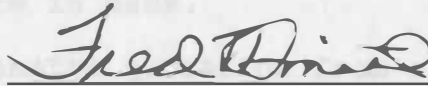


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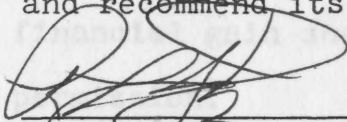
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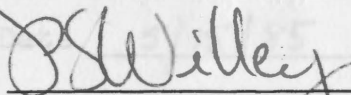


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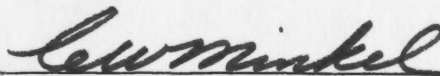
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THE ALLOMETRY OF THE PALATE OF
ARCHAIC HOMO SAPIENS AND
MODERN HOMO SAPIENS

A Thesis
Presented for the
Master of Arts
Degree
The University of Tennessee, Knoxville

Steven R. Leigh
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ABSTRACT

This research examines several aspects of allometry in the palate of archaic Homo sapiens and modern Homo sapiens. The allometry of the modern human palate is described. Comparisons between quantitative methods and comparisons between different types of samples are undertaken. Additionally, the allometry of the archaic Homo sapiens palate is described and analyzed. Finally, allometric comparisons between these groups are made.

The samples employed in this study consist of 132 Amerindian (Arikara) crania and 21 archaic Homo sapiens (primarily Neandertal) crania. Quantitative methods used for analyzing these groups include least-squares regression, reduced major axis regression, and principal components analysis. Analysis of covariance and principal components analysis are used to compare allometric relationships between the groups.

The results of this research indicate that least-squares regression techniques supply information which is generally substantiated by principal components analysis. Comparisons between samples indicate that static samples (samples derived from a single age group) do not provide the same information as ontogenetic samples (derived from several different age classes. These results are similar in both groups.

The most important aspect of this study concerns the allometric relationships between modern and archaic Homo sapiens. Comparisons suggest that archaic Homo sapiens begin growth at larger sizes than modern Homo sapiens, and that this difference holds throughout the growth period. Complementary multivariate analyses indicate that the pattern of general size increase between these two groups is very similar.

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CHAPTER I

INTRODUCTION

The study of allometry, defined by Gould (1966:587) as "the study of size and its consequences," has received considerable attention in the biological sciences. Contributions in biology, paleontology, genetics, and anthropology have been steady since the formal exposition of allometry by Sir Julian Huxley in 1932. Further refinements in both method and theory, particularly by Cock (1966), Gould (1966) and Jolicoeur (1963a), have greatly increased the applicability of allometry to biological problems.

Specifically, allometry may be defined as the quantitative exploration of size and shape relationships between anatomical units during growth and development. From quantitative expressions of growth, researchers may gain insight into complex developmental processes. Similarly, inferences concerning the direction of evolution and the nature of adaptations are extractable from allometric studies.

Several different approaches to allometric problems are identifiable in the literature (Cock, 1966). Generally, these approaches are limited by the types of data available for analysis. Growth data, whether longitudinal (derived from individuals at different points

in time) or cross-sectional (derived from individuals at a single point in time) comprise the most familiar and abundant type of allometric data. Allometric studies based upon growth data are referred to as "ontogenetic" studies. Data derived from individuals at one developmental stage, usually adult, are known as "static" data. Finally, subsidiary fields of study, such as "genetic" allometry have found frequent application in recent years. These topics are well summarized by Cock (1966) and Gould (1966).

The purpose of the present research is essentially three-fold. First, this work explores the allometry of the modern hominid palate, in a sample of American Indians (Arikara) from the Larson Site (39WW2) (Bass and Rucker, 1976; Owsley and Bass, 1979). Secondly, a study of the allometry of the archaic Homo sapiens (primarily Neandertal) palate is undertaken. Finally, an understanding of allometric relationships within each species allows a comparison between modern hominids and archaic Homo sapiens. Such a comparison provides valuable information regarding evolutionary changes between the two species.

Several ancillary problems require attention. A crucial problem involves the validity of using static data to estimate ontogenetic trajectories. In other words, do static data provide information from which ontogenetic

trajectories may be estimated? Secondly, information regarding the results of different statistical analyses of allometry requires examination. Different statistical techniques applied to a single data base may yield different results (Pilbeam and Gould, 1974). Research into the results of different techniques should provide information on appropriate techniques for future studies.

An investigation of allometric relationships in archaic Homo sapiens could provide valuable information pertaining to the position of this group in later hominid evolution. Specifically, are differences, if any, in the allometric patterns between modern humans and archaic Homo sapiens the result of allometric scaling involving purely size-required changes in proportions? Alternatively, are differences between these groups the result of natural selection for alteration of allometric relationships?

The solutions to these problems may provide insight into the role of archaic Homo sapiens (especially Neandertal) groups in the evolution of anatomically modern Homo sapiens. The results presented here may not be conclusive when considered in isolation. However, coupled with other anatomical and cultural evidence, an allometric study may aid in the understanding of later human evolution.

Finally, several contributions are necessary to avoid duplication of research. First, a general review of

allometric studies, with special emphasis on historical developments, seems necessary. Secondly, a synthesis of quantitative methods of allometry should provide a foundation for further investigations.

CHAPTER II

REVIEW OF ALLOMETRIC LITERATURE

1. ONTOGENETIC ALLOMETRY

Ontogenetic studies, or those which examine a growth sequence, are relatively common in the allometric literature. These studies generally attempt to isolate patterns of relative growth within and between species. Additionally, ontogenetic data are often used to compare quantitative methods. Finally, studies of the duration of ontogeny have attracted attention in order to investigate the role of ontogenetic timing in development and evolution.

Huxley (1932) examines an extremely wide range of topics in his major work, Problems of Relative Growth, the first definitive statement of allometry. His formulation of the equation of allometry, $y=bx^k$, (where k is the growth ratio between two body parts, X and Y , and b is a constant) forms the basis of most allometric studies. Huxley's ultimate goal was to "demonstrate the existence of certain broad empirical laws [of relative growth]" (Huxley, 1932:2). Generally, Huxley addresses quantitative issues, studies growth in a variety of species, and examines growth gradients and physiological components of growth.

Of particular interest and importance are Huxley's statements on recapitulation (1932:234-240). He attacks the Haecklian perspective on recapitulation (that ontogeny rigidly recapitulates phylogeny) and indicates that so-called evidence for recapitulation is often the result of different allometric trends. Additionally, Huxley suggests the existence of rate genes to account for evolutionary changes in morphology through changes in developmental timing (1932:229).

Gould (1977) provides a greatly expanded discussion of the problems of recapitulation theory originally raised by Huxley (1932). Gould presents numerous ontogenetic examples which support Huxley's original conclusions. However, the bulk of Gould's work is oriented toward evolutionary problems.

Brown and Davies (1972) provide an extremely detailed bivariate account of allometric growth in two species of cockroaches (Ectobius lapponicus and Ectobius panzeri). Although a major portion of the study involves comparisons of quantitative methods, several biologically relevant conclusions are reached. First, they note taxonomic and sex differences in isometric growth for the two species, probably indicating genetic differences in growth. Secondly, and perhaps more importantly, Brown and Davies (1972:109-110) suggest that simple allometric growth (i.e. constant slope value over the entire growth period) is

relatively uncommon. Instead, relationships between body parts tend to change through time. They also suggest that metamorphic changes in the thorax and abdomen cause deviations from simple allometry (1972:110). This result is not entirely unexpected, given that measurements were made at different instars, corresponding to developmental changes. Thus, each instar slope would be similar to a "statically derived" slope.

Brown and Davies (1972) also study growth gradients and growth contours between species. Differences in growth gradients and contours are explained as the result of genetic and adaptational differences.

In a second study, Davies and Brown (1972) analyze the growth of cockroaches using multivariate techniques. This research primarily investigates differences between quantitative methods. Taxonomic and sex differences in growth are again apparent between the two species. However, these differences appear more clearly in the multivariate analyses than in the bivariate analyses. Additionally, the extent of sexual dimorphism is more readily observed using multivariate methods.

Cock (1963) provides a study of limb growth in several breeds of fowl. Growth is examined cross-sectionally, longitudinally, and statically. Cock finds little difference between measures of ontogenetic allometry (measures based on cross-sectional and

longitudinal data). However, static estimates yield confusing results. Static estimates are, in some cases, similar to ontogenetic estimates, but usually bear very little similarity to ontogenetic results. Cock also notes allometric differences between breeds, and differences between sexes. Finally, Cock suggests that different ontogenetic trajectories may yield similar allometric relations in adults, a finding which can be based only on longitudinal data. Such a result illustrates the problems of estimating ontogenetic allometry from static data.

Cochard (1985) details the ontogenetic allometry of the dentition and cranium in rhesus monkeys. Based on longitudinal data, Cochard investigates sexual dimorphism in dental size. He finds that, relative to body size, females have larger post-canine dentitions than males. Cochard (1985:245) attributes this relationship to higher energetic costs during pregnancy and lactation for females. Conversely, Cochard links the relatively large canines in males to social and defense functions. Although the size of the viscerocranium as a whole is closely related to body size, Cochard notes poor correspondence between the size of the cranium and the size of the dentition. The lack of clear relationships between the cranium and dentition seems to result from the numerous functions performed by the skull. Cochard states that, "the face does not serve exclusively as an anchor

for the dentition" (1985:249). Finally, dental size may be more closely related to the size of the masticatory musculature, an hypothesis which Cochard did not test.

Jantz and Owsley (1984) present an allometric study of Arikara limb proportions. They find significant differences between burial populations in lower limb elements. Differences between groups in limb proportions are accompanied by spatial and temporal differences. The observed changes in proportions are explained by either selective pressures, resulting from migration into more northern habitats, or by gene flow from Mandan groups, already adapted to the more northern areas. In other words, climate, and the adherence to Bergmann/Allen Rules, is seen as a causal mechanism.

Another example of ontogenetic allometry is derived from the research of Gould (1977). These studies involve the application of Gould's "clock models," and are perhaps more properly summarized as parts of evolutionary allometry. However, Alberch (1980) has detailed the importance of ontogenetic studies, with special reference to clock models, in examinations of evolutionary morphology.

Alberch (1980) discusses the role of developmental dynamics in evolutionary morphology. Employing a three-dimensional model, which includes age, size, and shape as variables, Alberch (following Gould [1977])

suggests that regulatory changes in the timing of development are of primary importance in morphological evolution. This model, although currently difficult to apply, rests upon non-random changes in the timing of gene action (Alberch, 1980:660). In addition, Alberch suggests that developmental constraints limit the role of selection and thus limit phyletic trends (1980:664). Constraints are either epigenetically or environmentally controlled. Alberch concludes by stating that morphological evolution should be studied ontogenetically, primarily as a response to excessively "adaptationalist" methods of analysis. Developmental constraints should be identified so that the direction of selection can be more clearly understood.

2. EVOLUTIONARY ALLOMETRY

The study of evolutionary allometry has received considerable attention. Basically, evolutionary allometry usually involves the study of size and shape changes through time in a phyletic sequence. As such, examining allometric relationships through time could be of great importance in fostering an understanding of selectively induced morphological change (Gould, 1966:621).

Several different perspectives regarding evolutionary allometry appear in the literature. Cock (1966) presents one of the strictest definitions. He asserts that evolutionary allometry represents a special case of static

allometry. Thus, in Cock's view, the application of allometric methods to an evolutionary sequence provides researchers with a simple description, not an explanation of evolutionary events. Furthermore, allometric techniques are applicable only when a trend towards increasing or decreasing size seems evident (Cock, 1966:174).

In contrast, Gould (1966) presents a more positivistic view of evolutionary allometry. Gould, identifying size change as a major "theme" in evolution, uses allometric techniques to examine diverse topics, ranging from increases in metabolic efficiency (with larger body size) to brain-body evolution in hominids.

The two views presented above illustrate the polarized nature of the debate regarding evolutionary allometry. The difference in perspective of these two authors is, in some part, a result of historical factors. For example, in his discussion of evolutionary allometry, Cock (1966) cites Hersh (1934) and Lumer (1940) as providing poor examples of applying allometric methods to evolutionary problems.

Hersh's 1934 publication regarding horn growth and evolution in titantotheres represents one of the earliest attempts to apply Huxley's (1932) techniques to the fossil record. Basically, Hersh argued that titantothere horns would have reached a size, via selection, that would

increase birth hazards, possibly preventing successful parturition, and resulting in extinction (Hersh, 1934:550). Hersh concludes by arguing that, at least in the case of titantotheres, ontogenetic and phylogenetic patterns are similar (1934:560).

In a comparable study, Lumer (1940) employs measurements of dog skulls and long bones for allometric studies. His work tends to be more taxonomic, because he suggests that different groups of dogs form "allometric tribes." Additionally, Lumer argues that ontogenetic regressions provide results similar to phylogenetic regressions (1940:461).

Simpson (1953:287) provides a third case of evolutionary allometry. Simpson's example differs from that of Hersh because Simpson recognizes the existence of correlated genetic systems. Thus, if selection is strong for a particular attribute, correlated changes may occur in other phenotypic traits. The case of the Irish Elk (Megalaceros) presents a problem similar to the one encountered by Hersh (1934). As Simpson notes a common explanation that large antlers "'must have been disadvantageous'" is, in this case, naive (1953:286). He states:

Another possibility, or indeed probability, is that this was an example of selection in correlated trends. Body size and antler size were probably allometric in Megalaceros . . . with $k > 1$ for antler on body regression. In early stages, selection was for both larger body and large

antlers, the allometric relation then accelerated the trend. When the point was reached where antler size ceased to be advantageous, selection against further increase in antlers was weaker than that for further increase in body size. The latter trend continued, and therefore allometric increase in antler size continued, until the opposite selection pressures became equal. Body size was then somewhat under its optimum and antler size somewhat over its. That so specialized a creature might then be especially susceptible to extinction with environmental change is a different point, invoking no momentum effect. (Simpson, 1953:286-287)

Thus, Simpson avoids the problems encountered by Hersh (1934) by recognizing correlated responses to selection and separating evolutionary specialization and environmental change.

Cock (1966) clearly identifies the problems encountered by Hersh (1934) and Lumer (1940). Surprisingly, Cock (1966) does not comment on Simpson's (1953) view, despite the fact that Simpson recognized the same problems as Cock. First, Cock asserts that explanations of allometric overspecialization neglect considerations of genetic diversity. In other words, Hersh (1934) and Lumer (1940) implicitly suggest a total absence of genetic diversity in the allometric relations studied. Otherwise, as Cock suggests, selection on variable allometric relationships would prevent extinction due to increase in general size (1966:176). Secondly, these explanations tend to ignore genetically correlated responses in an organism. In other words, horn size in

titantotheres is not likely to be uncorrelated with other aspects of the anatomical system. Thus, a more cohesive explanation of titantothere extinction may include, but not be limited to dramatically enlarged horn size (sensu Simpson and the Irish Elk [1953]). Finally, Cock (1966) suggests that, in Lumer's (1940) case, ontogenetic results parallel phylogenetic results because of Lumer's use of a static data base as to represent an evolutionary data base. True ontogenetic data would, in Cock's opinion, lead to radically different results.

An article published by Bertalanffy and Pirozynski (1952) marks an important turning point in the study of evolutionary allometry. Their study, in which albino rats were used, indicates that ontogenetic and evolutionary allometry are not necessarily similar (contra Hersh [1934] and Lumer [1940]). This assessment is based on a comparison of relative growth of rat organs to relative growth of organs in other animals. These results do not seem overly important. However, Bertalanffy and Pirozynski were the first to synthesize interspecific data and compare these data to ontogenetically derived data. Secondly, their observation that evolutionary and ontogenetic allometries are not necessarily coincident is important, primarily because they were the first to document this pattern.

As a result, researchers could no longer use ontogenetic growth patterns to estimate evolutionary changes in morphology.

Researchers in human evolution have made significant contributions to the study of allometry (Gould, 1975). Several studies are important for current purposes, including research by Hemmer (1969; 1971) and Pilbeam and Gould (1974).

Hemmer (1969) provides an investigation of brain allometry in human evolution. He finds intercept differences in bivariate plots of cranial capacity on cranial length. These intercept differences take the form of upward transpositions, through time, between taxa. Hemmer explains these transpositions by arguing that differences exist in ontogeny: specifically, that the upward transpositions are the result of prolonged embryonic growth in modern humans in comparison to Australopiths. Finally, Hemmer (1969:180) attributes differences in cranial form to the allometric effects of increased size.

In a related article, Hemmer (1971) argues that allometric differences account for different "levels" between "true Neandertals and Neandertaloid types of Asia and Africa" (Hemmer, 1971:65). Hemmer finds transpositions of "Cro-magnoid men" significantly above the regression line for Neandertals. Additionally, Hemmer suggests that

three different transpositional episodes resulted in two different lineages, one leading to modern humans, the other leading to classic Neandertals. Finally, Hemmer sees "stagnation" of evolutionary rates in tropical and subtropical zones compared to "rapid evolution" in temperate climates (1971:69).

Hemmer's research contains abundant flaws. First, all the analyses are based on adult specimens. Thus, Hemmer's suggestion of ontogenetic differences is untestable. Secondly, Hemmer's statistical techniques are extremely weak. Correlations between variables, significance tests on regressions, tests for homogeneity of slopes, and tests for significant intercept differences are not presented. Consequently, Hemmer's "significant transpositions" (if they indeed exist) may be the result of sampling problems. Visual inspection of Hemmer's regressions (1971: Fig.2, Fig.3) shows a total of eleven "early and classical Neandertals" and eight "Cro-magnoid men." Finally, Hemmer's graph (1971:Fig. 2) shows a downward transposition of Australian Aborigines which, according to his criteria, suggests a "lower" evolutionary "level" than archaic Homo sapiens.

Pilbeam and Gould (1974) present a more informative study of brain/body evolution in hominids and pongids than Hemmer (1969; 1971). Their results suggest dramatic increases in endocranial volume relative to estimated body

weight in the Homo lineage compared to Australopiths and pongids. Australopiths possess large brains relative to pongids but within this lineage (gracile to robust) show an allometric brain/body slope similar to that for pongids ($a=.33$ for Australopiths; $a=.34$ for pongids). However, brain size in the Homo lineage scales with pronounced positive allometry ($a=1.73$); this lineage is characterized by larger brains relative to body size.

Dentally, a different situation is present (Pilbeam and Gould 1974). For the Homo lineage, teeth scale negatively relative to body size in contrast to Australopiths and pongids. Pilbeam and Gould (1974) conclude by arguing that Australopiths are primarily allometrically scaled variants. In other words, robust specimens simply represent larger versions of gracile specimens. Additionally, they argue that the relatively large teeth of Australopiths provide evidence for herbivory which is lacking for Homo habilis and Homo erectus. Thus, Pilbeam and Gould argue that differences in the Australopithecine face are primarily allometric. Rak (1983) mentions this view, but does not specifically examine this perspective.

The analysis undertaken by Pilbeam and Gould (1974) is a significant improvement over the analyses by Hemmer (1969; 1971). However, the lack of juveniles in their Australopith series (e.g. Taung) does not allow a detailed

understanding of the allometric differences between Australopith species. Thus, their results do not allow great confidence in hypotheses specifying allometric scaling or transpositional differences. This problem is not as acute in their analysis of the Homo lineage, because their evolutionary sequence is used simply to demonstrate the dramatic decrease of dentition through time in this lineage, not to examine allometric differences between species.

Gould may have recognized these problems in a later work, Ontogeny and Phylogeny (1977), in which he examines the roles of neotony and recapitulation in evolution. While not strictly an allometric study, Gould carefully dissects several problems encountered in the study of evolutionary allometry. Most directly, the problem of recapitulation (the repetition of ancestral stages in the embryonic or juvenile stages of development [Gould, 1977]) is addressed. Gould refines this concept and suggests alternatives to recapitulation theory. In addition, he considers evolutionary processes which serve to alter growth patterns. Gould's major refinement of the concept of recapitulation is the formulation and elaboration of the concept of hypermorphosis. Hypermorphosis may involve the extension of ontogeny beyond that of an ancestral stage. Conversely, neotony, the opposite of hypermorphosis, implies the abbreviation of ontogeny

relative to ancestral stages. A third concept, progenesis, is common in certain situations and involves accelerated maturation. These concepts fall under the general concept of heterochrony (literally, different timing).

In many ways, hypermorphosis is a "better" concept than recapitulation. First, it avoids strict adherence to classical recapitulation theory. Therefore, the vertebrate embryo need not "pass through" the "fish stage, amphibian stage, reptile stage, etc." Instead, morphological change in descendants may occur at later periods of life; most commonly, according to Gould (1977:344), hypermorphosis may be stimulated by delays in maturation. Secondly, Gould links hypermorphosis to generally accepted ecological theory, specifically "r" and "K" selection (Pianka 1978). According to Gould (1977:345), hypermorphosis may be the result of adaptation to K-selected regimes. Hypermorphosis leads to relatively rapid adaptation in "K-environments." However, this process may lead to overspecialization. According to Pianka (1978:122) environmental correlates of K-selection include predictable environments, density dependent mortality, longer life spans, greater competitive ability, and delayed reproduction, and other characteristics.

An important alternative to hypermorphosis is, according to Gould, neotony, or the phylogenetic retention

of formerly juvenile characteristics, produced by retardation during development (Gould, 1977:483). Both hypermorphosis and neotony are the results of similar processes. However, hypermorphosis involves the maintenance of ancestral rates of differentiation, and delays in maturation allow "extrapolation beyond ancestral conditions" (Gould, 1977:344). Conversely, neotony preserves evolutionary flexibility through the retention of unspecialized juvenile structures. According to Gould (1977:344), neotony is less common than hypermorphosis.

The differences between neotony and hypermorphosis, despite their apparent similarities, are important. In theory, each "pathway" should lead to more successful environmental adaptation. The most important difference, however, is the end result of each process: neotony generally confers evolutionary flexibility through the lack of specialization, while hypermorphosis leads to specialization, and thus more adequate adaptation to a particular environment. Obviously, Simpson's (1953:287) caveat suggesting the lack of a necessary relationship between specialization and extinction is of great importance in this case.

Gould suggests that neotony is an important factor in human evolution. Neotony, rather than hypermorphosis, is favored in human evolution because it confers evolutionary flexibility (Gould, 1977:352-404). Hypermorphosis, while

resulting in relatively rapid evolutionary advantages (Gould 1977:345) may lead to overspecialization. The example of the Irish Elk is used by Gould to illustrate this point. Additionally, Gould indicates that neotony may facilitate social bonding, and provides numerous examples to support his contention (1977:345-351). Obviously, the maintenance of strong social relationships in human evolution is of tremendous importance.

Analytically, the study of neotony and hypermorphosis which Gould advocates relies on a "clock model" (1977:246-282). This technique is poorly developed, especially in quantitative terms. Although Alberch et al., (1979) present a mathematical representation of clock models, their method is relatively rarely utilized. This method involves studying changes in developmental timing. A primary feature of this model (Alberch et al. , 1979) is that it uses shape to plot morphological change relative to size. Thus, shape is measured on the "Y" axis, and size on the "X" axis. Unfortunately, the difficulties in measuring "shape" tend to override the usefulness of this model. Nevertheless, the theoretical value of its contribution should not be underestimated.

As a result of the difficulties in the application of clock models, researchers have preferred more traditional allometric techniques, specifically regression and principal components analyses. Additionally, a large

portion of the work concerning heterochrony has been undertaken by anthropologists. Research by Giles (1956) and Shea (1981, 1983a; 1983b; 1983c) has significantly "bolstered" Gould's theoretical notions.

Giles (1956) suggests that chimpanzees and gorillas form an "allometric" group which is distinguishable from orangutans. Of considerable interest is Giles' (1956:56) statement that some differences between chimpanzee and gorilla morphology are:

due to similar growth patterns . . . [which during evolution have resulted in] . . . different terminal overall morphological configurations through the mechanism of general body volume increase. (Giles, 1956:56)

One important aspect of Giles' research is that Gould's (1977) considerations of heterochrony are empirically suggested. However, Giles does not suggest which heterochronic process (neotony or hypermorphosis) is responsible for the observed pattern.

Shea's work, which may be viewed as an elaboration on the work of both Giles (1956) and Gould (1977), demonstrates the presence of both neotony and hypermorphosis in African Apes (Pan paniscus, Pan troglodytes, and Gorilla gorilla). Shea (1983b) suggests that the morphology of the pygmy chimp results from neotonic processes relative to the common chimp. Shea argues that the opposite process (peramorphosis) from the pygmy chimp to the common chimp is untenable because of

ecological factors favoring neotony. These ecological factors are indicated by a K-selection environment inhabited by the pygmy chimp. Evidence for stronger K-selection on Pan paniscus takes the form of reduced sexual dimorphism in both behavior and morphology (Kuroda, 1980).

Elsewhere, Shea (1983a:275-289) indicates that rate hypermorphosis has resulted in differences between common chimpanzees and gorillas. Rate hypermorphosis involves a "speeding up" of developmental rates, leading to larger size and greater dimorphism in gorillas. Additionally, he notes that cranial and postcranial growth allometries of the pygmy chimp, common chimp, and the gorilla generally form a single ontogenetic trajectory. Thus, this assumed phyletic sequence is characterized by successively larger sizes via a common growth pattern, and accompanied by different rates of maturation. Consequently, selection, at least in the case of the African Apes, seems to act on the timing of maturation, rather than on body size alone (Shea, 1983a:283). Shifts in developmental timing and, therefore, body size, are associated with various ecological factors, such as adaptive radiations and niche differentiations (Shea, 1983a:286).

Analytically, Shea relies heavily upon age chronologies, primarily because traditional allometric techniques (bivariate plots, etc.) are relatively easily

combined with age chronologies. Thus, allometric methods achieve compatability with the newer and relatively untested methods based on Gould's (1977) clock models (Alberch, 1980; Alberch et al., 1979). Of critical importance is the fact that Shea relies primarily on ontogenetic data, rather than on static data. For example, Pilbeam and Gould's (1974) argument that Australopiths are ontogenetically scaled may be incorrect, primarily because no juveniles were analyzed. In other words, the absence of a true ontogenetic trajectory (i.e. Taung>graciles>robusts) may render their results insignificant. Pilbeam and Gould (1974) simply measured closely related paleospecies of differing size, not differences in ontogenetic scaling. Shea's work greatly expands the potential for studies of scaling in fossil populations, although the precision attained in his work may not be readily achieved in fossil studies. Additionally, juvenile fossil material is not usually abundant. However, studies of evolutionary allometry should attempt to analyze juveniles when possible, especially when research questions involve investigations of differences in scaling between closely related (ancestor-descendant) taxa.

In summary, the faults of earlier research into evolutionary allometry have been, to some degree, identified and avoided in later research. The primary

conclusion which emerges from this review is that juveniles should be included, whenever possible, in research of evolutionary changes in ontogenetic scaling. Results based on static data bases may be misleading, especially if developmental timing is to be considered. Results based on static data may, however, provide valuable results if researchers desire descriptive information on size changes in evolution.

3. GENETIC ALLOMETRY

Research into genetic aspects of allometry comprises a relatively small portion of the currently available literature on allometry. Huxley (1932) devoted a short, but relatively complete section of his book to the investigation of genetic factors in relative growth. At that time, only one case of the involvement of major genes in the rate of development was known: the development of eye pigment in Gammarus. As Cock (1966:157) points out, this example is not strictly morphometric, but represents one of the few examples of major-gene action in growth rates.

The lack of examples of major genes controlling development is not surprising. Unfortunately, the paucity of these examples greatly complicates the task of the geneticist in assessing the actions of genes on developmental rates. Another problem is, to a certain

extent, historical. The major historical factor is the contrast between the work of Gould (1966) and Cock (1966). Both articles are widely cited, but most researchers are more familiar with Gould's work. Cock emphasized genetic aspects of development much more than Gould. Both articles are extremely valuable reviews which summarize allometric research up to 1966. Several important differences exist between the two articles, primarily because Cock (1966) presents a review oriented toward geneticists, while Gould (1966) emphasized more general topics.

Cock (1966) notes and details differences in developmental rates which might be the result of genetic differences. For example, Cock's work focusses on comparisons of "breeds and strains." Differences in development are presumably the result of genetic differences.

Another valuable aspect of Cock's (1966) article is the attention he devoted to methodological considerations. Different types of data (longitudinal, cross-sectional and static) are meticulously defined and explored. Despite Cock's (1966) contribution, Gould's (1966) work is much more widely cited. Consequently, biases inherent to Gould's approach are more wide-spread, such as the bias towards paleontological data.

The major conclusions reached by Cock (1966) concerning genetic allometry are important. First, he identifies the optimal form of data (longitudinal) and contrasts these data with other forms (cross-sectional and static). Secondly, he notes that ontogenetic regression lines or trajectories of different breeds often intersect. Such observations may not be possible with "sub-optimal" data bases.

More recent investigations of the genetics of size and shape have been provided by Atchley and Rutledge (1980), Atchley et al. (1981) and Lande (1979). Lande (1979) presents an analysis which contributes to multivariate theories of selection and drift in allometric relationships. Lande applies mathematical constructs to the evolutionary relationship between brain and body size. He suggests (1979:412) that, in a short term situation (the amount of time necessary for subspeciation or speciation), the "coevolution" of brain and body size results primarily from selection on body size. Conversely, in a long term situation (in which differentiation at higher taxonomic levels occurs), natural selection should act primarily on brain size. Thus, changes in brain size would "close the gap" induced by more rapid body size change. Finally, Lande (1979) suggests that a low genetic correlation between brain and

body size would account for the dramatic increase in human brain size without a concomittant increase in body size.

Atchley and Rutledge (1980) examine aspects of size and shape in mice through quantitative genetic methods. They suggest that extrapolation from phenotypic correlations to underlying genetic correlations is unwarranted. Atchley and Rutledge (1980) show changes in covariance patterns throughout the developmental period studied (25 weeks). They explain changes in covariance patterns as the result of "differential activity of all the loci affecting the trait in question" (1980:1170).

Perhaps the most important suggestion made by Atchley and Rutledge (1980) is that changes in a particular allometric relationship could result in changes in others, provided a significant genetic correlation exists. This finding has far-reaching implications in terms of "mosaic evolution" (Mayr, 1963; McHenry, 1975). For example, evolutionary changes in a relationship between anatomical units (A and B) could result in alterations of seemingly independent units, C and D. This secondary change may not be the result of selection on both sets (A,B;C,D). Instead, changes in C,D may represent a correlated response to selection on A,B. Obviously, choosing between a correlated response model and a mosaic or independent selection model is difficult, especially in the case

of fossils. However, analogical evidence could prove valuable in such cases.

Atchley et al. (1981) expand the earlier study by Atchley and Rutledge (1980) through the examination of rat and mouse skull measurements. Again, they argue that inaccuracies may occur when attempting to extrapolate genetic relationships from phenotypic data. Atchley et al. (1981) argue that pleiotropic effects may mislead researchers concerned with phenotypic data. Furthermore, the genetic correlation and additive genetic variance of each trait determines the amount of change in related characters (Atchley et al., 1981).

Cheverud (1982) follows Atchley et al. (1981) in a study using rhesus macaques. In addition, he compares various types of data (ontogenetic, static, etc.). Genetic allometric relationships are a central part of Cheverud's research. He finds a lack of correspondence between genetic and phenotypic allometry. Cheverud (1982:146) suggests that a lack of correspondence between phenotypic and genetic size and shape relationships causes difficulty when inferring the action of natural selection based on phenotypic traits.

These studies, which reflect only a small part of genetic approaches to allometry, are all valuable. As a rule, they provide caveats to the study of phenotypic allometry. Geneticists studying allometric relationships

seem somewhat particularistic, however. Moreover, they do not discuss methods of circumventing the lack of correspondence between genetic and phenotypic analyses. Finally, the lack of genetic data does not necessarily render phenotypic data bases useless. It should, however, alert researchers to the potential problems with different types of data bases.

4. QUANTITATIVE METHODS IN ALLOMETRY

Several different quantitative techniques exist for the study of allometry. Generally, these techniques should yield similar results. The most commonly used methods will be examined and their similarities and differences illustrated.

Types of Data

Cock (1966) defines several different categories of data available for growth studies. These data are most conveniently expressed in matrix form, where, for each individual:

$$\begin{array}{ccccccc}
 a_1 & a_2 & a_3 & \cdot & \cdot & \cdot & a_k \\
 b_1 & b_2 & b_3 & \cdot & \cdot & \cdot & b_k \\
 \cdot & \cdot & \cdot & & & & \cdot \\
 \cdot & \cdot & \cdot & & & & \cdot \\
 \cdot & \cdot & \cdot & & & & \cdot \\
 n_1 & n_2 & n_3 & \cdot & \cdot & \cdot & n_k
 \end{array}$$

Each row marks the course of development of one

measurement. Concomittantly, columns indicate the form of an individual throughout development (Cock, 1966:132).

In addition to a matrix format of development, Cock specifies several distinct types of data. These are static, cross-sectional, and longitudinal. Two less common types of data include mixed cross-sectional and mixed longitudinal. These different types of data vary in their "usefulness" (Cock 1966). Optimally, longitudinal data are used, primarily because information concerning individual variation in size and shape through time is available. Longitudinal data bases may be "broken-down" into less reliable data bases, including static and cross-sectional forms of data. A more common data set is cross-sectional, in which data are derived from individuals at a variety of developmental stages. At this level, information concerning individual variation is unobtainable. Static data are derived from individuals at one developmental stage. Cock (1966:135-136) suggests that static data comprise single column matrices. As such, "the element of true (i.e. ontogenetic) growth is entirely absent" (Cock, 1966:135-136). Mixed cross-sectional data consist of measurements of individuals in populations from which independent age estimates are unobtainable. Finally, mixed longitudinal data consist of incomplete records for some individuals (Cock, 1966:136).

Gould (1966) recognizes the same types of data but does not explicitly describe them. In contrast to Cock (1966), Gould seems to accept static data more readily. In addition, Gould's discussion frequently includes examinations of inter-specific allometry, which is often necessarily based on static data.

Gould (1966:615-624) details uses of allometric methods in evolutionary studies, with specific emphasis on cause and effects of changes in allometric relations. Again, Cock (1966: 174) disputes the use of evolutionary allometry and indicates that these analyses should be confined to the investigation of trends; and are, therefore, only descriptive. Thus, evolutionary investigations based on static data are of limited utility.

Methods of Data Analysis

Rectangular coordinates. One of D'Arcy Thompson's (1961:288-323) contributions to the study of the relationships between size and shape is the method of "rectangular coordinates." Thompson's method (originally published in 1917) allows a rapid visual understanding of differences in proportions. Although not strictly statistical this method of "transformation" involves the superimposition of a grid on an organism or part of an organism. This original set of Cartesian coordinates is then "adjusted" and superimposed on another organism.

Coordinates placed at homologous anatomical points allow a quick visual understanding of differences between the two organisms.

Transformations allow a clear and objective understanding of morphological differences between forms. Unfortunately, several problems limit the usefulness of Thompson's method. First, characterization of forms by transformation grid is difficult in more than two dimensions. This may seem a minor difficulty. However, a third dimension could greatly enhance the usefulness of this technique. Secondly, a notion of population variability is difficult to obtain. Deriving a "mean" transformation would be an almost impossible task. Finally, transformations are difficult to express numerically, even at a typological level (Medawar, 1950).

Despite the problems with the transformation method, it remains a valuable heuristic device. Furthermore, recent research has attempted to circumvent some of the problems encountered by earlier efforts (see below).

The simple allometry equation. The most popular statistical method in the analysis of size and shape is linear regression. Huxley (1932:1-41) develops and explores the mathematical implications of "constant differential growth rates" which are generalized by the equation:

$$y = bx^k$$

where k is a constant and is the ratio of the growth rates of variables y and x . Similarly, b is a constant (Huxley, 1932:7). This formula may be simplified by conversion to logarithms where:

$$\log y = k(\log x) + \log b$$

Such an expression simply linearizes the original equation, allowing a clearer understanding of relationships between parts.

Huxley bases this empirical generalization on three "fundamental" facts about growth:

The rate of growth of an organism growing equally in all of its parts is at any moment proportional to the size of the organism
Second . . . the rate of self-multiplication slows down with increasing age Third . . . it [an organism] is affected by the external environment. (Huxley, 1932:6)

Huxley argues that this formula, while not a law, is sufficiently general to apply to a wide range of situations. Medawar (1950) has carefully considered the application of Huxley's formulation. While, as Medawar admits, not all growth can be considered multiplicative, examples of multiplicative growth are common enough to justify application of the formula to a number of situations. Additionally, Medawar (1950:477) suggests that additive growth may often be "subsidized" by multiplicative growth, further verifying the validity of the simple allometry equation.

Gould (1966:594) provides several basic guidelines for the biological interpretation of the allometry equation. The value of "a" (originally "k" in Huxley's formula), the slope, is of critical importance because it specifies the nature of the relationship between X and Y variables. If, according to Gould (1966), the value of a is less than 1, then the Y/X ratio decreases with increases in X. This situation is termed "negative allometry." Conversely, a values greater than 1 suggest a rapid increase in Y relative to X, a condition termed "positive allometry." A special case, where $a=1$, is known as "isometry," and implies equal rates of increase for both X and Y.

The interpretation of the intercept value (b) is considerably more difficult. Most authors have accepted Huxley's (1950:465) view that b (the value of Y when $\log X=1$) "has no biological or general significance." White and Gould (1965) have presented an extensive discussion of b. They find that, while b viewed simply as the value of Y at $\log X=1$ may have no universal biological significance, this value has some significance at other levels. First, differences in b without concomittant differences in a may indicate taxonomic differences. Secondly, differences in b may also indicate differences in sizes at the beginning of ontogeny.

Despite the efforts of White and Gould (1965), most researchers concern themselves only with the slope value (a). Intercept differences may be important, but some difficulty still exists in explaining these differences.

Regression Techniques. The primary statistical tool employed by allometrists is simple linear regression. The heavy use of regression is the result of the conversion of the simple allometry equation to the log-linear equation:

$$\log y = a(\log x) + \log b$$

where a is the slope of the regression, and b is the intercept. Essentially, regression is the study of relationships between variables (Younger, 1979:2).

Allometric studies generally apply simple bivariate regressions to problems under investigation. However, several different regression techniques are currently employed (Sokal and Rohlf, 1981).

The most commonly used technique is least-squares regression. This technique produces a regression line which attempts to minimize (on average) the squared deviations in the dependent variable (Younger, 1979:30). Thus, a line is found which is closest to all the points in the data set.

The least-squares method is not, however, without problems. Sokal and Rohlf (1981) indicate that least-squares, a type of Model I regression, assumes no

error in the measurement of the independent variable. When the independent variables are experimentally controlled, error is basically absent. However, when both variables are measurements, without external control, both are subject to error.

In cases where the independent variable is measured with error, Model II regression techniques may be appropriate (Sokal and Rohlf, 1981). Similarly, if specification of independence is impossible (i.e. in the case of two skull measurements), then use of Model II regression may be advisable. In allometric research, the most common Model II regression technique is reduced major axis regression. Two methods of calculating the regression coefficient are possible. First, the sum of the standardized Y variables is divided by the sum of the standardized X variables. The square root of this value is obtained, providing the regression slope (a) (Sokal and Rohlf 1981). Alternatively, the least-squares slope is divided by the correlation coefficient, yielding the reduced major axis slope (Pilbeam and Gould, 1974; Sokal and Rohlf, 1981). Other regression methods include major axis, and Bartlett's three group method, which are detailed by Sokal and Rohlf (1981).

The choice of Model I or Model II regression depends upon a number of factors. First, the questions formed by researchers may affect this choice. For example,

Goldstein et al. (1978) specify independence of some variables (e.g. body weight, dimorphism, and diet). They prefer least-squares for the problems they address. Secondly, Model II regression lacks certain advantages of Model I regression. Significance tests are difficult to perform with Model II regression. Additionally, statistical comparisons of regressions (analysis of covariance) are impossible to accomplish. Finally, Model II regressions are not generally available in packaged programs.

Multivariate techniques. The use of multivariate statistics in allometric research has become increasingly common since the refinement of these techniques by Jolicoeur and others (Jolicoeur and Mosimann, 1960; Jolicoeur, 1963a; 1963b). The majority of multivariate allometry studies employ principal components analysis, although other multivariate methods (discriminant function analysis, canonical variate analysis, and factor analysis) have been utilized (Blacklith, 1960, Albrecht, 1980). Generally, these different methods provide the same basic types of information. However, the analysis refined by Jolicoeur (1963b) has received the majority of attention.

The use of principal components analysis in morphological research was anticipated by Yates (1950). Yates seemed to express doubt regarding the applicability of principal components analysis, stating that, "there is

evidence that the measurements are primarily influenced by only two variates . . . however, the conclusion is tentative" (Yates, 1950:434). Jolicoeur's research (1963a; 1963b) has allowed greater confidence in the use of principal components to study allometric relationships. Nevertheless, some authors have expressed reservations concerning the accuracy of this technique, including Jungers and German (1981).

Principal components analysis involves the partitioning of variance into new variables (principal components). Transformation to principal components rotates the original data points (in multivariate hyperspace) to an axis of maximum variance. In so doing, points are projected onto a new set of orthogonal axes (Hope, 1968). In reference to canonical variate analysis, of which principal components analysis is a part, Albrecht (1980) states, "no extraordinary 'mathematical interventions' are involved. . . ."

The application of principal components analysis to allometric problems is relatively straightforward. Jolicoeur (1963a; 1963b) has indicated that the first eigenvector calculated from the covariance matrix of logarithms contains information concerning the general size of an organism. Typically, the first eigenvector accounts for the majority of the total variance. Concomittantly, the second and subsequent eigenvectors,

which usually contain a smaller portion of the total variance, provide information regarding the shape of an organism.

The information present in the first principal component is relatively easily interpreted. Jolicoeur (1963a; 1963b) has shown that the allometry coefficient may be "generalized" by derivation of a standardized loading, $1/\sqrt{p}$, where p is the number of traits (or measurements). Thus, if θ_i = the angle of the first principal component with the logarithmic coordinate axis of X , then $\cos \theta_i = 1/\sqrt{p}$ represents isometry for the i th trait (Jolicoeur, 1963b:499). Similarly, $\cos \theta_i < 1/\sqrt{p}$ and $\cos \theta_i > 1/\sqrt{p}$ represent negative and positive allometry, respectively.

Information concerning the shape of an organism is not easily extracted from subsequent principal components. Interpretation of these subsequent components involves the investigation of positively and negatively correlated variation between traits (Jolicoeur, 1963a:14). Finally, it is important to emphasize Jolicoeur's (1963a) attention to all principal components, regardless of the amount of total variation in each.

The advantages of principal components analysis are numerous. First, allometric relationships are expressed relative to overall size. Overall size is internally defined by the number of variables analyzed. Secondly,

the relationships between a vast number of dimensions may be explored simultaneously. Thirdly, by identifying dimensions of low variability, inferences regarding the degree of canalization (Waddington, 1957) are theoretically possible (Jolicoeur, 1963a).

Despite the numerous advantages of this method, various authors have challenged its applicability. Jungers and German (1981) argue that the variables used to define "general size" are sample specific. Furthermore, they note that variables chosen for analysis may not adequately reflect "independent" measures of general size, such as body weight. Jungers and German (1981) observed a high rank correlation between allometry coefficients derived from principal components analysis and allometry coefficients derived from regression based measures of allometry coefficients. However, they suggest that alternative methods to Jolicoeur's principal components method should be sought.

A potential problem with Jungers and German's analysis is the exclusion of body mass from the principal components analysis (1981:197). This variable was employed only in the bivariate regressions. Consequently, their results are probably biased because body mass was excluded. The inclusion of body mass may have provided more favorable results.

Principal components analysis seems to provide an adequate method for the analysis of allometric relationships. Comparison to bivariate results should, when possible, be undertaken. Obviously, such comparisons would be unwieldy when numerous variables are analyzed. Consequently, principal components analysis may be accepted as a reliable guide to allometric relationships, as has been suggested by Shea (1981).

The quantitative analysis of shape. Currently employed allometric methods generally supply only "inferential" data concerning shape. This deficiency is reflected in the problems of interpreting principal components subsequent to the first. Research is continuing in the direction of solving this problem. Therefore, a very brief review of this literature seems necessary. It is important to note that this field is in its infancy. Furthermore, a considerable amount of mathematical complexity is involved in these analyses.

Bookstein (1977;1980) has attempted mathematization of "Thompson grids." His approach utilizes engineering concepts, such as shearing stress, to understand shape transformation. Bookstein's "biorthogonal grids" involve only two dimensions. However, the mathematical complications are extreme. Additionally, the results of Bookstein's research seem abstract, primarily as a result of a general lack of additional empirical studies.

Cheverud et al. (1983) provide an expanded version of Bookstein's (1977;1980) technique. Their analysis employs three dimensions in the quantification of Thompson grids. Finite element analysis, a method of measuring form change in engineering, is used in their study. According to Cheverud et al. (1983:153) this method is, "based on the kinematics of mechanical continua." They seem able to quantify Thompson grids, providing measures of shape differences. Unfortunately, their method relies upon specialized computer programs, which may be subject to more empirical testing before general application becomes practical.

These methods should gain wider use in the future. Currently, however, the use of such techniques is somewhat limited. Additionally, further empirical applications are necessary.

CHAPTER III

MATERIALS AND METHODS

1. THE ARIKARA

A total of 132 Arikara from the Larson Site, Walworth County, South Dakota (Bass and Rucker, 1976; Owsley and Bass, 1979) were measured for this analysis. Of these, 36 are juveniles between the ages of 3 and 18 years old. Ninety-six are adults, and are older than 18 years of age. The majority of juveniles are older than six years of age, as defined by eruption of the maxillary first molars. Sexes are pooled.

Criteria for measurement included a relatively complete palate, meaning that at least two dimensions were measureable. In some cases, estimates seemed necessary, particularly with juveniles. However, estimation was kept to a minimum. Generally, the resilience of juvenile palates relative to other cranial structures proved to be an unexpected benefit. Exclusion of individuals or certain measurements occurred when excessive attrition and subsequent resorption distorted the palate. Observer error was not rigorously examined. A limited number of second measurements indicated that measurement error was minimal.

Eight measurements were taken for complete individuals and are described in the Appendix. All are standard

dimensions, described and illustrated by Bass (1981). Measurements were recorded to the nearest tenth of a millimeter. Palate depth, taken with a palatometer, was measured in millimeters. Consequently, these measurements were multiplied by ten.

The data were transformed to base-10 logarithms, a standard step in allometric studies, which reduces the effects of magnitude and indicates rectilinear plots (Gould, 1966; Huxley, 1932). Log-transformed measurements are presented unless otherwise specified.

Statistical analyses were generally performed by Statistical Analysis Systems (SAS) packaged programs (SAS Institute, 1982). Procedures employed include PRINCOMP for principal components analysis, and GLM (General Linear Models) procedures for least-squares regression. In addition, analyses of covariance were carried out using packaged SAS programs. Analyses not available in the SAS package, such as reduced major axis regression, were accomplished according to algorithms detailed by Sokal and Rohlf (1981).

The primary statistical technique employed in allometric studies is bivariate regression. Several different methods exist for bivariate regression. According to Pilbeam and Gould (1974) major axis regression should be used in allometric research. Major axis and reduced major axis regression techniques are

forms of Model II regression in which no specifications of dependency are made. In addition, measurement error is assumed for both the X and Y variables (Sokal and Rohlf, 1981:549). Often, the reduced major axis method, also known as geometric mean regression, is employed in allometric research (Sokal and Rohlf, 1981:550).

Proponents of least-squares regression (Model I regression) argue that the least-squares method is superior to Model II techniques, primarily as a result of difficulties in the calculation of confidence intervals for Model II regression (Simpson et al., 1960). Secondly, Model II regression is difficult to obtain in packaged programs, increasing the difficulties in the use of these techniques. In this study, specifications of independence and dependence will not be made. Consequently, two regression techniques, least-squares and reduced major axis, are used and compared.

The criteria for interpreting the results of bivariate regression have been detailed by Gould (1966). Transformation of the simple allometry equation,

$$y = bx^a$$

into logarithmic form, yields,

$$\log y = a(\log x) + \log b$$

Isometry, or a proportional increase in the size of Y relative to X, occurs when the slope (a) is equal to one.

Slope values greater than one indicate positive allometry, meaning that the Y variable increases in size at a faster rate than the X variable. Conversely, values less than one, indicating negative allometry, suggest a disproportionately slow increases in Y relative to X.

Interpretation of the intercept value (b) is considerably more difficult. However, the value of b may reveal taxonomic differences between groups (White and Gould, 1965).

The remainder of the Arikara statistical analyses focusses on multivariate descriptions of allometry, specifically through principal components analysis. The employment of principal components analysis follows Jolicoeur (1963a; 1963b) and Jolicoeur and Mosimann (1960). The use of principal components analysis has been described in Chapter II.

2. THE ARCHAIC HOMO SAPIENS

A total of fourteen adult and seven juvenile archaic Homo sapiens individuals are available for the present study. Measurements for several adults and Krapina juveniles were provided by Dr. F.H. Smith (personal communication). Additional adult measurements were derived from Coon (1963), Trinkaus (1983), and Suzuki and Takai (1970). Contextual information for the archaic Homo sapiens sample is provided by Murril (1981), Smith (1976;

Table 1. List of adult archaic Homo sapiens (N=14).

Specimen	Reference
La Ferrassie 1	Smith (pers. comm.)
Petralona	Smith (pers. comm.)
Gibraltar	Smith (pers. comm.)
Jebel Irhoud	Smith (pers. comm.)
La Chapelle	Smith (pers. comm.)
Broken Hill	Smith (pers. comm.)
Tabun 1	Smith (pers. comm.)
Le Moustier	Smith (pers. comm.)
Arago	Smith (pers. comm.)
Saccopastore 1	Coon (1963)
Amud	Suzuki and Takai (1970)
Shanidar 1	Trinkaus (1983)
Shanidar 2	Trinkaus (1983)
Shanidar 5	Trinkaus (1983)

Table 2. List of juvenile archaic Homo sapiens (N=7).

Specimen	Age (in years)	Reference (s)
Krapina Mx B	8	Smith (pers. comm.)
Krapina Mx C	10.5	Smith (pers. comm.)
La Quina H 18	6	Vlček (1970); cast
Teshik Tash	10	Ullrich (1955); cast
Gibraltar II	5	Vlček (1970); cast
Pech de l'Azé	2	Vlček (1970)
Subalyuk	3	Bartucz et al. (1940); Vlček (1970)

1984) Stringer et al. (1984), Suzuki and Takai (1970), Trinkaus (1983) and Wolpoff (1980). Several juvenile measurements were obtained from literature sources. Bartucz et al. (1940) contained measurements of Subalyuk. Measurements of Teshik Tash were extracted from Ullrich (1955). Other measurements were taken from scaled line drawings published by Vlček (1970), or from casts at the University of Tennessee Paleontology Lab. Bartucz et al. (1940), Ullrich (1955), and Vlček (1970) supply contextual information on the juvenile archaic Homo sapiens. Thus, a total of twenty-one archaic Homo sapiens comprise the study sample. Specimens are listed in Tables 1 and 2. Sexes are, presumably, pooled.

Considerable temporal and geographic differences characterize this sample. Broken Hill, Petralona, and Arago may be considered the earliest specimens (Wolpoff, 1980). Geographically, the sample ranges from Rhodesia to Western Europe. The sample tends to be concentrated in Eastern Europe, although a relatively "even" distribution seems to be represented. The temporal and geographic spread may bias results. In addition, the amount of missing data seems almost overwhelming. Nevertheless, a large enough sample is available to address the problem at hand.

A total of six measurements was obtained from the archaic Homo sapiens sample. These measurements are

listed in the Appendix. Limited estimation of measurements seemed necessary to maximize the sample size.

These factors combine to distort "biological reality" (sensu lato). Although discouraging, these shortcomings do not diminish the potential benefit of this work.

Bivariate techniques using the archaic Homo sapiens sample are similar to those techniques employed for the Arikara sample. These methods are calculation of least-squares and reduced major axis regression slopes. Furthermore, tests for homogeneity of slopes and for analysis of covariance should provide evidence of similarities and differences between regression lines for both samples. These procedures are performed by SAS GLM packaged programs (SAS Institute, 1982). These tests allow evaluations of hypotheses concerning allometric similarities and differences in palate morphology between the two groups. Additionally, the allometric relationships within the archaic Homo sapiens sample require attention.

Finally, the archaic Homo sapiens sample seems too small to allow judicious use of multivariate statistical methods. However, fourteen individuals (seven juveniles and seven adults) are available for a three-variable (bicanine breadth, inner palate width, outer palate width) principal components analysis. Additionally, nine individuals (three juveniles and six adults) are available

for a four-variable (palate length, bicanine breadth, inner palate width, outer palate width) principal components analysis. The approach to the multivariate analysis of the archaic Homo sapiens will parallel the approach taken for the Arikara.

CHAPTER IV

DEFINITIONS, ASSUMPTIONS, AND HYPOTHESES

1. DEFINITIONS

The boney palate includes the palatine processes of the maxillae and the horizontal plates of the palatine bones. The medial (lingual) and lateral (buccal) portions of the alveolar processes may be considered parts of the palate. The boney palate is lined with periosteum and mucous membrane. The palate serves as the roof of the oral cavity, and as the floor of the nasal cavity (Williams and Warwick, 1981).

Problems potentially caused by muscle attachment (e.g. "cresting") play a minimal role in the final morphology of the palate. Only two relatively small muscles, the musculus uvulae and the tensor veli palatini, attach to the boney palate. These muscles serve to alter the shape of the soft palate during deglutition and respiration (Williams and Warwick, 1981: 1271). Sensory innervation is derived from the greater and lesser palatine nerves, which ultimately arise from the maxillary division of the trigeminal nerve (Cranial Nerve V2). Arteries supplying the palate arise from the maxillary and facial arteries (Williams and Warwick, 1981:1271). The pathways of nerves and vessels contribute minimally to the final form of the boney palate.

As a unit of analysis, the palate presents several advantageous features. The palate should maintain an intimate relationship with adaptation, primarily because it serves as an anchor for dentition. Thus, changes in the masticatory apparatus through time should include the palate. Similarly, changes in the nasal cavity through time should also include changes in palatal morphology. A third advantage of studying the palate is that it may accurately reflect anatomical attributes which characterize archaic Homo sapiens populations (e.g. mid-facial prognathism) (Wolpoff, 1980). As Glassman (1978) has shown, the palate displays significant variability even between modern populations. Fourthly, the sample size of relatively complete archaic Homo sapiens palates is relatively large, allowing a moderately high degree of confidence in the results of statistical analyses.

Unfortunately, the dimensions of the palate may be modified by the environment through tooth wear, loss, or other pathological change. Thus, within any given population, considerable variability resulting from environmental factors presents potential analytical problems. The effects of these problems can be mitigated by careful selection of samples.

2. ASSUMPTIONS

Several assumptions must be advanced to simplify the problems at hand. A first assumption is that the archaic Homo sapiens sample represents only one group. The considerable time span covered by this sample necessitates this assumption. Although geographical and temporal variation undoubtedly exists, exploration of this variation is currently impossible as a result of the small number of archaic Homo sapiens. Secondly, the Arikara and the archaic Homo sapiens are assumed to adequately represent the group from which they are derived (anatomically modern Homo sapiens and archaic Homo sapiens, respectively). Third, the accuracy of statistical analyses must, to some degree, be assumed, particularly for the archaic Homo sapiens sample. Despite statistically significant results, small sample sizes reduce the confidence in these results. Finally, the variety of sources from which the archaic Homo sapiens data were derived may bias results. Thus, inter-observer error is assumed to be minimal.

These assumptions are not tremendously realistic. However, they should be specified before continuing this analysis. The paucity of the fossil record cannot simply be overlooked.

3. HYPOTHESES

The central hypothesis tested concerns the allometric relations of the archaic Homo sapiens and Arikara palate. This hypothesis specifies the absence of significant differences in the allometry of the palate between these groups. More specifically, the modern hominid palate represents a "scaled-down" version of the archaic Homo sapiens palate, implying the maintenance of similar allometric relationships between groups.

Graphically, this relatively simple hypothesis is represented in Figure 1. This figure represents a bivariate plot of dimensions X and Y for anatomically modern humans (represented by $\square$), and for archaic Homo sapiens (represented by $\circ$). As can be seen from this diagram, the relationship between X and Y is the same for both samples. Archaic Homo sapiens represent a larger version of modern humans, but the essential relationship between variables is unchanged. According to Shea (1983b:521) this diagram represents a "simple extension of common growth trajectories to different terminal sizes."

This hypothesis is testable with regression analysis. Ontogenetic scaling is apparent when the bivariate regression slope and the intercept remain unchanged between two groups. In this case, archaic Homo sapiens are expected to occupy the "upper portions" of the regression line. This expectation is based on the

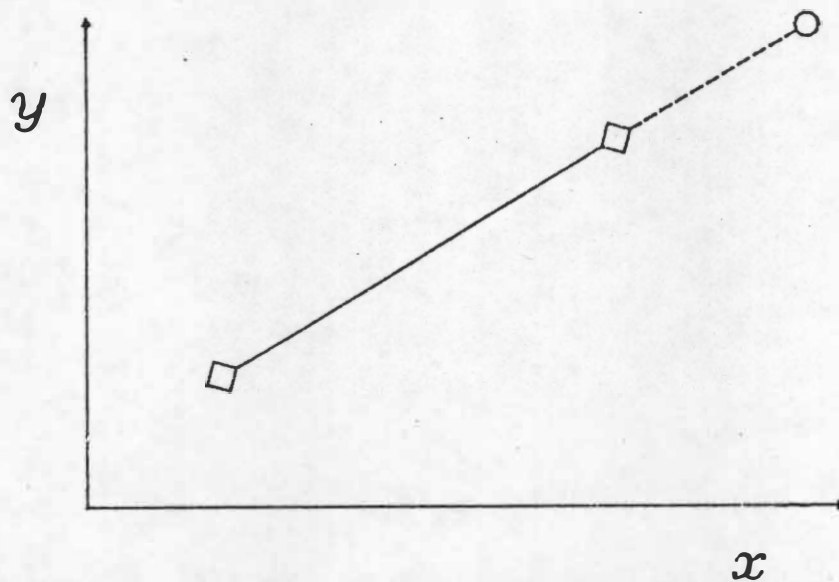


Figure 1. Graphic representation of Hypothesis I, Ontogenetic Scaling.

observation that archaic Homo sapiens cranial dimensions exceed those of modern humans.

In many ways, reduction of size along a common ontogenetic trajectory represents the simplest situation. Selection should, in this case, operate primarily on the general size of the organism, preserving shape relationships.

An alternative hypothesis specifies transposition (White and Gould, 1965) or shifts in the intercepts of regression lines, but without a concomittant shift in the slope value. Transposition is graphically represented in Figure 2. In this diagram, a downward shift of the regression line is present between the two groups. Although shifts in the intercept value are often difficult to interpret, White and Gould (1965:11) suggest that transpositions involve differences in proportions at the beginning of allometric growth.

Understanding the evolutionary significance of transpostions may be difficult. Explanations of these changes usually rely upon the need to retain functional abilities at different sizes (Kurtén, 1955). Size change underlies transpositions. Contrary to the case of ontogenetic scaling, however, size changes may occur in one dimension more than in another. Also, shape differences accompany transpositions.

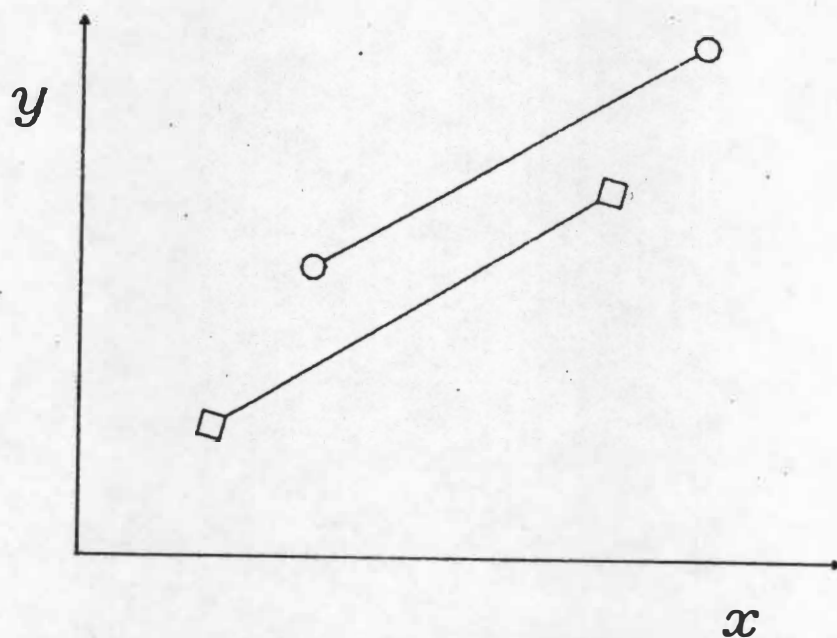


Figure 2. Graphic representation of Hypothesis II, Transposition.

A final hypothesis, which can again be illustrated graphically, involves a change in the basic allometric relationship. Figure 3 shows this alternative.

Intercept differences accompany changes in slope in this situation. Intersecting regression lines generally suggest the action of selection in altering an allometric relationship. In other words, selection for changes in body size (as a whole) may be absent in this case. Instead, the relationship between two parts is changed, not necessarily their size.

4. SELECTIVE IMPLICATIONS FOR THE PRESENT STUDY

Allometric relationships are controlled by natural selection (Cock, 1966; Gould, 1966; Brown and Davies, 1972; Atchley and Rutledge, 1979). Selection on general size should represent the dominant force in the changes in palate morphology occurring in later human evolution. Thus, confirmation of an hypothesis specifying reduced general size (Ontogenetically Scaled, Hypothesis I) should be anticipated.

Reduction of the masticatory apparatus is well documented for the transition from archaic Homo sapiens to anatomically modern humans (Fruyer, 1978; Brace, 1962; Wolpoff, 1980). However, questions regarding the specific nature of these reductions have not yet been fully addressed. For example, is the smaller palate of modern

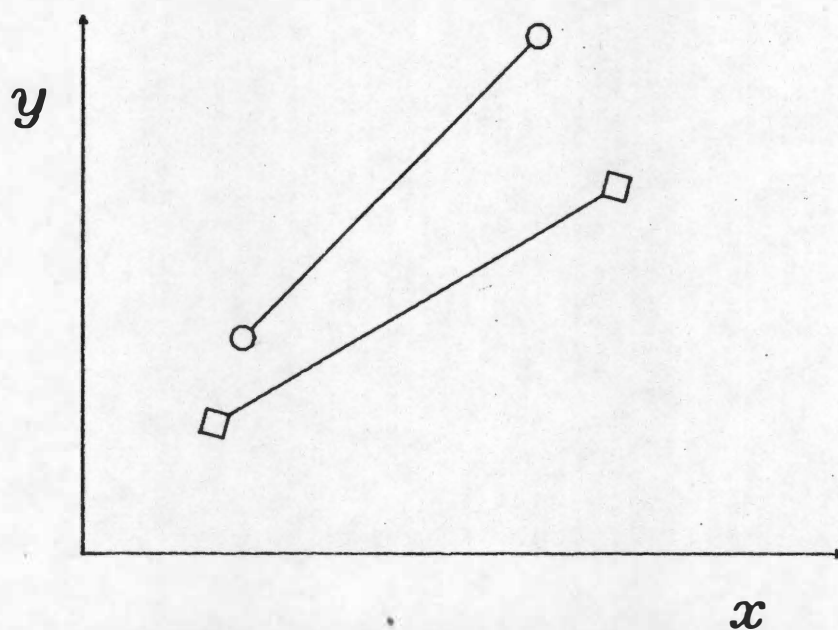


Figure 3. Graphic representation of Hypothesis III, Change of Slope.

humans the result of selection for smaller general size? Or, is the smaller palate of modern humans the result of small size at the onset of growth, which implies smaller and possibly less mature neonates. Finally, a third alternative implies a more "mosaic" pattern of evolution between these two groups. In this case, different anatomical units respond to specific selective pressures (assuming a lack of correlated genetic responses).

These possibilities are testable from an allometric analysis which includes both juveniles and adults for the two groups. The incorporation of juveniles into the analysis should provide clear evidence for increases or reductions of general size.

Comparisons of allometric trends between these groups should also allow inferences concerning their relatedness. Taxonomic investigations of allometry have found somewhat limited application. However, comparisons of growth trajectories are easily evaluated, especially through the use of multivariate statistics. The available data allow such an evaluation, and an additional hypothesis specifies similarity between archaic Homo sapiens and modern humans in overall growth of the palate. Strong similarities might be used as an argument for ancestry of archaic Homo sapiens to modern humans. However, similar ontogenetic trajectories do not necessarily dictate ancestor and descendant relationships.

5. ANCILLARY HYPOTHESES

A comparison of allometric growth between anatomically modern humans and archaic Homo sapiens cannot be fully understood without careful investigation of allometric trends within one of the two groups. The large sample of Arikara allows the use of this population to establish a "baseline." In this case, the research becomes primarily exploratory, and few specific hypotheses are readily deducible.

Within the Arikara sample, several issues deserve attention. Of primary interest is the degree of correspondence between static and ontogenetic allometry. The adequacy of static samples in estimating ontogenetic trajectories is an important issue, especially when fossil data bases are analyzed (Cock, 1966; Gould, 1966; Pilbeam and Gould, 1974; Cheverud, 1982). If static allometry accurately represents ontogenetic allometry, then the confidence of using only adult fossils in allometric studies is greatly enhanced. Thus, an hypothesis specifying close relationships between static and ontogenetic allometry in both samples is relevant to this problem. Finally, the variety of statistical techniques for allometric studies makes a comparison of these techniques a valid objective.

CHAPTER V

RESULTS AND DISCUSSION

1. THE ARIKARA

Ontogenetic Allometry

Bivariate Results. Table 3 presents the regression results for ontogenetic allometry of the Arikara palate. This table contains slope values, intercept values, r^2 values, measures of significance, and reduced major axis slopes for variable pairs. The X variables were generally the larger of the two measurements. All tables presenting bivariate regression results will follow the order of the analyses presented in Table 3. In all the regressions presented, the expected value for isometry is one ($a = 1$).

All regressions are highly significant ($p < .01$). Ten of the 21 relationships presented in Table 3 indicate positive allometry. The remainder suggest negative allometry. Most variables are well correlated, especially those pairs of variables for which the X variable is a measure of cranial length (prosthion-basion [LPRBA], prosthion-auricular point [LPRA]).

The first subset of Table 3 consists of regressions between palate measurements, generally presented with inner (LPWI) or outer (LPWO) breadth as the X variable. Palate length (LPL) is usually positively allometric with respect to outer width (LPWO), indicating that growth in

Table 3. Arikara ontogenetic regression results.

X	Y	a	b	r^2	F ^a	RMA a
LPWO	LPWI	.72	.57	.34	17.46	1.23
LPWO	LBICAN	.76	.44	.62	51.18	.96
LPWO	LPL	1.16	-.54	.68	67.00	1.41
LPWI	LBICAN	.49	1.26	.37	21.06	.81
LPWI	LPL	.79	.63	.50	30.63	1.11
LBICAN	LPL	1.06	-.04	.54	34.59	1.44
LPRA	LPWO	.79	.38	.62	33.78	1.00
LPRBA	LPWO	.95	-.06	.69	39.74	1.14
LPRA	LPWI	.74	.35	.80	85.28	.82
LPRBA	LPWI	.77	.29	.70	41.26	.92
LPRA	LBICAN	.47	1.12	.39	11.97	.75
LPRA	LBICAN	.66	.60	.58	25.13	.86
LPRA	LPL	1.24	-1.05	.88	158.31	1.34
LPRBA	LPL	1.52	-1.82	.90	157.24	1.60
LPRA	LPRBA	.78	.64	.87	109.35	.83
LPL	LMP	1.07	-.74	.63	45.28	1.36
LPWO	LMP	1.34	-1.58	.48	25.05	1.70
LPRA	LMP	1.48	-2.33	.65	36.46	1.84
LPRBA	LMP	1.46	-2.19	.56	21.86	1.95
LPL	LPD	2.27	-4.10	.72	78.20	2.82
LPWO	LPD	2.79	-5.74	.50	31.00	3.94

^a All F-values are significant at $p < .01$.

length "outstrips" growth in width. Bicanine breadth (LBICAN) shows a negatively allometric relationship to inner (LPWI) and outer (LPWO) width. Finally, inner palate width (LPWI) is negatively allometric with respect to outer width (LPWO).

Relative to measures of size defined by other cranial structures, palate length (LPL) generally seems positively allometric, indicating more rapid growth of the palate in length relative to other cranial structures. Contrary to the pattern observed for palate length, palate width measures (bicanine breadth, inner and outer widths) are generally negatively allometric relative to the length of the cranial base. Outer width approaches isometry relative to prosthion-basion (LPRBA). Bicanine breadth is consistently the most negatively allometric of the width variables.

The final two sets present the results of regressions with mid-palate (cruciate suture to posterior nasal spine [LMP]) and palate depth (LPD) at m^1/m^2 . Both variables show strong positive allometry relative to other palate dimensions. Palate depth (LPD), in particular, is the most strongly positively allometric dimension.

These results indicate that palate length increases in size at a rate generally exceeding the growth of the palate in width. A major component of this growth seems to occur at the posterior portion of the palate, between

the cruciate suture and the posterior nasal spine. Growth in length generally seems associated with positively allometric growth in depth. Thus, in the developmental relationships suggested by these regressions, relatively slow increases in width dimensions accompany relatively rapid growth in length and depth. Young individuals have relatively short, shallow palates relative to width, while older individuals have relatively deep, narrow palates. Finally, prosthion-basion (LPRBA) seems negatively allometric relative to prosthion-auricular point (LPRA).

Table 3 also presents the results of several different methods of calculating "a" (the slope value). Before continuing, a comparison of these results is necessary as a method of evaluating the reliability of the least-squares regression results. The different slope values in Table 3 are least-squares, reduced major axis, and principal component ratios (derived from analyses discussed in pages 70 - 78). Least-squares results were calculated using SAS GLM procedures (SAS Institute, 1982). Reduced major axis slopes were calculated by dividing the least-squares slope by the correlation coefficient (r) (Pilbeam and Gould, 1974; Sokal and Rohlf, 1981). Finally, principal component ratios were calculated by dividing the element in the first eigenvector corresponding to principal component of Y variables by the elements in the first eigenvectors corresponding to the

first principal component of the X variable (Jungers and German, 1981).

Correlation coefficients were calculated for the regression coefficients using SAS CORR procedures (SAS Institute, 1982). The results of the slope correlations are presented in Table 4. This method was employed by Jungers and German (1981) to compare coefficients of allometry derived by different methods. The highest correlation coefficient is between the reduced major axis method and the least-squares method ($r=.974$). The correlation between principal components ratios and the reduced major axis slopes is also strong ($r=.918$). The correlation between the principal component ratios and the least-squares slopes is the lowest ($r=.897$), but this relationship is still strong. All correlations are significant ($p < .001$).

Inspection of the results in Table 3 indicates that the reduced major axis method provides slightly higher slope estimates than the least-squares method. This is a result of correlations of less than 1.0 between variables. In several cases, the reduced major axis results suggest positive allometry, where the least-squares results indicate negative allometry. Viewed in this manner, the principal components results tend to corroborate the results of the least-squares analyses.

Table 4. Correlations between slope calculation methods.

		JLS	JRMA	JPCR
Juvenile Least-squares	(JLS)	1.00		
Juvenile Reduced Major Axis	(JRMA)	.97	1.00	
Juvenile Principal Components Ratios	(JPCR)	.90	.92	1.00

^a All correlations are significantly greater than zero ($p < .001$)

These correlation coefficients are somewhat lower than those presented by Jungers and German in a similar comparison (1981). They obtained a correlation coefficient of .99 between principal components ratios and least-squares slopes. For the relationship between principal components ratios and reduced major axis slopes, Jungers and German (1981) observed a slightly lower correlation coefficient ($r=.96$).

The results of this analysis suggest that the use of least-squares regression provides an accurate representation of allometric relationships because of the close correspondence, at least qualitatively, with the results based on principal components ratios. Although the reduced major axis slopes are more strongly correlated with the principal components ratios, the allometric relationships indicated by the reduced major axis method are frequently dissimilar.

Multivariate results. The next five tables present the results of allometric relationships estimated by principal components analysis (Jolicoeur, 1963a,b). These analyses include juveniles only. Additionally, different variables are used in each analysis so that the effects of excluding variables may be evaluated.

The results of the three-variable principal components analysis are presented in Table 5. The standardized loading, $1/\sqrt{p}$, is .577. The first principal

Table 5. Results of the Arikara ontogenetic three-variable principal components analysis.

	Eigenvalue	Proportion of Total Variance	Cumulative Variance	<u>Eigenvectors</u>		
				LPWO	LBICAN	LPWI
PC1	.0064	.7719	.7719	.5234	.5209	.6744
PC2	.0014	.1690	.9409	.5462	.4024	-.7347
PC3	.0005	.0590	1.0000	-.6540	.7528	-.0739

component accounts for 77% of the total variation. Inner palate width is positively allometric, with a loading of .67. Both outer palate width and bicanine breadth are negatively allometric, with loadings of approximately .52 each.

Table 6 contains the results of principal components analysis based only on the primary dimensions of the palate. The first principal component accounts for about 79% of the total variance. The standardized loading, $1/\sqrt{p}$, is equal to .5000. In this component, palate length seems positively allometric with respect to total size with an allometry coefficient of about 1.29. Inner palate width approximates isometry while outer palate width and bicanine breadth seem negatively allometric. The average allometry coefficient for widths is .88, indicating general negative allometry of widths relative to overall size. Thus, the growth in length seems to exceed growth in width.

In Table 7, the value of $1/\sqrt{p}$ is .41 and the first principal component accounts for 87% of the total variance. All loadings seem to indicate negative allometry, with the exception of LPD (palate depth), where $a=2.06$. Conversely, the average allometry coefficient for all other variables is only .72, indicating that the magnitude of increase in palate depth is very large. Of the negatively allometric dimensions, the mid-palate (LMP)

Table 6. Results of the Arikara ontogenetic four-variable principal components analysis.

	Eigenvalue	Proportion of Total Variation	Cumulative Variance	LPWO	<u>Eigenvectors</u>		
					LPWI	LPL	LBICAN
PC1	.0101	.7863	.7863	.4175	.5013	.6467	.3952
PC2	.0015	.1229	.9092	.4485	-.8358	.2181	.2295
PC3	.0008	.0598	.9690	.0321	.0871	-.5820	.8079
PC4	.0004	.0310	1.0000	.7896	.2061	-.4422	-.3721

Table 7. Results of the Arikara ontogenetic six-variable principal components analysis which includes palate depth and "mid-palate" variables.

	Eigenvalue	Proportion of Total Variance	Cumulative Variance	<u>Eigenvectors</u>					
				LPWO	LPWI	LPL	LBICAN	LPD	LMP
PC1	.0508	.8655	.8655	.1838	.1952	.2989	.1393	.8433	.3288
PC2	.0046	.0789	.9444	.2700	.0777	.2168	.2598	-.4900	.7525
PC3	.0020	.0341	.9785	.4020	.2235	.2419	.6502	-.1216	-.5406
PC4	.0005	.0084	.9869	-.1524	.2065	-.8049	.4907	.1214	.1748
PC5	.0005	.0077	.9946	.2494	.8372	-.1353	-.4527	-.1060	-.0497
PC6	.0003	.0054	1.0000	-.8039	.4030	.3728	.2108	-.0084	.0090

dimension is the closest to isometry, followed by palate length, inner width, outer width, and bicanine breadth, which is the most negatively allometric trait. The average length allometry coefficient is .76. The average width coefficient is .42, indicating a disproportionately slow increase in size of width variables to general size increase.

Table 8 presents the results of a principal components analysis of the palate with the introduction of cranial base measurements prosthion-basion (LPRBA) and prosthion-auricular point (LPRA). The first principal component contains 88% of the total variance, and the standardized loading is .41. Two measurements, LPRA and LPWO, approach isometry, an observation which suggests that LPRA partially measures width. Again, palate length exhibits strong positive allometry ($a=1.43$). Considered together, the two neurocranial measurements are slightly negatively allometric, with an average allometry coefficient of .93. Palate width measurements average .84, indicating negative allometry.

Results of the last multivariate ontogenetic analysis are presented in Table 9. The first principal component accounts for 88% of the total variance, and the standardized loading is .35. LPD (palate depth) shows very strong positive allometry, with a loading of 2.55.

Table 8. Results of the Arikara ontogenetic principal components analysis which includes cranial base measurements.

	Eigenvalue	Proportion of Total Variance	Cumulative Variance	<u>Eigenvectors</u>					
				LPRA	LPRBA	LPWO	LPWI	LPL	LBICAN
PC1	.0132	.8842	.8842	.4189	.3436	.4195	.3403	.5849	.2696
PC2	.0008	.0568	.9410	-.4381	-.1342	.4575	-.2479	-.1189	.7107
PC3	.0005	.0327	.9737	-.1287	-.3146	.6026	.5363	-.2884	-.3879
PC4	.0002	.0110	.9847	.0538	.7572	.3146	-.2842	-.4511	-.2010
PC5	.0002	.0100	.9947	-.0768	.2791	-.3839	.6573	-.4068	.4139
PC6	.0001	.0053	1.0000	.7792	-.3369	.0717	-.1493	-.4387	.2452

Table 9. Results of the Arikara ontogenetic eight variable principal components analysis.

	Eigenvalue	Proportion of Total Variance	Cumulative Variance	LMP	LPRA	LPRBA	Eigenvectors				
							LPWO	LPWI	LPL	LBICAN	LPD
PC1	.0489	.8680	.8680	.3547	.2222	.1770	.2002	.1717	.2980	.1167	.7882
PC2	.0044	.0782	.9462	.6784	.1273	.0780	.3050	.1677	.2149	.1401	-.5748
PC3	.0018	.0328	.9790	-.5626	.0433	.2093	.3615	.1047	.3232	.6113	-.1325
PC4	.0005	.0092	.9882	-.1046	.4845	.3517	-.6401	.0997	.4066	-.1397	-.1607
PC5	.0035	.0061	.9944	-.2122	.0648	-.1919	.1577	.8725	-.0649	-.3498	-.0334
PC6	.0001	.0028	.9971	.0063	.0270	.8016	.1253	.0861	-.5742	-.0593	-.0152
PC7	.0001	.0018	.9988	.1151	.3994	-.2982	-.3062	.1926	-.4971	.5990	.0367
PC8	.0001	.0012	1.0000	-.1679	.7302	-.1628	.4381	-.3399	-.1183	-.2979	-.0420

The variable LMP seems to be isometric. All other variables are negatively allometric, with an average coefficient of only .56.

These analyses share several features. First, palate length tends to increase at a faster rate than width. Secondly, cranial base measures show the expected negative allometric trends, resulting from the relatively slow growth of the brain-case after birth. Thirdly, palate depth grows the most rapidly relative to other dimensions of the palate.

Although each analysis contains different allometry coefficients, the rank-order of variables is similar in each analysis. For example, palate length tends to grow faster than width variables. Additionally, allometry coefficients derived from Table 9 agree quite closely with coefficients obtained through regression ($r=.897$ for least-squares coefficients; $r=.918$ for reduced major axis coefficients).

Static Allometry

Bivariate results. Table 10 contains the regression results for Arikara static allometry. Most regressions are significant ($p < .05$), however, most r^2 values are very low. Negative allometry ($a < 1$) is indicated by most regressions, with the exception of bicanine breadth relative to prosthion-basion and prosthion-auricular point.

Table 10. Arikara static regression results.

X	Y	a	b	r ²	F ^a	RMA a
LPWO	LPWI	.79	.40	.34	44.58	1.35
LPWO	LBICAN	.82	.28	.25	28.54	1.64
LPWO	LPL	.50	1.35	.17	17.28	1.19
LPWI	LBICAN	.21	2.01	.03	2.68*	1.21
LPWI	LPL	.24	2.12	.09	8.02	.79
LBICAN	LPL	.35	1.84	.27	30.74	.67
LPRA	LPWO	.58	.99	.22	23.65	1.22
LPRBA	LPWO	.58	1.03	.24	22.62	1.18
LPRA	LPWI	.59	.80	.13	12.65	1.61
LPRBA	LPWI	.51	1.08	.10	8.80	1.56
LPRA	LBICAN	1.01	-.52	.25	28.35	2.03
LPRBA	LBICAN	1.08	-.65	.29	29.77	2.01
LPRA	LPL	.95	-.16	.51	87.35	1.33
LPRBA	LPL	.96	-.15	.56	96.25	1.28
LPL	LMP	.96	-.41	.12	12.55	2.71
LPWO	LMP	.25	1.54	.01	.54**	3.22
LPRA	LMP	.79	-.19	.05	4.24*	3.71
LPRBA	LMP	.91	-.51	.07	5.68	3.95
LPL	LPD	.66	.35	.05	4.17*	2.95
LPWO	LPD	.75	.07	.05	4.28*	3.38

^a All F-values are significant at $p < .01$, unless designated with '*' ($p < .10$) or '**' (not significant).

The least-squares regression slopes for the adults show few clear patterns. In some cases, the results for adults contradict the results for juveniles. Bicanine breadth is positively allometric for adults in contrast to the negative allometry observed for juveniles.

Additionally, regressions with palate depth (LPD) suggest negative allometry, markedly contrasting with the results based on ontogenetic trajectories. Finally, palate length seems negatively allometric in the static regressions. Clearly, the static results provide different information than the ontogenetic results.

Regression slopes obtained from different regression techniques also provide varying results, due to the lack of size variation in the adult sample. Table 11 contains correlation coefficients between juvenile regression slopes derived from least-squares, reduced major axis, and principal components ratios, and adult regression slopes derived from the same methods. The least-squares slope values for the static adult regressions differ substantially from those based on ontogenetic analyses. The correlation between least-squares coefficients for adults and juveniles is .096. A much better relationship exists between reduced major axis regression coefficients between the two samples ($r=.62$). Least-squares estimates are generally much lower for the static regressions than for the ontogenetic regressions.

Table 11. Correlations between slope calculation methods for Arikara static and ontogenetic samples.

		JLS	JRMA	JPCR	ALS	ARMA	APCR
Juvenile Least-squares	(JLS)	1.00					
Juvenile Reduced Major Axis	(JRMA)	.97	1.00				
Juvenile Principal Components Ratios	(JPCR)	.90	.92	1.00			
Adult Least-squares	(ALS)	.10*	.05*	-.15*	1.00		
Adult Reduced Major Axis	(ARMA)	.60	.62	.43	.28*	1.00	
Adult Principal Components Ratios	(APCR)	.74	.79	.68	-.02*	.83	1.00

^a All correlations are significantly greater than zero ($p < .05$), unless designated by '*' (not significant).

Adult principal component ratios (derived from pages 83-88), show relatively high correlations with the ontogenetic slope estimates. The principal component method is fairly well correlated ($r=.738$) with the juvenile least-squares results. A better correlation ($r=.787$) is observed between the static principal components ratios and the ontogenetic reduced major axis slopes. A slightly negative correlation between static principal component ratios and static least-squares slopes is notable ($r=-.017$).

Clearly, the least-squares method for static data provides results which are least similar to the ontogenetic analyses. The fairly high correlations between the adult reduced major axis slopes and slopes derived from other methods are potentially important. The accuracy of static estimates may be improved when Model II regression techniques are used (although this result may be sample-specific). Similarly, the higher correlations between static principal component ratios and other methods may indicate greater reliability of this method when estimating ontogenetic trajectories from static data.

The relatively good performance of the reduced major axis method may be somewhat deceptive. All the static slopes indicate positive allometry, with two exceptions (LPWO,LPL; LBICAN,LPL). This observation contradicts the approximately equal mix of positively and negatively

allometric relationships observed for ontogenetic regressions. Such high slope values are the result of very low correlation coefficients for the static regressions. Therefore, the reduced major axis slopes may not provide accurate results.

The poor correlations between principal components ratios between adults and juveniles presents a similar problem. The extremely high loading for palate depth and bicanine breadth in adult analyses created very high slope estimates. Exclusion of these extremely high slope values improves the correlation between ontogenetic and static principal components ratios, but only slightly ($r=.39$).

Based on regression analysis, static allometry does not provide reliable estimates of ontogenetic allometry, at least in this sample. However, multivariate comparisons of static and ontogenetic allometry should be undertaken. Multivariate comparisons (following the method outlined by Cheverud [1982]) allow "measures of distance" between the two allometry estimates.

Multivariate results. Table 12 contains the results of the three-variable static principal components analysis. The standardized loading is about .57. The first principal component accounts for 61% of the total variation. Bicanine breadth loads the highest (.80). The other variables, inner and outer width, have loadings of .42 each. These results contrast with the analogous

Table 12. Results of the Arikara static three-variable principal components analysis.

	Eigenvalue	Proportion of Total Variance	Cumulative Variance	<u>Eigenvectors</u>		
				LPWO	LBICAN	LPWI
PC1	.0018	.6064	.6064	.4239	.7989	.4267
PC2	.0009	.3219	.9282	.2312	-.5510	.8019
PC3	.0002	.0717	1.0000	.8757	-.2413	-.4182

principal components analysis for juveniles, in which inner palate width had the highest loading.

The results of the second static multivariate allometry analysis are presented in Table 13. In this analysis, the first principal component accounts for only 59% of the total variance. The standardized loading is .50, and only bicanine breadth seems positively allometric ($a=1.44$). Conversely, the allometry coefficient for palate length is only .76, indicating negative allometry. The average coefficient for widths is 1.02, a value which seems to approximate isometry. These patterns do not agree well with the ontogenetic results for the same variables (see Table 6, page 73).

In the next analysis, the results of which are presented in Table 14, the first principal component accounts for only 47% of the total variance. As with the analogous juvenile analysis, the standardized loading is .41. Only two dimensions are positively allometric. These are LPD (palate depth) and LMP (posterior nasal spine-cruciate suture), with coefficients of 1.79 and 1.55, respectively. The average allometry coefficient for widths is .26, indicating a strongly negative allometric relation to overall size. The coefficient for palate length is .35, and the average of the two length measures (LMP, LPL) approaches isometry ($a=.95$).

Table 13. Results of the Arikara static four-variable principal components analysis.

	Eigenvalue	Proportion of Total Variance	Cumulative Variance	LPWO	<u>Eigenvectors</u>		
					LPWI	LPL	LBICAN
PC1	.0020	.5893	.5893	.3494	.4631	.3781	.7215
PC2	.0008	.2692	.8585	.3045	.7507	-.0980	-.5780
PC3	.0004	.1057	.9643	-.0578	-.1377	.9189	-.3652
PC4	.0001	.0357	1.0000	.8842	-.4505	-.0556	-.1099

Table 14. Results of the Arikara static six-variable principal components analysis which includes palate depth and "mid-palate" variables.

	Eigenvalue	Proportion of Total Variance	Cumulative Variance	<u>Eigenvectors</u>					
				LPWO	LPWI	LPL	LBICAN	LPD	LMP
PC1	.0059	.4663	.4663	.0665	.1163	.1439	.1400	.7337	.6350
PC2	.0040	.3132	.7795	.0349	.0944	-.0056	.1083	.6253	-.7661
PC3	.0015	.1175	.8970	.3202	.3921	.3176	.7571	-.2597	-.0443
PC4	.0009	.0703	.9674	.3264	.7791	-.0615	-.5299	-.0419	.0022
PC5	.0003	.0243	.9917	-.0131	-.1421	.9309	-.3237	-.0209	-.0879
PC6	.0001	.0083	1.0000	.8860	-.4433	-.0889	-.0979	.0292	-.0036

In Table 15, the first principal component contains 59% of the total variance, and the standardized loading is .41. Only bicanine breadth is positively allometric ($a=1.60$). The average width coefficient is 1.10, suggesting a slightly positive allometric increase. Palate length seems negatively allometric ($a=.91$). Finally, both cranial base measurements are negatively allometric, with an average coefficient of .74.

Table 16 presents the results of the final principal components analysis for Arikara adults. The first principal component accounts for 44% of the total variance, and the standardized loading is .35. The palate depth and "mid-palate" (LMP) measurements indicate marked positive allometry, with $a=1.76$ and $a=2.08$, respectively. All other variables indicate negative allometry. Bicanine breadth seems to be the least negatively allometric trait. The average coefficient for widths is .31, and for both lengths, the average coefficient is 1.10.

Comparisons of Static and Ontogenetic Results

The differences observed between ontogenetic and static allometry may be significant. Certainly, the first principal components for the static analyses account for relatively small portions of the total variances. This observation is expected because the variation in size in the ontogenetic (juvenile) sample exceeds the variation in size in the static (adult) sample. However, some static

Table 15. Results of the Arikara static principal components analysis which includes cranial base measurements.

	Eigenvalue	Proportion of Total Variance	Cumulative Variance	<u>Eigenvectors</u>					
				LPRA	LPRBA	LPWO	LPWI	LPL	LBICAN
PC1	.0024	.5881	.5881	.3074	.2974	.3050	.3865	.3734	.6596
PC2	.0009	.2124	.8005	.0534	.0251	.3346	.7352	-.0700	-.5822
PC3	.0005	.1216	.9221	.3509	.4228	-.1718	-.2709	.6158	-.4645
PC4	.0001	.0363	.9584	.5612	.4512	-.1156	-.0607	-.6813	.0097
PC5	.0001	.0284	.9868	.1082	-.0695	.8591	-.4812	-.0611	-.0997
PC6	.0001	.0132	1.0000	-.6728	.7236	.1181	-.0344	-.0919	.0049

Table 16. Results of the Arikara static eight-variable principal components analysis.

				<u>Eigenvectors</u>							
	Eigenvalue	Proportion of Total Variance	Cumulative Variance	LMP	LPRA	LPRBA	LPWO	LPWI	LPL	LBICAN	LPD
PC1	.0060	.4359	.4359	.6152	.1151	.1047	.0685	.0841	.1551	.1746	.7286
PC2	.0044	.3143	.7502	-.7781	.0493	.0193	.0317	.0798	-.0100	.1082	.6103
PC3	.0018	.1325	.8827	-.0806	.2906	.2743	.2919	.3765	.3087	.6450	-.3086
PC4	.0009	.0638	.9465	.0139	.0829	.0532	.3208	.7193	-.0276	-.6073	.0057
PC5	.0004	.0322	.9787	-.0899	.3655	.4342	-.1521	-.3248	.6120	-.4071	-.0252
PC6	.0001	.0100	.9888	.0305	.5020	.4467	.1322	-.1974	-.7002	-.0237	-.0041
PC7	.0001	.0075	.9968	-.0168	-.0073	-.2534	.8570	-.4251	.1166	-.0796	.0143
PC8	.0001	.0037	1.0000	-.0101	-.7121	.6769	.1761	-.0449	-.0335	.0032	.0187

analyses provide results which directly contradict the results of the juvenile analyses. Similar contradictions are present in the bivariate analyses.

In the multivariate case, the similarities between ontogenetic and static allometries may be estimated by vector correlations and derivation of angular values (assuming that the correlations are significantly different from zero [Cheverud, 1982]). Vector correlations are calculated by multiplying traits between sets for the first principal component. These products are summed, giving the correlation coefficient between vectors for each sample. This value may be misleading. As a result the $\cos x^{-1}$ of the summed products is calculated, providing an angular measure of the similarities between samples (Cheverud, 1982; pers. comm., 1984).

Angular values range from 21.32° to 27.54° for the analyses presented in Tables 5-9 and Tables 12-16. The angular difference in the three-variable analyses (Tables 5 and 12) is 22.22° . In the four-variable analyses (Tables 6 and 13), the angular difference is 24.82° . The angular divergence in the results presented in Tables 7 and 14 is 22.20° . In the final two analyses (from Tables 8 and 15; Tables 9 and 16), the angular divergences are 27.54° and 21.32° , respectively.

If ontogenetic and static allometries were the same, the summed products of the vectors would, in each analysis, equal 1. Since $\cos x^{-1}(1)=0$, then the angular divergence between the two measures of allometry is zero. Thus, in this example, the two measures of allometry are the same. The average angular divergence for the present analysis is 23.62° which is similar to the 23.94° angle presented by Cheverud (1982) for differences between static and ontogenetic allometry in the cranial dimensions of rhesus macaques. The divergence for the present analysis is graphically illustrated in Figure 4.

Thus, on the basis of the multivariate comparisons, static allometry fails to provide an accurate estimate of ontogenetic allometry. The method outlined by Cheverud (1982) is convenient, but the significance of these differences is difficult to assess. However, a notion of the magnitude of the differences may be derived from a comparison of inter-specific ontogenetic differences using multivariate methods. These comparisons, although on a limited scale, are presented in the following section.

2. THE ARCHAIC HOMO SAPIENS

Ontogenetic Allometry

Bivariate results. Table 17 presents the results of ontogenetic regressions for the archaic Homo sapiens sample. The sample is quite small in some regressions.

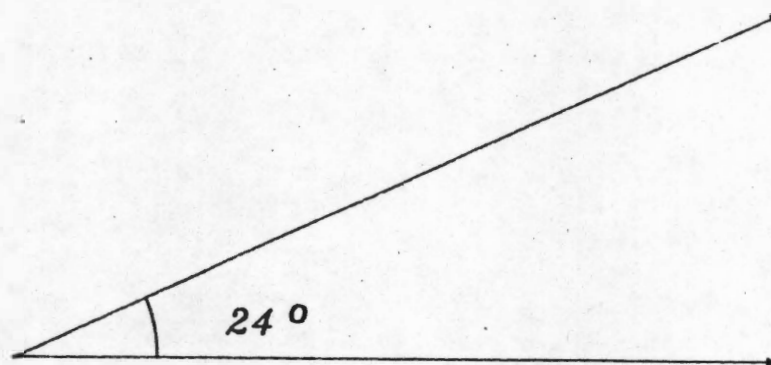


Figure 4. Average angular divergence for Arikara static and ontogenetic principal components analyses.

Table 17. Archaic Homo sapiens ontogenetic regression results.

N	X	Y	a	b	r ²	F ^a	RMA a
17	LPWO	LPWI	.86	.16	.78	55.81	.97
18	LPWO	LBICAN	.85	-.25	.64	28.44	1.06
14	LPWI	LBICAN	.68	.86	.46	10.22	1.00
15	LPWO	LPL	.84	.31	.68	27.30	1.03
11	LPWI	LPL	.52	1.37	.30	3.82*	.94
13	LBICAN	LPL	.84	.51	.54	13.19	1.14
9	LPRA	LPWO	.91	.008	.95	141.33	.94
7	LPRBA	LPWO	1.06	-.37	.63	8.57*	1.33
6	LPRBA	LPWI	.24	1.86	.04	.72**	1.28
6	LPRA	LPWI	.76	.27	.61	6.37*	.97
8	LPRA	LPL	.75	.41	.66	11.81	.92
7	LPRBA	LPL	1.12	-.62	.81	21.76	1.24
8	LPRA	LBICAN	.98	-.35	.78	20.03	1.10
6	LPRBA	LBICAN	.67	.63	.18	.89**	1.57
6	LPRA	LPRBA	.59	1.19	.78	13.98	.66

^aAll F-values are significant ($p < .01$), unless designated with '*' ($p < .10$) or '**' (not significant).

The most reliable regressions are those which include the entire juvenile sample (n=7). The variable pairs in these regressions are: LPWO, LBICAN; LPWI, LBICAN; LPWO, LPWI. The remaining regressions include only Teshik Tash and La Quina as representatives of the juvenile sample. However, a palate length measurement from Subalyuk allows the inclusion of this individual into certain analyses not possible for juveniles other than Teshik Tash and La Quina. Adult and juvenile archaic Homo sapiens are pooled for regression and principal components analysis. This procedure varies from the Arikara analyses, in which adults and juveniles were analyzed separately. (Several 18-21 year olds were included in the Arikara juvenile sample, however.) Pooling the archaic Homo sapiens sample is necessary because of the limited number of specimens.

Most archaic Homo sapiens regressions are significant at the .10 level. Two regressions (LPRBA, LPWI; LPRBA, LBICAN) are not significant. Concomittantly, r^2 values are fairly high, ranging from .95 to .30.

The first subset of variables includes intra-palate regressions. Relative to outer and inner width, bicanine breadth seems negatively allometric, increasing in size at a slower rate than other widths. The regression between outer width and bicanine breadth approaches isometry. Relative to outer breadth, inner breadth is negatively allometric.

Regressions of palate length and other palate dimensions (Teshik Tash, La Quina, and Subalyuk representing the archaic Homo sapiens juveniles) are only moderately correlated. The regressions are all significant. Palate length seems negatively allometric relative to increases in the size of the width variables. Differences between the archaic Homo sapiens and Arikara are most pronounced in these regressions (see Table 3).

The remaining archaic Homo sapiens regressions include only Teshik Tash and La Quina as representatives of the juvenile archaic Homo sapiens sample. Thus, these results may be less reliable than the results presented previously. However, these regressions supply information regarding the growth of the palate relative to other cranial dimensions.

Palate width dimensions are generally negatively allometric relative to measures of the cranial base. However, outer width and palate length seem positively allometric when regressed on prosthion-basion. The relationship between palate length and prosthion-basion is highly significant ($p < .005$) and the variables are well correlated ($r^2 = .81$).

A different pattern is present for the relationship between prosthion-basion and measures of bicanine breadth and outer palate width. Bicanine and outer breadth seem negatively allometric. The regression of bicanine breadth

and prosthion-basion should be excluded because of the poor correlation between these variables.

Dimensions regressed on prosthion-auricular point (LPRA) show relatively strong correlations. Increase in bicanine breadth seems isometric with increases in LPRA, and outer width increases in size at a slightly slower rate. Palate length and inner width regressions suggest negative allometry of these dimensions relative to LPRA.

Reduced major axis slopes, presented in Table 17, suggest that most Y variables are positively allometric. These high values are the result of division of the least-squares slopes by correlation coefficients (which tend to be relatively small). Reduced major axis slopes indicate positive allometry for palate length.

Palate depth and "mid-palate" measurements were not obtained for the archaic Homo sapiens sample. These may be positively allometric (as seen in the Arikara). This possibility deserves inquiry, but is beyond the scope of the present analysis.

Static Allometry

Bivariate results. The static allometry of the archaic Homo sapiens palate should be investigated for several reasons. First, the results of archaic Homo sapiens static allometry may be compared with the results of the ontogenetic regressions, allowing an assessment of the validity of using adult fossils to estimate

ontogenetic trajectories. Secondly, the static results of the archaic Homo sapiens may be compared with the results of static allometry in the Arikara. This procedure should allow identification of similarities shared by the adults of both groups.

In Table 18, the results of the within-palate regressions are presented. Only one of these regressions is significant. This regression, between outer palate width and bicanine breadth, indicates a negatively allometric relationship between these variables. The same relationship is present in the archaic Homo sapiens ontogenetic regression, and at about the same magnitude. The regression of bicanine breadth and inner width parallels the result of the corresponding ontogenetic regression, but the relationship in the adult regression is not significant. The regression between inner and outer width variables shows no correlation between these variables. In addition, a negative slope is obtained ($a = -.03$). This slope value indicates that inner width decreases with increases in outer width. Palate length seems negatively allometric relative to width variables. The relationship between inner width and palate length is negative ($a = -1.01$), indicating some negative interactions between length and widths. The negative slope value is probably the result of a small sample size and restricted size variation within the sample.

Table 18. Archaic Homo sapiens static regression results.

N	X	Y	a	b	r ²	Fa	RMA a
10	LPWO	LPWI	-.03	2.75	.001	.01	-.95
11	LPWO	LBICAN	.81	.36	.28	3.55*	1.53
7	LPWI	LBICAN	.45	1.47	.15	.39	1.16
12	LPWO	LPL	.59	1.06	.11	1.21	1.77
8	LPWI	LPL	-1.01	5.43	.75	18.14**	-1.16
13	LBICAN	LPL	.33	2.26	.08	.74	1.35
7	LPRA	LPWO	1.05	-.44	.79	18.36**	1.18
5	LPRBA	LPWO	.37	1.74	.21	.78	.82
4	LPRBA	LPWI	-1.09	5.94	.86	12.90*	-1.18
4	LPRA	LPWI	-.80	5.16	.28	.79	-1.51
6	LPRA	LPL	1.72	-2.63	.63	6.85*	2.16
5	LPRBA	LPL	1.22	-.96	.79	27.59**	1.28
4	LPRA	LBICAN	1.09	.89	.51	1.88	1.95
4	LPRBA	LBICAN	-.51	4.24	.14	.33	-1.36
4	LPRA	LPRBA	1.31	-1.08	.79	7.93*	1.47

^a F-values are significant at $p < .1$ when designated with '*', and are significant at $p < .01$ when designated with '**'.

The regressions of palate dimensions on other cranial dimensions show similar results. Negative slope values were obtained for regressions of inner palate width on prosthion-basion and prosthion-auricular point. Another negative slope value is indicated in the regression between prosthion-basion and bicanine breadth. Palate length appears to increase in size faster than the cranial base (prosthion-basion), a result which agrees with the archaic Homo sapiens ontogenetic regression. The regression of palate length and prosthion-auricular point indicates positive allometry of palate length, rather than the negative allometry indicated by the archaic Homo sapiens ontogenetic regression. The same pattern holds for the regression which includes both cranial base measurements.

The regression slopes calculated from the reduced major axis method do not improve the least-squares results. In cases where regressions slopes are negative, the reduced major axis slopes simply produce larger negative values. The poor correspondence between the two methods is an effect of the low correlation coefficients for the static regressions.

Table 19 presents correlation coefficients between slopes derived from different methods. Although the adult least-squares and adult reduced major axis methods are fairly well correlated, the results obtained for static

Table 19. Correlations between slope calculation methods for archaic Homo sapiens samples.

	JLS	JRMA	ALS	ARMA
Juvenile Least-squares (JLS)	1.00			
Juvenile Reduced Major Axis (JRMA)	.09	1.00		
Adult Least-square (ALS)	.56*	-.35	1.00	
Adult Reduced Major Axis (ARMA)	.54*	-.33	.92*	1.00

Correlations designated with '*' are significant at $p < .05$

regressions do not parallel the results obtained for the juvenile regressions. In some cases, these correlation coefficients are not similar, regardless of the method used. Correlations range from $-.35$ for the relationship between adult least-squares and juvenile reduced major axis to $.92$ for the relationship between adult least-squares and adult reduced major axis. These correlations are generally much lower than the correlation coefficients for corresponding Arikara results.

The poor correspondence between static and ontogenetic allometry in the archaic Homo sapiens sample results primarily from the small sample sizes analyzed. In addition, the variables are usually not well correlated. A more direct comparison of the differences between static and ontogenetic allometries, based on principal components analysis, is presented in a subsequent section.

Ontogenetic Allometry

Multivariate results. The results of principal components analyses using the archaic Homo sapiens sample are presented in the next four tables. Ontogenetic analyses include the entire juvenile and adult samples. For the three-variable analyses, which includes inner, outer, and bicanine widths, all seven juvenile specimens were analyzed. The three-variable ontogenetic analysis includes seven adult specimens.

In the four-variable ontogenetic principal component analysis, only three juveniles (Teshik-Tash, La Quina, and Subalyuk) were available for study. This analysis includes six adults. The procedures used for the multivariate analyses of the archaic Homo sapiens parallel the procedures employed for the Arikara.

In the three variable analysis, the results of which are presented in Table 20, the standardized loading, $1/\sqrt{p}$, is .577. The first principal component accounts for approximately 86% of the total variation. The remaining two components account for 13% and 1%, respectively. Inner palate width shows positive allometry in this analysis. The other variables seem negatively allometric, suggesting slow growth of bicanine breadth and outer palate width relative to inner palate width.

In the four-variable analysis (Table 21) the standardized loading is .5. The first principal component accounts for 85% of the total variation, while the second accounts for only 10% of the total variation. The remaining components account for 5% and 1% respectively.

Both inner and outer palate widths show positive allometry. Inner palate width loads the highest (.59), and palate length loads the lowest (.40). The results of the four-variable analysis are generally consistent with the three-variable analysis. In other words, the ranking of principal component loadings for widths is similar

Table 20. Results of the archaic Homo sapiens ontogenetic three-variable principal components analysis.

	Eigenvalue	Proportion of Total Variance	Cumulative Variance	<u>Eigenvectors</u>		
				LPWO	LBICAN	LPWI
PC1	.0203	.8588	.8588	.5666	.5579	.6047
PC2	.0030	.1266	.9854	-.2716	.8197	-.5034
PC3	.0003	.0146	1.0000	.7780	-.1215	-.6164

Table 21. Results of the archaic Homo sapiens ontogenetic four-variable principal components analysis.

	Eigenvalue	Proportion of Total Variance	Cumulative Variance	LPWO	<u>Eigenvectors</u>		
					LPWI	LPL	LBICAN
PC1	.0216	.8506	.8506	.5472	.5961	.4025	.4280
PC2	.0025	.0977	.9483	-.0164	-.3801	.8817	-.2789
PC3	.0011	.0422	.9905	-.2347	-.4502	.0731	.8584
PC4	.0002	.0095	1.0000	-.8032	.5455	.2348	.0465

between the two analyses (from largest to smallest, inner width, outer width, bicanine breadth).

Static Allometry

Multivariate results. In the three-variable static analysis (Table 22), the standardized loading is .577. The first principal component accounts for 65% of the total variation, followed by 25% and 10%, respectively, for the second and third principal components. In this analysis, bicanine breadth loads the highest (.76) followed by inner width (.54) and outer width (.35). These results contradict the results for the three-variable ontogenetic analysis, where inner width loaded the highest.

The four-variable analysis (Table 23) contains only 59% of the total variation in the first principal component. Palate length loads negatively on the first principal component, a result which implies that palate length decreases relative to increases in general size. This result seems spurious. Inner palate width seems positively allometric, and bicanine breadth is roughly isometric. Outer width is negatively allometric.

Comparison of Static and Ontogenetic Results

Qualitatively, the static results do not correspond well to the results obtained in the ontogenetic analyses. In the three-variable case, the ontogenetic bicanine

Table 22. Results of the archaic Homo sapiens static three-variable principal components analysis.

	Eigenvalue	Proportion of Total Variance	Cumulative Variance	<u>Eigenvectors</u>		
				LPWO	LBICAN	LPWI
PC1	.0027	.6449	.6449	.3520	.5481	.7587
PC2	.0011	.2512	.8961	.2297	.7352	-.6377
PC3	.0004	.1038	1.0000	.9074	-.3988	-.1329

Table 23. Results of the archaic Homo sapiens static four-variable principal components analysis.

	Eigenvalue	Proportion of Total Variance	Cumulative Variance	<u>Eigenvectors</u>			
				LPWO	LPWI	LPL	LBICAN
PC1	.0040	.5898	.5898	.2607	.6041	-.5553	.5087
PC2	.0019	.2763	.8661	.1311	-.2652	.5119	.8065
PC3	.0007	.1035	.9696	.8392	.2427	.3833	-.2999
PC4	.0002	.0304	1.0000	-.4589	.7112	.5316	-.0290

breadth loads the lowest, which contrasts directly with the high loading obtained for the static bicanine breadth. In the four-variable analysis, inner palate width loads the highest in each sample. However, palate length loads negatively, probably because of limited size variation in the small sample.

Quantitative comparison of the ontogenetic and static analyses yields similar results. The angular divergence between the three-variable analyses is 14.49° . Even more extreme are the differences between static and ontogenetic allometry in the four-variable static and ontogenetic analyses. Here, the angular divergence is 58.54° . The negative loading of palate length creates this large difference. Divergences are graphically depicted in Figure 5.

In summary, the poor correspondence between static and ontogenetic allometries observed in the Arikara population holds for the archaic Homo sapiens population. The problems of correspondence may be exacerbated by the small archaic Homo sapiens sample size. However, the bivariate results substantiate the results based on principal components analysis.

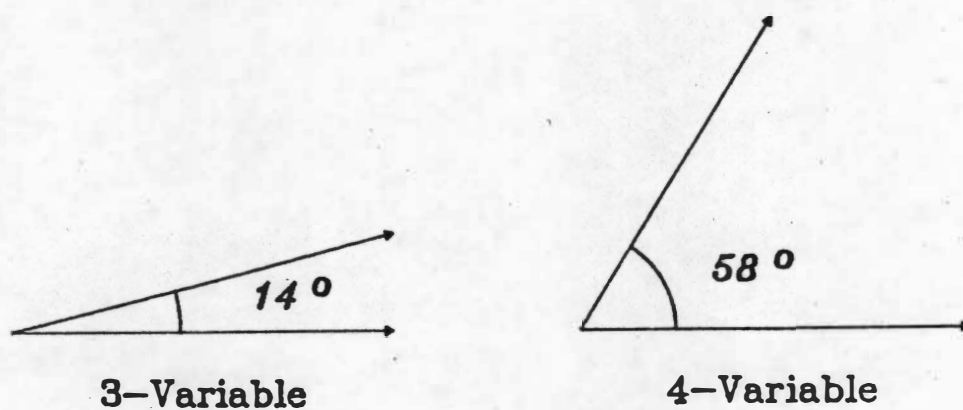


Figure 5. Angular divergences for archaic Homo sapiens static and ontogenetic principal components analyses.

3. COMPARISONS OF THE ARCHAIC HOMO SAPIENS AND ARIKARA

Regression-based Comparisons

Comparisons of ontogenetic regression lines between the archaic Homo sapiens and Arikara were accomplished in two stages. First, these regressions were tested for homogeneity of slopes. Second, the regressions were tested for significant intercept differences. Together, these procedures comprise analysis of covariance (Huitema, 1980; Sokal and Rohlf, 1981). Table 24 contains the results of these analyses. Presented in Table 24 are significance tests for homogeneity of slopes and tests for significant differences in intercepts. When the test for homogeneity of slopes is not significant, parallelism of regression lines cannot be rejected. However, when significant differences are present, parallelism of regression lines can be rejected as an hypothesis. The tests for significant differences in intercepts complements the homogeneity of slopes tests. If the intercepts of the regression lines are significantly different, then parallelism of regression lines again cannot be rejected as an hypothesis. If parallelism of slopes is not suggested in the homogeneity of slopes test, then the test for significant intercept differences is not necessary.

Allometrically, parallel regression slopes with significant intercept differences are important. Such

Table 24. Analysis of covariance results.

Sample size				F for slope				F for intercept	
Arikara		Arc. Homo sapiens		X	Y	F	p > F	F	p > F
Adult	Juvenile	Adult	Juvenile						
88	23	10	7	LPWO	LPWI	.20	.6530	188.08	.0001
87	34	11	7	LPWO	LBICAN	.04	.8400	178.45	.0001
87	34	7	7	LPWI	LBICAN	1.02	.3100	71.38	.0001
84	23	7	3	LPRA	LPWO	2.57	.1115	188.08	.0001
84	23	4	2	LPRA	LPWI	.00	.9500	122.40	.0001
86	31	10	3	LBICAN	LPL	.12	.7200	133.34	.0001
77	20	5	2	LPRBA	LPL	2.46	.1197	547.45	.0001
88	21	6	2	LPRA	LBICAN	1.28	.2600	89.44	.0001
76	20	4	2	LPRBA	LBICAN	.26	.6100	69.41	.0001
84	23	4	2	LPRBA	LPWI	3.16	.0785	122.40	.0001
83	33	12	3	LPWO	LPL	7.50	.0070	221.39	.0001
86	23	6	2	LPRA	LPL	14.61	.0002	458.78	.0001
79	19	4	2	LPRA	LPRBA	7.60	.0069	522.80	.0001

patterns are termed transpositions (White and Gould, 1965), and, although the biological meaning of different intercepts is often questioned (Huxley, 1950), transpositions may be of considerable importance. The significance of parallel slopes will be discussed after presentation of results.

For the analyses of covariance, adult and juvenile samples from each group are pooled. The paucity of archaic Homo sapiens juveniles makes this a necessary step. Sample sizes are listed in Table 24 so that the reliability of the results may be more adequately evaluated.

On the basis of sample size, the regressions which include the entire juvenile archaic Homo sapiens sample are the most reliable. These regressions all involve outer palate width, inner palate width, or bicanine breadth. For these regressions, presented first in Table 24, F-values are all very low and not significant. Thus, parallelism of regression lines cannot be rejected. In addition, the intercept differences are all significant ($p < .0001$). Thus, the archaic Homo sapiens allometric relationships for these variables are similar to analogous relationships for the Arikara. The differences (bearing in mind the inherent difficulties in the interpretation of the intercept) apparently result

from differences in size at the onset of growth (White and Gould, 1965).

The second set of regressions presented in Table 24 also indicate that parallelism of regression lines cannot be rejected as an hypothesis. In all cases, intercept differences are significant.

In the third set of regressions presented in Table 24, parallelism of regression lines is not suggested. Several of these regressions involve palate length, indicating that the allometric relationships of palate length to other variables are different between the two groups. In addition, the relationship between prosthion-basion and prosthion-auricular point seems to vary between groups. In general, the significance levels for the "non-parallel" regression lines are low, and in most cases, the sample sizes are very small.

These results indicate that, overall, allometric differences in palate allometry between archaic Homo sapiens and modern humans are relatively minor. Generally, allometric relationships in the palate seem similar between these groups. Before discussing these similarities, multivariate comparisons of the two groups should be undertaken. The results of multivariate analyses should provide additional comparative information.

Multivariate Comparisons

As a measure of the similarities between allometric patterns in the archaic Homo sapiens and Arikara, ontogenetic principal components analyses between the two groups may be compared using vector correlations and angular values. Both three-variable and four-variable analyses are comparable.

Figure 6 presents comparisons of the Arikara and archaic Homo sapiens in the three- and four-variable analyses. The divergence between the first principal component loadings for each group is only 5.08° . This value is quite low, considering the size of angular divergences between static and ontogenetic allometries for each population. The angular divergence between the second principal component (not presented in Figure 6) scores is 56.41° ; and for the third, 123.67° . The wide divergences between the second and third principal component loadings for each group may be the result of two factors. First, the differences could be the result of small sample sizes, especially when so little of the total variation is expressed in these components. Secondly, differences could be related primarily to shape differences between the groups. Obviously, both factors contribute to the observed differences. The most important point, however, is the small size of the divergence in the first principal components.

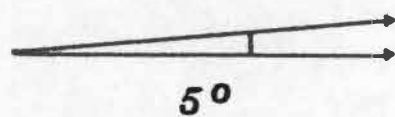
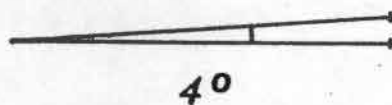
**3-variable****4-variable**

Figure 6. Angular divergences for archaic Homo sapiens and Arikara ontogenetic principal components analyses.

The results of comparison of the four-variable principal components analysis are also presented in Figure 6. An incredibly small divergence of 3.9° is present between the four variable analyses. The second, third and fourth principal components are more divergent, a result which is expected. Again, the between group differences are smaller than the static-ontogenetic differences.

4. DISCUSSION OF COMPARISONS BETWEEN THE ARCHAIC HOMO SAPIENS AND ARIKARA

Overall, the ontogenetic trajectories between the two populations show great similarities. The results of the analysis of covariance are similar to the results obtained through principal components analysis.

The probable parallelism of regression lines most clearly supports a "transpositional" hypothesis, formally expressed as Hypothesis II in Chapter III. Archaic Homo sapiens obtain larger sizes than the Arikara, but not in a strictly "ontogenetically scaled" manner. In other words, size differences at an early period during growth, rather than reductions in size along a shared ontogenetic trajectory, seem to account for the observed differences. Although this is not the case for all the relationships, most show this pattern. In addition, these relationships are often the most reliable because sample sizes are relatively large.

The results of the principal components analysis seem to support the results based on analysis of covariance. Between group differences are minimal in both the three and four-variable analyses. These differences are smaller than the differences in static-ontogenetic comparisons. Thus, considerable similarity in the pattern of general size increase is strongly suggested.

The multivariate results suggest that differences between the two groups are most probably the result of general size differences, but may also include shape differences. This conclusion is not readily apparent from the principal components analysis, but, taken in conjunction with the analysis of covariance results, this conclusion is stronger.

A sample of neonatal archaic Homo sapiens would confirm or reject an hypothesis of larger size at the onset of growth in archaic Homo sapiens relative to modern humans. Obviously, such a sample is currently unavailable. However, inferential support for this hypothesis is provided by Trinkaus (1983).

Trinkaus (1983:293-294) attempts to explain the differences between Neandertal and modern human pelvic morphology. He suggests that longer gestation periods in Neandertals may explain the observed differences. Trinkaus (1983:294) states that Neandertals could have given birth to neonates with heads 15-20% larger than

modern humans. Such features suggest a gestation period of 11-12 months for Neandertals, as opposed to 9 months in modern humans.

Trinkaus indicates that reduction of the gestation period may be adaptively important. Relatively early birth, according to Trinkaus, exposes the infant to environmental stimuli earlier, thus conferring selective advantages.

Although Trinkaus is vague concerning the selective processes favoring early birth, Gould (1977) provides considerable theoretical support for a general process explaining this pattern. Like Trinkaus (1983), Gould tends to skirt specific evolutionary mechanisms which might produce early birth. However, his argument is remarkably close to the argument presented by Trinkaus. Gould suggests that humans are "'essentially neotonous'," further suggesting that:

a general temporal retardation of development has clearly characterized human evolution. This retardation established a matrix in which all the trends in the evolution of human evolutionary morphology must be assessed. (1977:365)

Gould identifies "prolongation of fetal growth rates leading to larger [body] sizes" as a major factor in human evolution. In a sense, Gould's mechanism is primarily an "evolutionary inertia" (although he does specifically name this mechanism). Gould further suggests, in an argument almost identical to Trinkaus' (1983) that human birth has

accelerated in evolutionary history (1977:369), suggesting that relative to other developmental in other organisms, human birth should occur at about 21 months. Thus, instead of occurring in utero, a large portion of human "fetal" development occurs after birth.

Recently, Trinkaus' argument has been challenged by Frayer (1985) and Rosenberg (1985). These authors suggest that Trinkaus' argument is invalid, and suggest that Neandertal pelvic morphology is a result of larger overall size (Rosenberg, 1985). In other words, Neandertal pelvic morphology is not closely related to parturition or the length of the gestation period. The ideas of Frayer and Rosenberg are plausible, but they do not deal with Gould's theory of neotony in human evolution. Consequently, the arguments of Frayer (1985) and Rosenberg (1985) are incomplete, and they must respond to Gould's more general propositions before refuting Trinkaus' (1983) explanation.

Another alternative hypothesis suggests that developmental rates between each group are different. In this case, modern rates of development may be slower, resulting in smaller neonates. Finally, there may be considerable "interaction" between these hypotheses, producing the observed pattern of transpositions.

Although the specific evolutionary mechanisms resulting in progressively earlier birth or progressively slower development lie within a complex "matrix" of human

evolution (Gould, 1977:365), the implications of these processes are easily enumerated. First, increased infant care could result in changes in social relationships (produced by changes in infant care) within (and possibly between) groups. Secondly, decreases in gestation length may also bring about decreases in birth intervals. Shorter birth intervals would, ceteris paribus, increase the fertility rate, and thus lead to increased population size (Leridon, 1977).

Increased fertility rates, in addition to concomittant social changes, could either force expansion of habitats or create new social "environments," both of which are important in speciation (Mayr, 1963:575). As Mayr has indicated, purely behavioral changes may be a first step in speciation via "behavioral isolating mechanisms" (1963:415). These factors are somewhat speculative, but cannot be overlooked when considering a transition from archaic Homo sapiens to modern humans.

Finally, the "transpositional hypothesis" favored here applies only to the palate and the relationship of the palate to certain other cranial dimensions. More allometric research is necessary to allow greater confidence in transpositional patterns. Unfortunately, there are no clear guidelines regarding the acceptance or rejection of transpositional hypotheses. Often, as Shea (1985) has demonstrated, several different patterns

(ontogenetic scaling, transpositions) are apparent. In this case, the large number of regressions indicating transpositions, and the work by Trinkaus (1983) and Gould (1977) lend strength to the transpositional hypothesis.

CHAPTER VI

CONCLUSIONS

This research has explored the numerous aspects of allometry and has applied the methods of allometry to a fossil data base. In addition, the allometry of the modern hominid palate and other cranial structures has been explored and described. Finally, quantitative techniques for the assessment of allometry have been examined and compared.

The most important aspect of this research concerns allometric comparisons of archaic Homo sapiens and anatomically modern Homo sapiens. Basically, the results presented here indicate important similarities between these two groups. The allometric growth of the archaic Homo sapiens palate and anatomically modern Homo sapiens palate are, in many ways, quite similar. These similarities are indicated by the maintenance of similar slope values between each group. An important difference, however, is in the intercept value for each group.

The statistical descriptions (i.e. slopes and intercepts) indicate that differences in size at the onset of growth (presumably post-natal growth) are present between these groups. This result has several implications. First, the observation that archaic Homo sapiens are larger at birth lends support to Trinkaus'

(1983) explanation of the differences between Neandertal and modern human pelvic morphology. His argument, that the elongated superior pubic ramus of Neandertals is a response to long gestation periods resulting in large infants, seems supported by the allometric results presented in this research. Second, Gould's (1977) more general arguments concerning the increasing neotony in the Homo lineage are supported by the present results. Thus, the work of these authors seems independently substantiated. Recent commentaries (Fruyer, 1985) and research (Rosenberg, 1985) have not dealt with Gould's suggestions and are, therefore, incomplete.

The evolutionary mechanisms responsible for transpositional changes are difficult to identify, but the implications of such changes are more tangible. Reduction of gestational length (suggested by Trinkaus [1983]) could result in shorter birth intervals, allowing more rapid population increases. Changes in social behaviors may also have resulted from reductions in gestation period.

Comparisons of static and ontogenetic allometry yielded expected results. These measures of allometry are not necessarily similar, in accordance with observations by Cock (1966) and Cheverud (1982). The present research indicates that static allometry usually does not provide adequate measures of ontogenetic allometry in fossil as well as recent samples. Therefore, the use of static

samples should be limited to description, and should not be employed to illustrate evolutionary changes in growth trends between groups. Furthermore, juvenile fossils should be employed in allometric studies whenever possible. Even with the small numbers of individuals examined in this research, reasonable results were obtained, particularly in the between-group principal components analyses. Specifically, the principal components analyses indicate that static-ontogenetic differences within each group actually exceeded the differences between each group. This result clearly illustrates the difficulty in the use of static data.

The limited comparisons of quantitative methods indicated that, for these samples, the least-squares regression technique supplied results which were corroborated by the results of principal components analyses. A major benefit of using least-squares criteria is that the analysis of covariance is greatly facilitated, a procedure which is impossible when Model II regression techniques are used.

Clearly, more research is necessary to fully understand the allometric relationships of archaic Homo sapiens. Future research should focus on documenting allometric relationships between many body parts, not only the palate. Such information is needed to more closely

evaluate the significance of allometric relationships between archaic Homo sapiens and anatomically modern humans.

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APPENDIX

APPENDIX

MEASUREMENTS TAKEN

1. PWO Outer palate width, ectomolare to ectomolare, at M^1/M^2 and m^1/m^2 .
2. PWI Inner palate width, endomolare to endomolare, at M^1/M^2 and m^1/m^2 .
3. PL Palate length, prosthion to posterior nasal spine.
4. BICAN External bicanine breadth.
5. PD* Maximum depth of the palate (recorded with a palatometer) at M^1/M^2 and m^1/m^2 .
6. MP* Posterior-most aspect of the posterior nasal spine to the intersection of the cruciate suture.
7. PRBA Prosthion to basion.
8. PRA Prosthion to auricular point.

* Indicates measurements not taken for the archaic Homo sapiens sample.

VITA

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