Ontogenetic Changes in Orangutan Brain Evolution: Is it Heterochrony?

by

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A Master's Thesis

In

Anthropology

Submitted to the Graduate Faculty
of Texas Tech University in
Partial Fulfillment of
the Requirements for
the Degree of

Master of Arts

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May, 2012

Acknowledgements

I would like to thank the following people and institutions for their gracious help and support. First and foremost I want to thank my daughter, Infinity, for her patience with me throughout this process. She is the light of my life and the reason I put myself through this gauntlet. This is for her, in the hopes that it will build a better life for us.

I would like to thank my chair, Dr. Arthur Durband whose counsel, technical advice and general availability to listen to me vent about life and graduate school made a significant difference in not only my graduate work but in my quality of life as well. He has been a good friend and mentor throughout my undergraduate and graduate careers. I would also like to thank the other members of my committee, Dr. Sean Rice and Dr. Tamra Walter. Dr. Rice's expertise and technical advice was indispensible, and this project could not have gone far without his aid. Dr. Walter's willingness to join a project well outside her expertise and understanding is greatly appreciated. I want to thank the Department of Sociology, Anthropology, and Social Work for their financial support for this master's thesis as well as the opportunity to grow and be challenged as a person and student.

Finally, I would like to thank my close friends and family. Your love and devotion to me, and Infinity, has made all the difference in my success. I could not have done this without you and your support. Thank you.

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Chapter I

Introduction

The study of allometry is more than a century old. Beginning first with Otto Snell in 1892 and continuing with many contemporary scholars, allometric studies have shed tremendous light on evolutionary trends in organisms. Allometric studies have in particular increased our understanding of ontogenetic events of human and non-human primates. At various intervals in the early life history of primates, the brain grows at a given rate. This rate is different between the hominoids and the other taxa of primates, which is indicative of a derived character state in the ape lineage. The term for a change in timing or rate of some ontogenetic process is heterochrony. However, there has been much confusion as to how and when the term heterochrony should be applied (McKinney and McNamara, 1991; Rice, 1997). The change in developmental rate in the hominoids has been explained as paedomorphosis (neoteny) (Gould, 1977; Antón and Leigh, 2003), as sequential hypermorphosis (Shea, 1989; McKinney and McNamara 1991; Vrba, 1998; Rice, 2002) or as a combination of both heterochronic modes (Rice, 1997; Zollikofer and Ponce de Leon, 2010). It is undeniable that heterochrony has played an important role in the evolution of human and non-human primate ontogenies, yet the debate is not settled as to the type of heterochrony responsible for this change.

In the hominoid superfamily the growth rate is accelerated, perhaps due to having increased cognitive abilities relative to the non-ape taxa. There have been some studies done on the growth trajectories of humans and chimpanzees as well as a few of the New World monkeys (Vrba, 1998; Rice, 2002; Leigh, 2004; Zollikofer and Ponce de Leon,

2010). The Asian apes' growth trajectories have not been studied, and they have the potential to offer tremendous informative power to understanding when in the evolutionary history of the ape lineage this acceleration of brain growth occurred. Because the hylobatids and pongids diverged much earlier than either chimpanzees or gorillas, the importance of this research to our understanding the evolutionary history of the hominoids is significant. Recent molecular data has shed light on the phylogenetic relationships between the different primate taxa (Fabre et al., 2009; Locke et al., 2011). While these analyses are an important contribution to our knowledge of primate evolutionary history, they do not address ontogenetic relationships. The present study seeks to reveal the ontogenetic relationship of brain growth in Ponginae to the other members of the Hominidae and the Primate order in general.

It is widely agreed upon that heterochrony has played a role in human evolution (Rice, 2002). Heterochrony has been defined as "a uniform change in the rate or timing of some developmental process, with no other internal change to that process" (Rice, 2002: 154-155). In his study of chimpanzees, humans, macaques, and squirrel monkeys, Rice (2002) found that heterochrony alone did not completely explain the novel brain growth phase exhibited by humans and chimpanzees compared with the other primates. The difference between the human and chimp growth trajectories, however, is largely a result of heterochrony (Vrba, 1998; Rice, 2002). This indicates that sometime between the last common ancestor of apes and Old World monkeys a novel brain growth phase evolved. The most recent molecular data suggest that the lineage leading to the orangutans (*Pongo spp.*) branched off from the other great apes around 12-16 mya (Fabre et al., 2009; Locke et al., 2011). In contrast, the Hylobatid lineage branched much earlier,

at approximately 18-20 mya (Fabre et al., 2009; Locke et al., 2011). Given that these two lineages diverged much earlier than the chimpanzees, investigating these primates could give us a better understanding of when this novel growth phase first appeared in the ape line. Due to methodological constraints, at this time only orangutan ontogeny can be compared with those of chimpanzees and humans. Upon gathering the appropriate data from orangutans, a test will be conducted to determine if the resulting curves can be fit on the other, known, trajectories of humans and chimpanzees. If the curves of one or both of the study genera fit onto the known trajectory, this indicates that there was a change in timing or rate of the developmental process. If, on the other hand, one or neither of the curves can be transformed to fit on the known trajectories, this will indicate there was a fundamental change in the growth process itself.

Chapter II

Background

Before Charles Darwin published *On the Origin of Species by Means of Natural Selection* in 1859, the mechanism for biological change was unknown. For centuries, the great minds in biology struggled and failed to explain the panoply of variation in the natural world, nor were they able to satisfactorily explain the relationship between ontogeny and phylogeny. The leading explanation was that of preformationism, which has its roots in the scientific musings of Aristotle (see Gould, 1977). By the 19th century, preformationism became known as recapitulation and was championed predominantly by Ernst Haeckel (1866) in his most influential work, *Generelle Morphologie der Organismen*. Put simply, recapitulation asserts that during embryonic development the embryo would pass through the earlier adult stages of evolution. For example, the human embryo would pass through the fish stage of evolution, followed by the reptilian phase and finally the mammalian phase of development (McKinney and McNamara, 1991). As Haeckel put it, "ontogeny is the short and rapid recapitulation of phylogeny" (Haeckel, 1866: 300). However, there were many in the field of biology that did not subscribe to the theory of recapitulation. Thirty-eight years earlier, Karl Ernst von Baer (1828) published his book *Entwickelungsgeschichte der Thiere*, which asserted that recapitulation theory contained a fundamental flaw. von Baer argued that some features present in higher organisms were also present in lower life forms. He also argues that ontogeny occurs from the simple to the complex (von Baer, 1828). Even though von Baer's book attempted to demolish recapitulation (Darwin himself was a staunch anti-

recapitulationist), the concept remained an important part of evolutionary theory well into the 20th century. It was not until work by Walter Garstang in the 1920's and Gavin de Beer in the 1930's that recapitulation was truly threatened (McKinney and McNamara, 1996).

Working on tunicate larvae, Walter Garstang produced several works in which he suggests that rather than recapitulating phylogeny, ontogeny actually creates phylogenetic variation (McKinney and McNamara, 1996). Garstang coined the term *paedomorphosis* to indicate the retention of a juvenile morphology in the adult form. Continuing with de Beer, slowly the scientific community moved away from recapitulation and accepted paedomorphosis as the dominant force in phylogeny (McKinney and McNamara, 1996). However, the notion of recapitulation refused to disappear altogether. Indeed, even in the more modern synthesis of the relationship between ontogeny and phylogeny by Alberch et al. (1979), the term recapitulation is used in reference to the effects of peramorphosis (increased development). The key is that recapitulation is no longer considered the mode of phylogenetic change, rather it is viewed as the phylogenetic result of ontogenetic change.

It is from these early works that we get the core terminology regarding the different processes of ontogenetic change. Heterochrony, first used by Haeckel, refers to a change in the timing or rate of an ontogenetic event in relation to the ancestral condition. Underneath the umbrella term of heterochrony, there are two broad results of the various heterochronic modes: peramorphosis and paedomorphosis. In peramorphosis, development continues beyond the ancestral termination point. In contrast, paedomorphosis results in the termination of growth before the ancestral end point. There

are three 'types' or 'modes' of peramorphosis. Pre-displacement is the early onset of growth; acceleration is an increase in the rate of morphological development; and hypermorphosis is a late offset of growth (McKinney and McNamara, 1996). Likewise, there are three types of paedomorphosis. Progenesis is the early offset of growth; neoteny is a reduced rate of development; and post-displacement is a delayed onset of growth (McKinney and McNamara, 1996). Each of these different processes of heterochrony leads to different morphological developments. Neoteny is probably the most well known and controversial of the heterochronic processes, as this was reasoned to be the major mode of heterochrony responsible in human evolution (de Beer, 1958; Montagu, 1962; Gould, 1977; Godfrey and Sutherland, 1996). However, the general consensus has rejected neoteny as the primary heterochronic process involved in the evolution of most human characteristics (Shea, 1989; McKinney and McNamara, 1996; Vrba, 1998; Rice, 2002; Zollikofer and Ponce De Leon, 2010); though some still cling to the notion of humans as the neotenic ape (Godfrey and Sutherland, 1996).

Neoteny, or the slowing down of a developmental rate, should produce distinct characteristics in the descendant morphology. In the case of human evolution, Gould (1977: 353) argues that there are "striking resemblances between juvenile pongids and adult humans and the obliteration of this similarity during pongid ontogeny by strong negative allometry of the brain and positive allometry of the jaws." Gould (1977) continues by stating, "*a general temporal retardation of development has clearly characterized human evolution. This retardation established a matrix within which all trends in the evolution of human morphology must be assessed*" (p.365 italics original). However, as Shea (1989) and McKinney and McNamara (1996) note, this resemblance of

juvenile pongids and humans is only superficial. The similarity of the bulbous skull structure of adult humans and immature pongids is a result of a greatly enlarged brain in humans. The enlarged brain is produced by a late offset of growth, in other words, hypermorphosis (McKinney and McNamara, 1996; Vrba, 1998; Rice, 2002; Zollikofer and Ponce de Leon, 2010). Additionally, Gould (1977) argues that humans show a slow or retarded development in birth, maturation and longevity compared to chimpanzees. Yet as McKinney and McNamara (1996) point out, human ontogeny is not slowed down; each phase of growth is prolonged so that we stay in each phase longer. Again, this is hypermorphosis, not neoteny. Neoteny is a term to describe rate, how fast or slow something is occurring. The rate of growth is not slower in humans compared to chimpanzees, or even human ancestors (McKinney and McNamara, 1996).

Despite the hopes and efforts of early investigators to shoehorn human ontogeny into one heterochronic process, there is no single global mode responsible for the characteristics that make us distinctly human. Although Gould (1977: 365) leaves himself open to a non-global heterochronic mode by saying humans are '*essentially* neotenous (italics added),' he clearly views human ontogeny as being the result of global neotenic processes. It is now clear that human evolution involves more than a single mode of heterochrony, exhibiting instead a mosaic of ontogenetic changes. Some traits exhibit neoteny, while others show hypermorphosis (Shea, 1989; McKinney and McNamara, 1996; Rice, 1997, 2002; Vrba, 1998; Zollikofer and Ponce De Leon, 2010). Shea (1989) points to the overall size of the neurocranium and the size of the brain as evidence of neoteny in this organ. However, more recent work by Vrba (1998) and Rice (2002) has shown that neoteny is not responsible for the change in brain size relative to chimpanzees.

Instead these authors find that the heterochronic changes seen in human brain growth is best described by sequential hypermorphosis. In a multiphasic ontogeny, such as fetal growth, a heterochronic transformation may occur separately in each phase, this is called sequential heterochrony (McKinney and McNamara, 1996). Sequential hypermorphosis is a delayed offset of growth that is applied to each phase of the ontogeny in sequence. In the case of the human brain, the entire growth phase is extended relative to the chimpanzee. This produces a very different trajectory than does a general slowing down (neoteny) (McKinney and McNamara, 1996; Vrba, 1998; Rice, 2002). Perhaps one of the key misunderstandings of human ontogeny is that researchers have been drawing "comparisons between heterochronic apples and oranges" (Zollikofer and Ponce De Leon, 2010: 443). Here Zollikofer and Ponce De Leon are referring to the failure of previous studies to differentiate between size and shape in ontogeny. Size is a measurable quantity such as volume, mass, length, etc., whereas shape denotes a relationship of the different parts. Thus, a change in size is growth and a change in shape is development. It is important to distinguish between the two because there are distinct ontogenetic consequences of heterochrony in size and shape that may be independent of one another. For example, Zollikofer and Ponce De Leon (2010) find that the *shape* of the adult human cranium is neotenic compared with infant chimpanzees and australopiths. On the other hand, the authors also find that neurocranial *size* of infant newborns, which is similar to that of adult chimpanzees and *Sahelanthropus tchadensis*, and increases to four times the size of adult chimpanzees, clearly shows hypermorphosis (Zollikofer and Ponce De Leon, 2010).

With the issue of human heterochronic changes to ontogeny clarified, we are free to concentrate our efforts on the relationship of human ontogeny to our ancestors. Throughout the history of human ontogenetic studies, comparisons have been drawn between humans and chimpanzees. However, the richness of understanding heterochronic relationships with other primates and even ancestors within the human lineage has not been fully explored (but see Rice, 2002; Leigh, 2004; Zollikofer and Ponce De Leon, 2010). By investigating the ontogenetic relationships between humans and other primates (and human ancestors) we can begin to determine when in our evolutionary history certain changes in ontogeny occurred.

The evolution of the human brain has received a great deal of attention due to the highly specialized and unique nature of our brains. In order to understand the evolution of the human brain, comparative studies of pongid brains are of central importance. In terms of size (both relative and absolute), the human brain has increased more than threefold over the past 2.5 million years; this is more than 3.1 times larger than predicted by allometric scaling (Schoenemann, 2006). While the human brain has dramatically increased in size, much of this increase has been accompanied by a significant amount of cytoarchitectonic remodeling in the cerebral cortex (Rakic, 1988; Gannon et al., 1998; Hopkins et al., 1998; Schoenemann, 2006; Saki et al., 2011). Of particular interest are the language comprehension and production areas of the brain (Wernicke's and Broca's areas, respectively). Though homologs of these areas are present in all mammalian brains, these areas are highly specialized in humans (Butler and Hodos, 2005). In the great apes and humans there is a detectable asymmetry between the right and left hemispheres in the planum temporale, a region of the brain located in Wernicke's area that is thought to be

important in spatial location of sound (Deouell et al., 2007). The planum temporale is most often larger in the left hemisphere and is notably absent from New World and Old World monkeys (Hopkins et al., 1998). While only humans have language, chimpanzees, gorillas and orangutans show a remarkable amount of hemispheric specialization and gyrification of the brain (Gannon et al., 1998; Hopkins et al., 1998). This unique brain morphology is not shared with the lesser apes or monkeys (Gannon et al., 1998; Hopkins et al., 1998). It is therefore likely that this cytoarchitectonic restructuring had occurred by the split between orangutans (12-16 million years ago; see Figure 2.1 below) and the lineage that gave rise to the African apes and humans.

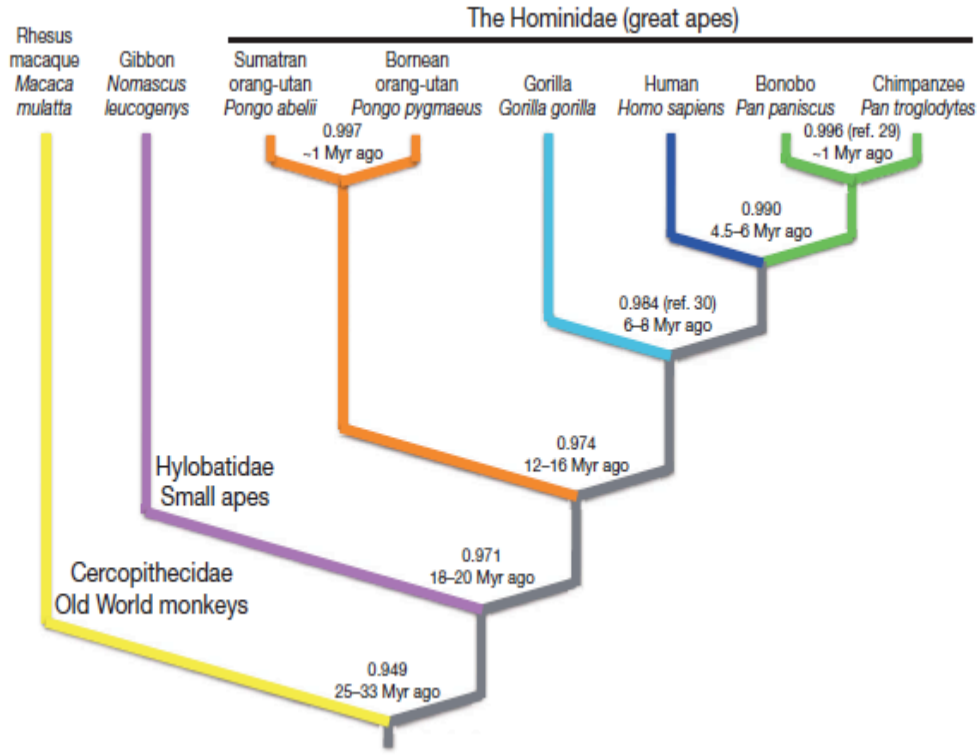

Figure 2.1 Recent molecular date illustrating the phylogenetic relationships of Old World monkeys and apes. From Locke et al. (2011).

This change in the cytoarchitecture of the brain is an important point for the application of heterochronic studies. In his study on the brain growth trajectories of macaques (*Macaca mulatta)*, squirrel monkeys (*Saimiri sciurius*), chimpanzees (*Pan troglodytes*) and humans, Rice (2002) found that the human brain is sequentially hypermorphosed compared to the pattern of brain growth seen in the chimpanzee. However, the chimpanzee and human brain trajectories cannot be related to those of the old world and new world monkeys by any combination of heterochronic transformations. Specifically, in the stage between birth and about one year of age there appears in the human/chimp curve a phase of intermediate growth that is not a simple heterochronic modification of the *Macaca* and *Saimiri* trajectories (Rice, 2002). A transformation of the monkey trajectory through neoteny or other heterochronic shift, while improving the fit between these species and the human/chimp curve, does not account for this modification. It appears that the rejection of heterochrony as the hypothesis for ape brain growth stems, at least in part, from the presence of more specialized structures of the chimpanzee and human brain and the lack of these structures in the more distantly related clades (Rice, 2002). In light of these conclusions, more questions must be asked regarding the origin of this unique growth phase. Is this growth phase unique to humans and chimpanzees, or is it present in other apes as well? Investigating more distant out-groups, such as orangutans, will enable us to determine when in the evolution of the human/chimp clade this novel phase of growth occurred. The orangutan is the most evolutionarily distant extant great ape related to humans. Recent molecular genetic evidence shows that the two species of orangutan (*Pongo pygmaeus*, the Bornean species, and *Pongo abelii*, the Sumatran

species) diverged from the rest of the ape clade between 12 and 16 million years ago (Locke et al., 2011). As already noted, orangutan brain morphology is similar to that of the other great apes; but, morphology does not necessarily indicate similar ontogenetic development. Indeed, chimpanzees share similar brain morphology with humans yet human brain ontogeny is generally described by sequential hypermorphosis with respect to the chimpanzee brain (Vrba, 1998; Rice, 2002). While the morphology of the orangutan brain confirms that the changes in brain structure were already in place by the time of the evolution of these species, it is important nevertheless to uncover the heterochronic changes, if any, to brain ontogeny in the orangutan. Male orangutan cranial growth, which is an indication of brain size, has been characterized as being peramorphic with respect to female cranial size (Leutenegger and Masterson, 1989). This, however, tells us nothing about the heterochronic relationship to other primate species. To date, I am unaware of any study that has explicitly investigated the heterochrony of orangutan brain growth with respect to other primate species. The purpose of the present study is to examine the relationship of orangutan brain ontogeny to humans and chimpanzees. In light of the findings regarding the similarity in brain morphology, it is hypothesized that the orangutan will show a similar growth trajectory to humans and chimpanzees. It is unlikely that given such important similarities in major brain cytoarchitectural structures that the orangutan would show a vast departure from the ontogenetic trajectories seen in humans and chimpanzees. Interestingly, the lesser apes (gibbons and siamangs) do not show the level of cytoarchitectonic modification (e.g. planum temporale asymmetry) that is present in the great apes and humans (Hopkins et al., 1998). This points to orangutans as the key to identifying when the human/chimp mode of brain growth first appeared.

Chapter III

Materials and Methods

The data for this project were collected at several institutions, the Anthropological Institute at Universität Zürich, the Natural History Museum in London (NHM), the Hunterian Museum at the Royal College of Surgeons in London (RCS), and the American Museum of Natural History (AMNH) (see Table 3.1). At the Anthropological Institute the data were comprised of CT scans of 42 fetal, neonate, juvenile and adult orangutan crania. Using the 3D analysis software Avizo, endocasts of the crania were generated and the volume of the endocast was calculated using the program ForMit V 4.0. This method produced cranial volumes for these individual specimens. No linear measurements were taken on these specimens, as many of the crania were not housed at the Anthropological Institute. At the Natural History Museum in London, the Hunterian Museum at the Royal College of Surgeons, and the American Museum of Natural History the specimens were dry skulls from the museum collections. Collections information for the specimens in England was taken from Jenkins (1990). Only 14 crania were usable from the NHM and eight from the RCS as many were damaged or missing from the respective collections. An additional 11 crania from the AMNH were measured.

Cranial capacity of these specimens was determined by filling the neurocranium with 5mm high-density polyethylene (HDPE) beads. The beads were then poured into a graduated cylinder to measure the volume. External linear measurements were taken on all crania from NHM, RCS, and AMNH. These measurements were taken in order to

Table 3.1: Number of individuals and age classes for the five species of primates in this study. Sources for the data are the Universität Zürich (UZ), Natural History Museum (NHM), Royal College of Surgeons (RCS), American Museum of Natural History, Manocha (1978), and Rice (2002).

Species	Number of individuals	Adult	Juvenile	Infant	Fetus	Source
Pongo	68	40	20	6	2	UZ, NHM, RCS, AMNH
Pan	95	30	30	25	10	Rice (2002)
Homo	223	0	47	77	99	Rice (2002)
Macaca	102	0	20	19	63	Rice (2002)
Saimiri	65	11	3	39	12	Manocha (1978); Rice (2002)

develop a linear regression function for calculating cranial capacity from linear measurements (see below). The measurements taken are presented in Figure 3.1 and Table 3.2. Sex of the individual was recorded when possible from collection records. Following previous examples by (Hofman, 1983; Leigh, 2004), brain weight was determined by multiplying the endocranial volume by the specific gravity of mammalian nervous tissue (1.6).

Figure 3.1 Location of measurements on crania

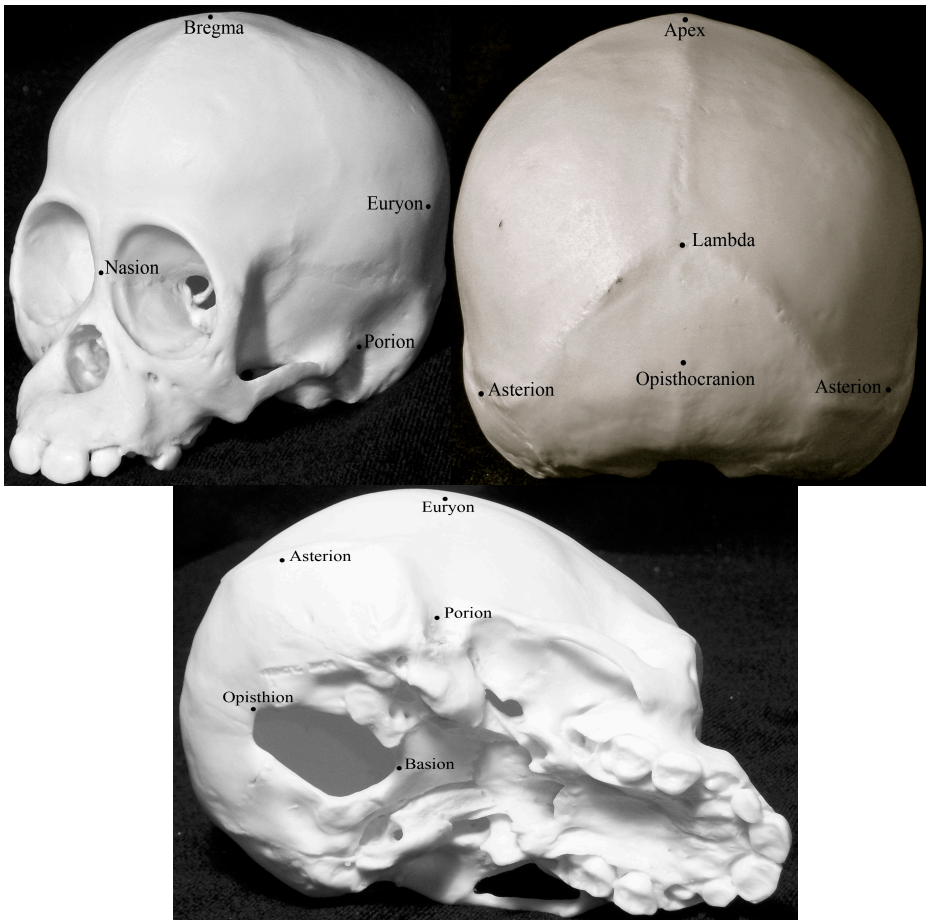

Table 3.2 Linear measurements taken on crania

Nasion-Basion	Maximum Frontal Breadth
Nasion-Opisthion	Bi-porionic
Nasion-Lambda	Bi-Asterionic
Basion-Apex	Nasion-Bregma
Bi-euryonic	Bregma-Lambda
Nasion-Opisthocranion	Lambda-Opisthocranion

To determine the ages of the individual specimens, the dental eruption stage was noted for each tooth and compared to the mean age for each tooth given in Smith et al. (1994). The more recent study by Kelley and Schwartz (2010) has shown that the mandibular M_1 in orangutans erupts at 4.6 years, which is later than the data presented in Smith et al. (1994) (approx. 3 years). For the mandibular M_1 eruption time, the value given in Kelley and Schwartz (2010) is used. However, Kelley and Schwartz (2010) do not investigate the eruption times of any other teeth and thus reliance on the older study by Smith et al. (1994) was necessary for the deciduous teeth and the other permanent teeth. Smith et al. (1994) present ages for individuals who only have deciduous teeth and some estimates for individuals with permanent teeth. Unfortunately, the numbers of individuals in the present study with only deciduous teeth are relatively few.

The orangutan data is compared to human and chimpanzee data from Rice (2002). In Rice's (2002) paper, the human and chimpanzee ages are calculated from time of conception. Therefore, the orangutan ages must also be calculated likewise. Due to the nature of the data collected (museum specimens with no life history information), it was not possible to unequivocally determine the ages of the individuals. Therefore an average gestation period of 244 days (Markham, 1995) was added to the dental age in order to approximate the age of the individual. Age at eruption is given from gingival emergence (emergence through the gum line). Kelley and Schwartz (2010) note that the time from gingival emergence to full eruption is 90 days. Thus, if M_1 is in occlusion, 90 days is added to the individuals' age. An example of the method used is illustrated below.

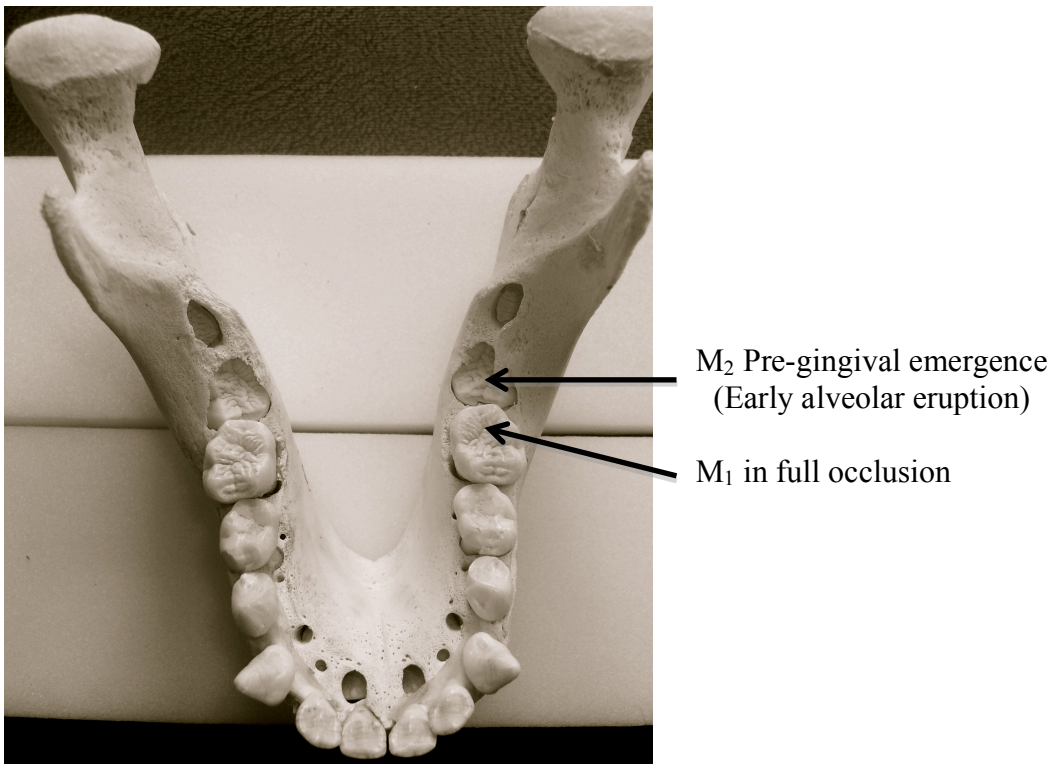

Figure 3.2 Mandible of a juvenile orangutan illustrating dental emergence patterns.

M_1 gingival emergence = 4.6 years (1679 days)
Gingival emergence to full eruption = 90 days
Average gestation time = 244 days

The specimen in Figure 3.2 has M_1 in full occlusion. Therefore, the age of this individual is: 1679 + 90 + 244 = 2013 days old. This is the youngest age capable of being calculated given the standards in the literature. Therefore, any age of an individual with permanent teeth contains a high degree of error by underestimating the true age due to the lack of any sufficient aging technique. A more precise method of aging skulls based on dental wear patterns would significantly increase the ability to age individual skulls. However, no such method yet exists for orangutans.

Both subspecies of orangutan were used in this study. Although there is a high degree of variability noted between subspecies, Ushida (1996) asserts that the amount of

variation in the eruption times and sequences between the subspecies is as great as across the Bornean orangutans. Therefore, both subspecies were grouped together to allow for a larger sample size.

Using a computer program designed and written by Sean Rice, I computed the probabilities of heterochrony being the agent responsible for similarities in the growth trajectories of humans, chimpanzees, macaques, squirrel monkeys, and orangutans. Using splines, the program fits a curve through the data sets to find the probability of getting a commensurate trajectory from each species. Commensuration in this context refers to probability of overlap and thus the likelihood of exhibiting the same allometry. The other set of points is then superimposed and the longest run of consecutive points on the same side of the line is found. If the trajectories are commensurate, then the probability (p) of getting a run as long or longer will be >0.05. For values of $p < 0.05$ heterochrony as the cause of changes in trajectories is rejected. The y-axis on the resulting plots represents the phenotype, which in this case is the log transformed brain weight. The x-axis represents age in days since conception.

Chapter IV

Results

The first analysis compares the growth trajectories of *Pongo* and *Macaca*. The untransformed trajectories can be seen in Figure 4.1. The orangutan curve resides significantly higher along the y-axis (the phenotype axis; in this case brain weight). This disparity is due to orangutans being much larger primates even as neonates than macaques. Additionally, the orangutan growth curve extends well beyond the termination of the macaque trajectory as a result of older orangutan individuals in the data set. The untransformed trajectories have a probability of commensuration of zero (p=0). We must therefore impose a transformation of the orangutan data along both axes to find a point of commensuration with the macaque. By multiplying the values on the phenotype axis by a factor of 0.77 and the values along the time axis by a factor of -111.55, we generate a best fit line with a probability of commensuration value of 0.05 as seen in Figure 4.2.

The second analysis compares the *Pongo* and *Saimiri* growth trajectories. In similar fashion to the macaque and orangutan trajectories, the squirrel monkey and orangutan show a wide separation in the untransformed graph (Figure 4.3). Again this disparity is due to the difference in overall body and brain size between these two species. The untransformed trajectories have a zero probability of commensuration. However, a transformation applied along both the phenotype and time axes, by a factor of 0.55 and -31.87 respectively, gives a commensuration probability of 0.62 (Figure 4.4). The shape of the earliest portion of the curve is also noteworthy. *Pongo* and *Saimiri* both appear to

show a deceleration of brain growth prenatally and then an onset of rapid growth a few months postnatally.

The next analysis compares the trajectories of *Pongo* and *Pan*. The chimpanzee and the orangutan are similar in body size and gross brain weight. Therefore, their respective growth trajectories overlap even in their untransformed state. However, the probability of commensuration in the untransformed state is p=0.05 (see Figure 4.5). This low probability indicates a transformation should be applied to the orangutan data to improve the fit. In Figure 4.6, the orangutan data was transformed along the phenotype axis only by a factor of 0.99. This improves the goodness of fit to a value of p=0.62. However, if we transform both the phenotype and the time axes by a factor of 0.99 and -135.18 respectively, we can improve the probability of commensuration to a value of 0.88 (Figure 4.7).

The final analysis compares the growth curves of the orangutan and human. In the untransformed graph (Figure 4.8), we see the human trajectory extends much higher than the orangutan. This is not surprising given the much larger brain and body size of the human with regard to the orangutan, neither is it surprising that the two trajectories show a p=0.0 value of commensuration. Only once a transformation of the orangutan data onto the human curve is applied along the phenotype axis can we see an improved fit with a probability of 0.889 (Figure 4.9). No additional improvement is gained by a transformation along the time axis.

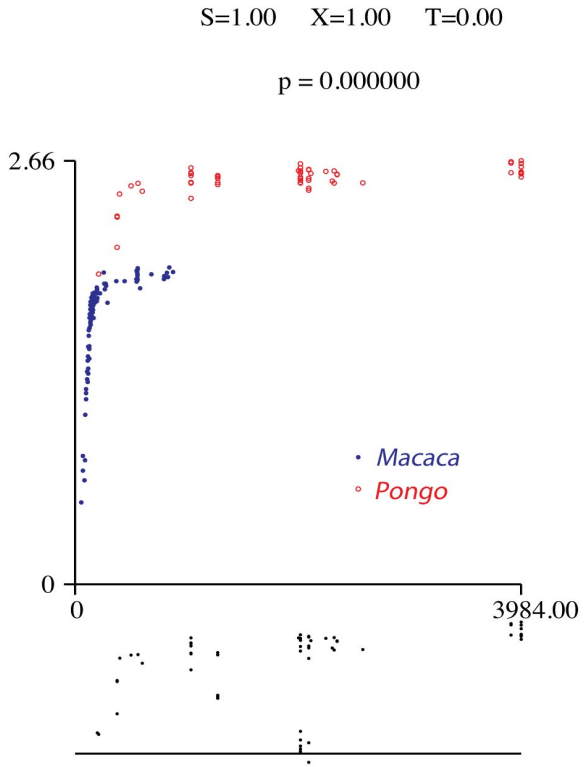

Fig. 4.1 Untransformed macaque and orangutan ontogenetic trajectories.

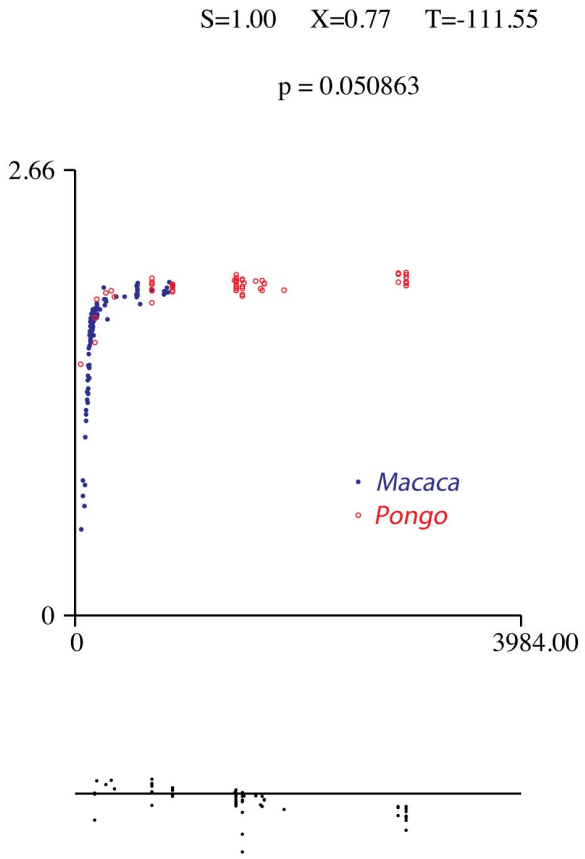

Fig. 4.2 Transformed macaque and orangutan ontogenetic trajectories.

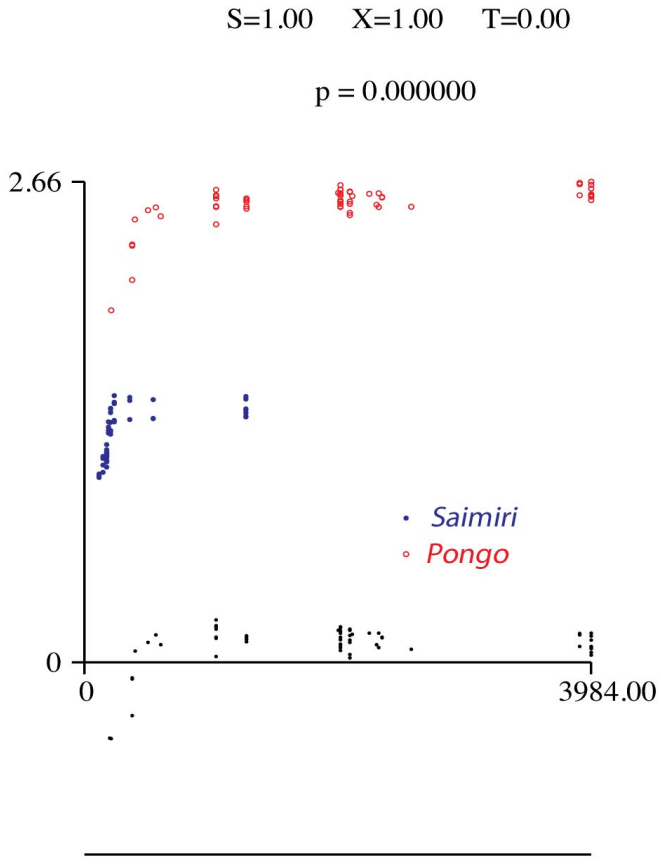

Fig. 4.3 Untransformed squirrel monkey and orangutan ontogenetic trajectories.

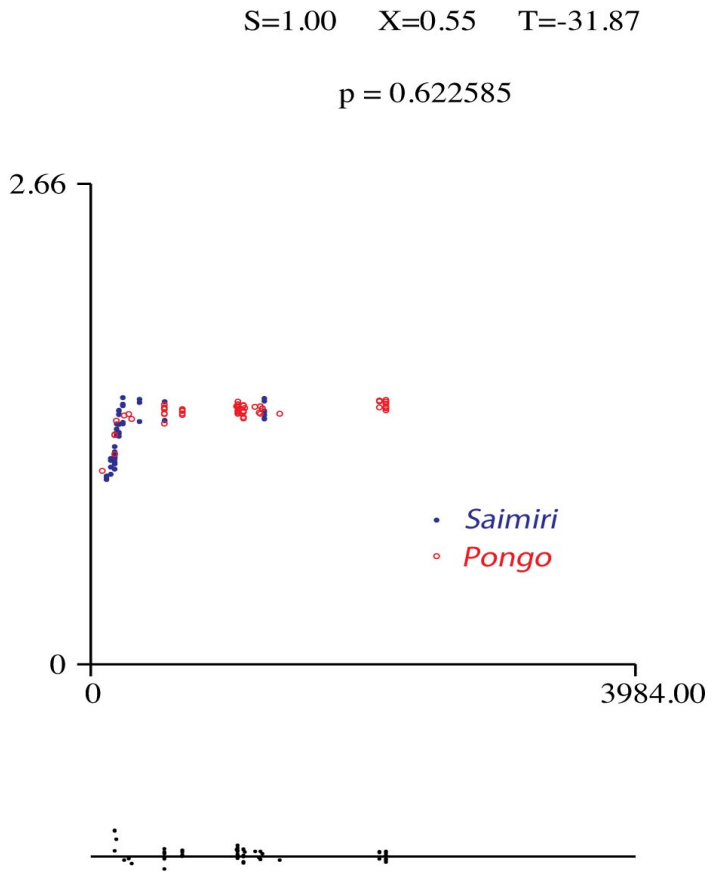

Fig. 4.4 Transformed squirrel monkey and orangutan ontogenetic trajectories.

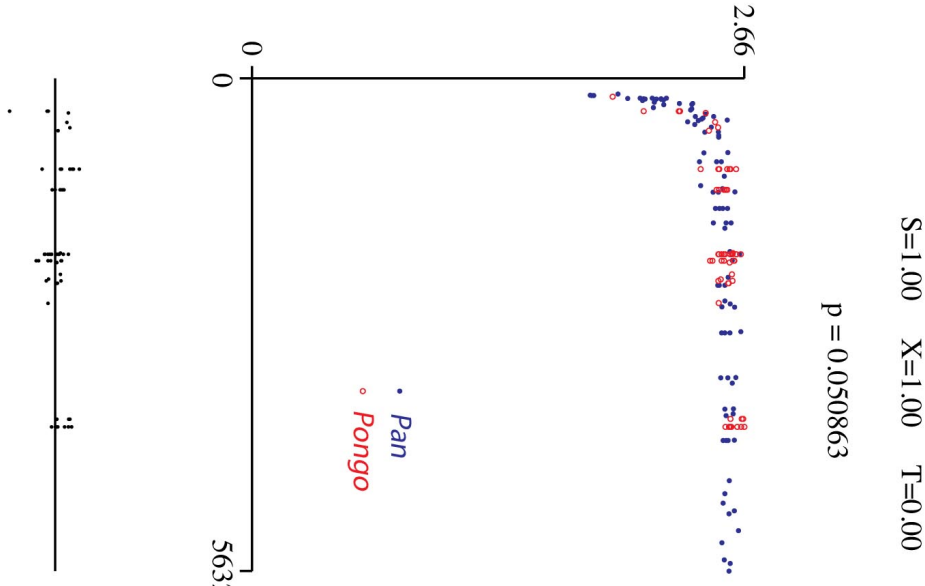

Fig. 4.5 Untransformed chimpanzee and orangutan ontogenetic trajectories.

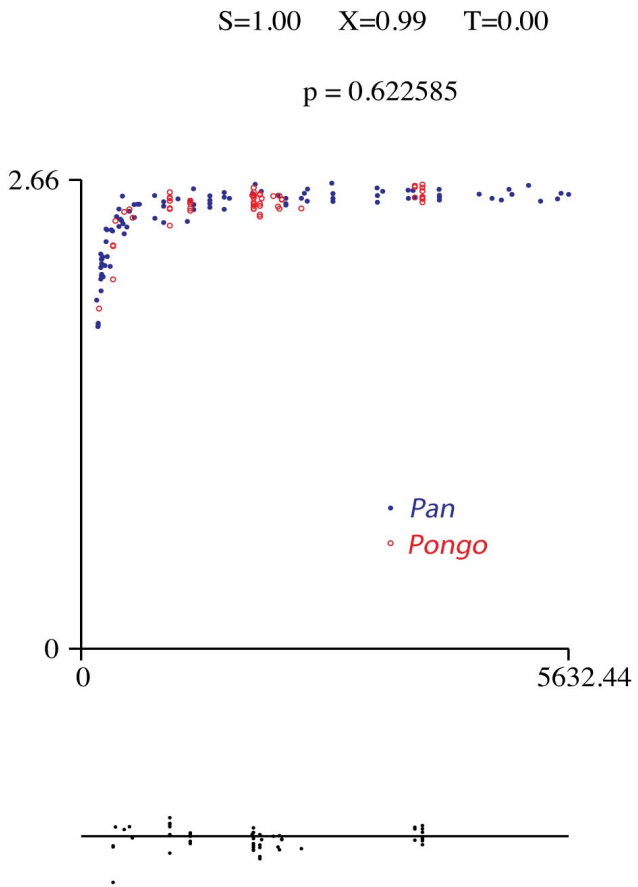

Fig. 4.6 Transformed chimpanzee and orangutan ontogenetic trajectories along the phenotype axis only.

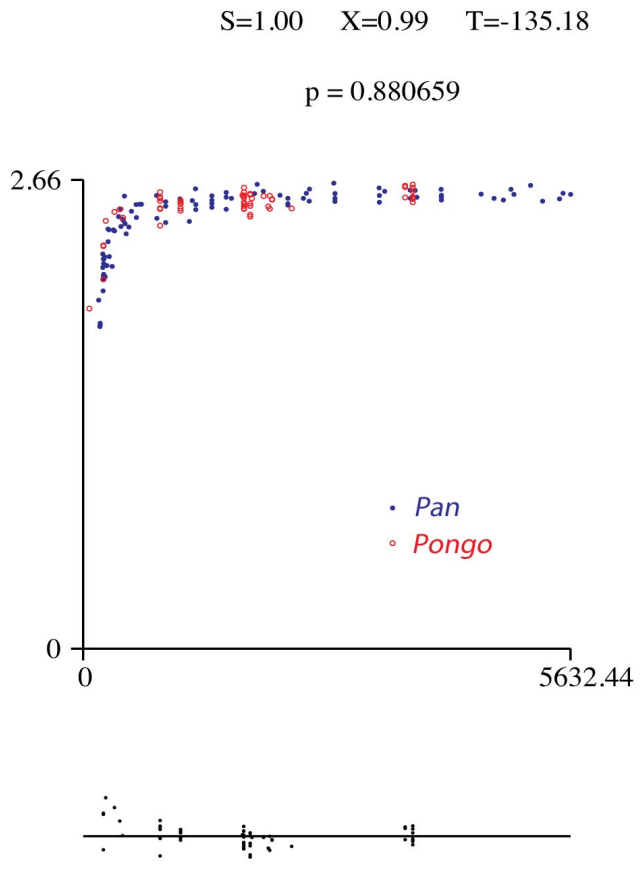

Fig. 4.7 Transformed chimpanzee and orangutan ontogenetic trajectories along phenotype and time axes.

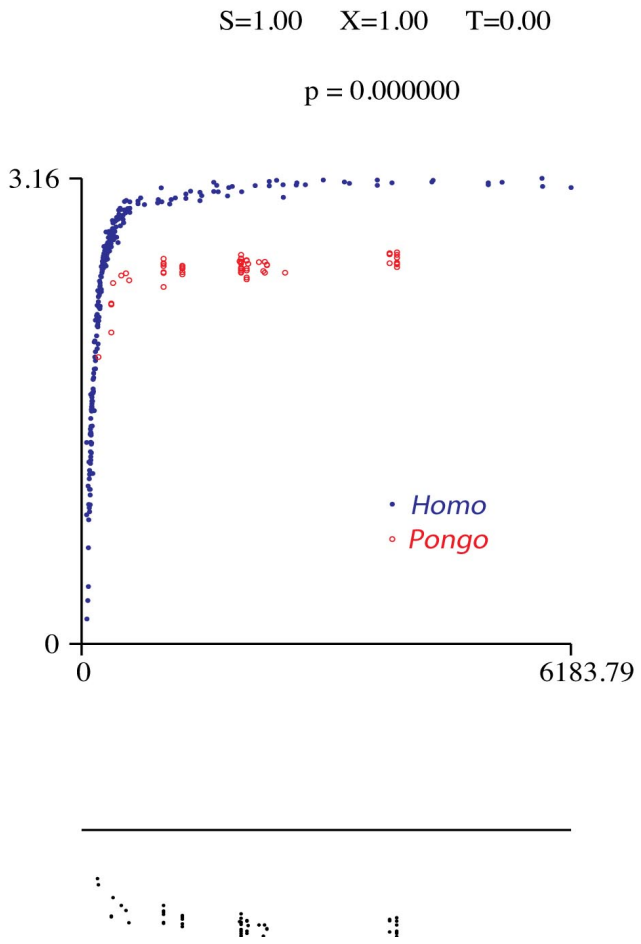

Fig. 4.8 Untransformed human and orangutan ontogenetic trajectories.

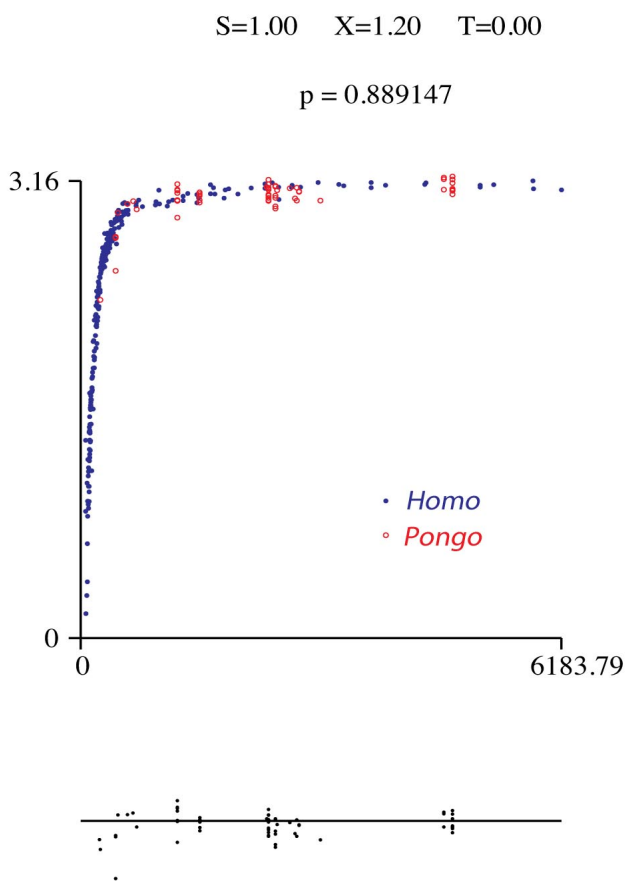

Fig. 4.9 Transformed human and orangutan ontogenetic trajectories along phenotype axis.

Chapter V

Discussion

It is undeniable that heterochrony has played a role in the evolution of primate brain size and growth rates. This is of particular interest and importance with regard to human evolution. Previous studies have suggested that human brain growth was heterochronically altered from the ancestral state by sequential hypermorphosis (Vrba, 1998; Rice, 2002). In this context the ancestral state is the chimpanzee/human common ancestor. These studies indicate that by the time of the human/chimp divergence, the pattern of relative growth rates of different parts of the brain was already in place, in addition to significant cytoarchitectonic remodeling with respect to the more distantly related monkey clades. However, the chimpanzee/human divergence occurred some 19 million years after the apes split from the monkey lineages (Locke et al., 2011). With approximately 19 million years of evolutionary history between these divergences, it is essential to identify with a higher resolution when these changes in cytoarchitecture and brain ontogeny occurred. By testing the orangutan against the macaque, the squirrel monkey, the chimpanzee, and the human, it is hoped that this greater resolution will be obtained.

The macaque represents the ancestral condition, relative to apes, of primate evolution; that is, a more primitive or less derived character state. A key difference, at least in terms of this study, is in the cytoarchitecture of the macaque brain when compared to the great apes. In the macaque brain, the planum temporale is symmetrical, whereas in the apes it is asymmetrical (Hopkins et al., 1998). There is also less

gyrification throughout the macaque brain with respect to the great apes (Hopkins et al., 1998). These cytoarchitectonic attributes of macaques are shared with other monkey species, such as baboons, capuchins, and squirrel monkeys among others (Hopkins et al., 1998; Buxhoeveden et al., 2001). Given these differences in brain cytoarchitecture, as well as other biological differences (life history events, overall body size, etc.) it is hypothesized that the orangutan and other ape ontogenetic trajectories will not be commensurate with the macaque, even with some kind of heterochronic transformation. In the statistical test run on the orangutan and macaque we find that the probability of commensuration is 0.050, a very low value. This indicates that the orangutan trajectory is not a heterochronic transformation of the macaque curve, and thus heterochrony alone is not responsible for the changes in the orangutan curve with respect to the ancestral (macaque) trajectory. This makes sense in light of the studies on brain cytoarchitecture. Heterochrony operates at the level of timing or rate in ontogeny, not in overall restructuring events. Thus, heterochrony is rejected as a hypothesis for the resultant ontogenetic trajectory of the orangutan with respect to the macaque. The resulting difference in ontogenetic trajectories suggests a change in the fundamental growth processes.

With heterochrony rejected at the orangutan/macaque node, we turn now to the orangutan/chimpanzee node of divergence. With chimpanzees and orangutans being more closely related than either is to the macaque, we expect to see more similar trajectories. When transforming the orangutan trajectory respective of the chimpanzee trajectory along the phenotype axis only, the resulting probability of commensuration is 0.622. However, if the time axis and phenotypic axis are transformed we arrive at a much higher

probability of commensuration at 0.881. Though we arrive at a higher probability of commensuration, there is an important alteration that argues against heterochrony. Shifting the orangutan trajectory along the x-axis we see the data points representing the earliest stages of brain growth exhibit a delay in growth until after birth (Figure 5.1). It appears that the orangutan has accelerated brain growth prenatally followed by slow growth until approximately six months of age postnatal.

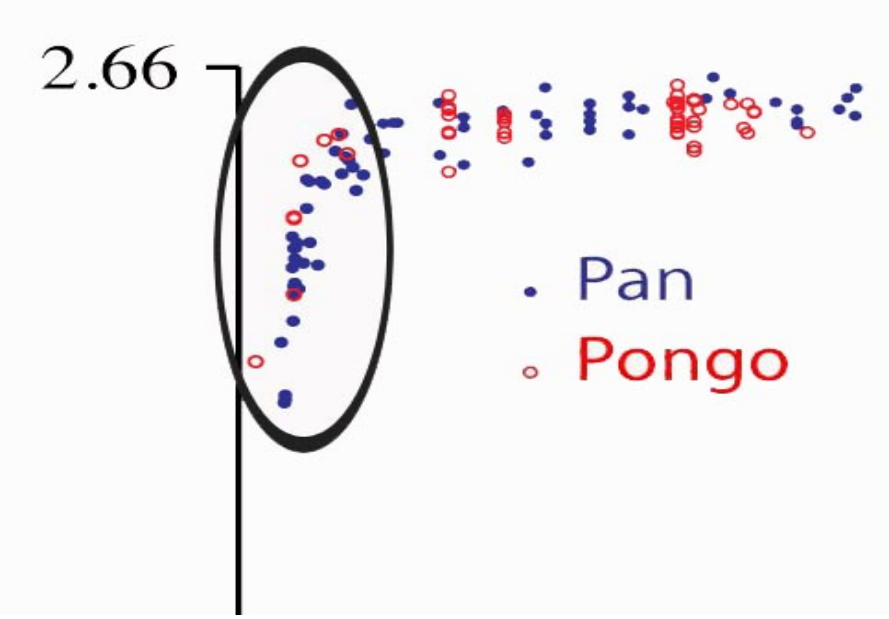

Figure 5.1 Highlighted area of chimpanzee and orangutan trajectories showing the rapid growth in the pre- and post-natal orangutan brain. Note the orangutan outlying individual is a fetus.

The discovery of this unique ontogenetic curve in the orangutan is quite unexpected. The shape of this portion of the growth trajectory resembles much more closely the curve for the squirrel monkey (*Saimiri sciurius*) growth trajectory (Manocha, 1978; Rice, 2002). Thus, it seems that the task of birthing large brained offspring is accomplished in diverse ways across distantly related primate species. Orangutans and squirrel monkeys

accomplish this by slowing brain growth down until after birth, after which brain growth accelerates quickly (Figure 5.2). In contrast, both humans and chimpanzees give birth earlier while keeping brain growth rate relatively stable.

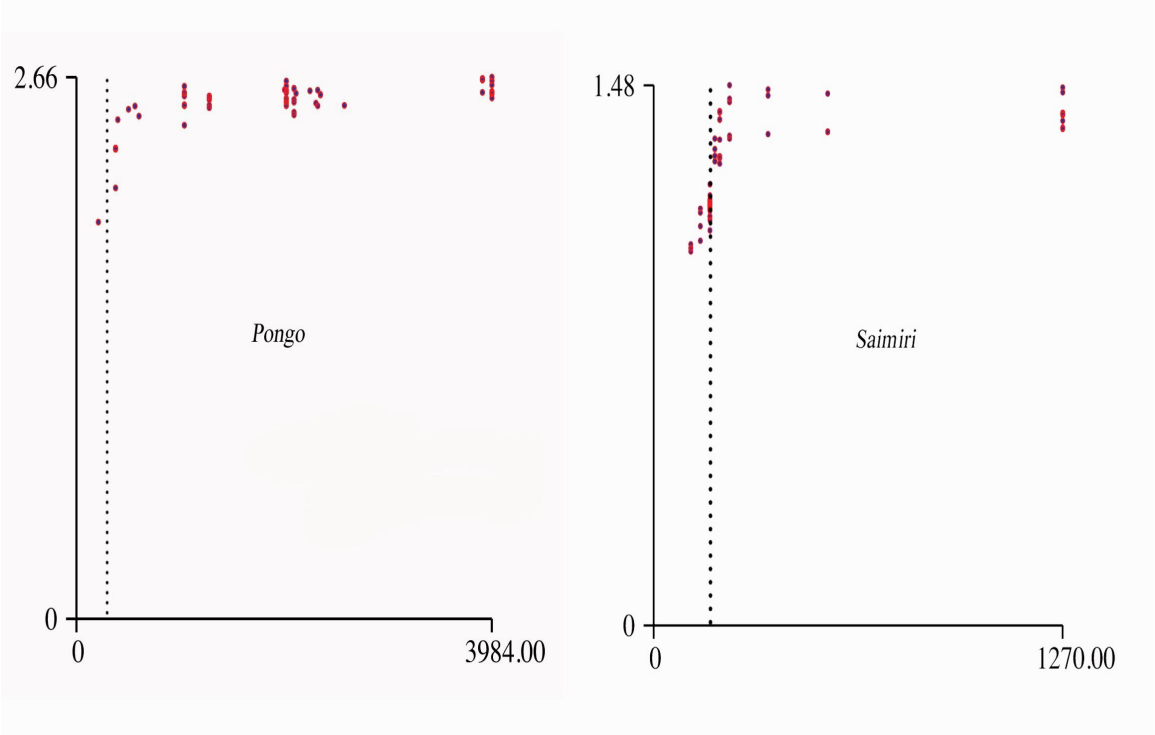

Figure 5.2 Orangutan and squirrel monkey growth curves respectively. Dashed lines denote age at birth. Note the difference in relative scales.

These results indicate that orangutans have undergone a change in the underlying mechanics of ontogeny rather than a simple heterochronic alteration. With regard to relative brain size, squirrel monkeys and orangutans have much larger brains relative to their body sizes than do macaques. Indeed, the encephalization quotient (EQ) for *Saimiri* and *Pongo* are 2.68 and 2.36 respectively, whereas the EQ for *Macaca* is 1.95 (Tartarelli and Bisconti, 2006). This difference in brain/body size between these primate species likely plays a role in the disparate birthing strategies of large brained animals. In contrast,

gorillas have a smaller EQ (1.61) than any of the previously mentioned primates. It would be intriguing, therefore, to conduct a study on brain ontogeny in gorillas to determine their growth pattern relative to the other primates.

Prior studies involving the role of heterochrony in human evolution have compared the human ontogenetic trajectory with the trajectories of chimpanzees, macaques and squirrel monkeys (Rice, 1997, 2002; Vrba, 1998). These studies conclude that relative to chimpanzees, human show sequential hypermorphosis in their brain ontogeny. We therefore suspect that humans will be sequentially hypermorphosed with respect to orangutans. Testing for heterochronic changes in human brain ontogeny we transform the ontogenetic trajectory of the orangutan along the phenotype axis only, and arrive at a probability of commensuration of 0.889. However, given the change in ontogenetic processes found in the orangutan we must reject heterochrony as an agent in the transformation of the human trajectory relative to the orangutan. If humans were sequentially hypermorphic orangutans, human brains would then grow quickly during prenatal development, essentially halt growth until after birth, and then resume growth at a high rate. This is not the pattern seen in human brain growth. Human brains grow steadily in utero and then after birth the rate decelerates slightly. In other words, humans have shifted nascency to happen earlier while keeping brain development relatively constant.

Putting these results in context of phylogeny, the Platyrhines diverged from the Hominoids approximately 40 mya (Goodman et al., 1998). Thus, with orangutans and squirrel monkeys being separated by some 40 million years of evolution they appear to show parallel evolution in brain growth strategies. Being so distantly related to the other

ape species, orangutans have approached the problem of giving birth to large brained offspring in a unique manner relative to other ape species that have been studied. One conclusion that can be drawn from these results is that heterochrony is not sufficient to explain brain growth across the ape clade. Additionally, heterochrony does not appear to be a common occurrence with regards to brain growth across disparate primate taxa. This is intriguing because a shift in timing or rate of a developmental process (heterochrony) would seem to be a simpler solution to the problem of getting a big brain out of a relatively small body, rather than changing the underlying mechanics of the growth process itself. A study of brain growth across many taxa of primates is thus warranted to uncover the array of approaches to this ontogenetic problem.

Chapter VI

Conclusion

Based on previous studies of ontogenetic events in the hominoid taxa, it has been revealed that the chimpanzee and human common ancestor showed a novel brain growth phase that is not exhibited in monkeys (Rice, 2002). In an attempt to further our understanding of the evolutionary history of these ontogenetic events, a study of more distant genetic relatives has been undertaken. Orangutans are the representative taxon for this study. The position of the orangutan in the hominoid phylogeny allow for a potential refinement of our understanding of heterochrony's role in the evolution of ape brains. Through the measurements of dry crania from various museums the volume of the endocranial cavity can be determined. Taking this volume and converting it to mass using the known specific gravity of mammalian brain tissue we can derive the approximate brain weight of these individuals. Analyzing this data with other established growth trajectories of humans, chimpanzees, squirrel monkeys, and macaques we are able to detect the ontogenetic changes in the brains of orangutans relative to these other primates.

The results of this analysis are quite intriguing. Ape brains have undergone a significant amount of reorganizing at the cellular level with respect to the Prosimians, Old and New World monkeys. Predictably, the orangutan does not have a commensurate growth trajectory with the Old World monkey representative, the macaque. However, when compared with the chimpanzee, a much closer genetic and phylogenetic relative, the orangutan exhibits a divergent growth pattern. Indeed, this pattern is much more similar to the squirrel monkey, whose lineage branched from the line leading to the apes

and humans some 40 million years ago and is thus very distantly related to the orangutan. The primates as a clade have very large brains for their body size (there are individual exceptions however; see Tartarelli and Bisconti, 2006). A significant challenge for most primates is getting large brained offspring out of a relatively small body. This present study reveals that there are several ways of accomplishing this feat. Chimpanzees and humans overcome this challenge by shifting accouchement to occur earlier while keeping brain growth relatively constant until after birth. Comparatively, orangutans and squirrel monkeys halt growth until after birth, while keeping the gestational period longer. This finding that orangutans have, through parallel evolution, developed a different pattern of brain ontogeny from the chimpanzees and humans is a significant revelation in primate brain evolution. While heterochrony has played a role in the evolution of the human brain, respective of the chimpanzee/human ancestor, heterochrony alone does not appear to be a sufficient explanation for brain growth across the ape clade. Overcoming the challenge of giving birth to large brained offspring seems to be approached in various ways across the primate taxa.

Additional tests on gorillas and gibbons would also be useful in helping to delineate the entire sequence of brain ontogenetic evolution in the ape clade. The value of exploring gibbon brain ontogeny is that they are the most distant relative of humans in the ape clade. As such, they show some ape like qualities and some monkey like traits (small body size for example) as well. However, a key problem with studying gibbons is there is no established methodology for determining age from dental eruption sequence. This foundational work would need to be undertaken before any comparison can be made with other members of the primate family. Gorillas on the other hand, have a well-

established dental eruption sequence that can be used to age individuals with accuracy. Additionally, the position that gorillas occupy in ape phylogeny makes them a prime candidate for brain ontogenetic studies. Gorillas diverged between 6-8 million years ago from the lineage leading to chimpanzees and humans. This position, in between the orangutan and human/chimp divergences, makes them a valuable source for understanding the evolutionary history of brain growth in hominoids. Both of these primate groups would be interesting and useful subjects for further testing of heterochrony in apes.

In conclusion, the role of heterochrony in the evolution of orangutan brain ontogeny, at least with respect to the other primates investigated here, seems to be nil. No transformation along either the time or phenotype axes can reasonably produce trajectories of related species. This discovery indicates that few things are as they seem when it comes to primates. This clade of organisms continues to mystify the host of researchers that investigate their biology and behavior.

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