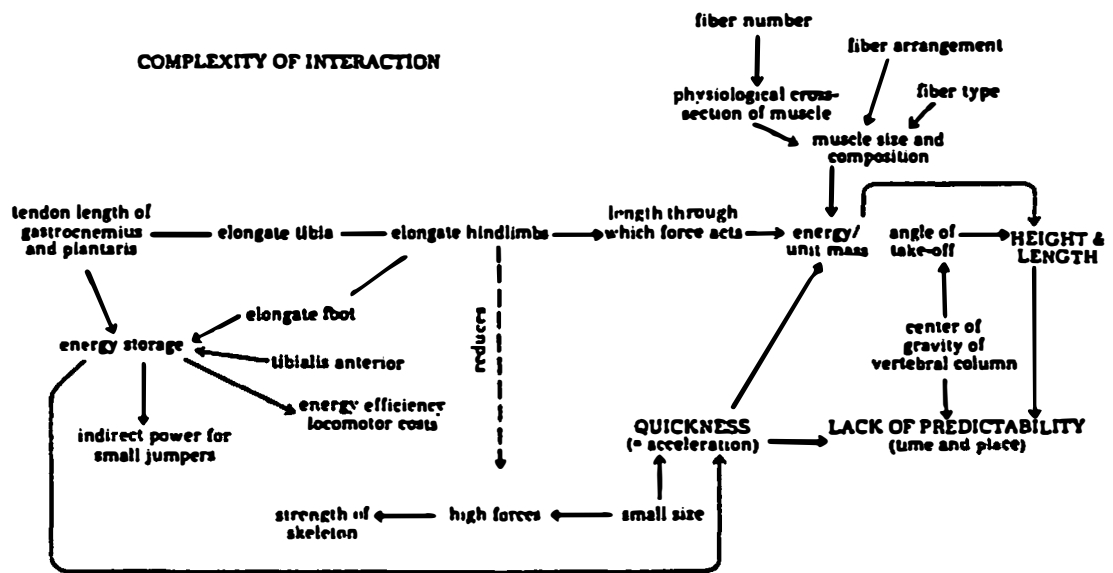
Figure 1. Schematic of Structure-Function Interaction in Frog Hindlimbs. From Emerson (1985).

taxa. Generally speaking, difference in ratios
translate into difference in locomotion performance with
low ratio frogs jumping shorter distances and vice
versa. "Given the known functional significance of
hindlimb length, workers have generally assumed that all
differences in relative hindlimb lengths among frogs
represent location adaptations for escaping predation"
(Emerson 1986: 169).

Emerson (1986) notes however, that predictable
relationships between jumping performance and
biomechanical predictions occur only with ratio
differences of greater than 10%. Citing previous work,
Emerson (1986) found there were no performance
differences in long and short legged populations within
two species of frog (Pseudacris triseriata and Rana
pipiens), even when there was small but significant
interpopulational differences in the hindlimb to body
length ratios. A case could at least be made that ratio
differences on the order of 10% and less are not the
product of natural selection acting on intraspecific
performance differences. Emerson (1986) suggests
that because of the dependency of frog hind-limb
differentiation on the hormones of metamorphosis,

heterochrony may be suggested. Emerson makes two
conditions mandatory if heterochrony is the underlying
mechanism. First, that the growth responses of hindlimb
and body length to varying levels of hormone (especially
thyroxin) be allometric. Second, differences must exist
in the total developmental time between both individuals
and species. Heterochrony will be especially probable
if the length of the larval period is disproportionate
relative to the other phases of development. As Emerson
demonstrates, both conditions are strongly met.

Probably the most important component of Emerson's
study is the relationship of these processes and life
history characteristics. In frogs, time to
metamorphosis is inversely correlated to the hindlimb
to body length ratio and the growth rate is positively
correlated to the ratio. On the basis of density
experiments, early-metamorphising, uncrowded individuals
had higher ratios relative to late-metamorphs. The
probability, therefore, is strong that the ultimate
cause of relative differences in hind-limb to body
length ratios in frogs is not selection upon
intraspecific performance variation but life history
parameters. Contrary to traditional explanation, ratio
differences may be contingent upon growth rate

variability within high or low density environments and not with the biomechanical considerations of predator avoidance.

In arguing for the importance of local (i.e. cellular and histological) developmental constraints, Alberch (1985) takes as his example the presence of dew claws in large dogs and its absence in smaller dog breeds. The normal condition in dogs is to have five digits on the forelimbs and four digits on the hindlimbs. In the larger breeds such as St. Bernards or Newfoundlands, there is a tendency to develop a sixth digit (dew claw) in the forelimbs. Smaller breeds do not exhibit a dew claw and are even prone to lose digits. According to Alberch, if there is a threshold value of available cells that must exist before a skeletal element can be specified and larger breeds have larger embryos and therefore larger limb buds with more cells, then the selection for large body size indirectly selects for larger limb buds. So, the appearance of an atavistic dew claw is governed predominantly by body size suggesting that it should be a difficult trait to select for in smaller breeds without making them larger breeds.

The realistic chance that natural selection has the power to break the correlation between body size and the presence of the dew claw (e.g. selection favoring a small dog with large limb buds) is small. For natural selection to be operative, there must be fitness differences coincident with inherited differences in phenotypes. In this case, "selection cannot operate on developmental parameters, such as the number of primordial cells in the limb bud; this is because the existing variation in the number of cells would still result in the same phenotype (i.e. a limb with four digits)" (Alberch 1985: 431-432). In other words, there is no overlap between the distributions of cell numbers in smaller breeds and the quantity of material necessary to generate a dew claw.

The two previous examples were used to illustrate three points that I feel are justification for the approach taken in this work.

The first point is that while the study of function is important in fossil and neontological materials, it may not shed much light on the problem of adaptation. Lewontin (1985) claims that hidden within adaptive analyses are three assumptions, based in part on a naive

Cartesianism. The first assumption being that the "partitioning of organisms into traits and the partitioning of environment into problems has a real basis" (1985:72). Second, an assumption is made that characters can be isolated in an adaptive analysis and that any interactions are secondary. Thirdly, a hidden assumption is made that all aspects of an organism are adaptations.

However one feels about how Lewontin (1985) and Gould and Lewontin (1979) have characterized the adaptationist paradigm, it should be clear once craniofacial development is reviewed below that the first and second assumptions are spurious. Philosophically, the third assumption is the most problematic. As Lewontin (1985) makes clear, the problem often becomes the finding of adaptations and not the questioning of their existence.

> If the assumption is allowed to stand, the adaptive explanation simply became a test of the ingenuity of theorists and of the tolerance of intellectuals for tortured and absurd stories (Lewontin 1985: 73).

Resting upon the assumption of a structure being an

adaptation, engineering analyses of that structure serve to "define" the adaptation. Because the process of adapting is necessarily historical, the adaptation is constructed on the basis of conferring some kind of fitness benefits, thus becoming a selective scenerio. The troublesome aspect of many adaptive scenerios is that differential fitness is inferred to account for these features without any evidence from fitness differences in modern groups with homologous variation. Under a functional/adaptational paradigm, the simple fact that differences exist is prima facie evidence for adaptive differences. Assumed in this association are necessary fitness differences conferred by trait performance, that have never been or will probably never be systematically defended (Cummings 1986).

A explicit example of this paradigm in paleoanthropology is the assessment of craniofacial morphology in archaic <u>Homo</u> <u>sapiens</u> as an adaptation to anterior masticatory and para-masticatory loading. While the anterior loading hypothesis is the intellectual product of C. L. Brace, Smith's (1983) review of the argument will be examined here because it is a sophistocated example of the paradigm.

Smith (1983) seeks to explain why differences in craniofacial structure between modern and archaic humans exist in order to better understand the emergence of modern humans.

> Attempts to determine the functional-behavioral basis for morphological features are critical to the understanding of an organisms evolution, because morphology and changes thereof reflect habitual behavior patterns (Smith 1983:142).

For any particular case, such an assumption is tautological. An association is assumed, then used as evidence for evolutionary importance because it exists.

Smith (1983) lists some difficulties encountered in any functional analysis, two of which deserve special consideration. Smith remarks that the testing of demand/morphology relationships is difficult, "because there are no really appropriate techniques for dealing with hypotheses, especially in fossil samples" (1983: 143). Problems of theory involve two considerations, both of which are contingent upon the observation that traits perform or are capable of multiple functions. Assuming the functional/adaptational paradigm to be the correct (or most useful) paradigm, how are morphological hypotheses based upon functional demand to be

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discriminated? If adaptations explain fitness
differences, and fitness can only be a relative measure,
then any hypothesis joining function-morphogy-fitness
must pose the question, relative to what? Also, Endler
(1986) discusses the problems associated with assuming
the synonomy of engineering design ideals with
adaptation and adaptedness, especially when the design
is near optimal for the function considered yet is
offset by many other disadvantages.

It is also necessary to consider our inadequate
knowledge of the mechanisms that control the growth and
development of the craniofacial complex (Smith
1983:143). The problems of development arise only as
the source of black box effects given differing
functional demands during growth and never as a conduit
of alterative explanations. All the problems of
functional analysis never serve to call into question
the value of the functional approach. Even such traits
as the expanded facial sinuses which defy explanations
based upon loading are made possible indicators of a
"slightly different" pattern of stress dissipation. The
functional program will shed light on a subset of trait
functions yet cannot extend itself into evolutionary

.

problems without making critical and self-perpetuating assumptions. Obviously, as will be discussed below, the importance of function is implied by the necessity of integrative harmony. The question then turns to whether functionalism (i.e. present operation accountable by natural selection acting upon performance variability) is a totally sufficient explanation.

The second crucial point relates to the fact that reasonable functional explanations could be derived for the relationship between hindleg length and body length in frogs. Alberch (1985: 431) quotes Prentiss's (1906: 347) functional interpretation of dew claws in St. Bernards and Newfoundlands as perhaps being of "some use for swimming, and walking through deep snow." The external check pouches of Geomyoid rodents are adapted to water conservation due to the larger size relative to interior pouches and furred epithelium. It would be tempting to argue for their presence as the historical products of selection acting upon those functional properties. In this regard, functional explanations for external pouches and limb/body ratios offer reasonable scenerios for mode of origin. However, like the dew claw, the external cheek pouch is a threshold trait with no intermediate between it and the ancestral internal

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pouch. The externalization, "appears to have resulted

from an anterior shift in the location of the

evagination to include the lip epithelium, or from a

change in the direction of the evagination" (Brylski and

Hall 1988: 393). These threshold features, being

discontinuous expressions of continuous genetic

variation may not be inconsistent with micro-

evolutionary theory but they pose problems for the

functionalist/selectionist paradigm. Similar to the dew

claw, selection cannot effectively act on existing

internal pouch variability in developmental parameters

since that variability results in the same phenotype.

Only sufficient knowledge of the development of these

morphologies afforded any insight into the origin of

these novel features or in the case of the frogs,

altered dimensions. As will be seen, the importance of

understanding development is critical to an

understanding of the Neandertal craniofacial complex.

The third major point is that the shift away from

simple functionalist/adaptationist explanations should

in no way be construed as an argument against natural

selection or its pervasiveness. Attending to the nature

of developmental processes and pathways expands our

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potential to understand variability itself, the raw material upon which natural can selection act. Without this understanding, we cannot estimate the routes taken by selection to shape the translation of genotype to phenotype and from phenotype to phylogeny. In fact, for this particular case, the ontogenetic model itself does not rule out the functional, dental anterior dental loading hypothesis outlined by Smith (1983) and Smith and Paquette (1989). One can interpret the model as a pathway by which selection brought about the effect of improved mechanical resistance since it does not address issues of differential tooth wear or anterior crown/root sizes. However, it will be argued that the variability that would have to be targeted by selection to generate the Neandertal facial form occurs too early to be relevant to the functional loading arguments.

Thus far, this introduction has concerned itself with constructing an epistemological justification for the study that follows. The present work is concerned with developing an ontogenetic model by which the Neandertal craniofacial complex may be understood. Mathematical and statistical analysis of modern craniofacial growth and somewhat detailed examination of its cellular biology will lead to a focusing on the key

structures and processes responsible for the adult differences between modern humans and Neandertals.

No extensive consideration will be given in defense of one phylogenetic scheme or another except in cautioning those who argue against the idea of Neandertal contribution to modern gene pools on the basis of morphological "over" specialization (Howell 1957). We know little of regulatory genetics, next to nothing of the composition of modern human regulatory gene pools, and absolutely nothing of the regulatory genetic suites that characterize groups of archaic Homo sapiens in Europe, Africa, and Southwest Asia. Ruling out the potential for in situ evolution or genetic intermingling between archaic and moderns in Europe on the basis of morphology is inappropriate. (c.f. Smith et al. 1989).

Overview

The theme of this work is the better understanding of Neandertal craniofacial morphogenesis. At this stage in our knowledge, such a discussion requires a broad brush approach incorporating such preliminary subjects as heterochrony, allometry and genetics. While the

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strokes of this brush will be wide they will also be purposeful.

Chapter I will be a discussion of the association between allometry and heterochrony. Allometry is the study of the relationship between size and shape; Heterochrony is the alteration in the timing or the rate of development of features or suites of features during phylogeny. These alterations are responsible for the size and shape differences between ancestors and their descendants, making the processes underlying heterochrony responsible for allometric differences in their homologous life cycle stages. As noted by Emerson (1983), heterochrony can only take place when their is differential (i.e. allometric) growth during ontogeny. Heterochrony then is the mechanism to transform ontogenetic size/shape variation in ancestral stages into size/shape variation between ancestral and descendent adults.

There are two important points to be taken from the first chapter. These are: that the mathematical junction between allometry and heterochrony lies in Gompertz equations and ultimately, meaningful biological connections between allometry and heterochrony occurs at

the cellular level.

Gompertz equations will add depth to our understanding of the allometric coefficient k, as it relates to initial specific growth rates and decay rates. If, according to Gould (1977) heterochrony operates to alter global to local developmental relations via acceleration and retardation, then Gompertz equations seem ideal for a mathematical trearment of heterochrony. With this in mind, it may one day be possible to dispense with the often confusing terminology associated with allometry and heterochrony and speak in more quantitative terms of growth rates, decay rates and initial sizes.

Also, emphasizing the cellular basis of allometry and heterochrony is particularly important for this work since patterns of differential chondrogenesis within the cranial base cartilages are critical keys to understanding the craniofacial differences separating modern humans and Neandertals.

Chapter II is a general discussion of the relationship between ontogenetic variability and its underlying genetic basis. Several aspects will be emphasized. First, there is no a priori coincidence

between morphological and genetical divergence. In other words, closely related fossil groups that differ in their morphology enough to be considered 'morphological species' may not be truly genetically isolated and incompatable. Only when development is considered can we judge with any degree of confidence the relationship between the two levels of divergence. Secondly, the nature of development calls for a highly interactive genome. Genes code for protein products that exhibit a norm of reaction (Lewontin 1983). Recalling Waddington's epigenetic landscape, reaction norms are the creodes, canalized pathways down which development proceeds. The greater the reaction norm, the greater the range of viable variation allowed. The fact that later ontogenetic stages exhibit the greatest observable variability does not however argue that later reaction norms are broader in scope. As development proceeds, increasing complexity as manifested in heightened numbers of components and their interactions translates into a greater number of available pathways with lesser morphological effects. This implies that complex structures, like crania, have their ranges of potential variability because they have larger ensembles of reaction norms. Also implied is that the pattern of this

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reaction norm ensemble changes during ontogeny, leading to age-specific responses to selection.

Also emphasized in chapter II will be the association between population genetics, demographics and ontogeny. Altering the epistatic genetic background by reducing population numbers and elevating the level of inbreeding may open up new morphological opportunities since development is the product of epistatic gene action.

Chapter III will be a detailed description of craniofacial development in modern humans. This description will be roughly chronological, beginning with the early mesenchymal formations of the basicranial floor and ending with the fusion of the basi-occipital synchondrosis. Several aspects will be stressed. First, the general pattern of craniofacial shape change during growth. Secondly, the developmental relation of the anterior and posterior cranial base to one another, each in relation to the face, and to the pattern of neural growth should be kept in mind. The literature certainly suggests that it is the anterior base that demonstrates the neural-like growth pattern. However, lines of evidence would implicate the posterior base as being

more greatly influenced by the growing brain. Thirdly, a description of the importance of cell kinetics to understanding the growth of the cranial base at its synchondroses will be given.

Chapter IV will outline the materials and methods used for the analyses and subsequent predictions. Chapter V will be an articulation of the model of Neandertal craniofacial growth and and an analysis of adult allometric relationships predicted on the basis of the ontogenetic analysis. Chapter VI outlines various statements and observations relating to Neandertal development and life history. The discussion will include the ultimate evolutionary cause for the life history patterns of Neandertals lying at the root of their craniofacial morphology. Chapter VII will summarize and conclude the work.

CHAPTER I

AllOMETRY AND HETEROCHRONY

Allometry/Scaling

The relationship between allometry and heterochrony
is biologically straight forward. While making
heterochronic inferences directly from allometric plots
(Cheverud 1982b, Shea 1983, McKinney 1988), can be
problematic, attention to patterns of life history and
development can alleviate these problems in
neontological cases. Attention will focus upon those
biological processes that underlie patterns of
heterochrony and how these relate to allometric
functions. These will be applied to the problems of
transfering the modern ontogenetic model to a model of
Neandertal craniofacial growth.

Allometry is the study of designating the
"differences in proportions correlated with changes in
absolute magnitude of the total organism or of the
specific parts under consideration... Allometry then is
the study of size and its consequences" (Gould 1966:
587). The appreciation of size as an important
biological adaptation is widespread (Calder 1984; Peters

1983; Schmidt-Nielsen 1984). Indirectly, paleontologists working within the Darwinian paradigm (descent with modification, the generation of adaptations via natural selection) have epitomized the evolutionary advantages of size increase in Copes Law. That is, through its phylogeny a lineage will tend toward size increase. Traditionally, Copes Law has been interpreted as representing the biological superiority of large forms over smaller. In many circumstances (such as predation, fat storage or environmental buffering) large forms do in fact have the greater advantage. However, the presence of smaller forms signifies size reduction or maintanence of small size as a perfectly reasonable adaptation.

For animals similar in design yet differing in size and shape, allometric analysis allows the discrimination between mechanically required shape change and adaptations with no specific relation to size (Gould 1975). In this way, allometry generates a criterion for judgement on the effects of size. Allometric size change allows more than just mechanically required proportional change. It opens up new morphological and therefore, adaptive potentialities in descendant groups with expanded size ranges (Gould 1966).

Of concern for this study is an accurate

representation of craniofacial ontogeny in modern

humans. From the fetal period to the adult stage, human

craniofacial form undergoes substantial shape change,

which makes it amenable to allometric analysis.

Afterall, what is ontogeny but the interplay between a

complex set of allometries. Before moving on to the

quantitative basis of allometric analysis, a brief

review of the types of allometry (scaling) will be

useful.

Ontogenetic Allometry

Ontogenetic allometry (also known as growth

allometry) is the analysis of proportional change during

growth of an individual or a species (Shea 1984). For

lack of prenatal Neandertal specimens, no comparisons

between growth allometries can be made with the prenatal

modern growth patterns to be analysed here. Ontogenetic

scaling also has an interspecific component. That is,

ancestral-descendent size and shape differences are

based upon the extrapolition to larger or smaller sizes

of ancestral ontogenetic trajectories (Alberch et al.

1979; Gould 1975, 1977; Shea 1983, 1984).

Biomechanical Allometry

Biomechanical allometry is size required shape
changes. Examples would include increased tubular
diameters in long bones of larger animals, reduced
relative metabolism with increased size (as a
consequence perhaps of reduced relative surface area),
and brain /body ratio (Stahl 1962; McMahon and Bonner
1985). The "purpose" of mechanical scaling is the
retention of physiological, functional, or behavioral
equivalence with size change. Predictions based upon
principles of biomechanics are determined and then
compared to observed scaling factors of interspecific,
static adult curves (Shea 1984). The predicted
allometric coefficients are what Gould (1975) termed for
interspecific comparisons, the "criterion for
subtraction."

Geometric Allometry

Geometric allometry would be the retention of
ancestral proportions at larger or smaller sizes, in
violation of predictions based upon biomechanical or
ontogenetic scaling. Patterns of interspecific
geometric plots would be exemplified by vertical

transpositions along the ordinate axis. The adaptive

implications of geometric scaling will be discussed

below. The limitations of this scaling are obvious,

especially for long bones. Because cross sectional area

is proportional to l^2 and volumes to l^3, the larger

the linear dimension of the bone, the greater the volume

to cross sectional ratio. At some point, the

discrepency between mass and strength (based upon cross

sectional area) will be too great, the result being

material failure due to elastic buckling (McMahon and

Bonner 1985).

Intraspecific Allometry

Intraspecific allometry involves the allometry of

adults within populations of a species. To Gould

(1975), intraspecific scaling represents the correlated

variability upon which evolution works. According to

Pilbeam and Gould (1974) and Riska and Atchley (1985),

intraspecific allometry coefficients are lower (.2 - .4)

than interspecific coefficients (.6 - .8). On account of

the declining correlation of growth rates as ontogeny of

the brain and body proceed higher taxic differences are

initiated earlier in ontogeny, so explaining the

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allometric effect. Comparison of closely related
species with intraspecific allometry coefficients (.2 -
.4) reveals similar design at different sizes.

Discussion

The mathematical basis of allometric studies was
given firm foundation in Huxley's Problems of Relative
Growth (1932). That formula, $y = bx^k$ according to
Huxley, is the relation between X, the absolute
magnitude of the organism and y, the magnitude of the
differentially growing organ. When plotted on a log-log
grid, the X, Y values describe a straight line.
Mathematically, this can be done by log transforming the
variables:

$$Log\ y = Log\ b\ and\ k\ (log\ x)$$

There are reasons that transcend mathematical
convenience for logarithmic transformation. For Huxley
(1932) and Medawar (1945), growth is a process of the
"multiplication of living substance" (1932:6). On a
logarithmic scale, equal spaces between increments
represents equal degrees of multiplication or
exponentiation. This is opposed to the ordinary
absolute scale where equal spaces represent equal

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addition. So far as growth is concerned, an increase
from 5 to 25 is equivalent to that from 25 to 125.
Thus, on a semilogarithmic plot, where the abscissa
denotes absolute time, the ordinate representing some
growing animal or organ should be represented
logarimithically. The curve described can be termed its
specific growth. The exponent k in the power function y
= bx^ k is the ratio of specific growth between whatever
variables are represented by X and Y. For Huxley, this
ratio remains constant with time in most cases. The
reason for this constancy will be related shortly.

In describing the constant b, Huxley credits no
particular biological significance since it merely
denotes the value of y when x equals unity (1932:5).
There are those that disagree (Anderson and Busch 1941,
Gould 1975) with this conclusion. Anderson and Busch
(1941) believe that k has been granted greater
biological meaning than b simply because it's more
easily interpretable. Gould (1971, 1975) and White and
Gould (1965) have done much for giving biological
meaning to b, making change along the ordinate for
interspecific curves an important evolutionary
adaptation. For instance, for an illustration of

geometric scaling and its effects on b, see Figure 2.

The individual slopes T1 and T2 have a slope of k = .75 and these represent the increase of brain weight with body weight in prosimians, T1, and Anthropods, T2. The dashed lines connecting the slopes represent size increase in adults without a necessary change in proportions since the dashed regression lines are equal to k = 1. That is, the difference in the 6 values of T1 and T2 is the product of geometric scaling in the adults described by T1 and T2. The evolutionary and adaptive importance of this shift via geometric scaling is that it results in greater encephalization in T2 since to produce the T2 intercept value, groups undergoing geometric scaling were undergoing positive allometry relative to mechanical expectations (KT2 - KT1 = .25).

Further, White and Gould (1965) find fault with Huxley's reasoning for the meaning of b when x = 1. First of all, regressions should not be extrapolated beyond the data set which they describe. White and Gould (1965:7) find it more mathematically correct to say $y = bx^k$, $x_i < x < x_j$, where x_i and x_j are the endpoints of the data interval described by the

31
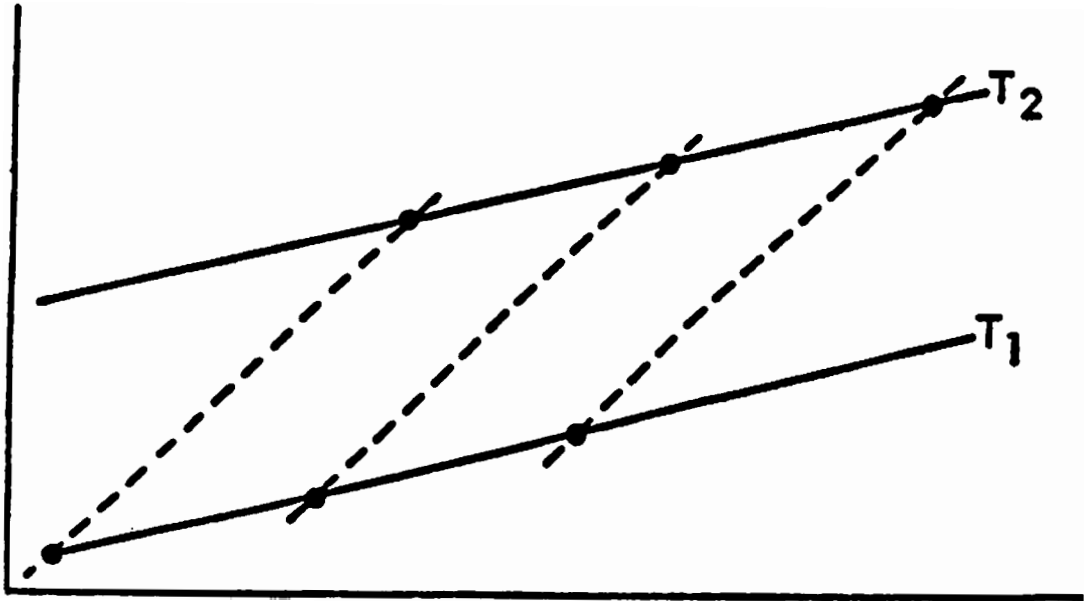
Figure 2. Relation Between Geometric Allometry and Vertical Displacement. From Gould (1971).

regression. As a further elaboration of this point, it is noted that patterns of relative growth may change, taking on more linear or curvilinear patterns at smaller size thus altering the value of b otherwise predicted from a more restricted portion of the growth curve.

As a constant within the formula $y = bx^k$ describing interspecific curves, meaning from b can be acquired in the following ways. For finding functional or physiological relationships that are independent of mass, b can give information. For instance, as a general rule CPR training specifies _five_ heart compressions for every one mouth to mouth breath. Stahl (1967) [see Calder (1984: 46-47) for reference and formula] noted that in resting mammals, a similar 4.5:1 ratio existed between heart rate and breathe. This was derived from the cancelling of k values and the ratio of b values.

$$241 \ M^{-.25} \ / \ 53.5 \ M^{-.26} = 241/53.5 \ M^{-.25 \ -(-.26)} = 4.5(M)^{0.01} \ (Calder \ 1984: \ formula \ 3-26).$$

A comparable method for comparing interspecific curves also makes use of differing b values. Making use of brain/body regressions supplied by Jerison (1961):

```
y = .055 * .655x    Oligocene Mammals
y = .115 * .664x    Recent Mammals
```

Again cancelling the K's and dividing the b's yields
.115/.055 or 2.09 meaning that the average brain weight
of a recent mammal is 2 times that of an Oligocene
Mammal. But is this the most meaningful expression of
b? White and Gould (1965) and Gould (1971) think they
have found one through a similarity criterion s. S
measures the difference in the size of animals on
different curves at which they would have the same
shape. Again, the slope k of the regression must be
invariant.

The most important aspect of the s criterion is
that contrary to the simple dividing of b's and the
cancellation of k's (thus making the relationship mass
independent), s measures the increase in size, via
geometric scaling (see fig. 2), in animals of similar
shape. The formula for the s criterion is:

$$s = (b1/b2)\char94 1/1-k$$

An example of the s criterion technique at work
will illustrate the difference between it and the
previous b ratio. Using the regression for brain/body
weights in Oligocene and recent mammals,

$$s = (.115/.055)^{1/1-.66} = (2.09)^{2.94} = 8.73$$

That is, a recent mammal is 8.73 times heavier, on average, for the same brain/body ratio as an average Oligocene mammal. Since volume scales as l^3, recent mammals are therefore, on average, $\sqrt[3]{8.73}$ or 2.06 times as long as those in the Oligocene. The conclusion seems clear that in a variety of ways, depending upon the researchers purpose, the constant b in the power function $y = bx^k$ yields important biological and evolutionary meaning.

Attention now turns to k, the coefficient of growth allometry. When the power function $y = bx^k$ is transformed logarithmically, it describes a rectilinear plot where k is the slope. The magnitude of k defines the differential rate of increase in Y relative to X. When variables of similar dimension are regressed, k = 1 defines isometry. When k > 1, y is growing at a greater specific rate than x. When k < 1, y is growing at a slower specific rate than x. If however, variables of different dimensions are regressed, then the criteria for isometry change. If y represents a surface or cross sectional area (l^2) and x is linear, then isometry is

defined as k =2. If x is a volume (l^3) and y linear,
then isometry is defined as k = .33 (1/3). If y
represents a surface (l^2) and x a volume (l^3), then
isometry can be defined as 2/3 or .66.

It is most interesting that as complex a process as
growth is, the allometric plots of x and y variables
remain rectilinear. That is, the ratio of the specific
growth rates of x and y remain constant. While this may
not always be so, understanding of the processes
responsible for rectilinearity will shed light on the lack
there of and ultimately, the patterns of heterochrony.

If embryonic growth rates were allowed to preceed
throughout ontogeny, before coming to an abrupt halt
(limiting condition), adult organisms would be
magnitudes larger than they presently become. Wright
(1926), commenting on populational growth (and equally
applicable to ontogenetic growth), finds it much more
likely, "that there will be increasing adverse pressure
as growth goes on, leading to damping off and reversal
of curvative, and ultimately, if conditions are uniform,
to an asymptotic approach to an upper limit" (1926:
494). As growth proceeds, it decays at a constant rate
(Huxley 1932). In fact, the decay is exponential (Laird

1965: 249 - 263). Taking growth data of the human embryo from Jackson (1909), Laird (1965) calculated the rate of growth decay for various regions and organs. What she found was that the rate of growth decay for the organs was very similar within a species. The invariable exponential rate of decay for bodily organs explains the linearity of the allometric plots. According to Lumer (1937), the only way in which the logs of two specific growth rates will yield a straight line is if their rate of decay is the same. When decay rates are dissimilar, the log-log plot becomes curvilinear.

A growth curve with a specific growth rate that undergoes decay with time that approximates an exponential function can be formalized by an equation of the Gompertz type (Laird et al. 1968),

$$W = WO \ EXP \ [AO/a \ (1 - EXP(-at)]$$

W is the weight at some chosen time to wO is the initial weight. AO is the initial specific growth rate and a is the rate of growth decay. The rate of decay can be calculated easily by regressing the log specific growth, $\frac{1}{W} \cdot \frac{\Delta W}{\Delta t}$, on absolute time. The line defining the regression will have a negative slope, the value of which is the rate of decay. The allometric exponent K,

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assuming identical decay rates between growth curve, can be defined as the ratio of initial specific growth rates or terminal specific growth rates for two growth curves.

Two curves, identical in rate of decay yet differing in specific growth rates, will have identical shapes. They will also pass through ordinate values at comparable periods in their growth yet displaced in time. For Laird et al.(1968: 349), since aO"/AO' is a constant, let k = dt/t where delta t is a constant time interval measuring displacement. When k = 1, dt = 0, meaning when the specific growth rates between two curves are identical (k = 1), they are not displaced in time.

Comparable points on two curves can be defined as such if they bear identical relations to their respective asymptotes (Laird et al. 1968). Because allometric curves do not include absolute time units, relative time units can be developed. Barton and Laird (1969) adopt as such a unit, the "standard doubling time" preceeding the inflection pool, which is mathematically TD = .527/a . Accordingly, the log time between two growth curves is expressed as a function of the slope of the allometric line and doubling time.

$$dT = \ln K * TD/.527$$

Both curves can also be time standardized, and therefore superimposable by a mathematical process described by Laird et al.(1968). This process results in the formula

$$W'(t") = Exp [-Exp (-t')]$$

which standardizes the time units t' and t of the curves to absolute units in t" which are equivalent to arbitrary units 1/a.

As already stated, two growth curves differing in their initial specific growth rates yet with identical decay rates will pass ordinate values at comparable periods relative to the upper asymptote yet at different times (Laird et al. 1968; Laird et al. 1965; Laird 1966; Laird 1965). Therefore, the allometric growth coefficient k is a measure of the displacement in time of two growth curves sharing identical decay rates. Complications do arise however. Laird et al.(1968) demonstrates the possibility that k may not only represent the ratio of differing initial specific growth rates between two curves but may also be a measure of the ratio of two curves with identical initial specific growth rates yet differ in their onset time.

The transformed calender units adopted earlier were equivalent to the reciprocal of the decay rate, 1/a, for growth along comparable segments of curve. Given that the ratio of the initial specific growth rates (AO) and the rate of decay are constant for any point t, then for prenatal growth periods differing in magnitude, N , the rate of decay will be 1/N and the initial specific growth rate will also be 1/N. For instance, Laird (1966) found that large newborn mammals such as calves and lambs have prenatal growth periods 10 times as long as various smaller animals. One would expect then that for the larger forms, Ao and a should be 1/10 as large as the smaller forms. This is in fact the case. For large animals, growth is executed with lower initial specific growth rates (AO) and rates of decay (a). As a consequence of this relationship, in large animals, the lowered a will result in the extension of higher average specific growth rates for longer calender periods, thus resulting in larger newborns.

It is clear then that there are important growth processes implied by the magnitude of the allometric coefficient k. Constant linearity of k implies identical ratios of initial specific growth rates. A slope that

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becomes curvilinear, especially towards it upper
asymptote, indicates a differential rate of growth
decay.

Interesting problems in allometric analysis of
growth curves have been reviewed by Barton and Laird
(1969). In Figure 3a, four ideal Gompertzian curves with
equivalent values of a are displayed. Time displacements
are due to differences in the initial specific growth
rates. Note the scales of the ordinate and abscissa are
in absolute values. In Figure 3b, each of the curves has
been allometrically plotted against curve 1. Notice the
value of time displacement corresponds to differences in
the specific growth rates. The magnitude of time
displacement is manifested as movement of the slope to
greater values of the abscissa. That the allometric
plots converge at point D, the asymptote, indicates the
equivalence of their a values.

Figure 3c shows two Gompertzian curves that do not
differ in their ratios of specific growth yet do differ
in their rates of decay by 20%. The curves have been
drawn through the inflection point to simplify the
comparison. In Figure 3c, curve 2 has the higher a level

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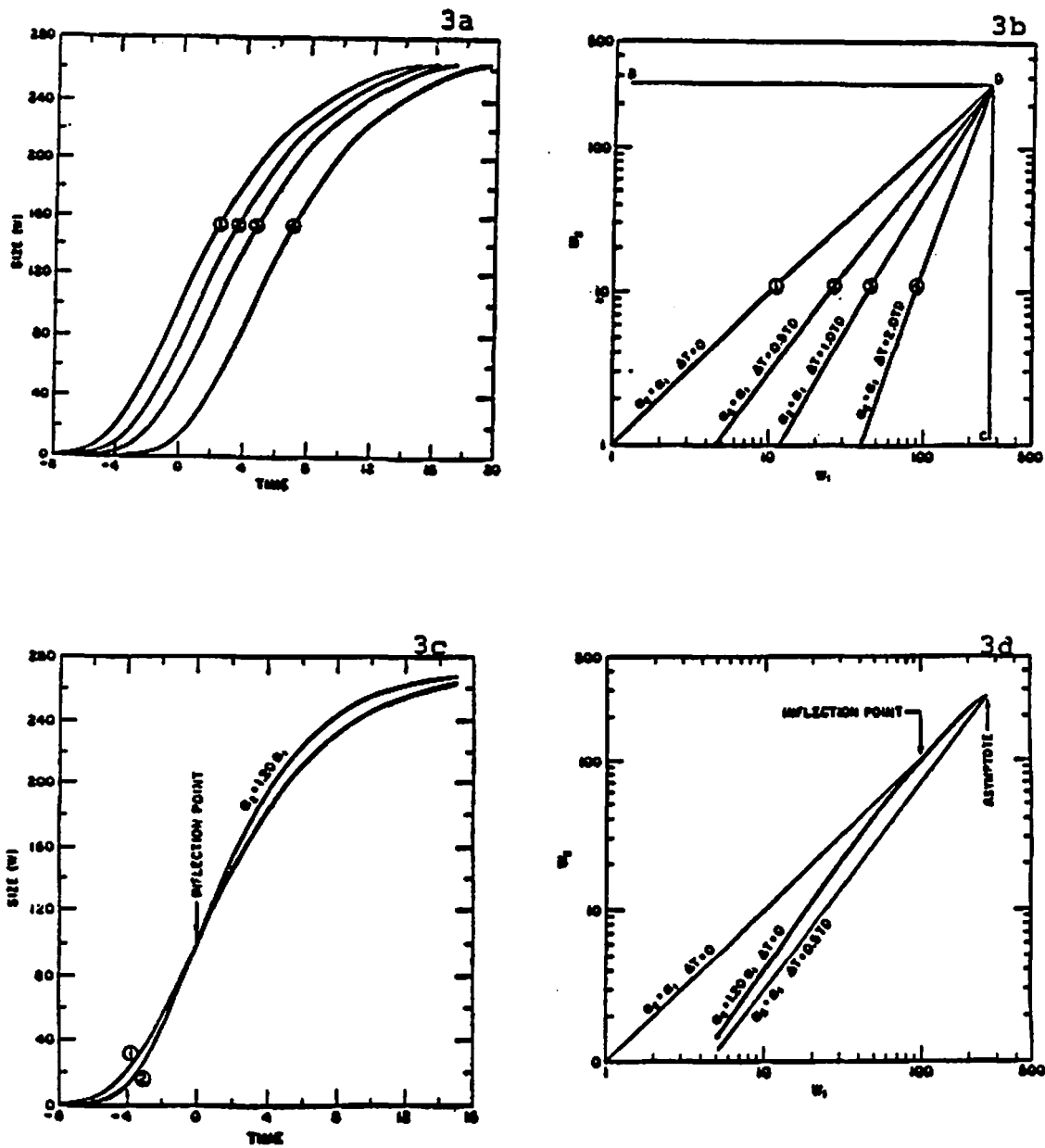
Figure 3. The Characteristics of Ideal Gompertz
Curves. From Barton and Laird (1969).

and so more vigorously checks its growth, resulting in the smaller terminal size. An allometric plot of these curves demonstrates some fascinating problems.

Smith (1980) commenting on the misleading visual impressions given by log-log comparisons notes that the absolute differences in log values are small between numbers that have great absolute differences. As an example, the antilog of 4.9 and 4.6 differ in their values by roughly 39,000 (79,000 - 40,000). When the antilogs of 1.2 and 1.5 are compared, they also differ by 2x yet their absolute differences are only 16 (31.6 - 15.84). The point being that as antilog values get higher, their log differences become increasingly reduced. A product of this 'squashing' of absolute differences can be seen in Figure 3d. Logarithmically transforming growth dimensions will expand disproportionately that segment falling before the inflection point and shrink the variance in growth occuring after the inflection point. As a result, curves with identical specific growth rates yet differ in their decay rates (in this case by as much as 20%) will mimic displacement along the abscissa normally indicating specific rate differences. Because curvature becomes visually manifest after the inflection point and this

region is artificially constricted, this curvature may be mistaken for random error and so disregarded.

Since the value of the allometric coefficient k is a measure of the time displacement, not recognizing the differences in displacement due to differences in AO (what k is supposed to measure) or unrecognized differences in the rate of growth decay may result in erronious interpretations of k. It is therefore suggested that before ontogenetic allometry plots are generated, the rate of a be calculated and compared for all units under investigation.

The evolution of adult phenotypes is a byproduct of the evolution of ontogenies. Size and shape differences between organisms closely related yet separate in time may be understood in terms of ontogenetic allometry. However, as has been demonstrated for ontogenetic allometry coefficients, a number of processes may be implied. These are the specific growth rates and the rates of decay. These processes, acting upon initial sizes, WO, will define the construction of the adult form and are therefore of great importance in the consideration of ontogenetic models. While these processes are not accessible from inter and intra-

specific static allometries, understanding the
consequences of their alteration can lead to a critical
evaluation of the ontogenetic changes neccessary to
explain adult size/shape differences in closely related
groups.

Heterochrony

However difficult (or impossible) it may be to
infer specific ontogenetic processes from static
allometries, it must be recognized that _time_ is at the
root of all allometry. Traditionally, allometry has been
defined as the relationship between size and shape.
Heterochrony, which has been defined as the, "change in
the relative time of appearance or rate of development
of a character during phylogeny"(Hall 1984:1),
incorporates the time element into the size/shape
relation.

Hall (1984) among others, has sought to understand
the patterns of heterochrony in terms of their
underlying cellular processes. In the discussion of
heterochrony that follows, only the parameters that can
be modulated will be outlined here since many specific
mechanisms may affect developmental events.

For Haeckel (1867), heterochrony was a mechanism that would explain discrepencies between the timing in appearance of organs during ontogeny compared to expectations from phylogeny. These 'Cenogenetic' discrepencies represented mechanical adaptations to the embryonic environment, thus clouding the 'Palinogenetic' (phylogenetic) pattern. Initially then, heterochrony was used as a salvage concept in Haeckel's revival of the Meckel-Serres law of recapitulation (Russell 1916). Today, we see the role of heterochrony a bit differently but recognize with Haeckel the importance of the parallel between ontogeny and phylogeny.

More than simply a route of major morphological change, heterochrony may also be a product of some ecological strategy. Gould (1977), Emerson (1985,1986), Emerson et al.(1988) and McKinney (1984) have pursued this line of investigation. Focusing upon progenesis(truncation of ancestral growth allometry) Gould (1977) argues that unstable environments favor precocious maturation. Morphological change may ensue from these life history adaptations since there are various degrees of covariance between somatic and gonadal structures. Lewontin (1965:85) mentions that in general,"... small absolute changes in developmental

rates of the order of 10% are roughly equivalent to
large increases in fertility of the order of 100%".

The patterns of heterochrony are easily understood.
Alberch et al.(1979) list eight patterns, only six of
which are usually listed by researchers (McNamara 1986).
The six patterns can be subdivided into two categories,
paedomorphosis and peramorphosis. Paedomorphosis is
defined as the retention of ancestral juvenile features
into the terminal stages of descendants. In other words,
adult descendents resemble the juveniles of their
ancestors. Peramorphosis on the other hand is the
extrapolation of ancestral shapes to larger sizes. There
are three categories of heterochrony for both
paedomorphosis and peramorphosis. These categories are
variants or combinations of four parameters:

    1) age at growth onset
    2) initial size at growth onset
    3) growth rate
    4) age at growth offset

Paedomorphosis is generated by neotony, progenesis,
and postdisplacement. Neotony represents the reduction
in the rate of shape change with size change in
descendents relative to ancestors. This results in a
disassociation of shape with size increase (McNamara

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1986). Progenesis is the precocious offset of descendent ontogeny relative to the ancestral condition (Gould 1977;McNamara 1986). Postdisplacement disassociates shape from size by reducing the initial size at onset or postponing the initiation of growth onset.

The categories of peramorphosis are acceleration, hypermorphosis, and predisplacement. Acceleration is the counterpart of neotony. It represents the increased rate of shape change with size change. Hypermorphosis does not initiate increased or decreased shape change relative to size change. It is simply the extrapolation of ancestral allometries to larger sizes (Shea 1983) by postponement of developmental offset. Predisplacement disassociates size and shape by increasing the initial size or initiating precocious growth onset.

Neotony, acceleration, predisplacement, and postdisplacement are categories of allometric disassociation. Progenesis and hypermorphosis are examples of ontogenetic scaling (McKinney 1988). The importance of growth and maturation data for heterochronic analysis is especially evident for interpreting patterns of ontogenetic scaling. Shea (1983) outlined the problem clearly using African great

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apes as an example. In many of their features, gorillas are ontogenetically scaled chimpanzees. That is, gorillas share similar patterns of ontogenetic allometry with Pan. Gorillas are shaped differently than chimpanzees because they extrapolate the chimp allometry to larger sizes. Yet, do gorillas differ in their size because they grow longer or because they grow faster during the same ontogenetic period? This would be a difficult question to answer in fossil materials. In the African ape example, gorillas share similar maturational schedules with the chimp and inspection of plots of growth weight indicate that gorillas grow faster during that schedule. Shea (1983) made two new additions to heterochronic terminology to describe the distinctions. If ontogenetic periods are similar, then the size differences become functions of rate and are termed either rate progenesis (McKinney 1988) or rate hypermorphosis. If size differences are a function of the length of ontogeny, then this would be an example of either time progenesis or time hypermorphosis. The real importance for making this distinction lies in the selective forces operating to produce the final effect. Selection for large body size would act to increase the rate of growth so that large sizes could be attained as

soon as possible. Changing offset times may be selected for because there are benefits to truncating or extending ontogeny (Shea 1983).

Focusing upon the fundamental parameters of offset, onset, and rate leads to vital conceptual connections between heterochrony, Gompertzian parameters, allometry, and ultimately cell kinetics. Sadly, at this time no formal linkages have been made between heterochrony and changing Gompertzian parameters. To illustrate the problem, superficially it would appear that all that needs changing in the Gompertzian function to produce hypermorphosis (time) is to reduce the rate of decay while maintaining the initial specific growth rates. This would explain the extended growth period and the larger size of time hypermorphs. However, a ratio of decay rates that differs from unity would generate complex allometries (i.e. curvilinear plots) (Lumer 1937). The fact that this pattern is not seen is not necessarily evidence that the decay rate hypothesis is erroneous since we know what effects log transformation have on curvatures late in ontogeny. These are questions and ideas that have rarely been asked or explored.

Ultimately, all growth is reducable to the dynamics of tissue proliferation and interaction. This dynamic is further reducable to the differential growth and differentiation of cell lineages. Can heterochrony and allometry be meaningfully reduced to the level of cell dynamics? and if so, will it aid our understanding of the overall process? Several examples will suffice in answering those questions in the affirmative.

The effects of selection for body size on increased muscle size has been demonstrated by Byrne et al. (1973). Muscle growth and development is controlled by at least four parameters: numbers of fibers, fiber length, rate of fiber formation, and rate of fiber growth. Fiber number is primarily determined prenatally whereas fiber length and diameter are determined after birth. As a result, selection for increased body size by selecting strains with higher growth rates increases prenatally determined cell numbers were in the larger strains. Falconer et al.(1978) selected for body size increase in Q-strain mice. They found that at all ages sampled, the larger strains had greater numbers of cells in their lungs, liver, spleen, and kidney. Regressing the log cell number to log organ weight determined that increased cellularity accounted for more

than 70% of the variation in organ weight. "The general
conclusion from the previous work on mice is that
genetic differences of size are mainly, but not
exclusively, due to cell number"(Falconer et al.
1978:288).

Selection for higher growth rates in Japanese Quail
(Lilja and Olsson 1987) resulted in increased growth
rates in the digestive organs, yolk sack, and allantois.
Much of the increased growth is connected to early rapid
growth, leading to the conclusion that selection for
more rapid growth rate affected early embryonic growth
parameters. Another interesting result from Lilja and
Olsson's (1987) work can be found in other organ
systems. As a product of early weight increase in the
digestive organs, a delay in the development of the
pectoral musculature and feathers occurred. In addition,
and probably as a product of delayed maturation, the
number of embryonic somites also decreased in the more
rapidly growing lineages.

Massive phenotypic changes occurring as a result of
aberations in early ontogeny illustrates upward
causation. Changes in embryonic growth accompanying
selection for rapid postnatal growth are not examples of

downward causation, a reversal of the normal cause-
effect cascade. Selection was acting upon rate/size
variability generated by variability in the initial
parameters governing tissue growth. This is in contrast
to the Geomyoid cheek pouch and the dew claw examples
given above. The effects on structures that covary with
those altered in early development may or may not be
profound yet a plausable avenue of major morphological
change is implied, making new designs not so different
or complex as they might appear.

Maderson (1975:322) sees two distinct categories of
evolutionary change: those that involve,"quantitative
modulations of the basic developmental program" or a
qualitative change involving the addition or loss of
structures. In many instances (e.g. polydactyly), once
the embryogenesis of added or lost structures is known,
the quantitative-qualitative distinction breaks down.
These quantitative modulations involve numerical
variability in such features as mitotic division rate,
topographical arrangement, and the logistics of
differentiation leading to specialization. In addition,
features that are prone to vary and determine
fundamental growth properties include sensitivity to

extrinsic chemical environments (e.g gradient effects [Wolpert 1982]), cell death (Stebbins 1969), and initial number of allotted cells in a growth region.

Maderson (1975) and Hall (1984) note that many of these variable features are controlled by inductive tissue interactions. Inductive tissue interactions are processes involving interregional contact to produce new cell types or patterns (Hall 1987). According to Hall (1984), development is a hierarchical sequence of these interactions and this mechanism is subject to genetic control. Recently, Edelman (1988:163) has theorized that variability in functional induction sequences caused by small changes in the response times of genes for "morphoregulatory" cell adhesion and surface adhesion molecules (CAM's and SAM's) can produce "large nonlinear changes in expression sequences and morphology" (1988:163). In other words, heterochrony can be, and is ultimately produced by affecting CAM's that act directly or indirectly on the 'primary processes' of cell division, cell motion, cell death, cell adhesion, and differentiation and induction(1988:1-22).

In not quite so ambitious a fashion, Hall(1984) credits inductive tissue interactions as driving

heterochronic change by regulating when and where cell condensations form. Even the onset of cell division of responding cells is a result of induction. Regulating the number and mitotic activity of cells in skeletal condensations is important because these emerge as the "fundamental control" over when growth starts (Hall 1984). In fact, the processes controling the formation of these skeletal condensations generate the fundamental parameters underlying heterochrony.

The cellular basis of growth onset and offset are similar. Onset is controlled early in development by the number of stem cells within the condensation, the number of mitotically active cells, the intrinsic rate of cell division, and the amount of cell death. Growth offset occurs when the growth plate runs out of dividing cells which is a function of initial number of cells in the plate and the number of times they divide (Kember 1983). Growth rate is much more open to modification by hormones, nutritional supply/demand ratio, activity levels, and other various growth factors. Hall (1984) and Kember (1983) both believe that the maximum and minimum growth rates are set by the number of dividing cells allotted to each skeletal element. Wolpert (1982) and Kember (1979) also acknowledge that for cartilage

growth, it is not so much the frequency of mitotic divisions that controls growth rate but the depth of the proliferative zones within the growth plates.

The cellular parameters underlying heterochrony outlined above, when altered, induce allometric changes between adults. These empirical observations by Hall (1984) and Maderson (1975) lack the formality to be found in Alberch et al. (1979). Katz (1980), by developing a cellular model to derive the allometric equation, has supplied the necessary first steps toward generating a mathematical link between allometry and heterochrony at the cellular level. Below is Katz's derivation:

If,

  y= the number of existing cells in a developing part.

  fy= the frequency of cell division in that part.

Then,

  $y = 2^{fyt}$ t=time

If to form a more complex y, additional germinal centers, m , are introduced, then

$$y = m(2^{f_yt})$$

Comparing two complex components, y and x, where

$$x = n(2^{f_xt}),$$

then the relative rate of x,y growth can be formalized.

$$y = m(2^{f_yt})$$

$$x = n(2^{f_yt})$$

$$= (m/n^a)[n(2^{f_xt})]^a \qquad\qquad a = f_y/f_x$$

$$= (m/n^a)(x)^a$$

The formula $(m/n^a)(x)^a$ is homologous to Huxley's allometric formula $y = bx^k$ where the constant k is the specific ratio of cell division between x and y, and b is the modified ratio of the germinal centers(Katz 1980:91-92).

This section has attempted to reduce the processes underlying allometry and heterochrony to the fundamental units most relevant and important to this analysis. While there is considerable literature available citing examples upon examples of heterochrony and allometry, I have tried to focus on biological processes responsible for generating particular patterns.

CHAPTER II

VARIABILITY, EPIGENETICS, AND POPULATION GENETICS

The evaluation of potential patterns of developmental variance in modern humans should go some way in addressing a fundamental issue pertinent to the debate on modern human origins. That is do the morphological differences that serve to separate modern H.sapiens from archaic H.sapiens warrant the assignment of the latter to a different species? Speaking strictly on the ontogeny of the basicranium and face, a case will be made that the differences are a result of minor quantitative modulations in a small subset of developmental parameters within a strategic structural determinant. To assign genetic isolate status to Neandertals based upon this morphological suite seems inappropriate. Especially so if these developmental differences could be generated with little genetic structural modification.

The separate species argument is critical to many who espouse a 'punctuated' origin of modern humans in southern Africa. The mtDNA variability in modern populations would seem to indicate that Africa is the continent on which all humanity last shared a common

ancestor (Cann et al. 1987). Stringer and Andrews (1988) use the calculated date for this hypothetical last common ancestor (ca. 145-290 kya) to argue that the early origin of modern humans in southern Africa represented a speciation event.

Factors affecting regional mtDNA variability, variation in the calculated mutation rate, and their influence on dating have been competently reviewed by Spuhler(1988). Spuhler (1988) contends that the evidence actually shows that most mtDNA diversity is shared by all modern groups and that what diversification has taken place has come by, "regional phyletic transition from H. erectus, starting in Africa in the Middle Pleistocene"(1988:15). The dating of a "speciation event" seems especially frought with problems given documentation that mtDNA may flow over "species" boundaries within hybrid zones (Ferris et al. 1983).

The remainder of this section will not focus on the meaning of mtDNA variability, even though in the debate over the origins of modern humans it is the most discussed application of gene data. There are other branches of genetics that offer insight into differences separating modern from archaic H.sapiens. First, a

somewhat heuristic discussion on patterns of ontogenetic variability is presented. Second, an illustration of how demographics (i.e. population genetics) can influence patterns of individual ontogeny is given.

Near the end of the last section, allusion was made to the relationship between variation in certain specialized molecules (i.e. CAM's and SAM's) and their suggested effects on the pattern and timing of induction sequences (Edelman 1988). Earlier, the connection was made between the process of induction and the generation of cellular parameters relevant to ontogenetic variability in general and heterochrony in particular (Hall 1984; Maderson 1975). These parameters and proteins are almost certainly some consequence of gene action.

Schopf et al.(1975) comparing the degree of genetic differentiation to some proxy of morphological complexity (anatomical terminology) conclude that there is a decoupling between the rates of morphological and genetic evolution. Wilson et al.(1974a,b) after comparing the patterns and rates of evolutionary divergence in frogs and mammals note that mammals have evolved morphologically at a much faster rate than frogs while at the

same time evolving more slowly at the molecular level. They also found that the average rate of chromosomal change in mammals was about 20 times higher than in frogs in contrast to the rate of protein evolution. It takes on average, 3.5 million years for a pair of mammalian species to develop numerical chromosomal differences whereas in frogs, it takes on average 70 million years. Accordingly, the authors attribute the decoupling in the molecular and morphological evolutionary rates to the importance of change in regulatory genes.

In a computer simulation designed to mimic the developmental rules that control cellular self assembly, Nijhout et al.(1986) found that within the generated phylogenies, genetic parallelism could not be superimposed upon morphological parallelisms. In other words, "genetic heterochronies do not lead to morphological heterochronies"(1986:455). The reason being that genetic effects are modified by their morphological, biochemical, physiological, and genetic contexts. It would seem that epistasis was also being modeled in these simulations.

For all the genetic variability contained within a species, it is nothing short of amazing that there is so

much phenotypic standardization (Mayr 1970). Some
genetic mechanisms must exist to constrain the filling
of all potential morphospace. Throughout the process of
meiosis and recombination, the genome still manages to
retain the capacity to generate stable entities in some
recurring morphospace. Regulatory regions of the genome
are supposedly responsible for such stabilization. The
concept of developmental homeostasis (i.e. canalization
according to Waddington (1975) and autoregulation
according to Schmaulhausen 1949)) was developed to
explain how it is that favored phenotypes are allowed to
persist across generations in the face of mutation and
recombination. Interestingly then, regulatory genes have
been used to explain both rapid morphological changes
(Goldschmidt 1940; Bonner 1982) and developmental
conservatism (e.g. constraints). This developmental
conservatism makes the genome a sort of privileged level
of the biological hierarchy since the accumulation of
micromutations can occur without immediate phenotypic
effect (Eldredge 1985). Therefore, morphologically
conservative groups can become genetically diverse.

The threshold effects of this gradually built-up
pool of micromutations are for Levinton (1988) evidence
that rapid morphological change can be easily

conceptualized into the Modern Synthetic idea of
evolution via simple gene frequency changes. Gould
(1982) on the other hand reasons in a reverse manner. He
(1982) argues that the morphological leap will occur as
a result of a regulatory mutation and that post facto
micromutations will modify its original effects. There
is no known reason to prefer one scheme over the other.
Threshold traits are easy enough to understand in
principle (Falconer 1981) as are models which suggest
that there are a small number of genes of major effect
and many more with minor, gradually decreasing effects
(Matthysse et al.1979). For example, the heading time in
wheat has 80% of the additive variance accounted for by
a single locus with 14% accounted for at 3 other loci.

Since the unveiling of the Punctuated Equilibium
theory, by Eldredge and Gould in 1972, its impact on the
way human evolution has been interpreted has been
profound. Arguments over the biological and statistical
meaning of stasis (Cronin et al. 1981; Eldredge and
Tattersal 1982;) especially regarding the evolution of
Homo erectus (Rightmire 1986; Wolpoff 1984) has
generated greater animosity than insight into the
biology of our genus' first out-of African migrant.

Perhaps studies similar to that of Michaux (1989), that relate synchronic variability in a species to asynchronic, temporal variability within the same lineage, will help in discriminating unidirectional trends from patterned oscillations. For Michaux's (1989) study, 10 measurements were taken on 700 shells of 4 distinct modern gastropod species. These measurements were then used to define the phenotype in multidimensional space. Species allocation rules were then developed via canonical discriminant analysis and subsequently applied to 644 fossil specimens of 3 of the 4 taxa. It was discovered that the fossil specimens occupied the same phenotypic space as their modern descendents. Through time though, the means of the fossil sample oscillated about the mean of the extant samples. These oscillations coincided with climatic temperature changes. While fossil samples of hominids may never be able to add up to the 'ideal' samples obtainable in invertebrates, the results of these types of studies should be kept in mind when interpreting patterned temporal variability within a lineage.

The debate over human origins has not been over the nature of stasis but the tempo and mode of change when change occurs. Of what taxic relevence are the changes

taking place in African archaic H.sapiens? Tattersal
(1986) contends, quizically in my opinion, that even
though taxic and morphological change may not coincide,
the fact that morphs assignable to archaic H. sapiens
can be recognized is reason enough to designate them to
the rank of separate species. He bases his judgement on
the observation that closely related primate species,
while distinct, are usually difficult to recognize
skeletally. Given fossil samples, Tattersal believes
species diversities to have been underestimated by
excessive lumping at the species level. This argument is
weak [for the same reasons that all such arguments are
weak] in that there is inherent circularity in equating
morphologcal with taxic variance (even though he
acknowledged that issue) (Larson 1989). Another reason
for being cautious of such arguments is that they
constrict the definition of Homo sapiens to variation
existing in modern populations. Modern humans have not
always looked as they do now. Frayer (1985) has studied
trends in dental reduction in anatomically modern humans
since their appearance in Europe. Smith (1985a) documents
the robusticity and even the retention of archaic
features in early moderns such as Mladec 5. Modern
skeletal biologists recognize the existence of unique,

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human geographic variability. Because the nature of traits 'defining' races is essentially continuous, it is the assemblage of these traits, their patterned covariance that makes racial identification possible. Why restrict this recognition to the biological present?

Genes do not code for proteins that have either single effects or singular magnitude of influence. Genes code for proteins that given their environments exhibit a _range_ _of_ _effect_ _magnitudes_. Individuals then are ensembles of these effect magnitudes (Lewontin 1983). These effect magnitudes are technically termed reaction norms. Studied in detail by Schmaulhausen (1949) and Stearns and Koella (1986), the norm of reaction is that range of environment in which gene products can perform adequately for the viability and performance of the organism. The propagating effects of early ontogenetic change will most often result in nonviability because the induced nonlinear consequences exceed the reaction norms of later or contemporary structural/regulatory products. So for evolution to occur at both the genetic and morphological levels, not only must there be sufficient allelic diversity but this must translate into a diversity of reaction norm ranges.

The norms of reaction and its genetic underpinnings are the raw material upon which natural selection can act (Lewontin 1983). There are several implications to be drawn from this statement. First, there should be a directrelation between structural complexity and rate of evolutionary change. The greater the number of components, the greater the norm of reaction ensemble translatable into phylogenetic transformation. In hominid evolution, I would argue that the most complicated skeletal structure, the cranium, shows the greatest degree of change. Zelditch (1988) studying ontogenetic variation and phenotypic integration found that the pattern of covariance between dimensions measured in the growing rat limb was time invariant whereas the covariance pattern of the cranium changed with time. The intensity of the integration also seemed to be greater in the limb than in the skull.

The cranium, as a composite of multiple tissue types (Gans 1988; Enlow 1975), is classified as a developmentally complex trait (Atchley and Newman 1989). Cheverud (1982a) concludes that the high genetic and phenotypic integration in the developmental and functional complexes in the adult Macaque cranium is due to intense stabalizing selection. However, genetic

correlations were found in traits that had no functional or developmental relationship. Cheverud (1982a) hypothesizes that these non-functional correlations arose as random processes (i.e. drift) and may indeed be a ready source of evolutionary possibilities.

In a discussion of evolutionary (developmental) constraints, Cheverud (1984) and Slatkin (1987) cite the degree of variability and the degree of trait correlation as important constraints on the path and rate of evolutionary change. Gans (1988) comments that evidence of congenital deformities would indicate that the cranium and face are not so tightly integrated to prevent substantial mosaic evolution. Similar to the nature of 'regulatory' genes, integration can lead to both homeostasis and radical design change.

Secondly, the changing variance-covariance structures during ontogeny (Atchley 1984; Atchley and Newman 1989) will result in reaction norm ensemble change proportional to the complexity of the structure. Because variance-covariance structures change during the course of ontogeny, phenotypic responses to selection will be age specific (Atchley and Newman 1989). Duration of developmental stages is also an important

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consideration since extended durations are more accessable selective targets (Slatkin 1987).

Riska (1986) observes that if the pattern of genetic variance-covariance is determined early in ontogeny and the genetic correlations between traits remain strong across age stages, then selection acting on variability in the adult stage may have effects on patterns early in development as seen earlier in the discussion on the Japanese quails.

Genes that regulate batteries of structural genes are important because when mutated, may cause disproportionate morphological divergence between individuals. Their potential for spread, fixation, and variation will for any given case determine their evolutionary importance. While discussions of the relationship between genetics and development have tended toward focus on the individual (i.e. rate genes) we must not neglect the fact that populations are the primary evolutionary units. Population genetics can offer great insight into the evolution of ontogenies.

Variation is everwhere, so what does it mean? Lewontin (1972), arguing for the banishment of the race

concept in human populations calculates that of the 15%
of total species blood marker variability found among
populations, only 6.3% is accounted for by racial
classification. Convinced that this small amount
counters biased perceptions of relatively large racial
morphological differences, Lewontin concludes that human
racial classification has, "no genetic or taxonomic
significance", and therefore,"...no justification can be
offered for its continuance"(Lewontin 1973:397).
Regardless of Lewontin's view on the value of racial
classification, of importance here is that if blood
marker diversity is indicative of the genotypic
diversity and human racial groups differ predominantly
in their frequncies, then the amount of phenotypic
variation we see in human populations is accounted for
by little allelic diversity. How can this occur?

Little concrete is known of the adaptive
significance of genetic variability (Koehn and Hilbish
1987). For what is known of phenotypic polymorphism, not
much is known of either its genetic basis or what
ecological circumstances might favor or disfavor certain
genotypes. That genetic variability is extremely
important is generally obvious. What is not so obvious,
for any specific case, are the forces acting to remove,

increase, or keep balanced the levels of polymorphism (Koehn and Hilbish 1987).

Brose and Wolpoff (1971) consider the magnitude of morphological variability in "classic" and "non-classic" Neandertal populations. They find enough craniofacial variability in these groups to eliminate both the classic/non-classic dichotomy and the idea that Neandertals were quite homogeneous (See also Smith 1976). What became apparent to Brose and Wolpoff (1971) was that, "Neandertals overlap with anatomically modern H.sapiens in almost every morphological feature, as well as almost every metric one"(1971:174). In fact, the "classic" Neandertals shared the greatest metrical similarity with Upper Paleolithic Europeans. For polygenic features, an assumption (not considered exclusive) is made that the genes contributing to the phenotypic variance of the trait each has equal, additive, and small effect (Falconer 1981). If Neandertals metrically overlap modern humans in the ways described by Brose and Wolpoff (1971), are the differences to be explained by gene frequency differences? Perhaps; this would be consistent with modern racial differences and thus expected if we see

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Neandertals as an extinct human race. How would these gene frequency differences come about? To better reflect the historical relationship between Neandertals and modern humans while generating a more specific question respecting their potential genetic differences, it would be better to ask -- what populational forces acting within and between populations of archaic H. sapiens in Africa and Europe would yield daughter groups (anatomically modern humans and Neandertals respectively) with relatively little structural genetic divergence?

Epistasis and recombination are important components of phenotypic variability. Development is, at the genetic level an epistatic phenomenon. Gene function must be consistent with, is influenced by, and influences the total genetic environment. According to Mayr (1970), the genome is internally coadapted."Regularity of gene function is thus the result of developmental regularity as well as a cause of it" (Oyama 1988:261).

While mutation may be the ultimate source of new genetic variation, recombination is the greatest proximate source of phenotypic variability in sexually

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reproducing organisms. According to Minkoff,

> Because genes interact with one
> another, and because many characters
> are controlled by several genes,
> genetic recombination may result in
> totally novel phenotypes, as well as
> in new combinations of previously
> experienced character states
> (1983:130).

Mayr(1988:446-47, 473-474) in defending his idea of genetic revolutions as the basis for peripatric (i.e. Type II allopatry) speciation, describes the genetical dynamics of founder populations:

"(1) The founders...carry only a fraction of the total genetic variability of the parental population.

"(2) The extreme inbreeding of the ensuing generations not only leads to increased homozygozity but also exposes many if not most of the recessive alleles (now made homozygous) to selection.

"(3) The elimination of many previously existing allelic and epistatic balances may result in a considerable loosening up of the genetic cohesion of the geneotype.

"(4) Such genetically unbalanced populations may be ideally suited to shifts into new niches such as will be

available under the changed environmental conditions of
the location of the founder population.

"(5) The genetic reorganization might be sufficiently
drastic to have weakened genetic homeostasis
sufficiently to facilitate the acquisition of
morphological innovations.

"(6) the drastically different physical as well as
biotic environment of the founder population will exert
greatly increased selection pressures"(1988:446)

The combination of these factors would initiate a
genetic revolution resulting in genetic reorganization
and rates of genetic turnover orders of magnitude higher
than the widespread parent population. The non-
representative genetic sampling would, because of
epistasis, alter substantially the genetic environment
at most loci at once. Furthermore,

> ...this 'genetic revolution',
> released by isolation of the founder
> population, may well have the
> character of a chain reaction.
> Changes in any locus will in turn
> affect selective values at other
> loci, until finally the system has
> reached a new state of equilibrium
> (Mayr 1988:446).

Interpopulational phenotypic variability then would be the product of differences in patterns of epistatic balance. Mayr (1988) with Carson and Templeton(1984) believe that the decisive factor in the process of genetic restructuring is recombinatorial rather than mutational.

Kauffman (1985) has generated a model of self-organizing regulatory networks. With special emphasis on mutational transpositions, Kauffman explains their effects as randomizing regulatory connections within developing systems. This scrambling of genetic elements to "new regulatory domains generate both more and novel regulatory couplings among loci"(Kauffman 1985:179). This scrambling, process wise, is comparable to recombination. Wright (1969:26-27) finds that mathematically, "ordinary recombination may indeed be treated as a sort of mutation"(1969:26).

Genetic drift may also open up ontogenetic variability by depressing heterozygozity. Palmer and Strobeck (1986) have reviewed the relation between protein heterozygozity and fluctuating assymetry. Fluctuating assymetry is assumed to be a measure of developmental instability (Soule 1979). There appears to

be an inverse relation between heterozygozity and
fluctuating asymmetry. Increased levels of
heterozygosity confer better buffering abilities to
developing organisms, reducing environmental noise.
Hence, there is low intraindividual variability when
populational variability is high. To Soule (1979), the
paradox of no positive correlation between morphological
and structural gene variability disappears if one
accepts that " heterozygosity is expressed among
individuals in a way different from that within
individuals"(1979:399).

So population genetics can offer insight into how
population structure can help direct groups into new
morphospace. As an application to the Neandertal
extinction 'problem', the principles outlined above
concerning the effects of genetic drift have been used
before. Howell (1952) anticipated this entire discussion
by stating that, "Differentiation will also take place
through recombination, or the rearrangement of genes
present beforehand in the genotype"(1952:402). He
continues:

            Actually so little is known of the
            significance of "racial"
            characteristics in living
            populations that any suggestions as

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to the adaptive nature of "Classic
Neandertal" morphology can only be
of uncertain validity at the present
time. The morphology of this group,
is to be sure, a distinctive and
peculiar one, so that it is possible
to recognize the group as a
geographically localized racial
entity, the result of prolonged
isolation during the first stadial
of the Fourth glaciation. The actual
mechanism of this differentiation
may have been drift(1952:402).

Howell (1952) cannot accept that the Neandertal

facial and cranial base morphology is either the direct

effect of drift or a by-product of some drift effect.

Although drift has undoubtedly
played an important role at times in
the evolutionary history of man, at
the food gathering level selection
is undoubtedly important. Since,
however, practically nothing is
known of the adaptive nature of
morphological traits in man, one is
too easily led to the conclusion
that certain phenomena may be the
result of drift and such an
explanation allowed to suffice. The
writer is convinced that, at least
in the structure of the "classic
Neandertal" facial skeleton and
cranial base, selective forces have
been the major contributing
evolutionary factor at work, genetic
drift having been of minor or
negligible import (1952:403).

Within the context of discussing the morphological

homogeneity of "classic Neandertals", Howell (1952)

comments on the potential effects of inbreeding. Suarez
(1974), testing and rejecting Brace's Probable Mutation
Effect, found that Neandertals had higher levels of
fluctuating asymmetry relative to modern humans. Given
the results, Suarez infers that Neandertals may have
been more inbred than modern human populations. In fact,
the pattern of asymmetry was similar to that found in
modern groups, suggesting that "Neandertal dentitions
were responding to approximately the same set of genetic
instructions as modern mans"(1974:415).

Given this information, an idea is suggested that
while necessarily speculative, is also compelling.
Dobzhansky (1937) reports that crossing races of
Drosophila pseudobscura leads to a developmental
disruption of testes size. Hybridization, which in this
case resulted in male sterility, could have resulted in
the disruption of cohesive, coadapted gene pools.
Introducing new alleles and gene complexes to new
genetic environments can have disruptive epistatic
effects. Gupta(1978:586), in back crossing experiments
with the sibling species Drosophila pseudobscura and D.
persimilis found no evidence of resultant developmental
instability. In fact, the F1 hybrids appeared to be
better buffered than parent groups. What could explain

the two sets of results? Gupta (1978) believes the developmental instability did not exist, "for the characters examined because the requisite genetic differentiation at 'regulatory loci' has not occurred during the differentiation of these two species"(1978:586). If the argument can be made that the fluctuating asymmetry observed in Neandertals is produced by inbreeding (Suarez 1974), then small effective breeding populations can be inferred. While inbreeding in some degrees tends to destabilize developmental pathways, it is only in the initial generations that genome destabilization is observed (Mayr 1988). In the ensuing generations, a "new state of equilibrium will be reached"(Mayr 1988:446).

Highly coadapted genomes can be found in small populations with small effective breeding sizes since high levels of inbreeding place restictions on recombination. Large populations do not display such highly coadapted states because of the large levels of outbreeding (Templeton 1986) and unrestricted recombination. When these small inbred populatiions outcross, internally coadapted genomes are disrupted, resulting in hybrids with reduced fitness. This

phenomena is termed outbreeding depression. Large populations are not so effected because their normal outcrossing levels are already high (Templeton 1986).

The implications for the punctuationalist and multiregional models for modern human origins are interesting. If, hypothetically, populations from Africa or Southwest Asia are characterized by high levels of outcrossing and lesser degrees of internal coadaptation and Neandertals by small populations with highly coadapted genomes (resulting form restricted recombination) what would be the consequences of their interbreeding. Assuming that the gene pools have been allowed to diverge sufficiently one might predict that the extinction of the Neandertal gene pool took place because of the differential response to outbreeding. In-coming populations could absorb Neandertal genomes with little effect on fitness. Neandertal gene pools on the other hand would have suffered from genetic instability as modern genes diffused into them. By sheer numbers, the effects of population history, and unrestricted recombination, the Neandertal genetic complex was lost.

An Alternative to Allopatric Model Dynamics

If my hypothetical assignments of population history are retained yet disparity in gene flow is not, then an interesting theoretical twist is produced. Hybrid depression would have served to keep the groups genetically distinct. If this were the case, then selection should act centrifigally to generate greater character displacement with time. The implication is that if there was going to be speciation, it would have been sympatric not allopatric. Also, the speciation process would have taken place in Europe or Southwest Asia and not Africa. Southwest Asia would be a likely hybridization zone since it is the only region where Neandertals and early modern humans are contemporary in time and proximate in space (Vandermeersch 1989).A prediction generated by this model would be that Neandertals and modern humans would become more morphologically differentiated over the period of temporal overlap. Late Neandertals such as St. Cesaire should be more morphologcally distant from temporally proximate moderns such as Cromagnon than the earliest modern humans from Skhul and Qafzeh would from the early Neandertals.

For this hypothesis, it could argued equally that Neandertals and early modern humans were very divergent populations within the same species or that they were closely related but different species. Biologically, the dynamics are identical. If these groups are different species, then the dynamics of their speciation, if this model has validity, has been grossly oversimplified. As oppossed to the total replacement model proposed by Stringer and Andrews (1988) and others who argue that speciation came before interaction and entailed no interbreeding, this model contends that speciation occurred synchronously with contact and took place because of gene exchange. If the archaic and modern H.sapiens were different species at the time of contact, it did not interfere with their gene exchange.

This model assumes population parameters and structures for which no evidence exists. There is certainly no indication, given the archaeological evidence that there were population structure disparities between early modern and European archaic H.sapiens either previous to or during their temporal overlap. I simply wish to point out that a wide variety of speciation scenerios can be used to interpret the fossil sample as it stands and the one proposed by

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Stringer and Andrews (1988) demonstrates nothing that would be prefered. Also, the later part of this discussion has focused on an aspect of genetics rarely linked to development, the relation between population structure, genome structure, and ontogeny . For paleontological interpretations, scenerios based upon nondescript regulatory genes are interesting but not very helpful since their identification may be impossible. It is for this reason that population level dynamics is emphasized.

CHAPTER III

CRANIOFACIAL DEVELOPMENT

Of all the skeletal elements, the growing cranium
can be singled out as exemplifying all three bony growth
processes-- endochondral, sutural, and
appositional (Enlow 1975). There is general concensus
that sutural growth is essentially passive, externally
regulated by an expanding neural mass (Moss 1976a).
Koskinen et al. (1976) find that the structural details
of the various cranial sutures, "appear to be related to
functional demands"(1976:515). In other words,
responsive to a mosaic of locally specific growth
fields. Similar commentary has been made for the
basicranial endochondral growth plates. Their growth,
according to Moss (1976a) is also directly responsive and
controlled by the expanding brain. One of the many
debates among students of craniofacial growth is the
predominance of intrinsic versus extrinsic factors
governing the active cartilaginous growth centers.
Patterns of remodeling, while quite complex and
important will be discussed but deemphasized since they
will not be analyzed in this study.

The evolutionary of the cranial base has been recognized by many workers. Huxley saw the cranial base as a 'relatively fixed baseline' for which to analyze evolutionary change in the cranium:

> It will be obvious from an inspection of the diagrams that the basicranial axis is, in the ascending series of Mammalia, a relatively fixed line, on which the bones of the sides and the roof of the cranial cavity and the face, may be said to revolve downwards and forwards or backwards, according to their position(1863:196-197).

Weidenreich (1946) associated the flexure of the cranial base with an evolutionary trend towards brachycephalization. The importance of cranial base flexure was due to its profound influence on the dorsal, anterior, and superior expansion of the vault (Weidenreich 1943). DuBrul and Laskin (1961) summarizing their experimental work, feel that the cranial base has "potent pre-adaptive value"(1961:117) and as a scaffold for the cephalic organs, permits differential growth directions and rates. For instance, DuBrul and Laskin (1961) conclude that both the frontal and overall vault curvature are the products of the bending pattern of the cranial base.

Much of human evolution involves changing patterns of vault curvature. The position of the base upon the cranial floor will influence its relation to the cranial roof, making cranial base morphology of special importance. On a more general note, Gould (1977) finds the basicranial axis yet another example of neotony. Refering to the spheno-ethmoidal angle (Ba-Prosphenion-Na), Gould (1977:379) argues that the relatively closed angle spheno-ethmoidal axis in newborn humans is a paedomorphic retention since its opening up does not proceed to the degree found in other primates. Dean and Wood(1984) take Gould (1977) to task and find the growth of the cranial base a composite of growth patterns and therefore resistent to any single heterochronic assignment.

Experimental evidence, gathered through surgical modification of specific growth sites in non-primates implicate the cranial base as a key structure in understanding the developmental pathways separating Neandertals from modern humans. All of the major craniofacial features: frontal angulation, facial projection, cranial length, degrees of flexure, cranial height, and occipital configuration are shown to be influenced by the cranial base. What is particularly

exciting is that strategic alterations in the
basicranial growth centers may alter all of these
dimensions at once. What follows is a brief summary of
the patterns, processes, and problems encountered in the
study of the developing basicranium. Prenatal growth
will be emphasized since, "Most investigators feel that
major postnatal growth patterns are determined
prenatally and that postnatal growth is a continuation
of a process that is established prior to birth" (Mauser
et al.1975).

Cranial Base Defined

While traditionally, the cranial base has been
defined as the length of an imaginary line joining
nasion and basion, this line masks the structural
complexity of the base. Before describing the segments
making up the cranial base, landmark definitions are in
order. Nasion is the most anterior point on the anterior
margin of the frontonasal suture. Basion is the lowest
and most anterior point on the anterior margin of the
foramen magnum. Sella point is the center of the bony
crypt forming the sella turcica and is determined by
inspection. Fronton is the lowest point in the frontal
wall as the skull bends in a more or less sharp curve to

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be continous with the roof of the nasal cavity. Fronton is found by inspection and is used by some to avoid the influence of appositional growth at nasion. Bolton point marks the height of the curvature at the junction of the occipital condyle with the lateral portion of the occipital bone. Brodie (1941) feels that Bolton is preferable to Basion in radiographic studies.

The cranial base itself is a composite of the midline frontal, ethmoid, sphenoid body, and the basioccipital. This composite lies along the inferomedial axis of the cranial floor. For most analyses, the various cranial base measures are artificial, crosscutting several segments. These artificial measures include Basion-Nasion length, anterior base length (Sella-Nasion), and posterior base length (Sella-Basion).

The anterior base includes that portion of the sphenoid body anterior to the midsphenoidal synchondrosis (unfused during most of fetal life) termed the presphenoid. Also included are the ethmoid (cribiform plate) and the midline frontal. Separating these components are two sutures. The sphenoethmoidal suture (considered a synchondrosis early in development)

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separates the presphenoid and the ethmoid plate along the lesser wing. The frontoethmoidal suture separates the frontal from the ethmoid. While Michejda (1972) plays down the importance of the sphenoethmoidal as an important determinant of craniofacial shape, it is probably this site where much of appositional postnatal growth anterior base growth occurs; this includes the late childhood growth spurt (Roche and Lewis 1976).

The posterior base shares anteriorly the midsphenoidal synchodrosis with the anterior base. It is made up of two bony segments; the anterior most segment, the postsphenoid (basisphenoid), will ultimately fuse to the presphenoid to form the sphenoid body proper. Posteriorly, the postsphenoid is connected to the basioccipital (the forward most extension of the occipital bone) via the spheno-occipital synchondrosis. The spheno-occipital, in humans, fuses in the middle teens and is responsible for most of the posterior growth of the posterior base and rearward migration of the foramen magnum (Schulter 1978). Attached to the flanks of the postsphenoid are the greater wings. The greater wings articulate, via sutures, with the frontal, parietal, and the petrous/squamous portions of the

temporal bone. Both the lesser and greater wings help to make up the eye orbits. Inferiorly, the pterygoid complex is continuous with the greater wings, and this complex is an important attachment site for the jaw (internal and external pterygoids) and laryngeal (superior constrictor) musculature (Leonard 1984).

Flexure dynamics of the cranial base will occupy a great deal of the following discussion. For most analyses, flexure is measured by the angle formed at the intersection of two planes formed by the anterior and posterior base. The anatomical point of intersection is the Sella point. An open or flattened base describes a large obtuse angle. A closed, flexed, or deflected base describes a smaller more acute angle. The dynamics of the flexure process has generated its share of the craniofacial literature, and for good reason, "The basicranium is the platform upon which the midface is constructed, and the dimensions and orientation of the nasomaxillary region relate directly to the corresponding size and alignment of certain parts of the basicranium" (Enlow 1976:198).

The cranium as a whole, and the sphenoid in particular would be classified by Atchley and Newman

(1989) as a developmentally complex trait; meaning
that it is made up of parts of differing embryological
origin with each having its own ontogenetic trajectory
of characteristic shape. To compound this developmental
complexity, the contributions of the differing
embryological tissues do not match the divisions of the
adult skull (Gans 1988:3).

The events that together generate the human cranium
and face are at their most impressive during the time of
preembryonic [fertilization to 2 weeks post conception
(PC)], embryonic [2 - 8 weeks PC], and early fetal life
[8 - 12 weeks PC](Ranley 1988). In early morphogenesis,
patterns of tissue differentiation, migration, growth,
and interaction are understood in basic outline.
According to Burdi(1976), an appreciation for how the
early mesenchymal model is transformed into a chondro-
osseous unit is mandatory because it is the mesenchyme
tissue that sets the pace for future cranial base
changes.

The basicranium initiates development during the
fourth week PC from mesenchymal cells that lie between
the cranial part of the neural tube and the foregut
(Ranley 1988). Specifically the bones of the

craniofacial skeleton form from or within mesenchyme surrounding the cerebral hemispheres. The facial region forms from within the pharangeal pouches (Burdi 1976). From this stage, bones of the cranial vault and facial skeleton bypass a chondrification stage and proceed directly to intramembranous bone tissue. Since the embryonic mesenchyme is the last developmentally common tissue type shared by the chondro- and intramembranous skeleton, the importance of mesenchymal pattern is underscored.

At around the fourth to fifth week PC, mesenchymal masses underlying the brain proliferate and condense, giving rise first in the occipital region to the earliest distinct cranial base elements (Burdi 1976:82). These condensations will go on to form the desmocranium (which in turn forms the intramembranous skeleton) and the chondrocranium which serves as the cartilaginous precursor to bone formation (Ranley 1988). Within the sphenoid, these condensations form numerous centers on intramembranous and endochondral growth. There are two centers of intramembranous growth in the sphenoid, the pterygoid plates and the greater wings, both of which appear 8 weeks PC. Endochondral centers are found in the pre- and postsphenoid bodies and in the lesser wings.

The appearance of 2 ossification centers within the presphenoid and postsphenoid takes place at nine and twelve weeks respectively. The lesser wing houses an ossification center on each side beginning at approximately 12 weeks PC (Mauser et al. 1975).

At this early stage in development, the growing brain demonstrates a stong influence on the size and shape of the mesenchymal model. These influences in turn serve also to influence the spatial patterning and development of the face, palate, and pharynx.

Until the late embryonic period, the sphenoid components are bilaterally distributed as condensation centers about the midline. At approximately the 7th week PC, widespread fusion of the elements takes place, forming the body and wings of the sphenoid. It is also at this time that the ongoing closure of the pontine flexure (a bend in the rhombencephalin) begins to raise the head from the ventral chest wall (Ranley 1988). This process initiates the wonderfully orchestrated closure of the palate that involves the mandible and tongue (Diewart 1985). This marks the end of the embryonic period.

Diewart (1982,1983,1985), in a series of studies
has filled a gap in our knowledge of basicranial growth
dynamics in the 7 to 10 week PC period. Some of her
major findings are summarized in the following
paragraphs.

Facial dimensions increased primarily in the
sagittal plane. The percentage increase in various
features emphasize this conclusion. From embryonic stage
19 to 10 weeks PC, the anterior base increases 213%,
maxillary length, oronasal cavity, and mandibular length
increase 309%, 258%, and 383% respectively (Diewart
1983). The rapid growth of the mandible reflects the
period when the Meckels cartilage forms the major
skeletal element in linear growth. In contrast, the
posterior base and crown-rump length increase only 158%
and 171% respectively. This would certainly imply the
incorporation of the anterior base into a facial growth
complex.

The greater sagittal growth stands in contrast to
the vertical and lateral growth. In association with the
anterior growth of the mandible, the growth of the
tongue and its everchanging position with respect to the
maxilla aids in the process of palatal closure.

Diewart(1983) and Ranley (1988) see no direct

relationship between vertical growth and lingual descent

but it does make sense that during this critical period

of palatal closure, lateral growth should be suppressed.

The second point made by Diewart (1983) is that

after the early fetal period, the cranial base angle and

overall craniofacial form remains stable.

> During the fetal period, the change
> in most craniofacial dimensions were
> similar, and facial growth appeared
> to be uniform(1983:507)...Results
> suggest that rapid forward growth of
> the face during the late embryonic
> and early fetal period creates a
> pattern of facial form that appears
> to be maintained during the later
> prenatal and postnatal growth of the
> craniofacial complex (1983:517).

During the embryonic period, the angulation between

cranial base components and the primary palate increased

between stages 19 and 20. After stage 20, the angulation

remained unchanged. The angular position of the maxilla

relative to the anterior base increased significantly

during this time and thereafter, remained unchanged.

With regards to the base angulation (Ba-S-Na), after an

initial increase between stages 19-20, an angle of 127

degrees was attained in stages 20-21 and remained

unchanged during the 7-10 week PC period. The similarity

to the postnatal angle leads Diewart to believe that this early period marks the establishment of the cranial base angle. Diewart(1983) goes on to claim that studies such as Ford's(1956) which show angulation change are either due to deformation or overrepresentation of near term infants. In defence of Ford (1956) and others such as Burdi(1969), if the angle was stable as Diewart supposes, it is difficult to see how representation of near term infants would alter her conclusions.

Muller and O'Rahilly (1980) in a study of 8 week postovulation embryos (stage 23, 27-32 mm CRL (crown-rump length)) found that a good deal of variability exists in the Ba-S-Na angulation. In embryos 20-31 mm CRL, angles ranged from 115-133 degrees. However for larger embryos (up to 93mm) a trend increased angulation was found. Two of the embryos, 50mm and 93mm in length were found to have angles of 102 and 106 degrees respectively. At this early stage, increasing angulation is not surprising and should even be expected due to the rapid forward and downward growth of the anterior base.

Trenmouth (1984) quantified and graphically represented fetal craniofacial growth between 1.8 and 5.4 months gestational age. He found that contrary to

the views of some workers who characterize the latter stages of fetal growth as simply the expansion of a static stable profile (Burdi 1969; Diewart 1982,1983,1985), there was indeed substantial shape change. After normalizing for size, he found that in lateral view, head shape changed from a square shape to an ovoid configuration. This relects rearward and forward expansion of the brain. As the cranial shape change was taking place, the face was rotating underneath with general downward displacement. The mandible increased its relative size by upward and backward extension of the ramus and condyle region. In the early groups(1.8 - 3.0 months), basal flattening was observed. The relation between this flattening and mandibular and maxillary rotation is well known. Postnatally, Kerr and Adams (1988) found an inverse relation between cranial base angle and mandibular prognathism, less so with maxillary prognathism.

In frontal view, craniofacial shape became less round and more ovoid due to vertical elongation of the upper face. Facial height increased and the mandible enlarged laterally in the ramus and condyle region altering the lower face from a 'V' shape to a 'U' shape.

In basal view, the foramen magnum migrated posteriorly as the occipital region expanded. Trenmouth (1984) sees neural expansion as going hand-in-hand with basal flattening in developing humans, " the cranial base flattens out as the brain expands in the frontal and occipital regions, tilting the face relatively downwards and backwards"(1984:649). As part of the flattening process, the anterior base moves downwards and forwards while the posterior base moves upwards.

As testament to the importance of brain growth to the process of flexion, Trenmouth (1989) examined and compared 11 anencephalic fetuses with the 60 'normal' fetuses used in the 1984 study. The fetal anencephalics ranged in age from 3.8 months to 5 months PC. What Trenmouth (1989) uncovered was a reduced cranial size, a cranial base that was much shorter than normal, and a basicranial angle (Ba-S-Na) with retained acuteness (app. 90 degrees). Of particular interest, and for future reference, is the pattern of shortening in the cranial base. The shortening was not simply a product of reduced Nasion-Basion distance by angular reduction (bringing the anterior and posterior arms closer together)."This discrepency was most marked posteriorly

and decreased anteriorly"(1989:219). This is most interesting in the light of the general concensus that the supposedly more rapid growth of the anterior base reflects the neural growth pattern. If this were indeed the case. one would expect to see the anterior base showing the greatest reduction.

Commenting upon the confusion over the lack of detection by Diewart (1983) of cranial base flattening, Trenmouth (1984) comments that the opening angle is masked by the upwards and backwards migration of sella (kinking) during flexure.

Lavelle (1974), feeling that multivariate methods best represent the multivectorial character of growth, analyzed 280 male fetuses ranging from 4 to 10 lunar months. Lavelle acknowledges that the study of the fetal period is important, "since it is during this time that the future proportions of the craniofacial skeleton are established"(1974:269). Using canonical analysis, review of the eigenvalues led him to conclude that the length of the anterior base and upper facial height contributed most to the separation of the age groups. The degree of separation was less in the 6 - 7 month period than in the 7 - 8 month period suggesting some fluctuations in

the growth patterns. Calculating percentage growth rates
of the anterior and posterior base, Lavelle (1974) finds
a 112% and 93% increase respectively. Cranial base angle
is concluded to change little during the analysis
period. However, Lavelle (1974) uses Bolton point
(defined by Lavelle as a location on the upward
curvature of the retrocondylar fossa) in the angular
measure instead of Basion. Since the foramen magnum
migrates posteriorly, it is difficult to see how Bolton
point fully represents the flexure process enough to
register flattening.

Ford (1956) analysed 72, 10 - 40 week old fetuses.
Regressing the anterior base to the posterior base, he
found that the posterior base grows only 48% as fast as
the anterior arm (Anterior base = 0.48(posterior base) +
2.5). Measuring various facial angles change with time,
Ford (1956) found that from 10 - 40 weeks, the Ba-S-Na
angle opened up 13.6 degrees. Ford interpreted the
flattening teleologically, saying that it was an
adaptation to maintain basal length as the brain and
cranium grew. Ford claims that the anterior base has a
more neural like pattern like that of the vault, which
does not explain its association with the facial
complex. Another angle analysed by Ford(1956) was the

Sella-Nasion-Prosthion angle which measures maxillary

prognathism. He found no significant change about a mean

of 78 degrees, leading him to conclude that the degree

of 'true' prognathism depends upon the position of the

nasal septum relative to the alveolus and is fixed by

the early fetal period. For Ford, a dominant component

of facial growth during the fetal period was the

cartilaginous nasal septum. Many workers such as

Latham (1970) and Copray (1986) believe the nasal septum

is a starter mechanism for facial growth. Moss (1976b)

after critically evaluating some experimental literature

finds that, "the nasal septum is a structurally complex

member of the facial framework whose growth is secondary

to, and compensatory for, prior passive translations of

midfacial bones"(1976b:196). It is the case that the

early nasal cartilages are contiguous with the anterior

base cartilages. This intimate relation with the

cartilaginous base may be an important component of

midfacial prognathism. On account of the intimate

relationship between the the brain and the base,

prognathism may intimately reflect this relation.

Burdi (1969) for the most part reiterates Ford's

(1956) conclusions for the last two trimesters of

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gestation. Linear regression with the base segments as dependent variables and crown-rump length as independent variable shows that the anterior base has a slope of .513 and the posterior base a slope of .295. The anterior base constantly contributed more than one half of the total base length, e.g. 55% at 70mm CRL and 61% at 420mm CRL and Burdi noted an increase of around 12 degrees in the Ba-S-Na angle over the last two trimesters. In fact, Burdi(1969) reports a significant relationship between 4 of 7 craniofacial angles and age yet claims that the prenatal profile is stable, increasing in size yet not altering its shape.

Johnston (1974) takes Burdi (1969) to task on this point. Johnston (1974) examined 32 human fetuses from 26 to 72 mm CRL. The age range was 11.5 to 25.3 gestational weeks. Johnston discovered after transformation, that **all linear measures, except those involving the posterior cranial base (S-Ba and Ba-Na) were independent of head length.** During the second trimester, the face and anterior cranial base, but not the posterior base grew proportionately.

> ...at the level of resolution
> provided by a sample of 32,
> allometry begins in the posterior
> cranial base during fetal life and

for the anterior cranial base,
nasomaxillary complex, and mandible,
not until sometime after birth. It
should be noted that in early fetal
life, the cranial base and nasal
septum are a continuous mass of
cartilage(1974:625-626).

This work emphasizes the intimacy shared between

the anterior cranial base and the facial complex. Since

the anterior and posterior base regressions coefficients

were .29 and .14 respectively, it falls into line with

many other studies that show the greater rate of growth

in the anterior as oppossed to the posterior base

throughout fetal life. There is a problem though. If, as

nas been claimed (Ford 1956; Scott 1958) the anterior

base demonstrates a neural-like pattern of growth, and

the anterior base is intimately involved in the growth

of the face, then how is it that the face doesn't

exhibit a neural-like growth pattern?

Lavelle (1974) in his study of fetal craniofacial

development documents the discrepency between the facial

and cranial growth patterns, "...facial growth is both

slow and commences late, such that when the cranial

growth is almost finished, the facial bones are growing

rapidly"(1974:285). Baer and Nanda (1976) also recognize

the discrepency, in rats, between incremental growth

patterns in the vault, face, and base. The vault attains

its greatest growth much earlier than both the face and the base. It is the base and the face that share the similar pattern. As will be reviewed below, the seeming independence of the vault and facial/basal complex does not exist yet it will not involve dynamically the anterior base. The developing brain acts on the base in a way not specifically addressed in the literature. The analysis that follows this section will attend to the issue pointed out by Baer and Nanda (1976:521) of why the clivus (posterior base) should adhere to a general somatic pattern while all other base components do not.

The greatest amount of shape change in the cranium and face comes before birth. As growth proceeds toward adulthood, it would not appear to be simply a stable continuance of prenatal processes.

Brodie (1941) finds that the morphogenetic patterns of craniofacial growth are established by the third postnatal month and once attained, do not change. In a later study, Ortiz and Brodie (1949) focused on the period between birth and the third postnatal month. They found that there was a continuance of anterior cranial base growth with continued forward and downward movement of the face as measured by the motion of the anterior

nasal spine. Using Bolton point in their work, they, not surprisingly did not detect much in the way of growth in the posterior cranial base, concluding that the spheno-occipital growth plate was not an important growth center. This conclusion is clearly mistaken and only underscores the confusion created by interpreting processes (posterior base growth) by movement of non-homologous points. This is not to say that the position of Bolton is not related to the Basion. I only argue that it doesn't monitor in an acceptable manner the vertical displacement of Basion with growth.

Monitoring the degree of postnatal cranial base angle change, from a period of one month to 5 years 9 months. George (1978) found that after 1 year 9 months, no appreciable change occurred. Of particular interest is that up to 1 year 9 months, the cranial base actually became more acutely flexed.

The midspenoidal synchondrosis, the actual site of flexure, fuses in late fetal life. Moss (1976a) notes that in neonates, it can be seen as a wedge of cartilage on the endocranial surface of the sphenoid body. After fusion takes place, any flexure that occurs will not be generated by the same pathways as in prenatal life.

Earlier mention was made of a 'kinking' of the
midshenoidal at the time of its fusion (Michejda 1972).
This results in the rise of the tuberculum sella.
Lestrel and Roche (1986) using Fourier analysis
discovered that there were age and sex dependent shape
variation in the cranial floor. From 3 to 15 years of
age, the sella turcica in both males and females drifted
in a superior and anterior direction. Drift in the males
differed only in degree over the females. Since most
endocranial surfaces are resorptive at this time (Enlow
1975) it is unlikely that this drift is a simple product
of remodeling patterns. These processes are probably
responsible for the increasing angulation described by
George (1978).

Knott (1969,1971) monitored growth of the Ba-S-Na
angle and cranial base components in males and females
with ages ranging from 4 years to adulthood. She found
that what growth took place in the anterior base between
6 and 17 years did so mostly in the area between Fronton
and Nasion. That is, sinus expansion was the primary
force. The segment homologous to the prefusion
presphenoid showed no growth during the growth period
while the ethmoid demonstrated minimal linear growth. In

other words, aside from sinus expansion and appositional growth at Nasion, the anterior base has ceased active growth by approximately 7 years. The basioccipital on the other hand demonstrated continous and steady growth until 17 years of age, the approximate time of the closure of the spheno-occipital synchondrosis (Scott 1958).

Scott (1958) describes 2 phases of postnatal facial growth. The first phase involves the thrusting forward and downward of the oronasal region (driven especially by growth of the nasal septum) and secondly, after 7 years, appositional growth. This first phase will be discussed here.

During the first phase, brain expansion lengthens the anterior base. The majority of this growth ceases at the fusion of the sphenoethmoidal suture at 6-8 years of age (Michejda 1972) with continued growth coming from appositional drift at Nasion. Aiding the anterior and inferior movement of the face is the expansion of the nasal septal cartilages. Vertically, the expansion of the face is striking, due mostly to the enlargement of the nasal cavity. At birth, the nasal floor is at the level of the inferior margin of the eye orbits (Ranley

1988). Bjork and Skieller (1975), using implants found
that along with the septal expansion, apposition at the
alveolus accounted for 53% of the growth. Lowering of
the orbital floors covered only 25% of the total
vertical lowering. This low percentage can be explained
by the appositional growth within the inferior orbital
margin and resorption along the nasal side (Enlow 1975),
thus countering to some degree the downward trend.
Ricketts (1976) and Enlow's (1976) work on mechanisms of
mandibular and maxillary growth would indicate that
Bjork and Skieller's (1976) review oversimplified the
actual pattern of vertical displacement. Through complex
and interacting remodeling processes, the lower face
actually rotates in a superoposterior direction.

Circa the seventh year when fusion of the
sphenoethmoidal suture occurs the perpendicular plate
of the ethmoid unites with the vomer just posterior to
the septal cartilage. The septal cartilage does not fuse
during this period by benefit of its separation from the
vomeral groove by a layer of fat (Roche and Lewis 1976).
The union of the vomer and perpendicular plate does not
impede the forward growth of the maxilla, a necessity if
growth synchrony between Nasion and the alveolus is to
maintained, thus preserving the S-N-A (sella-nasion-

alveolus) angle and 'true' prognathism (Ford 1956). The lengthening of the maxilla contributes to the projection of the face during growth. However, active growth does not occur anteriorly. Instead, most new growth occurs posteriorly, in the area of the maxillary tuberosity (Enlow 1976). In essence, the maxilla is being displaced forward while actually growing backward. As it grows, the nasal cartilage creates a space into which new bone may develop. It is into this space that the first, second, and third molars develop as they approach occlusion (Ranley 1988).

The importance of the nasal cartilage in the growth of facial projection is debated by Moss (1976b). He contests those claiming prime mover status of the septal cartilages , believing instead that either experiments showing such results were poorly designed or their results were misunderstood (e.g. Sarnat and Wexler 1966). Citing no particular mechanism, Moss instead prefers his functional matix model in which, like the sutures, nasal cartilage growth is passive, responsive to the tensile forces of surrounding soft tissues. Copray (1986) considers Moss's (1976b) criticism but in tissue culture experiments, seems to show Moss's

criticisms unjustified. In culture, the septal cartilage grew vertically and longitudinally to near in vivo dimensions, thus suggesting strong intrinsic growth potential.

At birth, the nasal septum is contiguous with the cartilages of the cranial base (Latham 1970). If, as will be argued, Neandertals differed from modern humans primarily in the dynamics of their synchondrosal growth, then the growth of the nasal septal cartilages may have been affected in a homologous way. Any histologically homologous structure bridging together the midface and the anterior base is of vital importance; especially so since many of the cranial features that distinguish Neandertals from modern humans are related developmentally to the cranial base and sagittal facial projection.

Enlow (1976) describes a facial/basal relationship that has great importance for the argument that follows. This summary will paraphrase and quote extensively Enlow's (1976) critical remarks.

The endocranial space has three fossae: the anterior, middle, and posterior. The midface interacts specifically with the anterior fossa. The anterior-most

boundary of the skull is shared by the anteriormost

boundary of the nasomaxillary complex and the posterior

boundary of the anterior fossa corresponds to the

posterior boundary of the nasomaxillary complex. So, in

the human cranium, the most anterior border of the

endocranial margin coincides with the posterior margin

of the maxillary tuberosity and ethmoid region. This

coincidence can be described by a vertical plane (See

Figure 4) which is termed the posterior maxillary line

(PM). The border separating the anterior fossa (a in

Figure 4) and the middle fossa (d in Figure 4) marks

the superoposterior border of the midface. The PM

separates the anterior fossa and nasomaxillary complex

(b in Figure 4) from the middle fossa and the

postmaxillary space (e in Figure 4).

> ... the nature of the alignment of
> the middle fossa relative to the
> anterior fossa directly affects
> positioning among the various
> principle parts of the face. If the
> middle cranial fossa is more
> horizontally placed relative to the
> PM line and anterior fossa, it has
> the effect of placing the midface
> more protrusively while, at the same
> time, the mandible is positioned
> retrusively. A more upright middle
> fossa, conversely has a mandibular
> protrusive effect (Enlow 1976:200).

Because an upright middle fossa is a characteristic of

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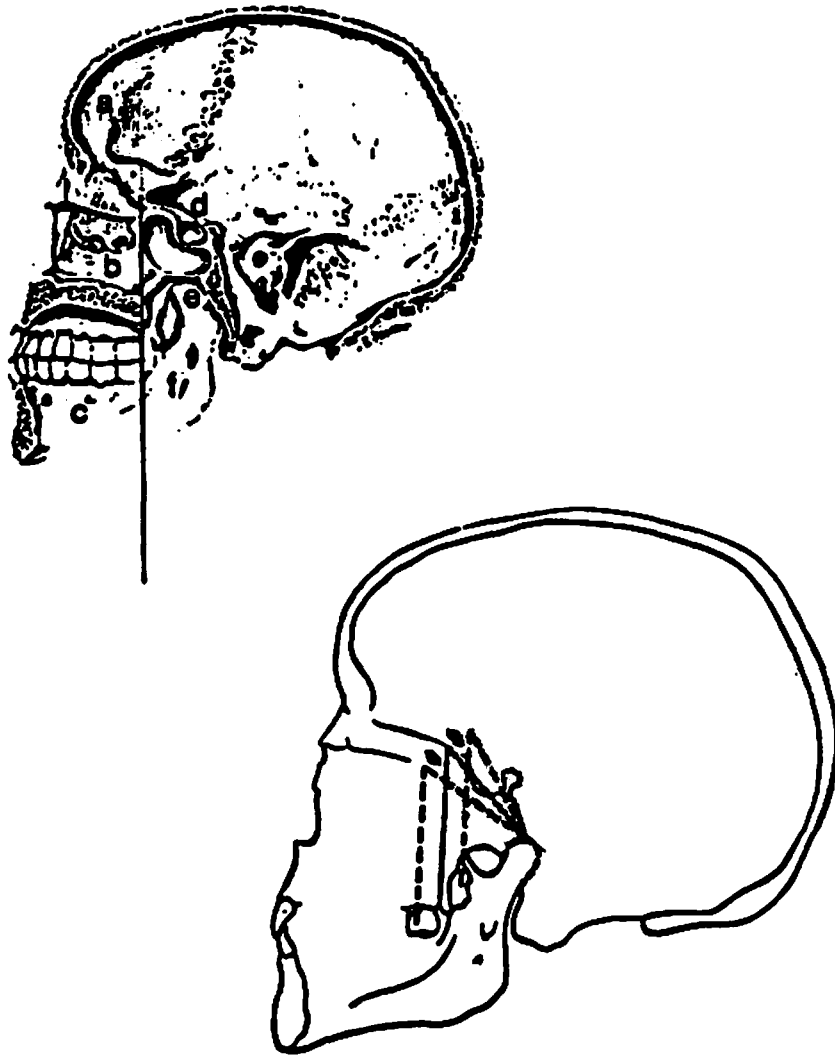
Figure 4.   The Placement of the Posterior Maxillary
Line. From Enlow (1976).

the brachycephalic skull (which has a short and flexed

base [Taylor and Dibennardo AJPA 53:151-158]),

> the nasomaxillary complex is
> correspondingly less protrusive, in
> contrast to the dolichocephalic
> headform with its longer basicranium
> and thus more protrusive face (Enlow
> 1976:200).

The angulation of the middle fossa is a

characterization of cranial base flexure. Kerr and

Adams (1988) study of the correlation between the

cranial base and jaw found an inverse correlation (r=-

.70) between the cranial base angle (Ba-S-Na) and

mandibular prognathism. The mandible then is in a

curious developmental position. It must grow anteriorly

to accomodate a midface being forwardly displaced yet it

is topographically congruent with the posterior base

that is migrating back backward and upward (Anderson and

Popovich 1983). Specifically, the mandibular ramus is

congruent with the middle fossa and pharyngeal space.

The mandibular corpus is associated with the body of the

maxilla (Enlow 1976). The PM line bisects the mandible

just posterior to the third molar and anterior to the

ascending ramus. As flattening procceeds, the mandible

is being literally pulled apart at the PM line. As

indicated by these patterns, the presence of prognathic

faces, flattened cranial bases, and a retromolar space
in Neandertals suggests a common developmental basis in
these features. This ends the discussion on general
(i.e. global) patterns of craniofacial growth. It is
time to go from the general to the specific.

The Cranial Base

We have seen that the developing cranial base has a
profound influence on the face. The components of the
base have demonstrated allometric growth during ontogeny
and as has been discussed, these allometric changes have
a quantifiable cellular basis. The greatest growth that
occurs along the cranial base does so at the two
synchondroses. These synchondroses, the last remnants of
the primary cartilages, are the midsphenoidal and the
spheno-occipital.

The midsphenoidal separates the pre- and
postsphenoid elements and it fuses at approximately the
eighth month of fetal life (Scott 1958). The
midsphenoidal is the most active site of prenatal growth
in the anterior cranial base and there is a well founded
concensus that flexure takes place at the midsphenoidal
(George 1978; Schulter 1978; Scott 1958).

The spheno-occipital synchondrosis is the major

growth site of the posterior base. It separates the

sphenoid body from the basioccipital bone. Without

consideration of the mechanical influences of the

posterior base on the growth patterns of the

midsphenoidal, Sirianni and Van Ness (1978) conclude

that at least in Macaca, it is the spheno-occipital that

qualifies as the site of flexure. The spheno-occipital

ceases its growth, and therefore the linear growth of

the posterior base (excepting remodeling at Basion) in

the middle teens (Knott 1971; Scott 1958).

There are those who believe cartilaginous growth

within the cranial base is intrinsically regulated,

playing itself out along some genetically preset course

(Copray 1986; DuBrul and Laskin 1961; Sarnat and Wexler

1966). On the other hand, there are those (e.g. Moss

[1958,1976] and Moss and Young 1960) who believe the

growth centers to be passive, like sutures, only

secondarily responsive to soft tissue growth. These are

the functional matrices models and their primary

emphasis is on epigenesis. For this discussion, the

outcome of this debate is not particularly critical. All

we are concerned with are the patterns that exist and

the effects of amplifying specific processes within those pathways. If it can be established that the cartilaginous growth plates are intrinsically regulated then so much the better.

The structure of the basicranial synchondroses are unique to the epiphyseal growth plates of the long bones in that they are bipolar. That is, long bone growth plates are histologically structured such that the transition from chondrogenesis to osteogenesis is unidirectional (proximal to distal). In basicranial synchondroses, the growth plates have two zones of growth, making expansion bidirectional (anterior to posterior)(Schulter 1978). Each of the poles is structured into five distinct zones:' central zone (CZ), proliferative zone (PZ), matrixogenic zone (MZ), hypertrophic zone (HZ), and erosive zone (EZ). The central zone acts as a protective covering to the proliferative zone and as the 'true' synchondrosis uniting the bones (Roberts and Blackwood 1983). The proliferative zone is the primary site of proliferative cell division within the cartilage (Kember 1972,1978,1979; Kvinnsland et al. 1975). Kember (1972,1978,1979) and Wolpert (1982) contend that it is the depth of the proliferative zones and the rate of

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cellular division within them that controls the rate of growth. The induction events that establish the initial sizes of these proliferative zones are in all probability under genetic control (Hall 1984). Many extrinsic factors (i.e. chemical and mechanical) can regulate the amount of cell division that takes place within the proliferative zones. One can see room here for both intrinsic and extrinsic determinants. The matrixogenic zones is the area in which appositional (i.e. matrix formation) growth takes place. The hypertrophic and erosive zones are primarily concerned with cell enlargement and osteogenesis.

In a series of studies measuring in detail the growth and cellular activities of the basal elements and cartilages in mice, Roberts and Blackwood (1983,1984) and Jones and Roberts (1988) have added significant contributions to our knowledge of basal cell kinetics. Included in all of their studies was the cartilage model of the rostral portion of the presphenoid (i.e. the caudal zone of the sphenoethmoidal synchondrosis). This, in addition to the two other cartilage plates, made it possible to monitor endochondral ossification in five zones. These were the rostral pole of the basioccipital,

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the caudal pole of the postsphenoid, the rostral pole of
the postsphenoid, the caudal pole of the presphenoid,
and the rostral pole of the presphenoid.

Jones and Roberts (1988) monitored each of these
zones and documented cell sizes within the hypertrophic
zones and the labeling indices of the proliferative
zones. The labeling indices were generated by
incorporation of 3H-thymidine which labels cells
expressing DNA synthesis activity (i.e. cell division).
Each proliferative zone was monitored and the indices
were calculated as the simple ratio of number of labeled
cell to total number of cells. Jones and Roberts (1988)
found within the normal mice strain a reduction in
hypertrophic zone cell sizes rostrally and temporally.
Their labeling indices also showed a rostrally
decreasing amount of proliferative zone activity.
Roberts and Blackwood (1983) calculated the growth rates
for morphometric data and concluded that the presphenoid
region grew faster than the more posterior elements up
to day 32 when the posterior elements became rate
dominant.

Roberts and Blackwood (1984) did tritiated
thymidine labeling of each of the five growth zones and

obtained results similar to Jones and Roberts (1988),
finding a decreasing caudorostral gradient of cellular
activity. Growth rates calculated from these labeled
materials also demonstrate a decreasing caudorostral
gradient. In other words, the cellular data tells us
that the posterior basal cartilages are more active than
the anterior cartilages. This is inconsistent with
results obtained from morphometric studies outlined in
the previous section.

Baer (1954), Bjork and Skieller (1976), Moss and
Baer (1956), and Sirianni and Van Ness (1978) observe
that within the midsphenoidal and spheno-occipital
cartilages, there are dorsoventral differences in
chondrogenic activity levels. For the midsphenoidal, the
greatest activity is found along the dorsal, endocranial
margin. For the spheno-occipital synchondrosis, the
greatest activity levels are found on the ventral,
ectocranial margin. These regions of greatest activity
can also be inferred from the fusion pattern since the
more active zones should be the last to cease growth.

Cartilage Dynamics of the Synchondroses

The cranial base cartilages are wonderfully complex
in their patterns of differential growth. The

anterior/posterior growth of the bones and the vertical

displacement during the flexure process are mirrored at

the cellular level. Refering back to Emerson's (1986)

criteria for demonstrating the potential for

heterochrony (i.e. allometric responsiveness and

temporal differences in growth timing), it is easy to

see that the cranial base offers great potential for

allometric change since,

> ...each endochondral site has a
> specific proportion of its cells in
> the proliferative zone engaged in
> proliferative activity and that
> this proportion is unique to each
> growth site(Roberts and Blackwood
> 1984:534).

Harkness and Trotter (1980,1982) make a strong

case, based upon observations of growth rates and growth

spurts in transplanted rat cranial bases, that the

synchondroses demonstrate the potential for intrinsic,

genetically coded growth patterns. The growth of each

base, when transplanted into older hosts (with mitogenic

environments typical of older animals), matched

comparably with donor age matched controls and not the

host groups perhaps illustrating the importance of

intrinsic controls of linear growth.

Moss (1976) would advocate the predominance of tensile forces, created by an expanding neural mass via attached dura matter, in base growth. Moss (1976) makes a strong case for the importance of tensile and compressive forces on patterns of chondrogenic activity within the synchondroses. In other words, Moss (1976) argues for the Heuter-Volkmann hypothesis adapted for cranial base shape change. Simply put, the Heuter-Volkmann hypothesis states,

> ...the rate of chondrocytic mitosis within a long bone growth plate is inversely related to the external loadings placed upon it; an increase in compression loading decreases mitosis and a decrease in compression increases chondrogenic multiplications (Moss 1976:556).

Based upon the Heuter-Volkmann hypothesis, the cellular/mechanical basis of flexure can be understood.

At the level of the proliferative zones, the posterior cranial base generates the greatest amount of activity (Roberts and Blackwood 1984; Jones and Roberts 1988). Also, the posterior base has a greater number of zones at its disposal. Within the midsphenoidal, the most dorsal activity aids in pushing the face down and forward. Within the spheno-occipital the ventral most activity pushes the posterior base backwards and

downwards. Since the posterior region enjoys the greatest cellular activity, it enjoys greater vertical displacement than the anterior base. The difference in net displacement generates stresses in the base which are compressive dorsally and tensile ventrally. Ventral tension will increase the ventral most activity of the spheno-occipital chondrocytes, increasing its magnitude of growth rate with time. Dorsal compression will act on the most active portion of the midsphenoidal to depress growth there and so check the magnitude of the input of the anterior base to facial vertical and anterior displacement. The result of these processes is the opening up of the cranial base. At the seventh or eighth month of fetal life, the midsphenoidal will begin the fusion process and flexion at this site will cease (Michejda 1972). When this occurs, there is a small pivoting that occurs at the spheno-ethmoidal. In left lateral view, the entire base complex will exhibit a small amount of counterclockwise rotation with respect to the ethmoid (Michedja 1972).

Whatever the ultimate starter mechanism, flexure can be understood as the product of mechanical forces generated by the differential cellular activity along a

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posterior/anterior gradient and differential activity levels within the synchodroses.

The importance of the spheno-occipital synchondrosis in this process would seem to be great. An intriguing study by DuBrul and Laskin (1961) illustrates its contribution to the entire process of craniofacial shape establishment. DuBrul and Laskin (1961) extirpated the spheno-occipital synchondrosis of the rat and the following effects were observed: skulls became shorter and rounder, the cranial roof showed more curvature, there was rotation of the nuchal crest, a markedly forward displacement of the occipital condyles, and an increased cranial base flexure. The arching of the vault was produced as the brain," growing as it must, by bending around the sharp, artificially created kyphosis"(1961:122). These sorts of cascading relationships should reinforce the view of the importance of cranial base development in better understanding the craniofacial differences between Neandertals and modern humans. Recalling Trenmouth's (1989) study of anencephalic fetuses, one must suspect that along with DuBrul and Laskin's (1961) results, a case could be made that the principle interaction between the base and the brain is with the posterior and

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not the anterior cranial base. This relationship has not
been given the attention that it deserves.

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CHAPTER IV

MATERIALS AND METHODS

The following analysis will serve two purposes. First, the patterns of prenatal relative growth in modern humans will be determined. Second, predictions will be made, based upon prenatal patterns of growth, of the allometric relation between a subset of variables in static adult samples.

In order to carry out such an analysis, six data sets were utilized. These data sets can be partitioned into two categories. One category will be used to determine patterns of ontogenetic allometry in the craniofacial growth of prenatal humans. The remaining five data sets are samples of adults from various populations. These will be used to test predictions of static relation based upon the ontogenetic analysis.

Data supplied by Ford (1956) was used for the analysis of craniofacial growth. This data was taken from a cross-sectional sample of 76 human fetuses between the post-menstrual ages of 10-40 weeks. Age was calculated by Ford on the basis of crown-rump length (CRL), foot length and weight when it was recorded.

Measurements made by Ford were taken on the prepared
crania. Ectocranial measurements were taken after the
removal of the soft tissue. Measurements in the sagittal
plane involving endocranial points were taken after the
crania had been sagittally sectioned. For ages 10-22
weeks, the fetuses have been arranged in weekly groups
and fetuses aged from 22-40 weeks were assigned to
biweekly intervals. There are 22 age intervals and
therefore 22 data points in total. The value assigned to
each interval represents the mean of all values within
that age group. The sample size per age group fluctuated
from 1-3 until week 30. For weeks 32, 34, 36, 38 and 40,
the sample sizes were 7, 8, 4, 13 and 11 respectively.
From Ford's (1956) data set, only six variables were
used for the analysis (See Figure 5). These variables
are:

 1) Facial Height -- Nasion to Prosthion (NPR)
 2) Cranial Length -- Glabella to Ophistocranium (MXL)
 3) Facial Length -- Basion to Prosthion (BPR)
 4) Anterior Cranial Base -- Sella to Nasion (PIN)
 5) Posterior Cranial Base -- Sella to Basion (PIB)
 6) Brain Weight -- (BRW)

    For the five remaining data sets, only two
measurements were utilized:

 1) Cranial Length -- Glabella to Ophistocranium (MXL)
 2) Facial Height -- Nasion to Prosthion (NPR)

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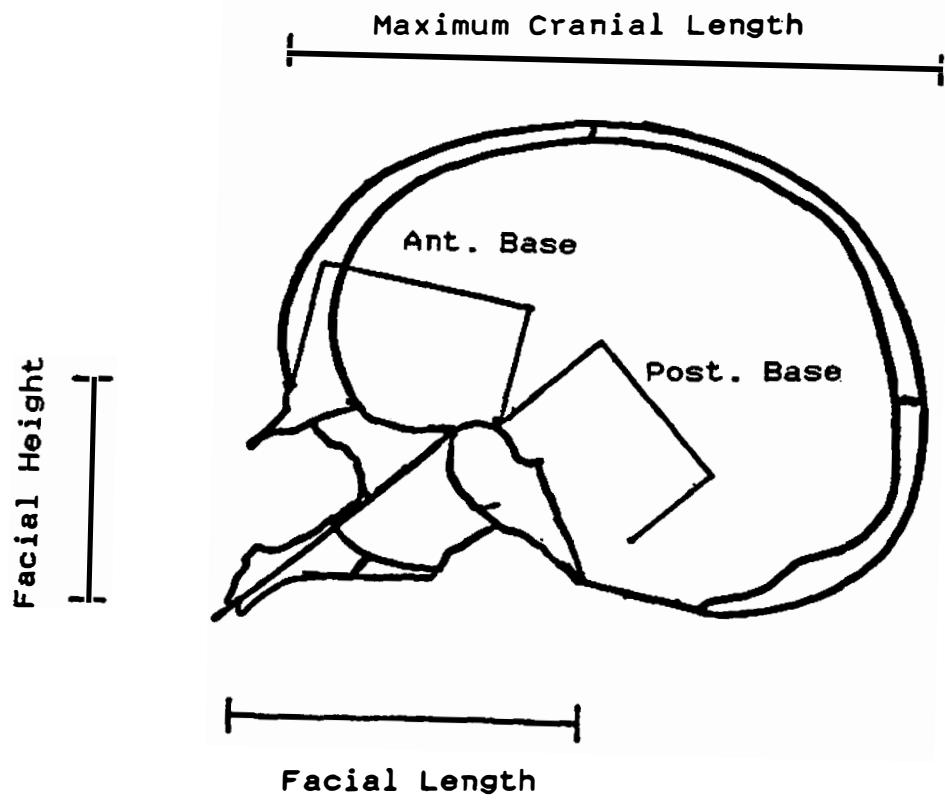
Figure 5. Graphic Representation of Study Variables

These measurements were not made by the author but were acquired from various sources.

Two forensic samples from the University of Tennessee Forensic Data Bank, representing both adult blacks and whites were employed. After pooling the sexes, 14 blacks and 39 whites were chosen (Table 1).

A sample of Arikara (N=100), from the Larson site, 39WW2, were measured by S. Donnelly and supplied to the author. All adult crania complete enough to measure were used (S. Donnelly pers. comm.) and pooled with regard to sex (Table 1).

A sample of 13 early modern Europeans (See Table 2) were commondeered from Suzuki and Takai (1970) and from Dr. Fred H. Smith (pers. comm.). The samples were collected regardless of sex.

A sample of 7 Neandertals, from Europe and Southwest Asia was taken from Suzuki and Takai (1970) and Dr. Fred H. Smith (pers. comm.). Any Neandertal crania complete enough to include both maximum length and facial height were included (See Table 3).

The data sets were all transformed to common, base 10 logarithms. In the case of static adult regressions,

TABLE 1

Samples of Recent Modern Humans

Sample	N	Source
Fetal Data Set	22	Ford (1956)
Forensic Black Adults	14	UTFDB
Forensic White Adults	39	UTFDB
Arikara (39WW2)	100	UT

UTFDB (University of Tennessee Forensic Data Bank).

TABLE 2

List of Adult Early Modern Humans

Specimen	Reference
Predmosti 3	Suzuki and Takai (1970)
Predmosti 4	Suzuki and Takai (1970)
Predmosti 9	Suzuki and Takai (1970)
Combe Capelle	Suzuki and Takai (1970)
Oberkassel D998	Suzuki and Takai (1970)
Oberkassel D999	Suzuki and Takai (1970)
Cromagnon 1	Suzuki and Takai (1970)
Kaufertsberg 01	Smith (pers. comm.)
Ofnet 2481	Smith (pers. comm.)
Ofnet 2486	Smith (pers. comm.)
Dolni Vestonic 3	Smith (pers. comm.)
Mladec 1	Smith (pers. comm.)
Abri Pataud *	Smith (pers. comm.)

* older sub-adult

TABLE 3

List of Adult Neandertals

Specimen	Reference
La Ferrasie 1	Smith (pers. comm.)
La Chapelle-Aux-Saints	Smith (pers. comm.)
Shanidar 1	Suzuki and Takai (1970)
Amud	Suzuki and Takai (1970)
Le Moustier	Suzuki and Takai (1970)
Gibraltar	Suzuki and Takai (1970)
Saccopastore	Suzuki and Takai (1970)
Monte Circeo	Suzuki and Takai (1970)

log transformation was used for the simple reason that most allometric analyses are done in this manner and comparable results were desired. For the ontogenetic data, log transformation was performed since according to Huxley (1932) and Medawar (1945) it best represents the multiplicative nature of growth.

In general, the analyses were performed using Statgraphics Version 3. The procedures employed were the principle components, simple regression (least squares) and multiple regression options. Calculations of the reduced major axis (RMA) was done by hand by dividing the least squares regression (LSR) slope by its associated correlation coefficient (r). For the principle components analysis, the raw data set were entered unstandardized into the program.

A principle components analysis (PCA) was performed on the fetal data subset supplied by Ford (1956). Brain weight was excluded because its dimension was variant to the other variables. Therefore, the five traits listed above were included in the PCA. PCA partitions variability along orthogonal axes. The first axis, termed the principle axis describes size variability. The second, minor axis, describes patterns of shape

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change (Jolicoeur 1963b). PCA is mathematically

generalizable to the allometric equation (Jolicoeur

1963b; Jolicoeur and Mosimann 1960) and offers some

fundamental advantages over bivariate allometry. PCA is

more efficient than bivariate allometry since by

considering large numbers of variables at once, a large

number of bivariate comparisons are reduced to a single

output. Because PCA defines size internally, no

subjective proxy for size need be considered. A feeling

for the organism as a coehesive unit is maintained

(Jolicoeur 1963b) while the opportunity for "discovering

biologically meaningful patterns of covariation among

interrelated variables that are not necessarily

discernable in the original data" (Shea 1985:369) is

enhanced.

Shea (1985) recommends that the first PC in PCA's

of ontogenetic data would be more properly termed the

allometric vector instead of simply a size vector. This

is done in recognition that the eigenvector loadings

(otherwise known as directional cosines) of the first

component are not equal. Size, being internally defined,

establishes in the first component a criterion for

isometry. The criterion being the reciprocal of the

square root of the number of traits used, or $1/p^{1/2}$

(Jolicoeur 1963a). Any eigenvector above or below $1/p^{1/2}$ is either positively or negatively allometric, respectively. The eigenvalue of each component is the percentage of variability explained by that component.

The chief mathematical technique employed in the analysis involves the calculation of third degree polynomials, formalized as:

$$\text{Log } Y = \text{Log } B0 + B1(\text{Log } X1) + B2(\text{Log } X2)^2 + B3(\text{Log } X3)^3$$

These polynomials were calculated by means of multiple regression. The independent variable X was defined as gestational age. The dependent variable Y was any one of the six traits taken from Ford's data set outlined above. As the polynomials were calculated for each of the variables, each additional term was monitored for its contribution to the model sums of squares. As linear functions, each regression had r values $>$ .90. However, the additional coefficients had p values $<$ .05, many with levels $<$ .01 (See Table 4) and therefore increased the previously high r values in a nonrandom way. This monitoring was especially necessary since Medawar (1945) has observed polynomials generated with 16 points (only six less than the number used in this study!) in the

TABLE 4

Polynomials Generated Using Multiple Regression

Dep. Var.	Ind. Var.	Coeff.	SE	P
MXL				
	B0	-.720	.364	.065
	X	.325	.072	.0004
	X^2	-.017	.005	.004
	X^3	.000422	.0001	.011
BRW				
	B0	-5.229	1.845	.015
	X	1.397	.355	.002
	X^2	-.076	.024	.008
	X^3	.001906	.0007	.018
PIN				
	B0	-.380	.088	.0005
	X	.168	.012	.0000
	X^2	-.0052	.0005	.0000
	X^3	.000058	$8*10^{-6}$	.0000
PIB				
	B0	-.871	.373	.033
	X	.268	.074	.002
	X^2	-.014	.005	.015
	X^3	.000351	.0001	.034
BPR				
	B0	-.242	.100	.027
	X	.1679	.014	.0000
	X^2	-.0052	.0006	.0000
	X^3	.000059	$9*10^{-6}$	.0000
NPR				
	B0	-.6017	.140	.0005
	X	.168	.020	.0000
	X^2	-.00489	.0009	.0001
	X^3	.000049	.000013	.0014

absence of any biological reason for departure from linearity.

Generally, such polynomials are calculated for growth curves in order to yield simple empirical fits to enhance prediction and not to illustrate elements of process. However, the application of basic, and simple, calculus methods furnishes a remedy to these criticisms. Following the Chain Rule Method, first and second derivatives were calculated. The first derivative, dy/dt, makes it possible to calculate the velocity at any part or point on some calculated trajectory. The following example will illustrate the technique.

For the formula, $y = 2 + 3x + 4x^2 + 5x^3$, calculating the first derivative involves several steps. First, the removal of the constant (in this case 2). Then for each term multiply the value of the exponent by the value of the coefficient, then subtract 1 from the exponent. This yields dy/dt =

$$3 + 8x + 15x^2.$$

So where x is some measure of time, at time 1, the velocity is 26 units for measure. The constant is removed for the simple reason that it adds nothing to the answer; Since $3x + 4x^2 + 5x^3$ is always 2 behind 2

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+ 3x + 4x^2 + 5x^3, the former neither falls further behind or catches up to the latter. Therefore the velocities are naturally the same.

The second derivative (dy/dt^2) involves applying the same principles on the first derivative formula, thereby transforming (dy/dt) = 3 + 8x + 15x^2 into (dy/dt^2) = 8 + 30x. This represents acceleration or the rate of velocity change in time. Since only third degree polynomials were calculated, the first derivative will include an x^2 term and be a parabolic function. The second derivative will then be a linear function. Given this, it will be clear when the curves are inspected that these functions are far from complete since the patterns of velocity demonstrate no point of inflection and constant positive acceleration is biologically absurd. The value of the technique, however, is not compromised. Because the data are log transformed, the first derivative will give the specific growth rate at any time during the duration of the growth period. If the ratio of first derivative values for two variables are plotted against time, then their ratios of specific growth (k) can be visually evaluated. In other words, ontogenetic allometry can be evaluated rigorously as a

series of changing allometries. This is similar to a
technique described by Carlson (1977) for orthogonal
polynomials. Medawar (1945) outlined this technique but
did not suggest taking the ratios of the first
derivative values.

Many investigations of complex allometry (e.g.
Dawood et al. 1988; Jolicoeur and Pirlot 1988; Jolicoeur
1989) differ from this study in an obvious way. Their
mathematics is often intractable. The simplicity of
interpreting the allometric formula has always been one
of the most widely accepted justifications for its use.
The technique I have outlined is elegant in its
simplicity and ease of visual interpretation.
Bivariate allometry is applied to static adult samples
to test the pattern of size covariability as predicted
by the prenatal growth analysis. Least squares and
reduced major axis regressions were calculated. Least
squares is preferable only when the dependent variable
is prone to error. Reduced major axis regression is
preferred when both dependent and independent variables
are prone to measurement error (Sokal and Rohlf 1981).

CHAPTER V

RESULTS AND DISCUSSION

Principle Components

Below (See Table 5) are the unstandardized PCA's
for MXL, PIN, NPR, BPR, and PIB. Isometry is defined as
1/ 5 or .447. The first PC accounts for 99% of the
total variability. This is not surprising since the data
is a growth series. There are three patterns within the
first PC requiring comment. First, facial length and
anterior base are both isometric and nearly identical
(.4461 and .4466 respectively). Second, maximum length
and facial height have the highest loadings and are
positively allometric. This will stand in contrast to
later predictions regarding the relation between cranial
length and facial height. Third, the posterior cranial
base has the smallest loading (.353) indicating that
with size change, it decreases in relative size. Super-
ficially, these results would substantiate the greater
growth of the anterior growth of the posterior base.
However, the patterns of the loadings reflect the small
size of the cranium, not the patterns of differential
size increase at larger size.

TABLE 5

Principle Components Analysis of Linear and Velocity
Measures.

Component	Eigenvalue	Variable Eigenvectors				
		MXL	PIB	PIN	BPR	NPR
Linear Dimensions						
1	99.43	.483	.353	.446	.446	.492
2	.24	.337	.739	-.246	-.142	-.510
Velocities						
1	99.47	.920	.389	-.018	-.021	-.032

The second component accounts for only .23 % of the total variance. These loadings could be dismissed as the product of random error. Perhaps a more appropriate interpretation (ala Jolicoeur 1963b) is that the patterns of variability in the directional cosines are either highly canalized developmental pathways or less sensitive to environmental disturbance. Patterns that emerge in the loadings are of particular interest. Maximum length and poterior base are positively loaded while the components of the facial complex are negatively loaded. Within the negatively loaded facial group, the greatest loading is facial height. Thus indicating that with growth, the height of the face gets relatively smaller. The patterns of component loadings almost suggest that the first component represents static proportions at small sizes and the second component the patterns of relative growth with larger size.

Since shape change is indicative of differential structural velocities, it follows that the second PC is the highly conserved relative velocity patterns of cranial growth. This would imply that the rate of posterior base growth is the fastest growing structure. To test this idea, a PCA was run on the data sets of

specific growth velocities calculated from the first

derivatives (See Table 5). The results are most

interesting. The first PC explains 99.47 % of the total

variance. Since the velocities are mathematically

independent of size, the first component cannot be

thought of as a size vector but only as a rate vector.

Notice that the general patterns of the loadings are

very similar to the second PC of the previous analysis.

Even within the negatively loaded facial complex, facial

height still has the greatest negative loading. Also,

maximum length has the highest loading indicating

greatest rate of growth. This is in contrast to the

opposite loading patterns of the first analysis. The

meaning of this reversal is unclear.

Polynomials

Figure 6

This plot shows the change in the calculated

specific growth velocities with time. The X axis

represents time, the Y axis represents millimeters or

milligrams growth per unit time. If the units of

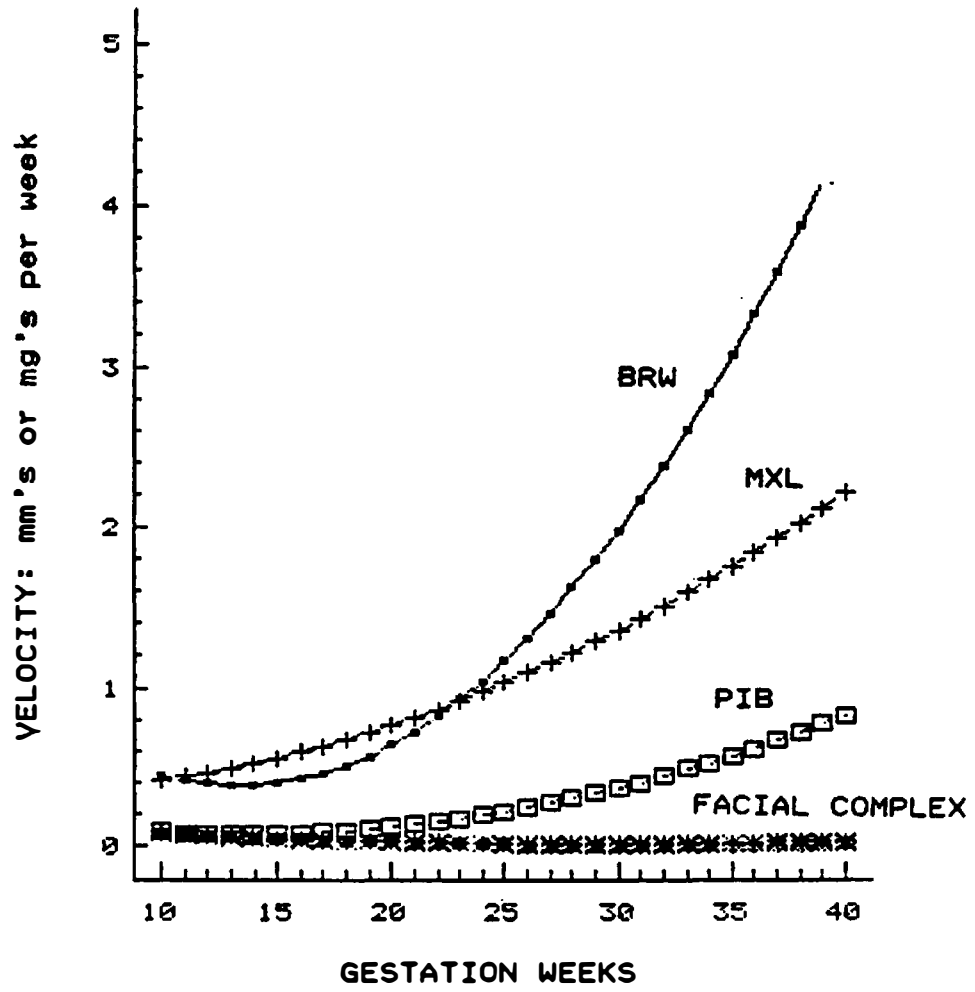increase seem unusually small to account for the total

Figure 6. Patterns of Specific Growth

distance covered during the course of the gestational
period, it must be remembered that derivatives cancel
the intercept (constant) and remove by n-1 the highest
power term in the polynomial. Also, growth is cumulative
process so that these rate calculations can be
translated by integration back into absolute units of
increase.

Another point needs mentioning. The anterior base
is always larger than the posterior base. The velocities
to be summarized would lead one to think otherwise.
However, in the original polynomials (See Table 4), the
Y intercepts and the raw data points indicate that the
anterior base maintains its larger absolute size because
it enjoys larger onset sizes. The steepest increase in
velocity is in brain weight, which is expected. The
second highest trajectory is maximum length of the
skull. Again this is to expected. The third steepest
slope is the **posterior base**. Its ascent from the
overprinted slope below begins at approximately 17
gestation weeks. The overprinted line represents the
near 'unity' in the velocity patterns of the facial
complex (PNV, Anterior Base Velocity; BPV, Facial length
Velocity; NPV, Facial Height Velocity). The differences
in the velocities between the anterior and posterior

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base disagrees with those studies that claim rate predominance of the anterior over the posterior base. These results are consistent with the findings of cellular activity gradients within the zones of the synchondrosal cartilages. So, in general, there are two patterns of growth; that pattern demonstrated by the posterior base and the cranial vault and that exhibited by the anterior base/ facial complex. Based upon this plot alone, it appears that the posterior base grows more like the brain than does the anterior base. Also, the fundamental agreement between expected and observed patterns of velocity gives some confidence that these patterns of specific growth are not spurious.

Figure 7

This plot demonstrates the pattern of change in the ratio of specific growth rates (k) between the anterior and posterior base through gestational life. At 10 weeks, the ratio is at its highest, proximate to the isometric condition. From that point, there is a steep descent in the ratio until a lower asymptote is reached between 25 and 30 weeks gestation. After week 30, the line flattens out to indicate a stabalization at low values of k. It is also about this time (lower
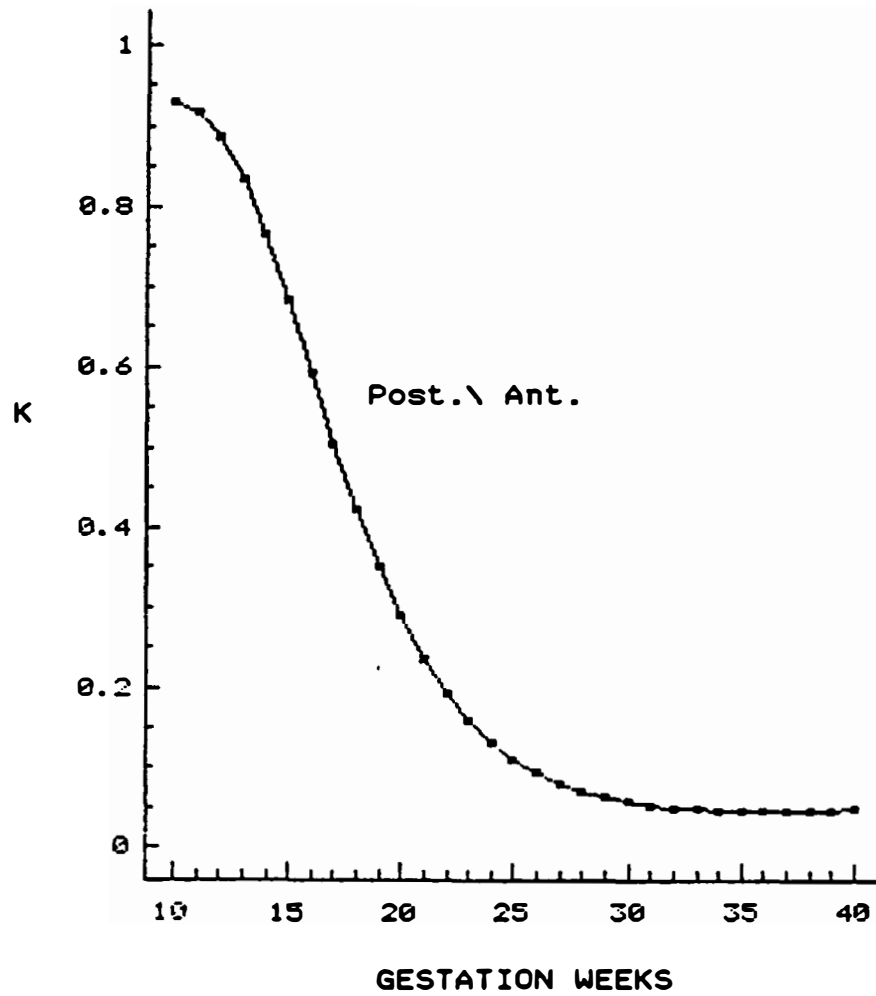
Figure 7.   Allometric Change in the Anterior and
            Posterior Cranial Base During Gestation.

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asymptote) that the midsphenoidal synchondrosis ceases
its active growth and is well on the way towards fusion.
The timing and rate differences in the base components
(especially the high rate covariance between the lower
and upper asymptotes) make them susceptable to hetero-
chronic alteration.

Figure 8

The growth rates of five variables are plotted as
ratios of brain weight velocity. The Y axis represents
k. the X axis is gestational age in weeks. Three
patterns are found. From 10 to 16 weeks, the maximum
length grows faster than brain weight. The ratio of
specific growth descends, after week 16 , to a value of
.5 at 40 weeks. Once again, the facial complex
demonstrates a near unified ratio of specific growth.
Most interesting is the near horizontal line
representing the posterior cranial base which argues
for the more neural-like growth pattern of the posterior
base. Unlike all the other variables whose pattern of k
changes with time, the posterior base retains a stable,
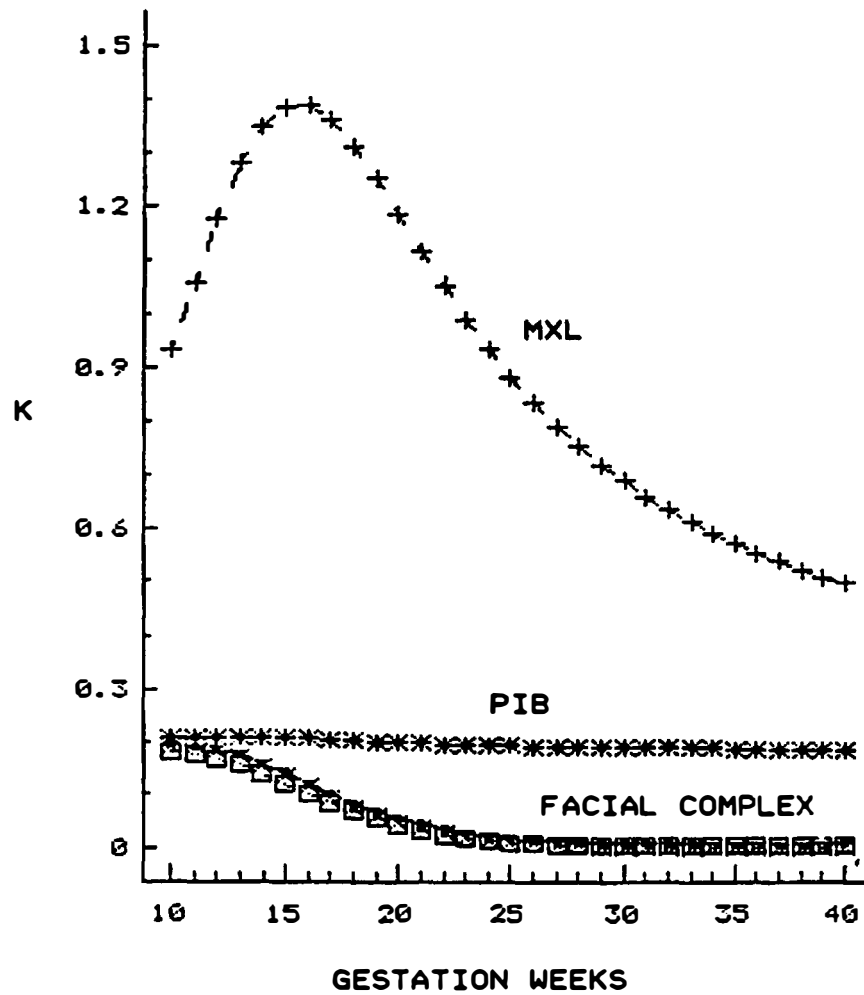relatively unchanging rate relative to the brain.

Figure 8.   Patterns of Changing Allometry in Five
            Variables with Respect to Brain Velocity.

Figure 9

This plot describes the positive increase in
acceleration during ontogeny for all the variables.
Notice the extreme slope of the brain weight (high
slope) and the facial complex (low slope). Also notice
the intermediate nature of the posterior base and
maximum length. Visually, the acceleration plots appear
parallel but actually the posterior base (refer to the
second derivatives) accelerates a litlle faster than the
maximum length.

Figure 10

The changing k of 4 variables with respect to
maximum length is displayed in this figure. Two
important patterns can be seen. First, the apparent
unity of the facial complex velocities starts to break
up at higher resolutions. Also, from 10 to 40 weeks, the
k of the facial complex declines rapidly. Late into the
gestation however, they seem to begin increasing their
velocity. The relationship between the posterior base
and maximum length is more complictated. From 10 to 16
weeks, the k of posterior base to maximum length
decreases from approximately k=.2 to .15. After week 16,
the k value rises almost in a linear manner up to k=.36

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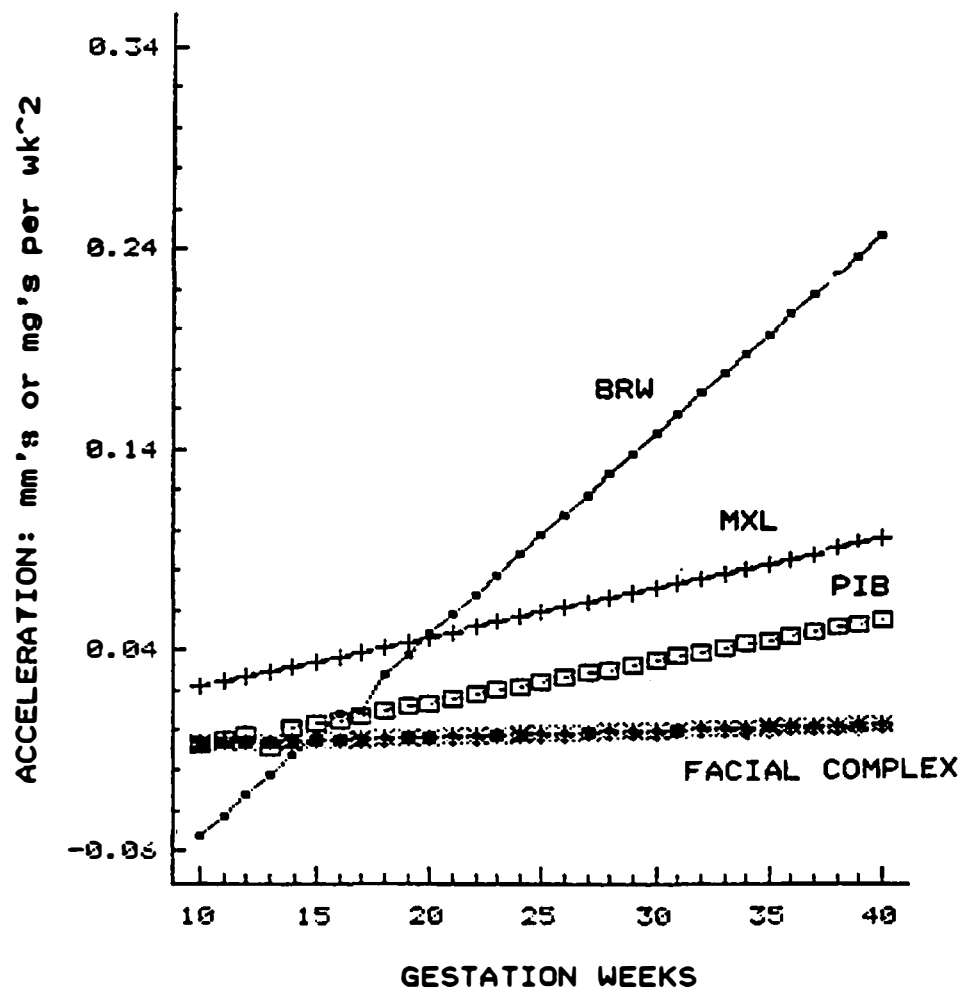
Figure 9. Patterns of Acceleration
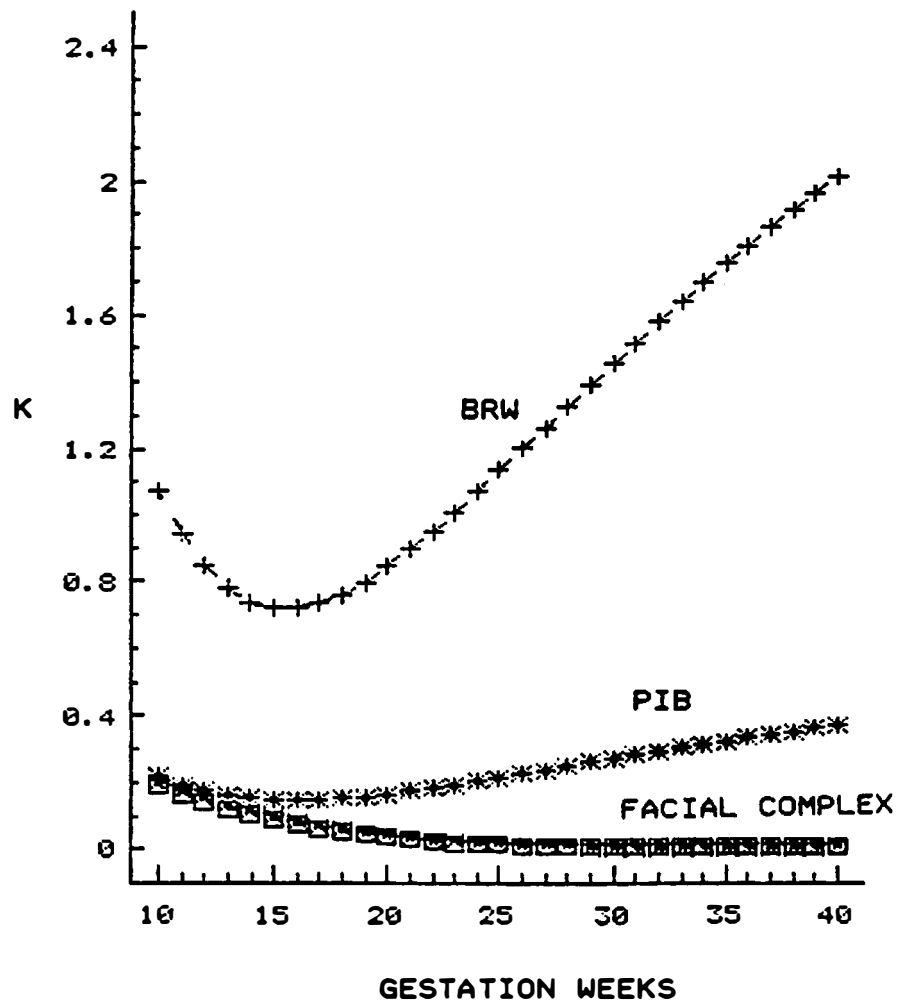
Figure 10. Patterns of Changing Allometry in Five
Variables with Respect to Maximum Cranial
Length.

at the end of the gestational period (40 weeks).

Figure 11

Figure 11 demonstrates at much higher resolution, the patterns of k change within the facial complex. The curve generating the greatest k is the growth of the anterior base relative to facial height. As growth proceeds, the size of the anterior base increases ralative to facial height. The same pattern but of lesser magnitude is seen in the relative growth of facial length to facial height. This makes sense relative to the anterior base/facial height ratio since this reflects to some degree the process of maxillary rotation. In essence, the greater the facial projection, the smaller the relative facial height.

Discussion

Before moving on to the implications of these patterns, it may be of interest to discuss what may lay behind the greater relative growth of the posterior over the anterior base. Thus far, the patterns match well with the expected partitioning of associated suites based upon the qualitative and quantitative studies discussed above. The facial measures show remarkable

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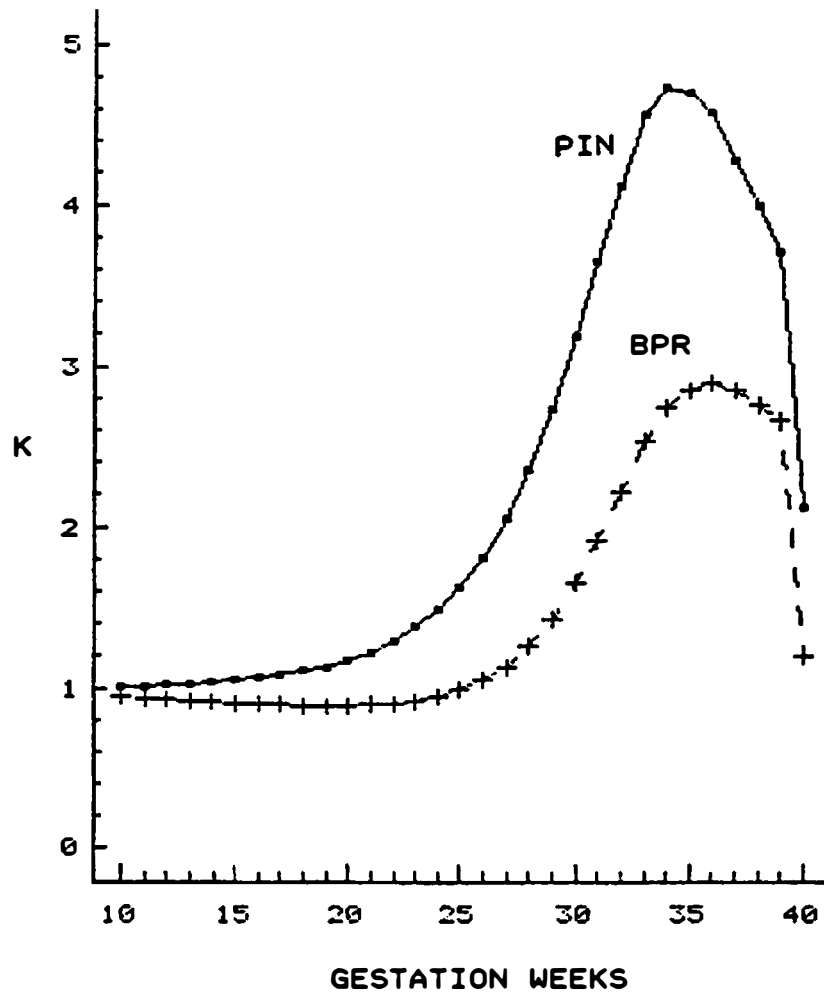
Figure 11. Patterns of Changing Allometry Between the
Anterior Base and Facial Length to Facial
Height.

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similarities in the pattern of velocity. This increases confidence in the technique.The more rapid growth of the posterior over the anterior base is supported by the literature on cell kinetics within the basal synchondroses.

Enlow (1976) and Moss (1976a) both imply that just the weight of the brain can have profound influence on the cranial base. In the case of the posterior base, the brain would exert its force via the underlying spinal cord which would choke off growth at the ventral spheno-occipital and so upset the opening process. Vectors of neural growth (implying both direction and magnitude) and not simple bulk weight may hold the key to understanding the relation between brain development and basal flattening.

Figure 12 is taken from Dobbing and Sands (1973:766) and illustrates the rate of increasing cellularity, as measured by the amount of DNA per gram of tissue, in various neural compartments. The cerebellum, from the caption, seems to initiate its growth later and finish earlier. Between onset and offset, the cumulative rate of cellularity in the cerebellum is much greater than either the stem or the forebrain. The forebrain lies in
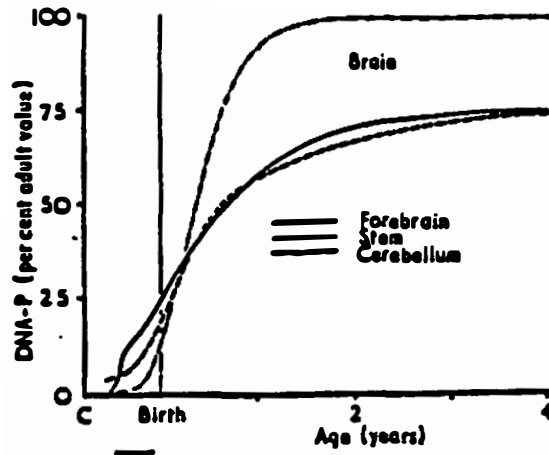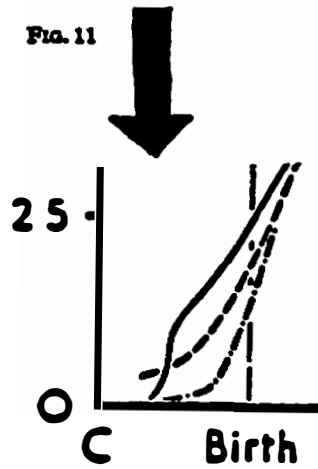
Figure 12. DNA Production in Brain Compartments,
Including the Cerebellum During Gestation.
From Dobbing and Sands (1973).

the anterior fossa and is associated with the anterior
base. Figure 13, also from Dobbing and Sands (1973:760),
illustrates the pattern more clearly. According to
Dobbing and Sands (1973), it is between 10 and 18 weeks
gestation that adult neuronal cell number is largely
achieved and though the cerebellum weighs only about an
eighth of the forebrain, it contains up to as much as
half of the number of cells. Referring back to Figure 7,
the time in which the greatest relative change in k
occurs between anterior and posterior base comes between
10 and 20 weeks gestation.

The cerebellum resides within the posterior fossa,
anteroinferior to the occipital lobes and posteriorly
contiguous with the midbrain-pons-medulla oblongata
group (See Figure 14). It is conceivable that it is the
rapid rearward and upward growth of the cerebellum that
indirectly affects the posterior base and middle cranial
fossa growth vector. During the earliest ontogenetic
periods, rapid phases of multiplicative neural growth
are the most sensitive to disturbance (Dobbing and Sands
1973). Factors influencing growth during these early
periods may have disproportionate effects in later
ontogeny. Riska and Atchley (1985) have discussed the
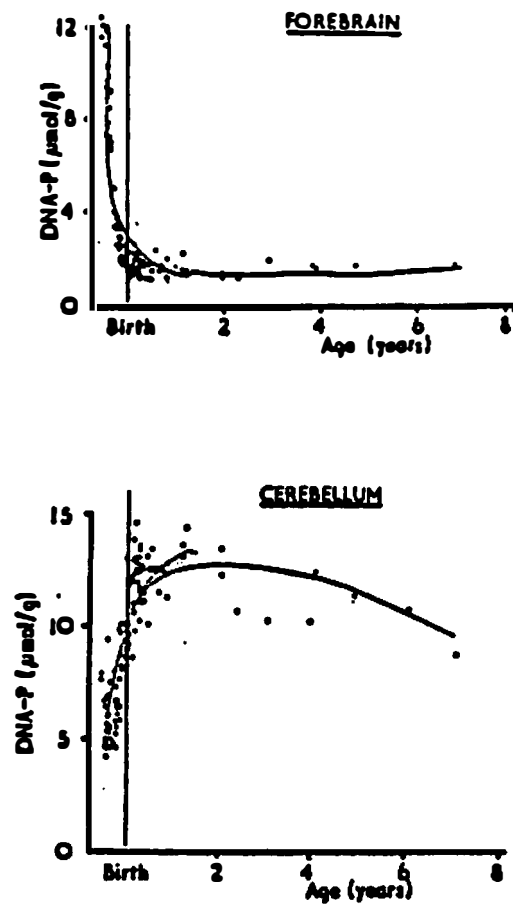
Figure 13. Patterns of Cellularity in the Cerebellum
and Other Cerebral Compartments. From
Dobbing and Sands (1973).
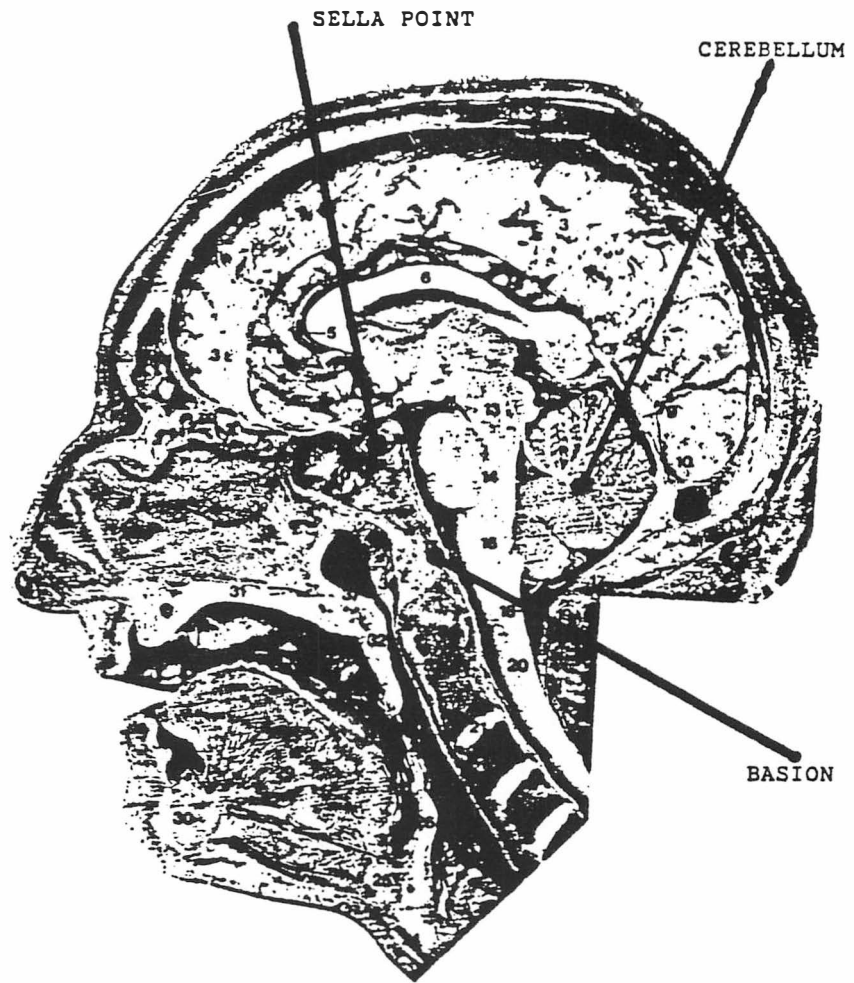
Figure 14.   Sagittal Section of An Adult Human Head.
            Modified from McMinn and Hutchings (1985).

high correlations between brain and body growth rates
early in ontogeny. It is not beyond the realm of
plausability to argue that forces selecting for larger
neonates will have secondary effects on structures such
as the cranial base. Specifically, the amount of
allometric growth of the cerebellum during global size
increase and its subsequent effects on the posterior
base.

Hormonal Environments

For heterochrony to occur, growth must be
allometric. During growth, it has been established that
these allometries change.It has been suggested by
Brothwell (1975) that Neandertals are hormonal variants
of modern humans. This condition is not inconceivable.
Smith (1985b) even mentions the plausability of
regulatory genes being active in the transition from
archaic to modern humans.The morphological affects of
global mitogen level changes, especially in amphibians,
is well known (Gould 1977), but an appreciation of
global mitogen environmental influence on differential
activity in cartilages is necessary to fully evaluate
Brothwell's general argument. Examples of important
global mitogens would be the insulin-like growth factors

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(IGF-1 & 2) and human growth hormones.

IGF-1 is a growth promoting protein otherwise known as somatomedin C. Secreted in the postnatal liver, IGF-1 is similar in function to insulin and is regulated by growth hormone, cortosol, insulin, and thyroid hormone (Canalis 1985). Vetter et al.(1985) have demonstrated IGF-1 to be an effective stimulus for colony formation in postnatal septal and and articular chondrocytes. The absence of somatomedins, coincident with inhibited growth hormone production in the Snell (dw/dw) dwarf mouse (Jones and Roberts 1988) leads to global growth reduction with particular diminution in the snout and tail.

IGF-2 or MSA (Multiplication Stimulating Activity) is secreted by the peripheral fibroblasts where its synthesis is regulated by placental lactogens (Canalis 1985). Like IGF-1, MSA is a systemic mitogen but unlike it, MSA is independent of growth hormone production (Sara et al. 1981). MSA stimulates DNA and collagen synthesis (Vetter et al. 1985) and is primarily a circulating factor in the fetus. Moses et al. (1980) measured fetal rat serum levels of MSA at 20 to 100 times the level of maternal and 25 day old rats.

Canalis(1985) and Sara et al.(1981) note high fetal MSA levels in fetal humans.

Variability in the expression of IGF-1 in human populations is best illustrated in the African Pygmies. The short stature in Pygmies may well be a secondary effect of "subresponsiveness to the growth promoting properties of hGH"(Merimee and Rimoin 1986:1973). In other words, Pygmies DO NOT have abnormally low levels of hGH but they DO have abnormally low levels of IGF-1.

Shea (1988) observes that the pygmies are ontogenetically scaled. That is, while the absolute growth rate is reduced, the allometric patterns of that growth are not. As a result, Pygmies have limb proportions similar to other Africans of SIMILAR SIZES but not at SIMILAR AGES. This effect is made possible because most limb proportional change goes on postnatally. This is the same pattern that can be seen in the ontogenetic trajectories of Snell (dw/dw) dwarf and transgenic mice (Shea in press). The IGF-2 (MSA) serum levels in Pygmies are not appreciably lower than in "control" (non-Pygmy) Africans (Merimee and Rimoin 1986). According to Shea and Gomez (1988), Pygmies lack size and shape change in the skull and dentition

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relative to "control" Africans. While their cranial
bases are shortened (probably due to a late stunting of
the spheno-occipital synchondrosis), there is
considerable overlap with other Africans. Why? Because
the critical growth period of the cranium and dentition
predates the occurrence of IGF-1 deficiency during
ontogeny and prenatally is under the control of IGF-2
(MSA). Pygmies do not demonstrate lower levels of MSA
and therefore do not initiate size/shape changes in
structures under its control.

In a study on the effects of high hGH treatment on
subjects diagnosed with idiopathic growth hormone
deficiency, Poole et al.(1982) found significant, but
variable effects on the posterior base. While not all
subjects reflected this response, "all subjects do not
show any differences in values for any of the other
parameters of cranial base (sic)"(Poole at al. 1982:505).
The late closure of the spheno-occipital synchondrosis
is probably responsible for this pattern of
responsiveness and coupled with the example given by
Shea and Gomez (1988) demonstrates the importance of the
critical interaction between systemic mitogens and
endochondral growth. The most critical aspect of the
interaction is the timing of the critical growth periods

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and the presence or absences of growth stimulants.

A Model of Neandertal Craniofacial Growth

Thus, with changing endocrine environments, there are differential effects depending upon synchrony or asynchrony with critical period growth. What would be the potential outcome if the pathways described thus far were accelerated? That is, what structural results could be found by extrapolating the allometries to larger sizes by enhancing the cellular processes responsible for those allometries. Since the allometries will be maintained with only the rate of their unfolding accelerated, the heterochronic pattern described is global acceleration.

Refering back to Figure 7, accelerating the rapid growth of the posterior base would magnify the basicranial unbending by initiating greater compressive loads to the dorsal midsphenoidal at an earlier time. Since these global effects would also act on the midsphenoidal, its activity too would be enhanced. If this were not so, then its activity would be depressed earlier, stunting the flattening process. The magnified flattening process is made possible by the existing

ontogenetic allometries. Neandertals have

characteristically unflexed bases (Howell 1951, 1952,

1957). In Figure 15, an early modern human

(characterized by Howell (1951) as an early Neandertal)

from Skhul is compared to a "classic" Neandertal from

Monte Circeo. Note the magnitude of the difference in

the base angulation. Howell's(1951) characterization of

the early Neandertals includes specimens now believed by

many to be modern human (Smith et al. 1989). This does

not necessarily refute Howell's point since Howell

(1951) himself noted the similarities between the

craniobasal morphology of the early Neandertals such as

Saccopastore and modern humans, i.e. these being smaller

faces, shorter rounder vaults, and more flexed bases.

Using the sphenoidal angle, Howell (1951) calculates the

early Neandertal-early modern group as having bases

flexed at angles averaging 109 degrees (101-117

degrees). "Classic" Neandertals on the other hand had

angles averaging 129 degrees (123-135 degrees).

The accelerated flattening will have a number of

potential effects on the shape of the cranium and face.

Beginning in the occipital region the

marked climb of relative growth rate in the
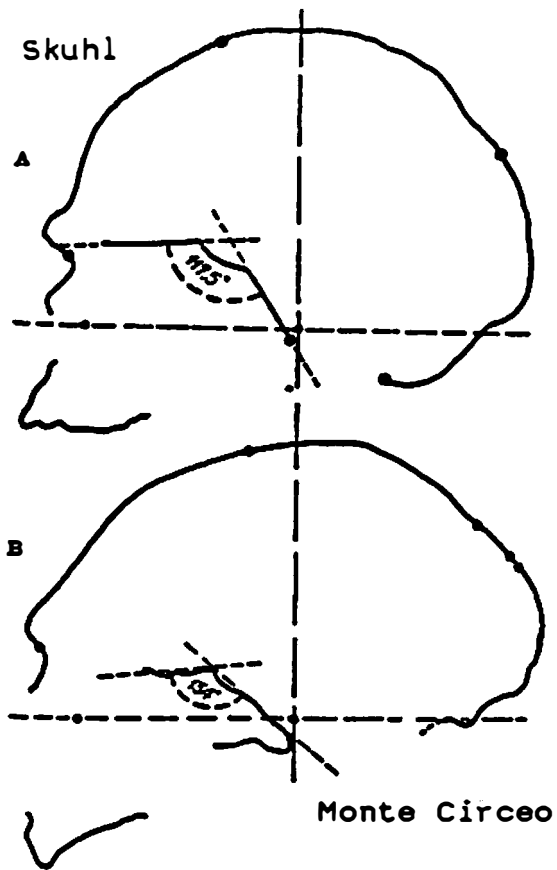
Figure 15.   Comparison of Cranial Base Flexure Between
             A Neandertal (Monte Circeo) and An Early
             Modern Human (Skuhl). From Howell (1951).

posterior base to maximum length would not be without

consequences. The posterior base would grow posteriorly

and bend upward with increasing relative speed. The

result may have been a progressive buckling in the

rearmost occipital region. The magnified upward and

rearward migration of the posterior cranium will bring

that area just posterior to the lambdoidal fontanelle

into a more horizontal orientation. The end product of

the accelerated allometry of the posterior base will be

a reduction in cranial height due to the loss of

cerebral rotation over a site of acute flexure, a

flattened area in the lambdoidal region and a

mechanically buckled occipital. This agrees well with

European Neandertal occipital morphology (Trinkaus and

Lemay 1982; Smith 1983).

One line of evidence that would argue for the

association between flattening and bunning is to compare

Neandertal occipital regions and cross check that with

their flexure status. Figure 16 taken from

Lieberman (1989) illustrates various flexure

configurations in archaic and modern H.sapiens. Fossils

such as Steinheim (pre-Neandertal archaic from Europe

which demonstrates some distortion) and Kabwe (archaic
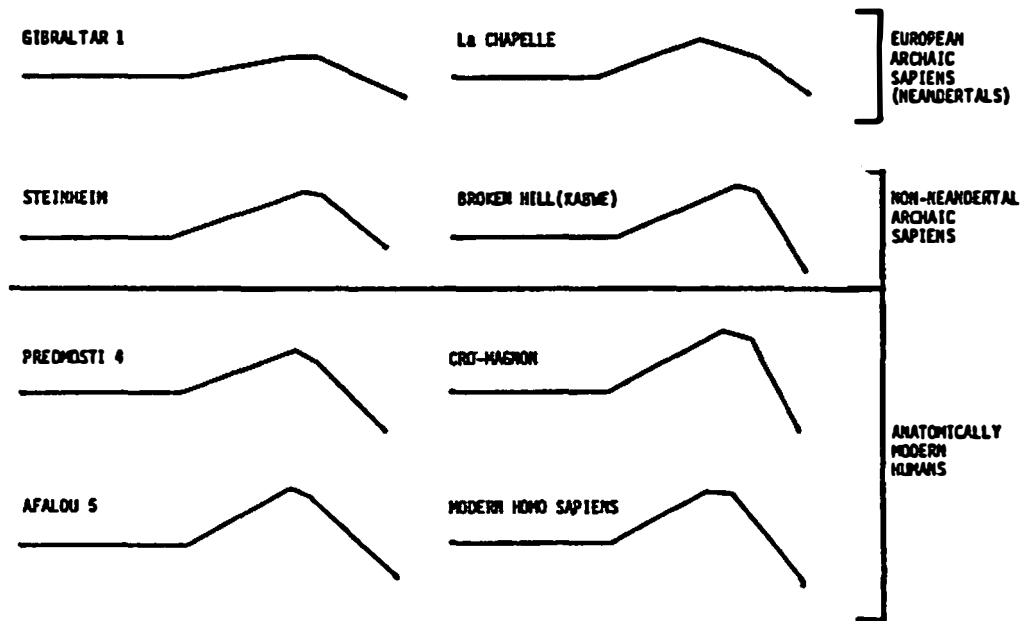
Figure 16. Pattern of Cranial Base Flexure in Modern
and Fossil Hominids. From Lieberman (1989).

H.sapiens from Africa) do not exhibit the Neandertal-like occipital bunning and their bases are flexed in a way more closely related to modern humans. Analysis of the association would be optimal in such specimens such as Shanidar 1 where the occipital bun does not exist and the basal flexure can be measured. For the sample of archaic H.sapiens supplied by Lieberman (1989), the association between bunning and flexure holds.

What actually drives the base into a more flexed state may be the accelerated growth of the cerebellum. Earlier, it was conjectured that the growth vector of the cerebellum influences the growth pattern of the posterior base. Kochetkova (1978) finds that in Neandertals, cerebella may have been were larger and that this is what contributed to the unique Neandertal occipital morphology.

Another effect of this cranial flattening was described by Enlow (1976). As the accelerated process of unbending proceeds, the increased forward movement of the face is compounded by the horizontal shifting of the middle fossa with respect to the posterior maxillary (PM) line. The flattening which drives this reorientation will result in the greater projection of

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the face. Because of the continuity between the nasal

septal cartilages and the cartilaginous sphenoid early

in ontogeny, midsagittal projection may be emphasized.

Coon (1973) recognized the association between facial

protrusion and the expansion of the nasal chamber,

concluding that the midsagittal prognathism demonstrated

by Neandertals was associated with an adaptation for

cold air inhalation. Here it could be argued that the

midsagittal prognathism in Neandertals would not be a

localized adaptation to a selective problem but the

product of global developmental adaptation to glacial

environments. In other words, the acquisition, as soon

as possible, of larger sizes via speedy growth.

Laitman (1985) commenting on the importance of the

cranial base in making taxonomic assignments, discusses

the relationship between highly flexed bases in archaic

H.sapiens specimens such as Steinheim, Kabwe, and

Petralona and less projecting faces. Howell (1951) noted

the small face of the Saccopastore specimen relative to

the "classic" Neandertal group, leading him to conclude

that " There is a tendency to smaller faces in the

early Neanderthals...and these may be correlated with

the difference in basal flexion"(1959:399). Howell

(1973) compared the Nasal Radius length (External

Auditory Meatus to Nasion) in early archaic H.sapiens
such as Petralona and Broken Hill (Kabwe) with that of
Neandertals and modern humans. He found that the Nasal
radius in the Petralona and Kabwe specimens were lower
(103 and 104mm? respectively) than in Neandertals (107
to 117mm) and higher than in modern humans (mean equals
94).

In Figure 17, compare the angle in the
zygomaxillary region of Neandertals and modern humans
(Trinkaus and Howell 1979) with the illustration
below (Enlow 1976) describing the pattern of middle
fossa horizontality with respect to the PM line. It ap-
pears that even though the angles were measured from
nonhomologous points, they measure the same thing,
prognathism. The similarity in the geometries of the
triangles would suggest that the differences seen
between Neandertals and modern humans can be understood
as simply an extrapolation of an orientation process
active during modern ontogeny. The association by Enlow
(1976) between dolichocephaly and facial projection
would certainly characterize the Neandertal cranium and
face.

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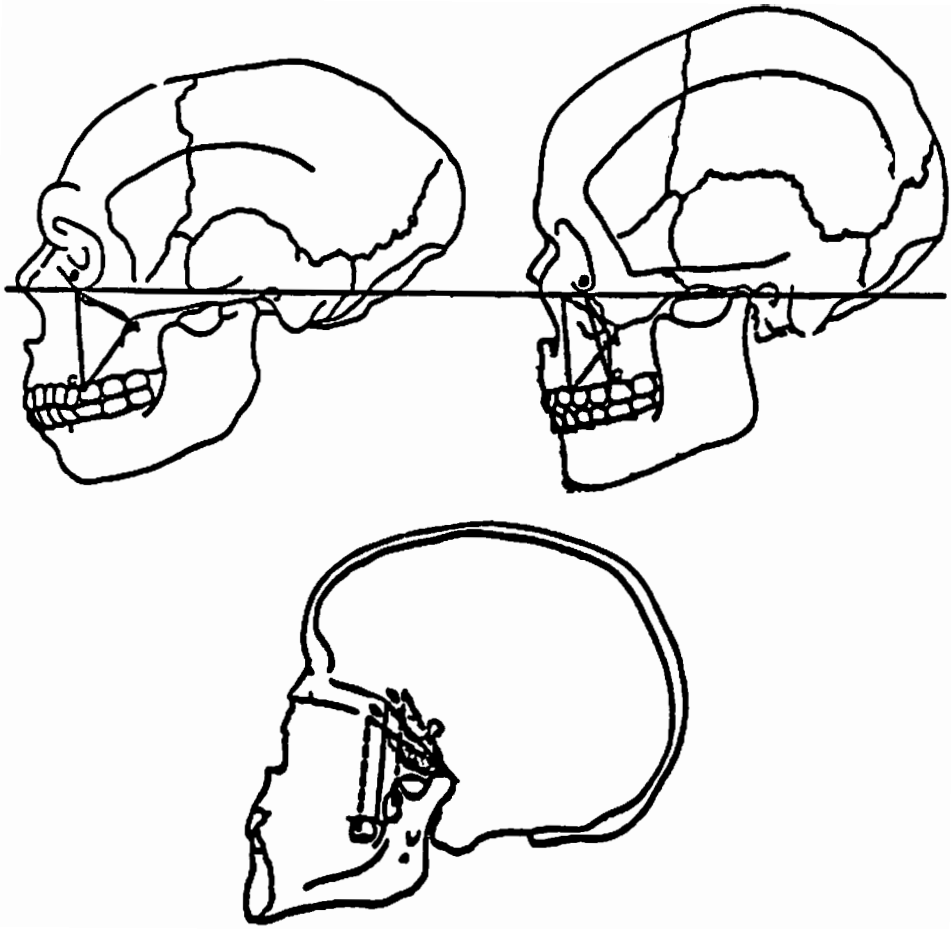
Figure 17.   Geometry of Facial Projection as a Product
              of Middle Fossa Orientation. Taken From
              Enlow (1976) and Trinkaus and Howell
              (1979).

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Another projected result of accentuated basal flattening can be conjectured based upon the relationship between the jaws and the base. Kerr and Adams (1988) found an inverse relationship between cranial base angulation and mandibular prognathism. This would be consistent with the pattern of mandibular rotation seen during development. The mandible is in an interesting developmental situation. It must track the rearward and upward movement of the posterior base given its topographical congruence with the middle fossa yet it must maintain occlusal relations with the maxilla. The maxilla is itself rotating but if Kerr and Adams (1988) results are any indication, not to such a degree as in the mandible. The critical structural landmark here is the intersection of the PM line and the mandible. The PM line intersects the mandible just posterior to the third molar and anterior to the ascending ramus. The posterior migration of the condyle/ramus area coupled with the necessary forward growth of the corpus will pull the mandible apart along the PM line. This could create the retromolar space characteristic of Neandertals. Of course, there is no active growth center along the PM line so that there must be differental growth via anterior-posterior

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gradients of remodeling along the anterior ascending ramus (resorptive) and anterior mandible (appositional). Also, the massater muscle is inserted onto the inferior border of the ascending ramus. The magnified rotation of the posterior mandible may serve to pull the zygomatics backward. This in conjunction with the maxillary displacement may set up a situation that would reorient the zygomaxillary region with respect to the face and perhaps even initiate a more sagittal orientation of the infraorbital plates (Rak 1986). The oblique, posterior orientation of the zygomaxillary and the inflation of the anterior maxillaries may in fact not be due to selection for efficient dissapation of force (Smith 1983; Rak 1986; Demes 1987) so much as it is a product of accentuated tensions created by a mandible that needs to maintain functional integrity with craniofacial structures growing in opposite directions.

Predictions for Modern Humans

More quantifiable predictions can be made in adult populations based upon their early growth patterns by projecting ontogenetic allometries to predict static adult relationships between cranial length and facial height. In the first PCA, the first component

eigenvector loadings were interpreted as structural relations between components at small sizes. The nearly identical loadings in the facial height and cranial length can only be interpreted as a pattern to be found in small crania. The second component loaded facial height negatively and cranial length positively. This means that as the head increased in size, the facial height would get relatively smaller.

Inspection of Figure 11 shows that anterior base and facial length grow relatively faster than facial height. Extrapolating the allometries by increasing their rate of actualization toward adult form translates into long heads having ABSOLUTELY LONGER but RELATIVELY SMALLER facial heights. Allometrically, this could be predicted by larger heads having shallow slopes while smaller heads would have steep slopes. Variation in the prenatal growth rates of modern humans would seem to offer some opportunity for populational variability and predictability in the allometric relation outlined above.

According to James (1985) and Overfield (1985), blacks have lower birthweights than whites. This does not of itself demonstrate rate differences since

Papiernak et al.(1986) have shown blacks to have
slightly shorter gestation lengths (7 to 9 days
shorter). Since the close of gestation occurs in
temporal proximity to prenatal maximum growth
rate (Tanner 1978), this shortening could indeed be
responsible for the lower weights. However, shown cross-
sectional data that show blacks having slower prenatal
growth rates than whites (Freeman et al. 1970). If this
pattern holds, blacks should demonstrate steeper allo-
metric slopes than whites.

Amerindians and Eskimos have precocious dental
development compared to Whites (Mayhall et al. 1978;
Hyman 1987). In these more northern Mongoloid
populations, lower slopes relative to whites should be
observed.

Several recent studies on the growth and
development of Neandertals implicate this group as
having precocious growth relative to modern humans (Dean
1985; Dean et al. 1986; Minugh-Purvis 1988; Wolpoff
1979). If this is indeed the case, the predicted slopes
based upon modern humans prenatal allometries should be
the most shallow. The slopes of the earliest modern
Europeans should fall somewhere between whites and

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Neandertals, an indication of ancestry.

In the allometric analysis of facial height and maximum cranial length, if the least squares slopes are compared,(See Table 6) a gradient of low to steep slopes would run White > Arikara > Neandertal > early modern Europeans > Blacks. This does not agree with expectations based upon the ontogenetic allometries themselves and their relation to our 'knowledge' of early growth rate. However, if the reduced major axis slopes are calculated and compared, the predicted pattern more or less emerges. Neandertals have the lowest slope, followed by whites, Arikara, early modern Europeans, then blacks. In the initial allometric analysis of Neandertal facial height and cranial length, the slope was very low (LSS= .251; RMA= .79) and statistically insignificant (T=0.88) with a correlation of .31 . After the removal of a single outlier that had an unusually long face for its cranial length, the slope increased dramatically (LSS=1.01; RMA= 1.19) and acquired statistical significance (T=3.49) with a correlation of .81. This outlier was Saccopastore 1, a specimen characterized by Howell (1951) as an early Neandertal with a smaller and rounder brain case, more basally flexed, and with an absolutely smaller face.

TABLE 6

Comparative Allometry in Adult Samples Using
Facial Height as the Dependent Variable and
Maximum Cranial Length as the Independent
Variable

Population	N	GM MXL	LS	r	RMA
Blacks	14	174	1.91	.767	2.51
EME	13	190	1.46	.769	1.89
Arikara	100	177	.81	.538	1.50
Whites	39	178	.67	.551	1.22
Neandertals	11	199	1.04	.876	1.19

EME (Early Modern Europeans)

When comparisons between the geometric mean of
cranial length for each group is made with their
respective slopes, an interesting pattern emerges. Early
modern Europeans have cranial lengths more comparable to
Neandertals than to modern groups yet their slope falls
almost perfectly intermediate between the slope of
Neandertals and the modern black group. The modern white
group has a cranial length comparable to that of the
blacks but a slope that is very close to Neandertals.
The Arikara are more closely related to the whites and
Neandertals than to blacks but fall intermediate between
Neandertals and early modern Europeans. Interestingly,
the early modern Europeans , in their slope values, fall
almost perfectly intermediate between Neandertals and
the modern black sample. Models of regional
continuity (Smith et al. 1989) involve high levels of
gene flow between populations of Neandertals and
anatomically modern humans. With this in mind, it is
both interesting that the earliest modern humans to date
can be found in Southern Africa and that the earliest
modern Europeans demonstrate an allometric pattern
intermediate between modern blacks and Neandertals. This
result would suggest two things. First, that early
modern Europeans are the genetic products of both

indigenous Neandertal and early modern African populations. This would imply that Neandertals contributed to modern gene pools. Second, because the allometries suggest patterns of growth rate, perhaps some insight into the physiological life history of Neandertals and their immediate descendents has been acquired.

CHAPTER VI

DISCUSSION

> Much valuable information could be
> gained from the comparative study of
> the juvenile specimens of the two
> Neandertal groups and the growth
> pattern in modern man (Howell
> 1951:392).

In recent years, considerable attention has been

given to the assessment of developmental patterns in

hominids (Bromage and Dean 1985; Smith 1986; Dean 1987;

Grine 1987; Benyon and Dean 1988). Most of this research

has focused on the australopithecines with an eye

for making heterochronic and life history inferences

about these groups. This study has taken a lead from

these workers and gone a step further. It is not enough

to gather a generalized life history scenerio.

Imperative is the need to say something concrete on the

development of Neandertals and how that can help us

understand both the details of their morphology and the

life history patterns.

The size/age problem in paleodevelopmental studies

is quite profound and this is the reason why research on

dental increments is so important. Tying absolute ages

to the developmental stages of hominids is quite

important since significant errors in aging fossils can play havoc with any heterochronic analysis. While continued work is being done in order to better judge the meaning of these increments and their accuracy, this study has come at the problem from a new angle. By making minimal assumptions, a model is proposed that exposes the developmental pathways leading to the adult Neandertal cranium and face. Among all workers, it was Howell (1951,1952) who appreciated most the nature of this approach. In recent years, Minugh-Purvis (1988) has surveyed the majority of preadult Neandertal remains and has drawn important conclusions. Her work will be reviewed below.

Giacobini et al. (1984) document the relative sizes of frontal measures of juvenile Neandertals of comparable age. In general, for traits such as mimimum frontal breadth, bistephonic breadth, and interorbital breadth, Neandertals (Le Fate 1, Carigela, La Quina H18, and Teshik Tash) fall either at the high end of the modern range for that age or exceed it. Vlcek (1972) studied the 5 to 7 month old Kiik-Koba infant. He found that at even at this early stage of development, typical Neandertal traits were exhibited. From the intramembral indices, to the robusticity of the long bones, and

thickened axillary border of the scapula these features reinforce our view that the Neandertal morphotype is established early and must be understood in terms of processes acting at these early stages.

Tompkins and Trinkaus (1987) made comparisons of the pubic bone morphology between a 3 to 5 year old infant from La Ferrassie (#6) and modern children of comparable age. Evident is the typical Neandertal elongate superior pubic ramus (as measured from the acetabulum to the symphysis) at this early age. The authors conclude that the appearance of this morphology in children this young, before the start of the reproductive career, is evidence for strong genetic determination of this trait.

Recently, Dean et al.(1986) have reevaluated the age of the Gibraltar child from the Devils Tower. Based upon the association with an aged temporal bone and a dental perikymata count, Dean et al. interpret the large Gibraltar child as indicative of advanced development in Neandertal children relative to modern children at 3 years of age. The authors believe that the evidence indicates accelerated development in Neandertals along pathways very much similar to modern humans. From this

it is concluded that,

> Neandertals emphasised a greater
> proportion of total brain growth in
> utero but had gestation periods
> similar to modern humans. It then
> follows that they would have
> required a greater pelvic outlet to
> cope with a neonate of greater
> endocranial capacity and would have
> achieved adult cranial capacities
> earlier in their growth periods than
> do modern humans (1986:307).

In an analysis of the developing root cone angles in various hominids, Dean (1985) found that the root cone in the Gibralter child from Devil's Tower had steeper angles (29°) than modern humans (app. 57°). This would indicate precocious development of the root system and is consistent with the accelerated patterns of dental eruption found by Wolpoff (1979). Whether this is indicative of global acceleration cannot be said but the results are consistent with the relative acceleration of their growth respect to modern humans.

Trinkaus (1984) has argued that the size of the Neandertal pelvic outlet, as indicated by the elongation of the superior pubic ramus, implied a gestational period of 11 to 12 months. The precociousness of Neandertal growth almost implied that its gestational

period be elongated. Rak and Arensberg (1987) after
study of the Kebara 2 Neandertal pelvis find that the
elongated pubic ramus stems from an externally rotated
pelvis and not from an enlarged pelvic outlet, In fact,
it was found that the area of the pelvic outlet was
comparable to that of modern humans. In a recent review
of Neandertal gestational hypothesis, Anderson (1989)
finds no support for the gestational hypothesis,
prefering in its place locomotor, environmental, and
baby size determinants of gestational timing.

Rosenberg (1988) discusses a model of Neandertal
development based upon the functional significance of
the pubic bone. There exists a strong relationship
between maternal and neonatal body and brain weights.
Rosenberg proposes that Neandertal children were large
simply because their mothers were large and the enlarged
outlet and pubic lengths were a product,"of their
extreme weight and body proportions"(1988:597). This of
course begs the question of why Neandertal mothers are
so large in the first place. Size is important for sure
but it doesn't explain the unique shape of the pubis.
Only a deeper analysis of the actual development of the
pubic ramus will yield deeper answers. For instance, it
would be interesting to know in humans the rate of

cellular activity in the pubic symphysis and the early proximal end of the ramus.

Minugh-Purvis (1988) has compiled the most complete set of descriptions for Neandertal juveniles and developed a basic outline for their postnatal craniofacial development. Minugh-Purvis (1988) utilizes a comprehensive battery of aging techniques to minimize the size/age problem. She rejects claims that dental banding offers reliable age predictions and opts for more traditional dental/skeletal techniques. The problem with this approach is the application of aging techniques in modern groups to fossil groups whose aging life history status is unclear. There is a real possibility that many of the specimens have been systematically overaged. However, if correction is one day appropriate, then there will be a body of specimens that have been aged in a consistent way by a single worker. This alone is a great service.

Minugh-Purvis (1988) finds the following patterns in Neandertal craniofacial growth and development. Cranial circumference continues to grow into the postadolescent period. This a product of both supposed breadth increase and the developing browridge. At all

stages of development, Neandertal juveniles have larger facial heights. In modern juveniles, upper facial projection increased early in childhood and exhibited throughout the rest of the growth period, continued increase. This is probably due to apposition at Nasion and the expansion of the sinus. Neandertals on the other hand have a pattern that is essentially established in early to middle childhood.

A number of basioccipitals were available for study by Minugh-Purvis (1988). Until late childhood, the Neandertal basioccipital falls within the modern range. By late adolecscence, Neandertals such as Teshik-Tash 1 and LeMoustier fall outside of the modern range, "Thus, the morphological pattern of a long basilar occipital, known from the few adult Neandertals preserving this region, appears to emerge during late childhood during Neandertal ontogeny"(1988:232). This is curious given the model proposed. However, a familiar pattern emerges in the relation to the face. About the time of basilar lengthening beyond the modern range there occurs the development of the lateral browridge. This is coincident with anterior growth of the glabellar region of the torus. Also, this is in association with the marked

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frontal flattening seen in Neandertals. This period of
greater activity would be developmentally homologous to
the late childhood-early adolescent growth spurt seen in
the cranial base and face in modern children (Roche and
Lewis 1976).

Occipital curvature in Neandertals is reached early
in infancy and exhibits stable expansion throughout
growth (Minugh-Purvis 1988). According to Minugh-Purvis,
all of the Upper Pleistocene children are in possession
of some degree of lambdoidal flattening.

The maxillary facies are established early in the
growth period. The 2.5 year old Subalyuk 2 Neandertal
showed no evidence of a canine fossa and throughout the
growth period, the maxilla were either flat or
inflated.In modern children, an early canine fossa is
evident which is then lost with the eruption of the
permanent dentition (Minugh -Purvis 1988).

Two important conclusions made by Minugh-Purvis are
that Neandertal children are generally larger in their
craniofacial features than modern children of comparable
age. With this accelerated development relative to
moderns, there is the early ontogenetic acquisition of
typical Neandertal autapomorphies. Also, the Neandertal

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children demonstrated no anomolous growth patterns that would lead her to believe Neandertals and modern humans traverse different developmental pathways. This conclusion is consistent with the assumption made in this study of the retention of ancestral pathways and the possibility of recovering ancestral growth patterns from present ones.

Leigh (1985) in an analysis of ontogenetic and static allometry in archaic and modern H.sapiens palates, found the Neandertal allometries predisplaced relative to the modern human allometry. In other words, their slopes were nearly the same but they were displaced along the Y-axis. Leigh(1985) interpreted these results by disassociative allometric differences in the size of growth onset. Leigh (1985) gives minimal attention to the alternative of more rapid growth but cites it as an alternative.

Recalling the relation between the Gompertz equations and patterns of heterochrony, the displacement found by Leigh (1985) may be indicative of another process altogether. A control Gompertz curve was calculated (See Figure 18 , curve 1) and plotted. Then, a 10 % increase in both the initial specific growth rate

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GOMPERTZ FUNCTIONS

$Ao_2 = (1.1)Ao_1$

$a_2 = (1.1)a_1$
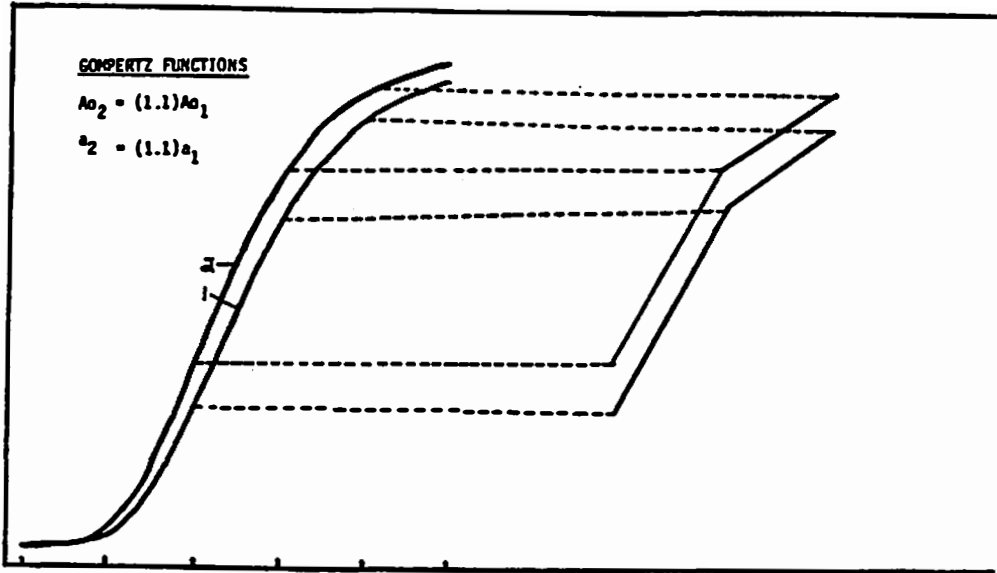
Figure 18.   Simulated Gompertz Curves Which Differ in Their Initial Specific Growth and Decay Rates.

and decay rate was calculated and a new curve generated
(Figure 18, curve 2). The curves are displaced in time
because they have different initial specific growth
rates which translates into different allometric
coefficients. The curves have differing decay rates yet
still pass ordinate values at homologous points because
the RATIO of the specific growth and decay rates remains
the same. In affect, the whole process of early growth
has been speeded up and this early acceleration results
in early senescence. Trinkaus and Thompson (1987) have
found that the post reproductive survival of Neandertals
at Shanidar is much lower than in modern humans. Forty
five to fifty are the oldest these groups seem to
become. This conclusion is based upon gross
morphological criteria and histological techniques
(osteon counting).

Increasing both the initial specific growth and
decay rates without changing the ratio of these
processes qualifies as GLOBAL ACCELERATION, leading to
the conclusion that Leigh's (1985) interpretation of
DISPLACEMENT is not strictly correct. It is not
difficult to see how Leigh(1985) would have come to that
conclusion. The two curves throughout their lengths are
displaced with respect to one another and essentially

parallel. If sizes at identical time periods (X axis)
are plotted, any subsegment of the curves will
demonstrate a pattern similar to displacement.
Neandertals reach larger sizes at earlier ages when
compared to moderns because they are growth accelerated.
The Neandertal craniofacial morphological pattern,
relative to the modern condition is the product of
higher growth velocities early during prenatal life
acting on complex and everchanging allometries.

Ultimate Causation

Earlier in this work, various speculations over the
adaptative nature of the Neandertal craniofacial
architecture were reviewed. It is the authors opinion
that the Neandertal craniofacial complex is a secondary
effect of global growth acceleration (relative to modern
humans) acting early in development. The question
remains, why rapid growth?

There are two alternative explanations that are
thought to best explain the morphological and life
history evidence. These alternatives can work as
independent agents or in concert.

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The postcranial morphology of Eskimos (short, robust, and reduced brachial and crural indices) is convergently reminiscent of the Neandertal condition (Trinkaus 1981). This morphological pattern, based upon the Bergmann and Allen Rules, is consistent with a thermoregulatory adaptation to polar or polar-like environments. I propose that the rapid growth rate in Neandertals occurs as a result of intense selection for increased body sizes at earlier, postnatal ages. Lilja and Olsson (1987) found that selecting for larger sizes in Japanese Quails initiated more rapid growth in still earlier stages of development. Barnett and Dickson (1987) document the association between mice adapted to cold and 'superior' rapid growth rates. Selection would be most intense, and have its greatest effects on morphology, when acting in early postnatal life for several reasons. The correlation between factors affecting growth reduces as growth proceeds. That is, selection acting on early postnatal size (and therefore growth rate) is best able to affect early growth parameters because of their higher correlations (Riska and Atchley 1985). Also, Meban (1983) has clearly shown the classical surface-to-volume relation (A/V=.66) to be operative in human fetuses. It makes sense that

selection favoring the relative minimization of heat exchanging surface will be the greatest when the relative surface area is at its zenith in the postnatal life cycle.

Stearns (1982) and Stearns and Koella (1986) cite examples in which the risk of mortality is reduced if developmental stages or morphologies with high intrinsic mortalities are passed through quickly. Williams (1966:88) has noted that natural selection will always, everything being equal, favor more rapidly developing organisms since "the sooner an organism matures, the less likely it is to die before maturing and reproducing". In a classic paper on the evolution of senescence, Williams (1957) postulated a pleiotropic relationship between rapid early development and early senescence. This pleiotropy may indeed explain the apparently early senescence noted in Neandertals by Trinkaus and Thompson (1987).

Another interesting, alternative and not necessarily mutually exclusive explanation for rapid Neandertal growth rates could be that Neandertals were tending toward an r-like life history adaptation. Of course, relative to most of the animal kingdom,

Neandertals (like Primates in general) are extremely K-like animals. However, like all things biological, life history orientations do vary and there is no a priori reason to believe that this variance should be skewed to an even more K-like condition. According to Gould (1977), Stearns (1977), and Calder (1984) situations favoring r-selection might include large, frequent, and unpredictable environmental fluctuations, abundant resources and density independent catastrophic mortality. Common features shared by r-selected groups (Stearns 1977; Calder 1984) are rapid development, early reproduction and short lifespan. This would coincide with the proposed Neandertal life history pattern. However, r-selected organisms tend toward high reproductive productivity with smaller adults and young. The larger body sizes of Neandertal juveniles may be only superficially inconsistent with these characteristics. The constraining influence of singleton births must be recognized and entered into the reproduction/maintanence equation. High productivity, given this constraint could translate into more energy being channeled into the developing fetus, increasing the individual infant's birthweight. According to Boyce (1979), selection for large body size could be a

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response to resource limitations imposed by episodic resource inavailability. Thus, what has come to be characterized as a typical k adaptation (large body size) can be expected in r-type environments, making it a facultative r-type strategy. However, Boyce (1979) unnecessarily associates low fecundity, long developmental periods, delayed first reproduction and low intrinsic rates of increase with these larger body sizes. It is likely that larger sizes can be acquired not only by growing longer but also by growing faster. This accelerated maturation actually reduces the intergenerational turnover.

Lastly, another factor perhaps critical to the long term survival of Neandertal populations is the relationship between rapid growth and the length of gestation. As discussed previously, many of the arguments surrounding Neandertal gestation length focused upon whether they were longer than or more like the modern durations (9 months). There is another possibility, made possible by Rak and Arensberg's (1987) analysis of the Kebara 2 pelvic inlet. If Neandertals were growing faster earlier in ontogeny and this generated larger fetuses while possessing a modern inlet size, it is certainly possible that they were born

chronologically earlier than modern humans. This would occur to avoid the problem of cephalopelvic disproportion. The shorter gestation lengths of Neandertals may have increased the number of birth attempts within their reproductice career. This would be consistent with an r-like strategy.

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CHAPTER VII

SUMMARY AND CONCLUSIONS

This study has been an effort to tease from the complex and interactive ontogeny of the cranium and face, those features most critical to the establishment of the adult phenotype. Reviews of the literature consistently indicated that the cranial base was a structural and developmental "key" determinant of craniofacial form.

Discussion regarding allometry and heterochrony were directed towards an understanding of the growth process itself. Their relation to classes of Gompertz equations yields a critical set of parameters that may reduce allometry and heterochrony to the various permutations of initial specific growth rate and decay rate. These permutations can be applied at local and global levels to account for all heterochronic change.

Using a data set supplied by Ford (1956), polynomials and their derivatives were calculated so that instantaneous specific growth rates could be attained. If ratios of these rates between structures are plotted against time, the pattern of the allometric

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coefficient as it changes can be analyzed. Since growth is a changing array of rate covariances, this technique is in a much better position to reflect biological reality than the characterization of ontogenetic allometries with a simple, unchanging allometric coefficient.

Several important results were obtained from the analysis itself. The most important of which, finding that the posterior base is growing at a faster pace than the anterior base and that the posterior base exhibits the neural-like growth pattern. It is hypothesized that the growing cerebellum is the primary force behind these patterns. It was also found that facial length, facial height, and anterior cranial base length grow with similar patterns of instantaneous rate change. These traits are then characterized as the facial complex. Zones of greater and graded growth are found in the cranial base cartilages and these are responsible for the flexure process. The pattern of rate change found here in the posterior base agrees well with cellular expectations. The influence of the base on the face is profound and is contingent upon the nature of the flexure process.

A model involving the extrapolation of the present
allometry patterns to larger sizes by increasing their
relative rates was proposed and tested. It was
postulated that the effects would resemble many of the
features differentiating modern humans and Neandertals.
Predictions based upon postulated growth rate
differences were made and static adult allometries were
run. It was found that given the patterns of ontogenetic
allometry uncovered, Neandertals could be infered to be
fast growing relative to modern humans. Also, dramatic
differences in the least squares and reduced major axis
slopes between a sample of forensic blacks and all other
populations supports the link between prenatal growth
rate and facial allometry.

Previous conclusions of Neandertal displacement
were evaluated in terms of Gompertz functions differing
only in the absolute values of their initial specific
growth and decay rates; The ratios remained the same. It
was found that the period of rapid early growth is
checked by early senescence. Since Neandertals have been
postulated by many workers to be precociously large at
birth and suffer early post reproductive mortality, this
set of growth parameter change may best characterize

Neandertal growth relative to modern humans.
Leigh'(1985) conclusion of allometric displacement is
reinterpreted as global acceleration.

Contrary to functional scenerios that fragment the
cranium and face into parcels and then explain each in
terms of some beneficial effect, the developmental
approach has yielded the following conclusion.
Neandertals are variant to modern humans in their rapid
prenatal growth velocities and this acceleration
produces the characteristic patterns of the Neandertal
cranium and face. Because of the degree of covariability
in developing cranial components and the importance of
the minor changes in the development of the cranial base
cartilages, minor genetic changes need only be
responsible for such differences.

The finding that early modern humans demonstrate in
their adult allometries intermediate features relative
to blacks and Neandertals has interesting implications
for the debates on the origin of modern humans. Since
the static adult allometries are meant to be proxies for
prenatal growth rate variation between modern
populations, perhaps the intermediate status of early
modern humans represents the joining and assimilation of
two or more regulatory gene pools. This would be

consistent with the Assimilation Model proposed by Smith et al. (1989) and inconsistent with the Total Replacement Model which suggests that the extinction of Neandertals took place without contributing to modern human gene pools.

This study is an example that the analysis of development generates biological insight unmatched by functional/adaptational scenerios based upon current utility. If mechanics is to ever hold the key to undertanding the morphology of fossil humans, it will be developmental mechanics. If analyses of size/shape change are to ever contribute to our knowledge of the biology of fossil humans, then embryology, development, and cell kinetics must become the conceptual currency of allometricians.

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VITA

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