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Incisor Heteromorphy within Anthropoids and its significance to the *Sivapithecus* - *Pongo* Clade

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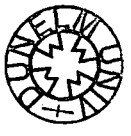

17 JAN 2001

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1999

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Jacob Hogarth, Department of Anthropology, University of Durham, M.Sc. Thesis

Abstract.

Incisor heteromorphy, the size of I^1 relative to I^2, has been considered a synapomorphy of the *Sivapithecus – Pongo* clade. Recent examinations of this condition within the fossil record, however, indicate the presence of this character within a number of fossil hominoid species. *Dryopithecus*, *Ankarapithecus* and *Ouranopithecus*, for example, appear to retain some form of this condition. No research, to date, has attempted to clarify the frequency of incisor heteromorphy within fossil hominoids and extant anthropoids. The purpose of this research is to examine incisor heteromorphy, in the wider context of anthropoids to shed light on the phylogenetic and functional importance of this characteristic.

In total, 383 individual sets of measurements, from 24 anthropoid genera were analyzed. To discern the phylogenetic usefulness of incisor heteromorphy it was coded and then optimized through existing cladograms. To examine the functional aspects of incisor heteromorphy this character was correlated with dietary consumption percentages using standard regression techniques and independent contrasts.

The analysis of incisor heteromorphy indicates widespread presence of this characteristic within extant anthropoids. Other than moderate / high incisor heteromorphy appearing to be the primitive condition for anthropoids, this characteristic is of little phylogenetic use. The phylogenetic analysis indicates a large number of anthropoid genera independently acquired this condition after the last common ancestor. Widespread homoplasy indicates the susceptibility of this characteristic to the immediate environment. The analysis of diet supports this fact. It appears that frugivory is the main force behind the adaptation of incisor heteromorphy. Frugivores, in general, have a higher degree of heteromorphy than folivores. Within frugivores the broader and more abrasive the diet, the more incisal preparation hence the higher the degree of incisor heteromorphy. These results indicate that hyper-incisor heteromorphy within anthropoids and, in particular, in *Sivapithecus* and *Pongo*, is due to frugivory rather than shared ancestry.

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Introduction

The importance of dentition in the field of palaeoprimatology cannot be stressed enough. It is the dentition that most commonly survives the decomposition and fossilisation processes (Fleagle 1988; Aiello and Dean 1990). Although other skeletal features do survive, it is the dentition that survives *en mass.* An exceptional example of this is the continuing discoveries of primate dental material alongside numerous fossil species of rodents, creodonts and hyracoids in the Fayum, Egypt (Groves, 1989; Gagnon, 1997). It is the particular composite nature of teeth, that enables the teeth to survive better than many bones. The composition is a mixture of mineral and organic material, as in most skeletal material. The teeth, however, have a higher mineral content (nearly 97%); this is the main contributor to their better preservation and survival (Aiello and Dean, 1990). The high survival rate and structure has allowed for phyletic comparisons (Pilgrim, 1915; Brown *et al.*, 1924; Simons and Pilbeam 1965; Kay, 1982; Kelley, 1988; Bonis and Koufos, 1993; Alpagut *et al.,* 1996) of fossil primates. Later techniques, such as cladistic analysis, have also used teeth (Andrews and Cronin, 1982; Strasser and Delson, 1987; Begun, 1992; Begun and Kordos, 1997; Cameron, 1997; Ross *et al.*, 1998) to discern common ancestry. Dental remains can also be used to reconstruct extinct primate diets and niches (Leakey, 1982; Andrews, 1983; Ungar, 1998), based on the studies of modern primates and the role of diet in forming dental adaptations (Hylander, 1975; Kay, 1981; Kinzey 1990; Ungar, 1994; Anapol and Lee, 1990; Dumont, 1995; Strait, 1997).

In any examination that involves fossil material, especially tooth morphology, it is possible to incorporate two important aspects of palaeontology and evolutionary biology, phylogeny and function, into any observations. The former is concerned with the relationship of species, whilst the latter is concerned with the action / performance that a trait performs. Although it is possible for phyletic and functional interpretations to be based on the same characteristics, each examines the same characteristics in a different light and it is here that

deductions concerning fossil material become problematic. It is from these seemingly incompatible points of examination that many important arguments, deductions and advances concerned with fossil species have been made.

In the strictest terms, a phylogeny is "a genealogical history of a group, hypothesising ancestor – descendant relationships" (Harvey and Pagel, 1998: 50) that is based on morphological and, more recently, genetic similarities (Fleagle, 1988). A phylogeny shows which pairs of species are more closely related to each other through common ancestry, be it a common ancestor or ancestor – descendent relationship, to the exclusion of other species. There are a number of methods that can be used to deduce phylogeny, of which the most important and most commonly used are the cladistic, phenetic and evolutionary taxonomic approaches.

Since the discovery of the first fossil hominoids in St. Gaudens over 140 years ago (Simons and Pilbeam, 1965), similarities in dentition have been used to infer the phyletic position of both extant and extinct anthropoids to one another. The material assigned to *Sivapithecus* is a good example when considering the use of dentition for phyletic inferences. Since the first placement of fossil material into the genus *Sivapithecus* (Pilgrim, 1910, 1915) this taxon and its junior synonyms (Table 1) have been seen as "ancestral stock" to Hominidae (Pilgrim, 1910, 1915; Lewis, 1934; Simons, 1961; Prasad, 1962; Simons and Pilbeam, 1965), and to *Pongo* (Lipson and Pilbeam, 1982; Andrews and Cronin, 1982; Ward and Kimbel, 1983; Ward and Brown, 1986; Begun and Kordos, 1997; Begun *et al.*, 1997). The former theory, that of an ancestor - descendant relationship between *Sivapithecus* and hominids, was first put forward by Pilgrim (1910, 1915). Pilgrim assigned material to *Sivapithecus* and placed this genus firmly into Hominidae on the basis of the dental and mandibular / maxillary evidence. Specimens assigned to *Sivapithecus* also appeared to share a number of traits with the gibbon, which Pilgrim (1915: 50) used infer that *Sivapithecus* was "near to the Gibbon than any other of the living apes. The chief of those (similar characteristics) are... the hinder cusp of the lower canine, the bicuspid character

Year Proposed	Original Designation	Reference	Year Revised	Revised Assignment	References
1879	*Paleopithecus sivalensis*	Lydekker, 1879	1937	*Sivapithecus indicus*	Lewis, 1937
1915	*Sivapithecus indicus*	Pilgrim, 1915	1983	*Sivapithecus indicus*	Andrews, 1983
				Sivapithecus sivalensis	Andrews, 1983
	Drypoithecus punjabicus		1937	*Bramapithecus*	Lewis, 1937
			1964	*Ramapithecus punjabicus*	Simons, 1964
			1979	*Sivapithecus sivalensis*	Greenfield, 1979
	Drypoithecus chinjiensis		1937	*Sivapithecus sivalensis*	Lewis, 1937
	Paleosimia rugosidens		1937	*Sivapithecus sivalensis*	Lewis, 1937
	Dryopithecus giganteus		1949	*Indopithecus*	Simons and Pilbeam, 1965
			1951	*Sivapithecus indicus*	Simons and Pilbeam, 1965
1924	*Dryopithecus pilgrimi*	Brown *et al.*, 1924	1934	*Sivapithecus sivalensis*	Lewis, 1934
	Dryopithecus cautleyi		1934	*Sivapithecus sivalensis*	
	Dryopithecus frickae		1934	*Sivapithecus indicus*	
1927	*Sivapithecus himalayensis*	Pilgrim, 1927	1937	*Sivapithecus indicus*	Lewis, 1937
	Sivapithecus orientalis		1937	*Sivapithecus indicus*	
	Sivapithecus middlemissi		1937	*Sivapithecus indicus*	
	Paleopithecus syvaticus		1937	*Sivapithecus sivalensis*	
1938	*Ramapithecus brevirostris*	Gregory *et al.*, 1938			
1961	*Ramapithecus hariensis*	Simons, 1961	1965	*D. (S.) sivalensis*	Simons and Pilbeam , 1965
1962	*Sivapithecus aiyengari*	Prasad, 1962	1983	*Sivapithecus sivalensis*	Martin, 1983
1980	*Sivapithecus meteai*	Andrews and Tekkaya, 1980	1996	*Ankarapithecus meteai*	Alpagut et. al., 1996
1988	*Sivapithecus parvada*	Kelley, 1988			

Table 1: Synonyms and assignments of *Sivapithecus*

of the Pm_3, the inward position of the mesoconid in the molars." These similarities led to the placement of a gibbon- like ape as the "ancestral stock" to *Sivapithecus* and *Dryopithecus.*

Later studies (Lewis, 1934; Simons, 1961, 1964) withdrew *Sivapithecus* from any major evolutionary relationship with hominids on the grounds that the dental traits observed were too primitive. Instead, another fossil species, 'Ramapithecus', was seen as ancestral to hominids because it alone shared a number of characteristics solely with hominids; these characteristics included small canines and incisors, 'progressive' upper premolars and crown pattern. 'Ramapithecus' was seen as the first hominid in anatomy and behaviour (Simons, 1967). Such inferences appeared conclusive and dominated phyletic inference for close to 20 years. When the material assigned to 'Ramapithecus' and *Sivapithecus* were eventually compared to each other, however, it became evident that 'Ramapithecus' exhibited "no more similarities to Plio-Pleistocene hominids than did the species of *Sivapithecus*" (Greenfield, 1979: 527). In fact 'Ramapithecus' and *Sivapithecus* shared a number of dental features, including angled incisors, similar canine / premolar complex and molar dimensions, that indicated a shared ancestry (Kay, 1982). In fact the only difference between 'Ramapithecus' and *Sivapithecus* was in overall size, comparable to the difference in size seen between the two species of *Pan* (Greenfield, 1979). This reasoning, and the subsequent discovery of G.S.P.15000 (Pilbeam, 1982; see below), eventually led to the sinking of 'Ramapithecus' into the genus *Sivapithecus.*

Better material and new approaches to analysis (such as cladistics) have led to better recognition, identification and evaluation of morphological traits. This has enabled researchers, when making inferences about phyletic relatedness, to take into consideration shared primitive characteristics (sympleismorphies), which are not significant for discerning relationships and shared derived characteristics (synapomorphies). It is the latter that is most important when constructing a phylogeny. In the case of *Sivapithecus*, due to the discovery of G.S.P. 15000 (a partial *S.indicus* cranium and facial skeleton) and the application of cladistic concepts, a shared

common ancestry has been indicated between *Pongo* and *Sivapithecus* to the exclusion of all other hominoids (Andrews and Cronin, 1982; Kelley et al., 1995; Cameron, 1995; Begun and Kordos, 1997). The majority of the synapomorphies in support of this phylogeny are craniofacial (Andrews and Tekkaya, 1980; Andrews and Cronin, 1982; Bonis and Koufos, 1993; Kelley *et al.*, 1995).

These methods, however, do have problems, in that there is a great deal of uncertainty in any reconstruction of a phylogeny, especially when several phylogenies appear to be equally likely (Harvey and Pagel, 1994). It is even more important that, regardless of the number of phylogenies that can be reconstructed, there always will be a number of parallel (homoplasy) characteristics present. This forces any deductions, based on a set of morphological characteristics, to consider the function of the characters concerned (Begun and Kordos, 1997). The function of a characteristic is determined by a species' adaptive response to selective pressures. Selective pressure from a specific environment can make it possible for two species to share similar adaptive responses; in other words, each species independently acquires a similar morphological trait. When this occurs, it is called parallel evolution. Both species have the same trait, which in turn has a similar function, but the trait has not been acquired through a common ancestor. An example of this is the tail loss in apes and a few monkeys, such *Macaca sylvanus* (the barbary macaque); the monkeys have lost their tails independently of the tail loss seen in the apes (Fleagle, 1988; Rowe, 1996). There are a number of variants on this adaptive response, which include different characteristics responding to similar forces, and different forces moulding the same characteristic. An example of this is the different forms of adaptation to nocturnal living, as evident in a number of different lemurs, the tarsier and *Aotus*, the owl monkey (Rowe, 1996). If this independent acquisition is not considered when constructing a phylogeny, then it is possible that a phylogeny could turn out to be problematic. By considering

the functional role of adaptations, it may be possible to resolve the 'independent acquisition' of characteristics.

Sivapithecus provides a good example of the use of structure-function relationships in explaining homplasy in phylogeny (Anapol and Lee, 1994; Begun and Kordos, 1997). The alledged homplasies are certain similarities in morphology between *Sivapithecus*, *Pongo*, *Dryopithecus* and 'hominines' (*Pan*, *Gorilla* and *Australopithecus*) (Begun and Kordos, 1997). The characteristics that appear to be in dispute include "very large upper central incisors, and still more elongated premaxilla with longer, reduced caliber incisive canals", and molar morphology (Begun and Kordos, 1997: 298). Two phylogenetic inferences are possible; the first is that the similarities between *Sivapithecus* / *Pongo* and the 'hominines' are synapomorphies, making the same characteristics seen in *Dryopithecus* homoplasy. The second is that the similarities between *Dryopithecus* and the 'hominines' are synapomorphies, which makes the same characteristics seen in *Sivapithecus* / *Pongo* homoplasy. It would appear that the *Sivapithecus* – *Pongo* clade contains the "largest number of homplasies in a single clade" (Begun and Kordos, 1997: 308).

By examining the functional anatomy of these characteristics, the problems evident from phylogenetic inferences could be resolved. As stated earlier, the structure and function of the jaws and teeth are closely related to each other and can allow "palaeofeeding behaviour to be interpreted by analogy" (Anapol and Lee, 1994: 240). For instance, similarities in molar, and incisor, morphology and microwear can be put down to dietary similarities (see Dental Function and Inferring Behaviour from Fossils below). The characteristics shared by *Sivapithecus*, *Pongo* and the 'hominines' show adaptations to a frugivorous diet, in contrast to the more folivorous adaptations seen in *Dryopithecus* and *Gorilla*. These frugivorous adaptations include enlarged incisors, molars with low, rounded cusps and relatively shallow basins. The increase in the size of the premaxilla is in turn related to the increase in the size of the incisors that are housed in the

alveloi of the premaxilla. The "parallel acquisition of enlarged incisors has led to the parallel increase in the premaxilla in response to higher levels of stress" (Begun and Kordos, 1997: 309). It is possible to base a phylogeny on certain dental characteristics as long as it is remembered that the teeth have an important functional role in the adaptation of a primate to a specific niche. This also is important when considering the phylogeny and adaptations of fossil primates.

Background

Dentition

Each dental row (teeth in the maxilla and mandible, respectively) can be divided into two identical halves, due to bilateral symmetry. Each of these quadrants (upper left and right, lower left and right), in turn, is comprised of four different distinct types of teeth: incisors, canines, premolars and molars (Fleagle, 1988; Bilsborough, 1992). Within primates, the incisors are generally flat and blade-like (Bilsborough, 1992), with conical tapering roots in the upper incisors and more flattened roots in the lower incisors. The maxillary incisors tend to be larger than the mandibular incisors and in apes, especially *Pan* and *Pongo*, the incisors are larger relative to the cheek teeth (Aiello and Dean, 1990). In the incisors, the cingula and marginal ridges of the lower incisors tend to be less developed than in the upper incisors (Aiello and Dean, 1990) and the upper central incisor (I^1) tends to be larger than the upper lateral incisor, I^2.

The canine, of all the types of dentition, is that is most closely associated with sexual dimorphism in primates (Fleagle, 1988; Aeillo and Dean, 1990; Bilsborough, 1992). In most primates, the canine is long, sharp and conical. In anthropoids, with the exception of *Homo sapiens*, both the upper and lower canines project beyond the occlusal plane and interlock. A by-product of this type of morphology is a gap (diastema) in the upper jaw between the lateral incisor and canine, and in the mandible between the lower canine and the first premolar (Aiello and Dean, 1990, Bilsborough 1992). The occlusion of the upper canine and the P_3 creates honing facets. The premolars, be they 2, 3 or 4 in number, are similar to the molars in morphology (albeit smaller). The exception to this is the morphology of the anterior lower premolar (either P_2 in strepsirrhines, tarsiers or New World monkeys or P_3 in catarrhines). Primates with large canines tend to have a canine-like first lower premolar that tends to have one cusp (the protoconid) that is very large with a curved anterior face which, in turn, shears against the back

of the upper canine (Aiello and Dean, 1990; Bilsborough, 1992). The molars, in general, are large multicusped teeth. Their topography is such that the upper molar cusps will fit into the hollows of the lower molar surface (Bilsborough, 1992). Upon closer examination, it is the molars, and to a lesser extent the premolars, that seem to vary most in morphology depending on the diet of the primate.

In catarrhines (apes and Old World monkeys), the dental formula (the number of each type of tooth) is 2.1.2.3, which represents a more derived condition than the 2.1.3.3, found in platyrrhines (New World monkeys), tarsiers (1.1.3.3 in the mandible) and the majority of strepsirhines.

Dental Function

The primary role of the dentition is in "the acquisition and initial preparation of food" (Fleagle, 1988: 15). To this end, the dental arch can be divided into 2 different areas, the anterior and cheek dentitions, which are distinguished by their functional roles in food processing. The anterior dentition, and the incisors in particular, is used primarily to slice and chop the food into smaller parts; in a very few primates, the canines also function to pierce food items enclosed within a tough core (i.e., insects, nuts and hard fruit). The cheek teeth (molars and premolars) tend to be used when further preparation of the food is needed. This process of ingestion makes swallowing easier by breaking larger food items into smaller, more manageable pieces (Fleagle 1988; Bilsborough, 1992). The type of food preparation can vary from puncture crushing, to shearing, and to crush grinding, depending on the food type (Fleagle, 1988). No matter the type of preparation, the action itself serves to increase the surface area of the food exposed to the enzymes within the digestive tract (Bilsborough, 1992). The dentition is the first stage in the digestion of the food; once processed, the food is then absorbed by the gastrointestinal tract. Both

these stages, the dentition and the gastrointestinal tract, are often adapted to the specific diet of a primate (Richard, 1985).

It is also "possible to relate various characteristics of both the anterior teeth and cheek teeth to diets of different consistencies" (Fleagle, 1988: 17-18); in other words, the anatomical characteristics of the teeth (size and shape) are related to the physical properties of the food items consumed. Such adaptations can, and often do, lead to specialisations in dental anatomy and behaviour, so as to exploit one type of food source, frequently to the exclusion of other types (Anapol and Lee, 1994; Strait, 1997). Many studies have succeeded in correlating certain dental patterns with specific diets and dietary consistencies. It has been shown that there is a strong correlation of incisor size to diet, particularly by Hylander (1975), who examined and compared the relative incisor size of 57 species of anthropoids with their diet. Frugivorous primates, such as the cercopithecines, tend to have larger incisors than those with a more folivorous diet, such as the colobines (Fleagle, 1988; Richards, 1985; Hylander, 1975). Even when the body weight of a primate is taken into consideration, folivores tend to have significantly smaller incisor widths than frugivores (Goldstein *et al.*, 1978; Shellis and Hiiemae, 1986).

Although this is sweeping generalisation, more recent research (Ungar 1993; 1996) has suggested a more specific adaptive explanation for an increase in the size of the incisors. An adaptive increase is perhaps due to difference in one aspect of ingestive behaviour, incisal preparation. It appears that incisor size not only relates to food preferences, but also to ingestive behaviours of the primates. The more foliage or soft fruit consumed by a primate (for example, by *Presbytis thomasi* and *Hylobates lar*, respectively) the less incisal preparation is required, since much of the initial break-up of foliage and soft fruit is done by the cheek teeth (Ungar 1993; 1996). It is worth noting that these types of diet are quite specific. It is also apparent that primates with a mixed, non-specific diet of hard fruit, animal matter, nuts and bark, as seen with

Pongo pygmaeus and *Macaca fascicularis*, undertake an increased amount of incisal preparation (Ungar, 1994).

Enamel distribution on the lower incisors also appears to support differential tooth use (Shellis and Hiiemae, 1986). Primates with a folivorous diet tend to have a substantial layer of enamel on the lingual and labial aspects of the lower incisors, which results in the formation of blunt edges. Frugivores, however, have little or no enamel, which forms a sharp edge, on the lingual aspect of the incisors. Folivores tend to use their incisors to grip the food items and their hands to reduce the food ingested, whilst frugivores, such as *Cercopithecus*, use their incisors to reduce the food ingested. It has been suggested that, when using incisors for ingestion, it is better for a primate to have sharp edges. If the incisors are regularly used for holding, not ingestion, however, then a blunt edge is more efficient (Shellis and Hiiemae, 1986). The differences in the use of incisors for food preparation can be seen in platyrrhines. *Chiropotes*, for example, has enlarged incisors that are used to remove the hard pericarp of unripe fruit and gouge out the seeds inside (Anapol and Lee, 1994), whilst *Alouatta*, a folivorous primate, has smaller incisors, a condition that "de-emphasises the use of the anterior dentition" (Anapol and Lee, 1994: 253). The consistency of the fruit consumed and its initial processing are responsible for an increase in the amount of attrition and abrasion on the incisors. The enlargement of the incisors, therefore, is an adaptive response to sustain their usefulness in the initial stages of digestion.

It has been suggested that the morphology of the cheek teeth is not food-specific but specially adapted to particular structural properties of food (Goldstein *et al.*, 1978; Fleagle, 1988; Strait, 1997). The best documented morphological character of dietary adaptation visible in the cheek teeth is the presence or absence of shearing crests. To enhance the digestion of structured carbohydrates, it is necessary for the food particle size to be reduced. This process is more efficient when carried out by shearing crests on the molars and premolars. The shearing crests act as scissors to shred the food (Kay, 1981; Richards, 1985; Fleagle, 1988; Bilsborough, 1992;

Strait, 1997). Folivorous primates, such as *Colobus*, who have opted for a structured carbohydrate diet, tend to have thinner enamel and more shearing crests (along with smaller incisors) than fruit eating primates. The adaptive rationale for thinner enamel has been to associate it with the lack of crushing and grinding needed to process foliage (Kay, 1981). Folivorous primates slice and dice their food; this requires more scissor-like adaptations than crushing- grinding adaptations. Conversely, less structured carbohydrate foods, such as soft fruit, require less dicing and more crushing and grinding. Frugivorous primates, therefore, tend to have thicker enamel, lower crown relief, more rounded cusps and basin like crowns that occlude with the upper molar cusps (Bilsborough, 1992). Those primates who feed on hard fruit and nuts (such as *Pongo*, *Cercocebus* and *Cebus apella*) tend to have similar adaptations to soft fruit eaters but thicker enamel (Kay, 1981; Dumont, 1995). All these adaptations facilitate the crushing and grinding actions and aid in resisting attrition and prolonging the use of the cheek teeth.

Other dental characteristics, such as enamel microwear (Teaford and Walker, 1984; Grine, 1986; Ungar, 1996), have also been used to infer the diet of both extant and extinct primates. It appears that the enamel microwear of a folivore tends to have a high percentage of striations, whilst the microwear of a frugivore comprises of a high percentage of pits in the enamel. Overall, frugivorous primates tend to rely on both the anterior and cheek teeth for reducing and processing fruit, whilst folivores and insectivores rely solely on their cheek teeth to preform the necessary first stages of ingestion.

Inferring Behaviour in Fossils

The studies outlined above have not only shed light on the dental adaptations and ingestion behaviour of extant primates, but have also enabled inferences concerning the diet and ingestion behaviours of extinct primate to be made. These inferences are impossible to make without comparisons to extant material. This is because direct observations of extinct diets and

behaviours is not possible. All that is available are skeletal and dental remains. It then becomes necessary for deductions to be based "on comparitive studies of modern species" (Teaford and Walker, 1984: 191). By comparing adaptations of modern primates with those of fossil primates, there is a greater chance that similarities in morphology will indicate a similar diet and ingestive behaviours, although this can be plagued with problems when relatedness is not taken into consideration. It should be remembered, however, that when undertaking such comparative studies, it is best to treat similar characteristics as broad indicators of dietary habitats, instead of using them as specific definer (Dumont, 1995). This is mainly due to the fact that extinct primates are not identical to modern primates.

According to Ungar (1996: 335), "one key to understanding the ecology and evolution of primates is the inference of their feeding behaviour." The comparison of ingestive behaviours associated with dental adaptations in modern primates with those in European Miocene catarrhines (*Ouranopithecus macedoniensis*, *Dryopithecus*, *Pliopithecus* and *Oreopithecus bambolii*) demonstrated that there was a diversity of dietary specialisation that is not seen in extant hominoids. For example, the incisor microwear of *O.macedoniensis* indicated a variety of ingestive behaviours that included stripping foods laterally across the incisors. In fact, it would appear that most of these fossil primates used their incisors more regularly in ingestive behaviours than the extant folivore, *Alouatta seniculus* or the soft fruit eater, *Hylobates lar*. Molar microwear analysis indicates that *Ouranopithecus* was a hard object feeder to the same magnitude as *Cercocebus albigena* and *Cebus apella* (Ungar, 1996; 1998). Similar comparative studies show that the dentition of *Sivapithecus* is indicative of a fruit eating, hard object feeder with enamel thickness values similar to *Cebus apella* (Kay, 1981). Folivorous dental adaptations (shearing crests and striations) are also present within the fossil record. The dental morphology of *Oreopithecus* (Ungar, 1996; 1998) and *Rhinocolobus* (Leakey, 1982) indicate dietary tendencies similar to those of the extant primates *Alouatta* and *Colobus*, respectively. Finally,

dental adaptations to faunivory have been shown to be present within the fossil record. Faunivores have well developed shearing features on their molars similar to folivores, but with more pointed cusps for puncturing and processing the tough insect exoskeleton (Strait 1993; 1997). Nearly 30% of omomyid species, including *Washakius insignis* and *Omomys cantei*, show such adaptations. When the microwear was compared to the diet of extant faunivorous primates it became evident that the majority of these omomyids were generalised faunivores consuming a high percentage of hard insect matter, such as beetles (Strait, 1993; 1997).

Phyletic inference

With the application of the cladistic methodology, phyletic relationships concerning fossil and extant species are is becoming easier to discern. The importance of the cladistic approach has grown since the 1980s with many studies using dental characteristics to determine common ancestry (Strasser and Delson, 1987; Begun, 1992; Begun and Güleç, 1998; Ross *et.al.*, 1998). For example, out of 37 characteristics that Strasser and Delson, (1987) used to examine cercopithecid relationships, 10 were dental. Even more substantial was the cladistic analysis of anthropoids that used a total of 291 characteristics, of which 182 were dental (Ross *et al.*, 1998). In the case of *Sivapithecus* the discovery of G.S.P. 15000 (a partial *S.indicus* cranium and facial skeleton), coupled with the application of cladistic concepts, indicated a shared common ancestry between *Pongo* and *Sivapithecus* to the exclusion of all other hominoids (Andrews and Cronin, 1982; Kelley *et al.*, 1995; Cameron, 1997; Begun and Kordos, 1997). The majority of the synapomorphies are craniofacial, but there is one important dental characteristic, a great discrepancy between the size of I^1 and I^2. It has been put forward that this characteristic is apparently only evident within one extant species, *Pongo*, and the extinct hominoid species, *Sivapithecus* (Begun *et al.*, 1997; Aiello and Dean, 1990; Fleagle, 1988; Andrews and Cronin, 1982). This characteristic has been important in the diagnosing of a *Sivapithecus – Pongo* clade

but has recently been shown to be problematic (Andrews and Tekkaya, 1980; Andrews and Cronin, 1982; Bonis and Koufos, 1993; Kelley *et al.*, 1995).

Incisor Heteromorphy

Incisor proportionality is the size of I^1 relative to I^2. If the I^1 is more or less equal to the I^2 in size, then that condition is termed incisor homomorphy. Where the I^1 is greater than I^2 in size then that condition is termed incisor heteromorphy. There is no evidence for a reverse of this condition (I^2 greater than I^1) in anthropoids. It has been suggested that incisor heteromorphy is related to extensive incisal preparation prior to mastication and the type of diet (Hylander, 1975; Ungar, 1996, 1998); the tougher the fruits in a diet, the larger the I^1. This characteristic, to date, has been important in discerning the relationship of *Sivapithecus* to other hominoids, in particular *Pongo*. When G.S.P. 15000 was compared to other facial morphotypes it became evident that it was very similar in overall appearance to *Pongo*. Upon closer examination it became even more apparent that *Pongo* and *Sivapithecus* shared a number of synapomorphies. This points to them sharing a more recent common ancestor to the exclusion of all other hominoids. Incisor heteromorphy was one of the diagnostic clade characteristics (Andrews and Tekkaya, 1980; Andrews and Cronin, 1982; Preuss, 1982; Pilbeam, 1982). In *Sivapithecus*, the I^1 is near double the mesiodistal length of I^2, giving an index value of 205% (*S.inidcus*) and 212% (*S.parvada*). In African apes and *Dryopithecus* the condition was more homomorphic with index values between 120 - 150%. Only *Pongo* appears to come close to the *Sivapithecus* value with 200% (see Table 2). The African ape condition was considered primitive in Hominoidea (Andrews and Tekkaya, 1980; Andrews and Cronin, 1982; Kelley *et al*, 1995). The reasoning for this was that incisor homomorphy appeared to be widespread, being found in hominids, *Pan*, *Gorilla* and *Hylobates*. The derived condition was considered to be incisor size heteromorphy, which was found only in the *Sivapithecus-Pongo* clade.

It should be noted that, although the view that incisor heteromorphy is a synapomorphy of the *Sivapithecus-Pongo* clade was predominant in 1980s research, there was some criticism and over-looked research. For example, it was shown (Andrews, 1978) that incisor heteromorphy, to some degree, was found in *Proconsul africanus*, *Limnopithecus* and *Dendropithecus* (see Table 2). This was subsequently overlooked when incisor proportionality was examined in *Sivapithecus* and *Pongo*. Groves (1986), in his parsimony analysis of hominoid relationships, hypothesised that *Pan* and *Gorilla* shared incisor homomorphy to the exclusion of other hominoids, and so this condition was derived and not primitive. In the 1990s, further examinations and more complete finds have challenged the extent of incisor heteromorphy in hominoids. Both *Ouranopithecus* (Bonis and Koufos, 1993) and *Ankarapithecus* (Alpagut *et al.*, 1996) have incisor heteromorphy (see Table 1), with similar values to *Sivapithecus* and *Pongo*. In fact, until 1996 *Ankarapithecus* was considered to be a junior synonym of *Sivapithecus* (Alpagut *et al.*, 1996).

At present, research seems to point to incisor heteromorphy being more widespread in hominoids (see Table 2). Incisor proportionality based on incisor area (Cameron, 1997) also appears to be as varied. Variation in incisor proportionality occurs in varying degrees throughout the extant and extinct hominoid record. It has been *suggested* that very small (e.g., *Homo sapiens*) and large indices (e.g., *Pongo*) are derived and that the moderate indices are indicative of the primitive condition (Bonis and Koufos, 1993; Begun and Güleç, 1998). Another view is that the condition seen in *Pongo* is primitive and that the decreases and increases in size proportionality, seen elsewhere, are derived occurring at different times (Bonis and Koufos, 1993). If, however, the condition in *Pongo* is derived, there may be a considerable amount of homplasy in the hominoid record. There may even be so much incisor variation in hominoids that it would be difficult to establish polarities and distinguish homology from homoplasy (Bonis and Koufos, 1993; Kelley *et al.*, 1995). Owing to this, incisor proportionality may have little use in

phylogenetic analysis (Bonis and Koufos, 1993; Kelley *et. al.*, 1995; Begun and Güleç, 1998). It should also be noted that incisor heteromorphy does not appear to have been examined in anthropoids other than hominoids.

The purpose of the present work is to examine the extent of incisor proportionality within the extant and extinct anthropoid record. Analysis of this feature, in the wider context of anthropoids, will shed light on the phylogenetic and/or functional importance of incisor heteromorphy and clarify the uncertainty surrounding this interesting characteristic.

Hypotheses

1. Are varying degrees of incisor heteromorphy visible within anthropoid genera?
2. Is incisor heteromorphy homologous or homoplastic within anthropoids?
   -What is the primitive condition?
3. What functional and adaptive reasons are there for incisor heteromorphy?
4. What does this mean for inference concerning fossil anthropoids and the *Sivapithecus-Pongo* clade?

Table 2 : Previously published incisor heteromorphy values for hominoids

Species	I^1	I^2	Index Value	Proportionality	Reference
			I^1 x100/ I^2	I^1/I^2	
Ankarapithecus	10.1 / 10.5	6.3 / 6.4	179	*1.79*	Alpagut *et al.*, 1996
Ouranopithecus	10	6.4	156	*1.56*	Bonis and Koufos, 1993
	10.8	6.5	166	*1.66*	
Sivapithecus parvada	15.5	7.3	*212*	2.12	Kelley *et al.*, 1995
Sivapithecus indicus	12.3	6	*205*	*2.05*	Pilbeam, 1982
Dendropithecus	5.1	3.6	141	1.41	Andrews, 1978
Rangwapithecus gordoni	7.4	5.8	122	*1.22*	Andrews, 1978
Proconsul africanus	7.4	4.9	151	*1.51*	Andrews, 1978
Proconsul nynanze	9.3	4.9	151	*1.47*	Andrews, 1978
Proconsul major	10.9	8	136	*1.36*	Andrews, 1978
Pongo p. pygmaeus	13.7*	8.8*	*155*	1.55	Kelley *et al.*, 1995
Pongo p. abelii	13.9*	12.4*	*178*	1.78	Kelley *et al.*, 1995
Gorilla	12.5*	9.1*	*138*	1.38	Kelley *et al.*, 1995
Pan	11.5*	9*	*129*	1.29	Kelley *et al.*, 1995
Hylobates spp.	–	–	138	*1.38*	Andrews, 1978

Values in *italics* are calculated from published data using the formulae given above. All others are as reported.
* indicates mean values
– values not reported

Materials and Methods

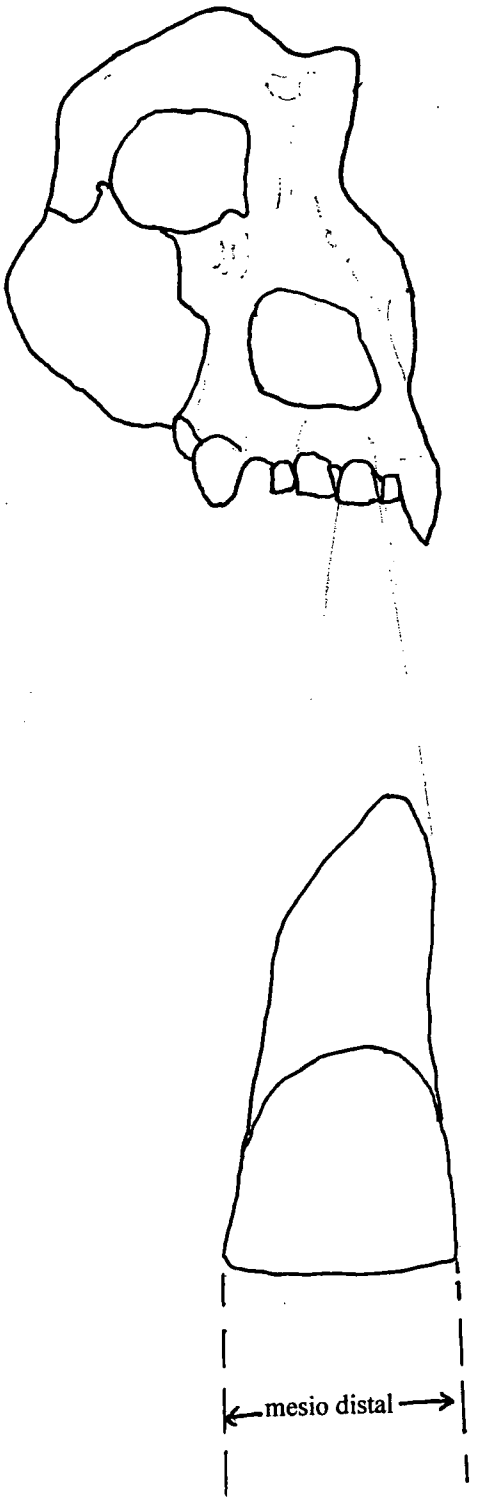
Materials

To test the hypotheses listed in Chapter One, incisor heteromorphy data were collected from adult dry crania of a number of anthropoid species. Incisor proportionality is a condition found in the upper incisors, and so for each specimen four measurements were obtained, one for each upper incisor, using medial-distal length (see Figure 1). Measurements to the nearest 0.1mm were taken using Mitutoyo Digimatic digital callipers.

As can be seen from Table 3, the number of specimens of the genera sampled tends to vary considerably. This is mainly due to a disproportionate number of specimens that were available for study and the availability of specimens that contained the associated incisors . Many specimens were not included within this sample because they lacked associated incisors or had extensive wear. For each specimen that was included, the sets of measurements were arranged into pairs, representative of the central and lateral incisors. The sample (Table 3) consisted of 24 different anthropoid genera, representing nearly 44 different species (Table 4). These crania were examined at the Natural History Museum, London. A total of 383 sets of measurements were obtained (Appendix 1). All the measurements are primarily of associated incisors from the left and right sides. In the 89 cases where one or two incisors were missing , or where a measurement from one side could not be obtained, an antimere (the tooth on the opposite side) measurement was used (see highlighted specimens in Appendix 1).

Strepsirhines were excluded from the analysis due to their dental specialisation, the dental tooth comb, in the lower jaw and the impact it has had on the upper incisors (Eaglen, 1986). The tooth comb has caused the upper incisors to become much reduced and separated by a large cleft. The type of incisor proportionality in the upper incisors of strepsirhines is not strictly comparable to the type seen in anthropoids. This study, therefore, will centre on the incisor proportionality within Anthropoidea. The genera represented below includes the majority

Figure 1: Mesio-distal measurements



Facial skeleton of XIR 1, *Ouranopithecus macedoniensis* (after Bonis and Koufos, 1993; Cameron, 1997)

of platyrrhines, with the exception of the five genera in the Family Callitrichidae (*Callithrix*, *Cebuella*, *Saguinus*, *Leontopithecus* and *Callimico*). The exclusion of Callitrichidae is mainly due to the overall size of their incisors, which are very small and therefore difficult to measure. Specimens from Cercopithecinae (*Cercopithecus*, *Macaca*, *Cercocebus*, *Papio*, *Mandrillus* and *Theropithecus*), Colobinae (*Colobus*, *Presbytis*, *Nasalis* and *Pygathrix*) and Hominoidea (*Hylobates*, *Pongo*, *Gorilla* and *Pan*) were all examined and measured.

Table 3: Sample size

Genus	No.	Male	Female
Gorilla	60	40	20
Pan	42	20	22
Pongo	48	33	15
Hylobates	58	31	27
Colobus	23	12	11
Presbytis	9	4	5
Nasalis	6	3	3
Macaca	12	6	6
Mandrillus	10	5	5
Theropithecus	7	6	1
Papio	12	9	3
Cercopithecus	22	11	11
Cercocebus	12	7	5
Aotus	6	3	3
Alouatta	6	3	3
Cebus	6	3	3
Saimiri	6	3	3
Ateles	6	3	3
Brachyteles	4	3	1
Lagothrix	6	3	3
Callicebus[1]	6	3	3
Cacajao	6	3	3
Chiropotes	6	3	3
Pithecia	4	2	2
Total	383	219	164

Table 4: Species present within sample

Common Groupings	Genus	Species
Apes	*Gorilla*	*gorilla*
	Pan	*troglodytes*
	Pongo	*pygmaeus*
	Hylobates	*hoolock*
		lar
		pileatus
		agilis
		moloch
		concolor
		syndactylus
Old World Monkeys		
Colobines	*Colobus*	*angolensis*
		polykomos
		cottoni
		palliatus
	Presbytis	*rubicundus*
		palliatus
	Nasalis	*larvatus*
Cercopithecines	*Macaca*	*fuscata*
		nigra
	Mandrillus	*sphinx*
	Theropithecus	*gelada*
	Papio	*hamadryas*
		urinus
	Cercopithecus	*diana*
		campbelli
		mitis
		cephus
	Cercocebus	*torquatas*
	Lophocebus	*abigena*
New World Monkeys		
	Aotus	*trivirgatus*
	Alouatta	*palliata*
		seniculus
	Cebus	*apella*
		capucinus
	Saimiri	*sciureus*
	Ateles	*paniscus*
	Brachyteles	*arachnoides*
	Lagothrix	*lagothricha*
	Callicebus	*torquatas*
	Cacajao	*calvus*
		rubicundus
	Chiropotes	*satanas*
	Pithecia	*pithecia*

Methods

Proportionality

To evaluate and determine the extent of incisor proportionality within anthropoids, two formulae were used (I^1 / I^2 and $I^1 x\ 100/ I^2$). Both formulae have been used successfully to ascertain incisor proportionality of fossil hominoids (Kelley *et al.*, 1995; Bonis and Koufos, 1993; Andrews, 1978). By using these formulae on extant genera, comparisons with incisor heteromorphy values obtained from fossil material will be easier to make. These values enable further analysis into the phylogenetic and functional value of incisor heteromorphy.

Phylogenetic Analysis

Coding characteristics for phylogenetic analysis proceeds by ascertaining if the sampled taxa are 'the same' or 'different' (Rae, 1998). Although there are a number of possible methods that could be applied, such as segment and gap coding (Rae, 1998), one particular method, the homogeneous subset coding (HSC) method is used here. The main reason for this selection is that the HSC method fulfil the theoretical requirements of repeatability and lack of arbitrary criteria for grouping and separating taxa. Analyses byHSC use " a posteriori multiple comparisons test" (Simon, 1983: 380). In cases where the sample variance is homogeneous, HSC coding is based on GT2 test (MCPAIR) contained within the BIOM computer analysis package (Rohlf, 1982). Where samples contains heterogeneous variances the Games and Howells method (MCHETV) is applicable. To ascertain if the sample variances were homogeneous, the program HOMOV was applied (Rohlf, 1982).

The resulting means of each taxon were then grouped into homogeneous subsets using the significant value (see Results). Each taxon that belongs to the same subsets is given the same code. The use of the HSC method is outlined in more depth by Simon (1983) .

With the data coded, it then becomes possible to evaluate the extent of homoplasy in incisor proportionality by reconstructing the evolution of this character. The character coding was applied to existing cladograms which were optimised by MacClade ver. 3.01 (Maddison and Maddison, 1992). By using previously determined cladograms, a characteristic can be compared to the probable pattern of evolution determined by other characteristics in a single most parsimonious phylogeny. In this case, Ford (1986), Strasser and Delson (1987) and Fleagle (1988) provide the cladograms for platyrrhines, cercopithecoids (cercopithecines and colobines) and hominoids, respectively (see Figure 2).

Function

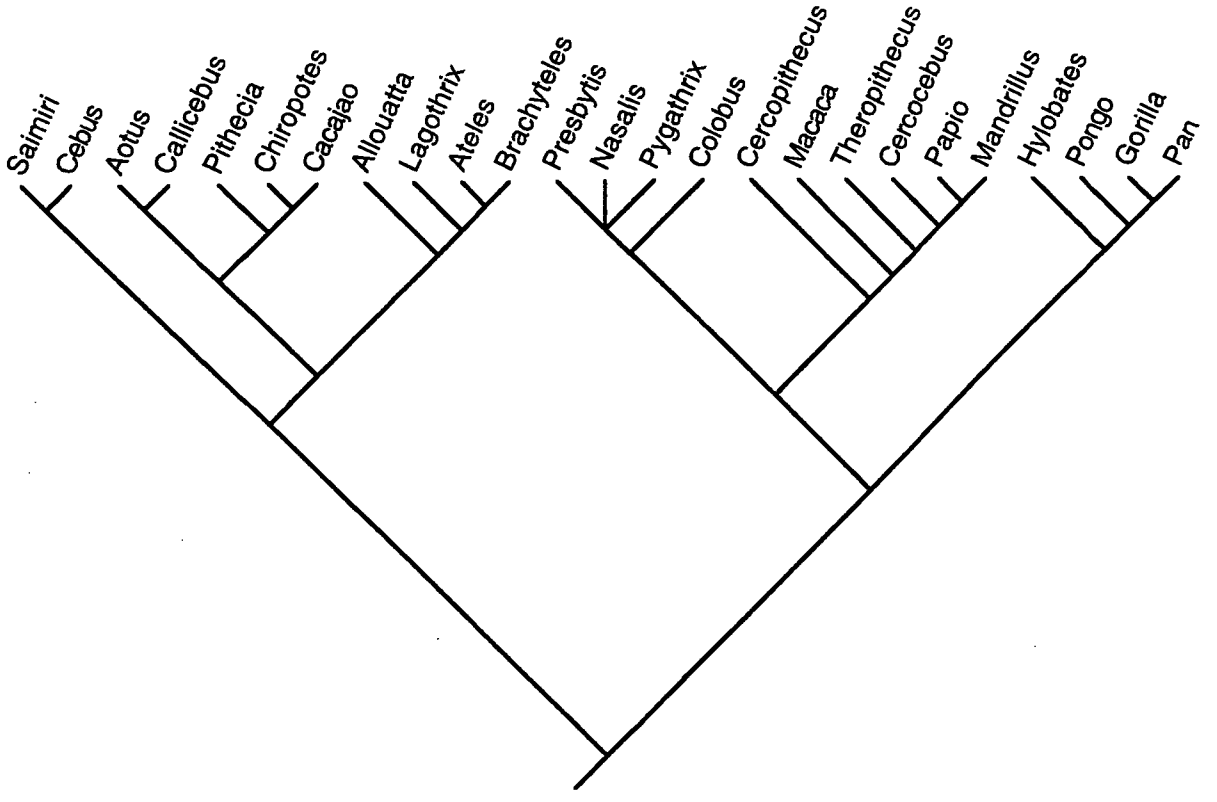
The function of a characteristic depends strongly on external factors such as diet and environment. To ascertain and evaluate the relationship between a structure and another factor regression analysis was undertaken. The application of this method allows for comparisons, for example, between incisor heteromorphy and the percentage of fruit consumed.

Standard regression techniques, however, do not take into consideration the effects of phylogeny (Harvey and Pagel, 1998), and in particular the scope of independent acquisition of a certain characteristic. This important because any regression analysis that includes a number of members from the same clade can create an artificial "significant" correlation between two variables. Rather than treating all characters individually, and so assuming that the characteristic is independently acquired, the CAIC (Comparative Analysis by Independent Contrasts) computer program makes contrasts that consider these sorts of changes only once (Purvis and Rambaut, 1995). CAIC computes the contrasts from continuous variables, such as dietary consumption and incisor heteromorphy, by using 'Crunch' algorithms.

In order to achieve standardised linear contrasts CAIC will calculate the linear contrasts at bifurcating nodes (i.e. within a group of two taxa). In its simplest form, a linear contrast is the difference between two taxa. The difference, or variance, of a two-taxon contrast appears to be

proportional to the sum of the branch lengths between two taxon and their common ancestor. Contrasts between "distant relatives will have a higher expected variance than contrasts between sister species" (Purvis and Rambaut, 1995: 24). The branch length, therefore, is accepted, by CAIC, as the expected variance; the difference between two taxa. The next step, if these contrasts are to be used in standard statistical techniques (e.g. regression), is to take the heterogeneity of variance out of the equation. CAIC does this by dividing each contrast by its expected standard deviation (i.e. the square root of the expected variance). The resulting output are standardised linear contrasts that can be used in regression analysis.

Figure 2: Composite phylogeny used for character optimisation analysis (MacClade)



Results

Incisor heteromorphy

The conversion of the raw data into ratios shows that incisor heteromorphy is a widespread phenomenon within anthropoids. Table 5 shows the incisor means and the incisor proportionality ratios. All the sampled genera have, to some varying degree or another, incisor proportionality. Those with a high degree of incisor heteromorphy include *Pongo*, *Cercopithecus* and *Mandrillus*, whilst those with a low degree of incisor heteromorphy include *Brachyteles*, *Alouatta* and *Lagothrix* (as indicated, respectively, by the bold and underlined data in Table 5). These anthropoids mentioned represent two ends of a spectrum with the values of the other 19 anthropoids examined falling in between.

Genera	I^1 Total	I^2 Total	I proportionality
Gorilla	25.11	17.88	1.40
Pan	22.27	16.86	1.32
Pongo	**26.58**	**16.07**	**1.65**
Gibbon	9.59	7.71	1.24
Colobus	9.3	7.84	1.19
Presbytes	8.43	7.13	1.18
Pygathrix	9.69	7.92	1.22
Nasalis	10.84	7.97	1.36
Macaca	12.95	9.36	1.38
Mandrillus	**17.44**	**10.76**	**1.62**
Theropithecus	12.23	10.2	1.20
Papio	18.51	12.98	1.43
Cercopithecus	10.63	6.07	1.75
Cercocebus	14.49	9.26	1.56
Aotus	6.86	4.31	1.59
Alouatta	7.57	6.9	1.10
Cebus	8.73	7.02	1.24
Saimiri	5.49	3.86	1.42
Ateles	10.41	7.28	1.43
Brachyteles	7.6	7.42	1.02
Lagothrix	8.74	7.6	1.15
Callicebus	6.08	4.42	1.38
Cacajao	8.4	6.14	1.37
Chiropotes	6.49	4.89	1.33
Pithecia	6.84	4.83	1.42

Table 5: Incisor totals and proportionality (heteromorphy)

When placed in rank order (Table 6) there would appear to be very little correlation between incisor proportionality and actual body size. For example, *Pan*, the third largest anthropoid, appears in the middle of the spectrum with a number of smaller anthropoids, *Saimiri* and *Aotus*, appearing higher in the spectrum. When the incisor proportionality was correlated with body weight (Fleagle,1988) a r value of 0.150 ($p = 0.474$, $p > 0.05$) was obtained. Any correlation, therefore, between these two characteristics is due to random chance.

Genera	Incisor proportionality	Body weight (kg)
Brachyteles	1.0325	12
Alouatta	1.1017	6.69
Lagothrix	1.1533	7.255
Presbytes	1.1844	6.187
Theropithecus	1.1971	14.85
Colobus	1.2113	8.85
Pygathrix	1.228	9.55
Cebus	1.2467	2.62
Hylobates	1.2467	10.75
Pan	1.3233	53.5
Chiropotes	1.3267	2.98
Nasalis	1.3617	15.015
Cacajao	1.3717	3.167
Callicebus	1.38	1.377
Macaca	1.3842	7.63
Pithecia	1.4175	1.8
Papio	1.4242	16.65
Gorilla	1.4256	120.5
Ateles	1.4317	9
Saimiri	1.4317	0.875
Cercocebus	1.5633	7.69
Aotus	1.61	1.22
Mandrillus	1.612	19.2
Pongo	1.67	59
Cercopithecus	1.7523	6.88

Table 6: Incisor proportionality and body weight.

Homogenetity of sample

A test for homogeneity of variance concluded that the incisor proportionality sample was heterogeneous. A X2 value of 42.3717 was obtained and using 24 degrees of freedom. The critical value of the Chi at $p<.05$ is 36.415 (Sokal and Rohlf, 1982: Table 14). Therefore the sample is significantly heterogeneous at $p< 0.05$. This resulted in the use of the non - parametric Games and Howells method, rather than the GT2 method, to obtain HSC.

Homogeneous subset coding (HSC)

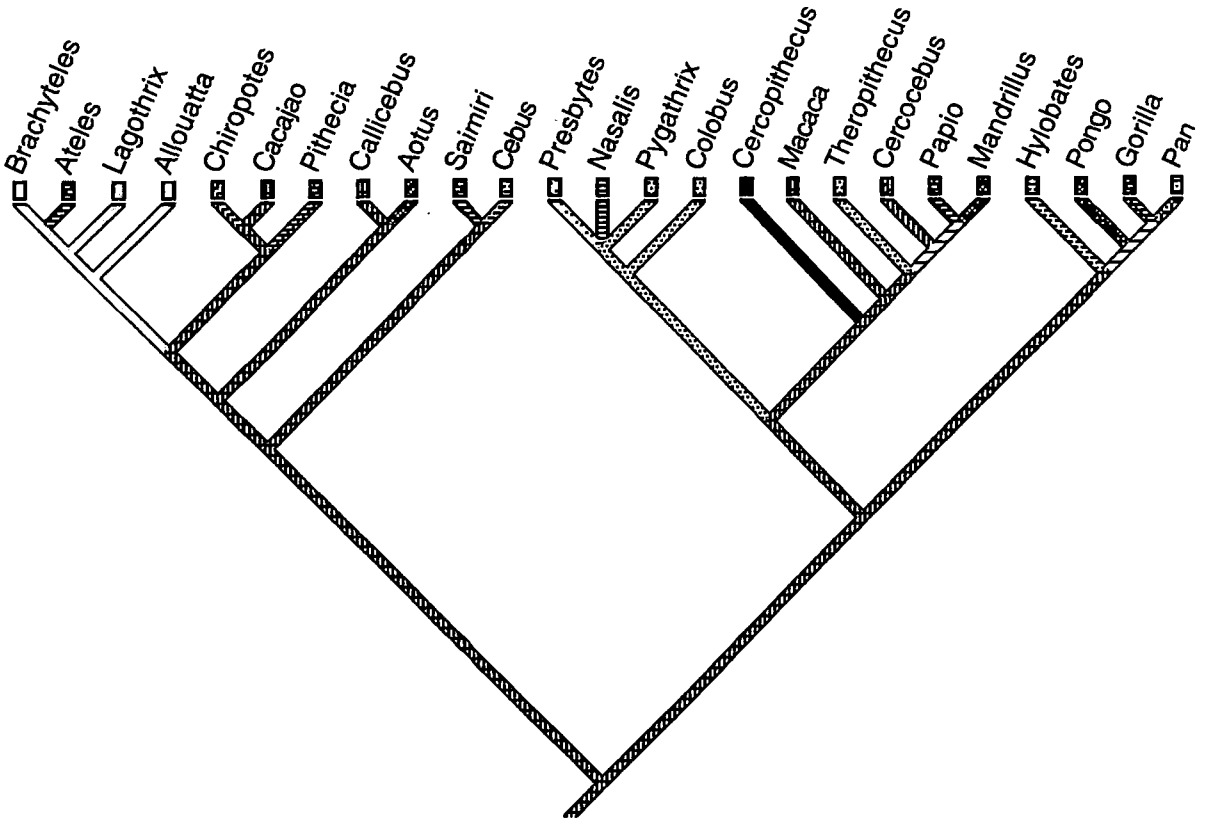
The application of the HSC method grouped the 25 anthropoid genera into 14 character states. For example, *Brachyteles* and *Alouatta* share character state 0. When compared with the other anthropoids, both species are significantly different from the same species. The application of the Games and Howell method (using MCHETV) and the HSC method resulted in a code that was used for subsequent phylogenetic analysis (Table 7).

Genera	HSC	Order of Means
Brachyteles	0	1.0325
Alouatta	0	1.1017
Lagothrix	1	1.1533
Presbytes	2	1.1844
Theropithecus	3	1.1971
Colobus	3	1.2113
Pygathrix	3	1.2280
Cebus	4	1.2467
Hylobates	4	1.2514
Pan	5	1.3233
Chiropotes	6	1.3267
Nasalis	7	1.3617
Cacajao	8	1.3717
Callicebus	8	1.3800
Macaca	8	1.3842
Pithecia	9	1.4175
Papio	9	1.4242
Gorilla	9	1.4256
Ateles	9	1.4317
Saimiri	9	1.4317
Cercocebus	A	1.5633
Aotus	B	1.6100
Mandrillus	B	1.6120
Pongo	C	1.6700
Cercopithecus	D	1.7523

Table 7: HSC coding and order of means

Phylogenetic analysis

The use of recognised cladograms and the coding, coupled with the McClade program, resulted in character state optimisations of the 14 states for incisor

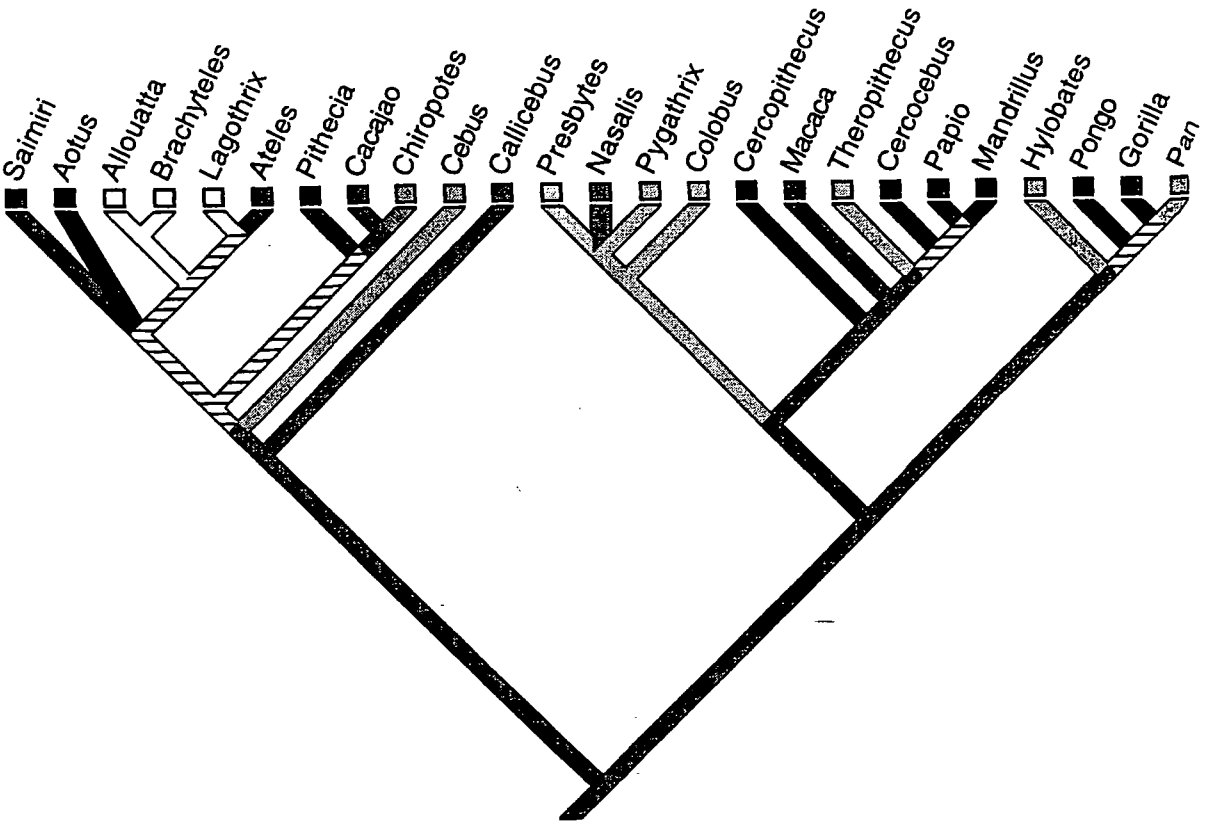


(Ford, 1986)

Character 1
64 steps
ordered

0
1
2
3
4
5
6
7
8
9
A
B
C
D
equivocal

Figure 3: Optimization of proportionality using Ford (1986).



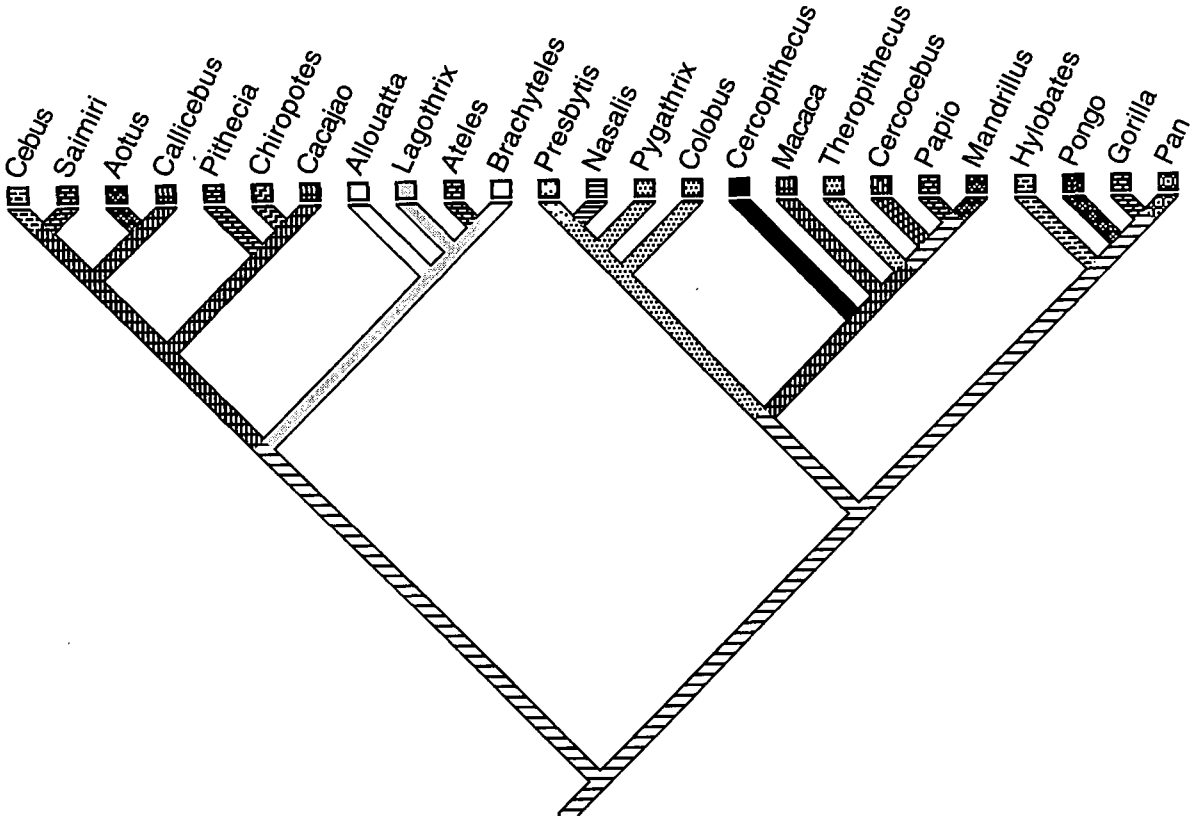
Kay, 1990

Character 1
63 steps
ordered

0
1
2
3
4
5
6
7
8
9
A
B
C
D
equivocal

Figure 4: Optimisation of incisor heteromorphy using Kay, 1990.

Figure 5: Optimisation of incisor proportionality using Rosenberger (1981)



(Rosenburger, 1981)

Character 1
64 steps
ordered

0
1
2
3
4
5
6
7
8
9
A
B
C
D
equivocal

heteromorphy (figures 3 - 5). The polarity of the cladograms depends strongly on which platyrrhine phylogeny was used. Although Figures 3 and 4 (Kay, 1990; Ford, 1986) differed in their placement of several platyrrhine genera, there was a great deal of similarity in polarity. The polarity of figure 5, however, differs substantially. The platyrrhine phylogeny of Rosenberger (1981) is based on similarities in molar morphology and genitalia, soft tissue rather than extensive dental, cranial and postcranial comparisons of Ford (1986) and Kay (1990). The lack of soft tissue preservation makes comparisons, and inferences of relatedness, with extinct fossils complicated, if not impossible, therefore, further analysis will be based on the skeletal phylogeny supplied by Ford (1986).

There are three trends that are immediately evident when examining this cladogram. First, and most important, there is a recognisable primitive condition. The incisor proportionality ratio of 1.37 to 1.38 (code 8) is the primitive condition in anthropoids. Three anthropoids, *Cacajao*, *Callicebus* and *Macaca*, appear to retain this condition. Of the remaining 13 character states, eight show a derived reduction whilst five show a derived increase.

A second result is that the majority of the different states appear to be recent events; in other words the derived conditions, in extant anthropoids, have evolved since their the last common ancestor, independent of one another. Only two clades out of seven have taxa that share derived conditions; atelines and colobines.

Finally, in support of the independent acquisition of this characteristic, there is widespread homoplasy within the incisor heteromorphy states. Figure 3 points towards code 4, as represented by *Cebus* and *Hylobates*, as being a homoplasy. The New World monkey *Cebus* shares the same coding and ratio as *Hylobates* but is not related by recent common ancestry. By far, the largest occurrence of homoplasy involves the

taxa with code 9. The genera possessing this state include three New World monkeys from different families, a cercopithecine and a hominoid. There is no way in which to relate these five genera with each other by means shared recent common ancestry. The final state, as represented by *Aotus* and *Mandrillus*, also appears to be homoplastic. The two anthropoids concerned are, in phyletic terms, poles apart on all three cladograms, yet share the code B. All other character states (1, 2, 5, 6, 8, A, C, and D), with the exception of the primitive condition state 8, are autapomorphic.

The widespread and autapomorphic nature of incisor heteromorphy within extant primates is of particular interest when examining the condition in fossil anthropoids. The independent acquisition of this character would seem to indicate a force other thanshared ancestry at work. Even though there is a great deal of homoplasy, incisor heteromorphy may still be of some phylogenetic use, in that this analysis has identified a moderate degree of heteromorphy as the primitive condition for anthropoids. The widespread homoplasy, however, indicates another force acting upon this character. According to Fleagle (1988: 241) "the best - documented morphological adaptations to diet are those found in primate teeth". In trying to deduce possible reasons for incisor heteromorphy, other than phylogeny, it would be worth while considering significance of diet to incisor proportionality.

Diet

To examine possible dietary adaptive forces behind incisor heteromorphy, the ratios were correlated with diet composition. The average values of incisor heteromorphy were regressed against percentage of leaf values taken from Rowe (1996). A r value of -0.467 ($p = 0.092$, $p > 0.05$) was obtained. This, in turn, indicates no significant correlation between the percentage of leaf matter consumed and the incisor ratios. This correlation is indicative of the lack of use of a folivores anterior dentition during initial mastication.

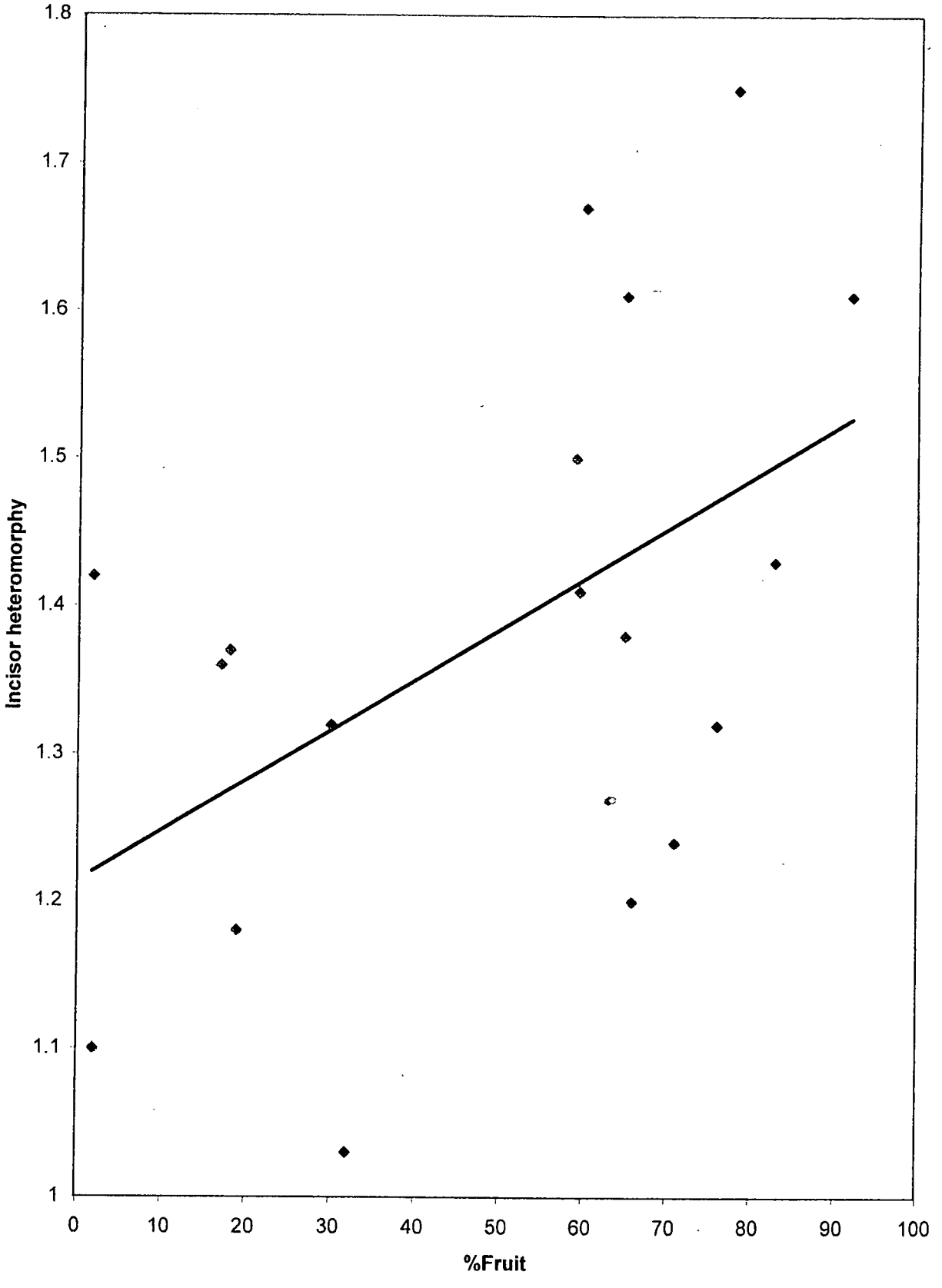
Although there is no significant correlation between leaf percentages and incisor ratios, the correlation between percentage of fruit consumed and the ratios is significant. Table 9 also shows the fruit percentages and the incisor ratios that were available for 18 of the 25 anthropoid genera examined.

Table 8: Incisor proportionality and dietary percentages (Percentages taken from Rowe 1996)

Genera	Incisor	Fruit %	Leaf %
Brachyteles	1.03	32	51
Alouatta	1.1	2	66
Presbytis	1.18	19	36
Theropithecus	1.19	N\A	2.2
Cebus	1.2	66	N\A
Hylobates	1.24	71	11
Pan	1.32	76	12
Chiropotes	1.32	30	N\A
Nasalis	1.36	17	44
Cacajao	1.37	18	N\A
Callicebus	1.38	65	15
Pithecia	1.41	59.5	N\A
Gorilla	1.42	1.7	85.8
Ateles	1.43	82.9	6
Cercocebus	1.56	59	5
Aotus	1.61	65	5
Mandrillus	1.61	92	2.2
Pongo	1.67	60	N\A
Cercopithecus	1.75	78	6.5

When a correlation analysis on these two characteristics was performed a r value of 0.504 was obtained ($p = 0.033, p < 0.05$) . This indicates a positive linear correlation between the percentage of fruit consumed and incisor heteromorphy (Figure 6). Although this correlation indicates a relationship between these two characteristics, there is, however, a concern that must be addressed. Phylogeny must be taken out of the equation if this correlation is to be acceptable.

Figure 6: Regression fruit % / incisor heteromorphy



Comparative analysis of independent contrasts (CAIC)

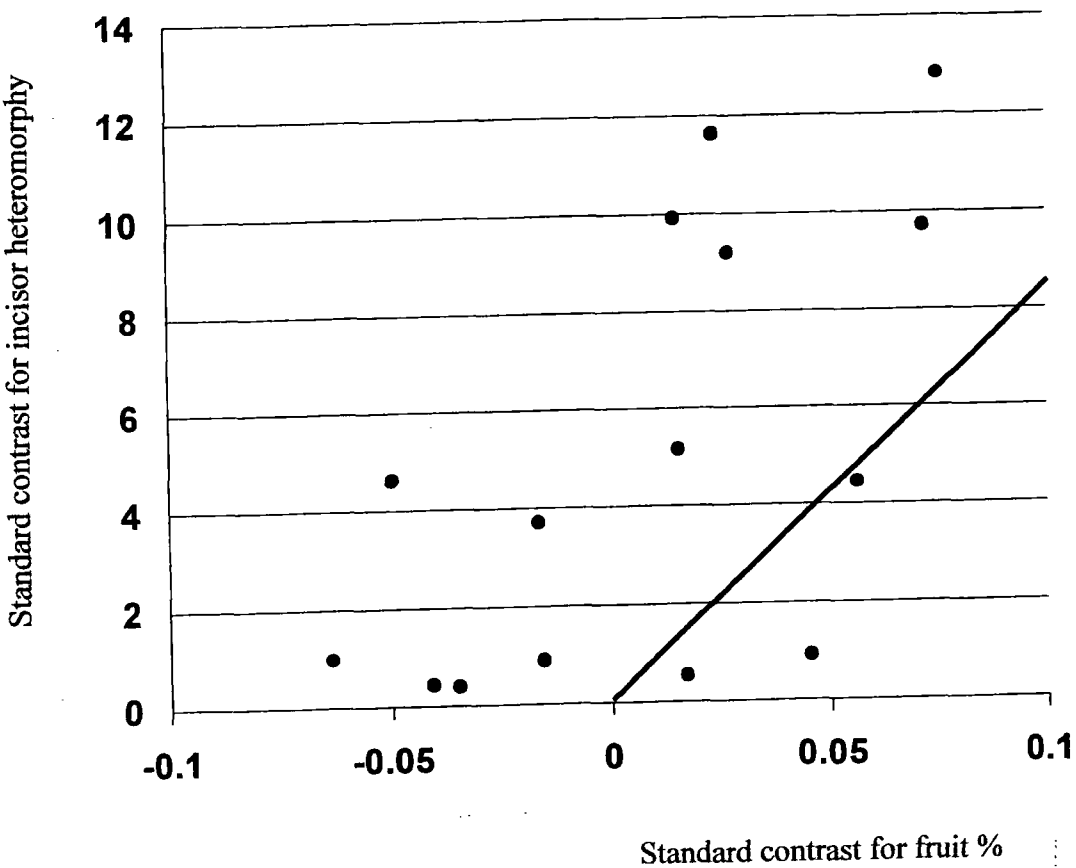
A CAIC analysis will take a data set and an established phylogeny and compare the variation between bifurcating nodes. This can include sister taxa or higher nodes representative of distant relatives. In the case of this analysis, Table 9 shows the data set for the two continuous variables in anthropoids and the the phylogeny of Purvis (1995) was used. As can be seen, 18 of the 25 genera sampled for this research are present. The other seven genera have been excluded from this analysis because the values for the percentage of fruit consumed were absent. Of these seven anthropoids, four, *Papio*, *Macaca*, *Pygathrix* and *Lagothrix* have been recorded (Rowe, 1996) eating fruit, but no percentages were available at this time.

The end product of this CAIC analysis, suitable for use in standard statistical techniques, are standardised linear contrasts in which the heterogeneity of variance has been overcome. These contrasts were then compared through least squares regression. It became clear that there was a problematic comparison. One comparison of the phylogenetic independent contrasts was a outlier that lay more than two standard deviations from the regression line. For a clearer correlation, this outlier had to be removed. With the removal of the outlier, a correlation with a r value of 0.64, significant at $p < 0.05$ ($p = 0.0075$), was ascertained. To ascertain a direct correlation the regression must be forced through the origin (Figure 7). Once done the correlation remains significant at $p < 0.05$ ($p = 0.0177$). This indicates a significant positive relationship between the percentage of fruit consumed and incisor heteromorphy independent from the effects of phylogeny.

Table 9: Data set for CAIC analysis

Genera	Fruit % (Rowe, 1996)	Incisor Heteromorphy ratio
Alouatta	2	1.1017
Aotus	65	1.61
Ateles	82.9	1.4317
Brachyteles	32	1.0325
Cacajao	18	1.3717
Callicebus	65	1.38
Cebus	66	1.2467
Cercocebus	59	1.56
Cercopithecus	78	1.7523
Chiropotes	30	1.3267
Gorilla	1.7	1.4256
Hylobates	21	1.2467
Mandrillus	92	1.612
Nasalis	17	1.3614
Pan	76	1.3233
Pithecia	59.5	1.4175
Pongo	60	1.67
Presbytis	19	1.1844

Figure 7: Regression using Caic contrasts.



Discussion

The above results are directly relevant to decisions concerning the usefulness of incisor heteromorphy in relation to phylogenetics and in discerning its adaptive role. The latter case, that of adaptive responses, is important because it enables possible dietary reasons for incisor heteromorphy to be clarified. Adaptive responses are also important in discerning the dietary behaviour of extinct anthropoids. By comparing ratios of extant taxa (and their diets) with ratios from extinct anthropoids, it is possible for a broad deduction concerning the diet of extinct anthropoids to be made. From a phylogenetic point of view, incisor heteromorphy has, in the past, played an important role in phylogenetic interpretations of the *Pongo* lineage (Andrews and Tekkaya, 1980; Andrews and Cronin, 1982; Bonis and Koufos, 1993; Kelley *et al.*, 1995). It is only recently that doubts have been aired over the utility of this characteristic in determining shared ancestry (Kelley *et al.*, 1995; Begun and Güleç, 1998). With comparisons to extant genera the utility of this characteristic might be clarified.

Phylogenetics and fossils

The results have indicated a number of important phylogenetic implications to both extant and extinct anthropoids. Incisor heteromorphy has been discussed frequently with respect to Miocene hominoids (Andrews and Tekkaya, 1980; Andrews and Cronin, 1982; Bonis and Koufos, 1993; Kelley *et al.*, 1995; Begun and Güleç, 1998) and when incisor heteromorphy data concerning these fossils is applied to the results the doubts over the phylogenetic usefulness of this character seem to hold true. As can be seen in Table 10, the fossil hominoids include a number of different species, of which four genera, *Dendropithecus* (RU 1849, 1850, 1901), *P.hesloni* (RU 1769, 2036, 7290), *Ouranopithecus* (XIR – 1, RPL 128) and *Ankarapithecus* (AS 95-

500, MTA 2125), show ranges in their incisor heteromorphy ratios. These values are based on more than one fossil specimen with associated incisors. The values for *Kenyapithecus* (Pickford, 1985), *Griphopithecus* (Alpagut *et al.*, 1990) and *Lufengpithecus* (Kelly *et al.*, 1995) are based on isolated incisors (not associated in any one particular maxilla). These values are thus provisional. The incisor ratios for the other fossil hominoids, which include *Sivapithecus indicus*, are based on single associated specimens. When the incisor heteromorphy ratios for these fossil hominoids are consolidated with the extant anthropoid ratios (Table 10), very few phylogenetic inferences can be made.

The incisor ratio results from extant anthropoids, as this research has shown, would appear to support the growing doubt over the usefulness of incisor heteromorphy in phylogenetic inferences. The fossil and extant evidence indicates widespread variation of incisor heteromorphy within anthropoids as a whole, with few clear synapomorphies evident. This is not to say, however, that incisor heteromorphy is a useless characteristic, especially when differing states of this character are viewed in a spectrum. When considering the variation, and taking homoplasy into consideration, within the consolidated sample there are essentially two character trends of interest; a primitive condition and a hyper increase in incisor heteromorphy.

A recognisable primitive condition for anthropoids and, although only extant anthropoids fall directly into this range, it is worth noting that the incisor heteromorphy for *Dendropithecus* (RU 1849, 1850, 1901) significantly overlaps the range of the primitive condition. *Dendropithecus*, at present, is the only fossil anthropoid that comes close to retaining the anthropoid primitive condition hypothesised here.

The majority of the remaining extant and extinct anthropoids either show decreases or increases in incisor heteromorphy. These states coupled with a great amount of homoplasy and dietary analysis supports the overall phylogenetic uselessness of this character. Those anthropoids that do show a supposedly derived decrease, or increase, do not share a common ancestry but probably do share similar dietary tendencies (see *Diet, Incision Behaviour and Abrasive Quality*, and *Diet, Incision and Fossils*).

The second trend of interest involves those anthropoids with incisor heteromorphy ratios of 1.73 +. These few anthropoids can be classed as having 'hyper incisor heteromorphy'. Only two fossil genera, *Ankarapithecus* and *Sivapithecus* (*S.indicus* and *S.parvada*) fall directly within this range. One extant species, *Cercopithecus* (1.75), also falls within this category. The inclusion of *Cercopithecus* can probably be placed down to its diet. *Cercopithecus* is a highly frugivorous, more so than most extant anthropoids. On the whole, these three genera do show an extra increase in the amount of heteromorphy relative to the other 'increase' range and to the primitive condition. Although *Ankarapithecus* (1.64-1.95), and probably *Cercopithecus* (owing to the number of species used), have overlapping ranges with some of the later Miocene hominoids, such as *Ouranopithecus* (1.66) and *Griphopithecus* (1.66), as well as with *Pongo* (1.67), the average ratio indicates the presence of 'hyper incisor heteromorphy'.

It is here that the phylogenetic usefulness of incisor heteromorphy runs out. The majority of anthropoids have acquired this adaptation independently of one another, since splitting with their last common ancestor. This trend also includes the majority of the Miocene fossil hominoids. There is, however, one notable exception, the *Sivapithecus* - *Pongo* clade (see below).

Table 10: Fossil hominoids and extant anthropoid incisor heteromorphy ratios

Genera	Incisor heteromorphy ratio	Range	Specimens
Brachyteles	1.03		
Alouatta	1.1		
Lagothrix	1.15		
Presbytis	1.18		
Theropithecus	1.19		
Colobus	1.21		
Rangwapithecus [1]	1.22		SO 550
Pygathrix	1.228		
Cebus	1.24		
Hylobates	1.24		
Pan	1.32		
Chiropotes	1.32		
Dendropithecus [3]	1.35	1.27-1.43	RU1849/1850/1901
Mortopithecus [2]	1.36		UMP 62-11
Nasalis	1.36		
Cacajao	1.37		
Callicebus	1.38		
Macaca	1.384		
Papio	1.424		
Gorilla	1.425		
Ateles	1.431		
Saimiri	1.4317		
Proconsul hesloni [3]	1.44	1.39-1.51	RU1769/2036/ 7290
Proconsul nynanze [1]	1.47		isolated incisors
Cercocebus	1.5		
Kalepithecus [3]	1.52		
Mircopithecus [3]	1.53		
Afropithecus [3]	1.53		WK 16999
Proconsul africanus [1]	1.55		M32363, RU 1769
Lufengpithecus	1.6		isolated incisors
Aotus	1.61		
Mandrillus	1.61		
Kenyapithecus [3, 5]	1.65		KNM MB 17, 104, 9729.RU 1681MJ 9734FT 49, 3637
Drypoithecus [3]	1.66		RUD 15
Ouranopithecus [3, 4]	1.66	1.56-1.79	XIR-1, RPL128
Pongo	1.67		
Griphopithceus [3, 6]	1.68		85 isolated incisors
Cercopithecus	1.75		
Anakarapithecus [2]	1.79	1.64-1.95	AS 95-500, MTA 2125
Sivapithecus indicus [3]	2.07		GSP15000
S. parvada [3]	2.12		GSP46460

[1]- Andrews, 1978
[2] - Begun and Güleç, 1998
[3]- Kelley *et. al.*, 1995
[4]- De Bonis and Koufos, 1993
[5]- Pickford, 1985
[6]- Alpagut et al., 1990

The confidence behind inferences concerned with a primitive condition and hyper-heteromorphy can be doubted when one considers the widespread homoplasy evident within fossil and extant anthropoids but it is worth noting that optimisation models (see Figures 3 and 4) based on differing skeletal traits point to similar trends in the primitive condition and the acquisition of incisor heteromorphy.

Sivapithecus - Pongo *clade*

The phylogenetic relationship of *Ankarapithecus*, *Sivapithecus* and *Pongo,* which originally gave rise to the interest in incisor heteromorphy, has proved problematic in the past, especially when incisor heteromorphy was taken into consideration. Originally it was thought that incisor heteromorphy was a synapomorphy (a shared derived characteristic) of the *Sivapithecus – Pongo* clade (Andrews and Tekkaya, 1980; Andrews and Cronin, 1982) shared by these two genera to the exclusion of all others. It was one of several characteristics that indicated common ancestry of *Sivapithecus* and *Pongo*. This remained the case until recently when research showed that incisor heteromorphy appears throughout both the fossil and, as this research has shown, extant anthropoid record. This is what has questioned the phylogenetic usefulness of this characteristic. With the discovery of AS 95-500, and the subsequent resurrection of *Ankarapithecus meteai*, this picture has become even more muddled. *Ankarapithecus*, along with *Sivapithecus*, has 'hyper' incisor heteromorphy. This, and a number of other characteristics, suggests that *Ankarapithecus* and *Sivapithecus* share a common ancestry. The problem occurs when *Pongo* is added to the equation. There is some doubt, as to whether *Sivapithecus* and *Pongo* are sister taxa, especially when postcranial morphology is taken into consideration (Pilbeam *et al.*, 1990). When the incisor heteromorphy ratios of this

clade, however, and are compared to that of *Ankarapithecus* more confusion is evident. *Pongo* shows a smaller ratio relative to *Sivapithecus* and *Ankarapithecus*. When considering the extent of incisor heteromorphy within these three genera it would appear that "it could be a synapomorphy of the clade subsequently lost by *Pongo*, or it could equally have arisen independently in *Ankarapithecus* and *Sivapithecus*" (Begun and Güleç, 1998: 307). The cladistic analysis performed on the extant anthropoids, and the subsequent results, supports the latter possibility. Incisor heteromorphy is a highly homoplastic characteristic, with the majority of extant anthropoids acquiring the condition since the split with their last common ancestor. The same can be cautiously applied to the fossil hominoid record and in particularly to *Ankarapithecus*, *Sivapithecus* and *Pongo*.

Diet

The results from CAIC have shown that the dominant force behind incisor heteromorphy is that of diet, in particular the percentage of fruit consumed by an anthropoid. There are, however, other trends visible when diet and dietary behaviour are applied to spectrum of incisor heteromorphy. The latter, dietary behaviour, is of great importance when discerning adaptive responses of incisor heteromorphy.

As can be seen from Table 11, the first trend that is evident is the separate grouping of folivores and frugivores. Those anthropoids with a foliage diet tend to fall towards the lower end of the spectrum. These anthropoids, *Brachyteles*, *Alouatta*, *Lagothrix, Presbytis*, *Theropithecus, Colobus* and *Phygathrix*, tend to have a diet dominated by leaf matter, with some consumption of fruit (Rowe, 1996). There are two notable exception to this grouping. The two exceptions, *Gorilla* and *Nasalis*, fall outside of this grouping. The diet of *Nasalis* indicates that it is a seasonal specialist

(Yeager, 1989) switching between leaf and fruit consumption with the changing of the seasons (Yeager, 1989; Rowe, 1996). The increased consumption of fruit (40% - Yeager, 1989; Rowe, 1996) in comparison to those anthropoids whose diet is dominated by foliage, supports the placement of *Nasalis larvatus* higher in the incisor heteromorphy spectrum. *Gorilla*, however, is a problem. The diet of *Gorilla* is predomiently made up of foliage (although there is variation in the amount of fruit consumed between sub-species), which mainly comprises of leaves (85%), wood (6.9%), roots (3.3%), and flowers (4%). Also consumed is wild celery, thistle, nettles and bamboos (Rowe, 1996). The broadness of this diet is comparitively similar to that of *Theropithecus* and yet these two genera are literally poles apart. There is no consumption of fruit, similar to *Theropithecus*, and yet *Gorilla* shows a derived increase in incisor heteromorphy that cannot be explained, as *Nasalis* was, by the consumption of fruit. The answer may lie, however, in the quality, and broadness, of the diet and the dietary behaviour undertaken (see below). The remaining anthropoids can all be classed as frugivores. The degree of incisor heteromorphy, evident in the spectrum, can be explained by the properties of the fruit consumed and the broadness of the diet (Table 11).

In general there appears to be a number of dietary trends, in relation to the degree of incisor heteromorphy, amongst the remaining anthropoids. At the lower end of the spectrum there are those anthropoids, *Hylobates* and *Pan*, which consume a high percentage of soft fruit (on average 55% and 50% respectively) which is supplemented with folaige and insects (Rowe, 1996). Those anthropoids who fall near or within the primitive condition, *Chiropotes*, *Cacajao*, *Callicebus* and *Pithecia*, tend to consume fruit with a hard endocarp (outer exterior) and a high percentage of seeds (Kinzey, 1992; Rowe, 1996).

Table 11: Spectrum of proportioanlity, abrasive quality and incisal preparation

Genera	Homo	Folivore	Frugivore	Specific diet	Abrasive Quality (-)	Incisal Preparation (-)
Brachyteles *Alouatta* *Lagothrix* *Presbytis* *Theropith.* *Colobus* *Phygathrix* *Cebus* *Hylobates* *Pan* *Chiropotes* *Nasalis* *Cacajao* *Callicebus* *Macaca* *Pithecia* *Papio* *Gorilla* *Ateles* *Saimiri* *Cercocebus* *Aotus* *Mandrillus* *Pongo* *Cercopithecus*	↕	↓	↓	↕	↕	↕
	Hetero			Non-spec.	+	+

For example, seed consumption comprises of 60% of the diet of *Chiropotes satanas*. Whilst *Cacajao* and *Callicebus* consume similar amounts of seeds, they also supplement their diet with a broader range of food items, which includes animal and insect prey (Kinzey, 1990; Rowe, 1996). When examining the diets of those anthropoids with a derived increase in incisor heteromorphy, two trends are evident. Firstly, there is the continued consumption of hard skinned fruit. Anthropoids such as *Cercocebus* and *Pongo* tend to consume a high percentage of hard fruit similar to *Cacajao* and *Callicebus*. Secondly there is emphasis on more broader non-specific diets. A number of anthropoids, such as *Macaca*, *Papio*, *Mandrillus* and *Pongo*, are inclined to supplement there hard fruit diet with increased amounts of leaves, bark, stems, shoots, flowers and animal prey (Hoshino, 1985; Rowe, 1996; Knott, 1998; deVore and Washburn, 1963). The harder the fruit and greater range of diet, the greater the degree of incisor heteromorphy.

The exceptions to these generalised trends, *Cebus*, *Ateles* and *Saimiri*, (coupled with *Gorilla*) indicate the influence of other factors, than just diet, to the degree of incisor heteromorphy present in a species. Although *Cebus* falls at the lower end of the frugivore spectrum, with *Hylobates* and *Pan*, it is not a soft fruit eater. *Cebus* tends to consume hard coated fruit (Dumont, 1995), similar to the types consumed by *Cercocebus*, yet it shows a decrease in the degreee of heteromorphy relative to the primitive condition. The diet of *Ateles*, mainly soft fruit such as figs and some foliage (Nunes, 1998; Rowe, 1996), should indicate a lower position in this spectrum, similar to *Hylobates*, *Pan* or *Nasalis*, but instead *Ateles* falls well within the

"increase" class. *Saimiri* is even more of an exception than the other two species because it shows a increase in incisor heteromorphy that is due to the consumption of animal prey and insects, not the consumption of fruit.

Although the percentage of fruit consumed is a driving force behind the adaptation of incisor heteromorphy, it is quite clear that other factors are involved. Any adaptation to food consumption will also be adapted to the abrasive content of a diet and the different kinds of ingestive behaviour.

Incision Behaviour and Abrasive Quality

In the case of incisor heteromorphy, the use, or lack of use, of the incisors will have an effect on the degree of incisor heteromorphy. In other words, the amount of incisor manipulation, influenced by the properties of food matter, has an effect on the degree of incisor heteomorphy. The use of incisors in mastication is varied throughout anthropoids.

Folivores, such as *Alouatta* and *Presbytis*, vary rarely use their incisors for ingestion (Ungar, 1990, 1994). Instead, there is a reduction in the use of the anterior dentition in favour of specially adapted molar crests for the slicing of foliage; folivores, such as *Presbytis* and *Theropithecus*, to place leaves directly into the back of the mouth, rather than use the incisors. On the odd occasions of incisor manipulation, very little mastication takes place. Usually the leaves are either bunched together and incised, as with *Presbytis*, or a branch is pulled to the mouth, incisors clamped on a leaf and the branch released, as with *Alouatta*.

With frugivores, there is an increased tendency towards incisor manipulation, as well as more heteromorphic incisors. Even *Cebus*, at the lower end of the spectrum, uses its anterior dentition more often than *Alouatta* (Ungar, 1990). *Cebus apella*,

however, relative to other frugivores such as *Hylobates*, *Chiropotes* and *Pongo*, rarely uses the incisors. Instead, the initial processing of hard fruit objects is undertaken by the molars instead of the anterior dentition. This action is reinforced by thick molar enamel (Dumont, 1995). Similar trends are also evident when considering the diet of *Hylobates*. *Hylobates* prefers soft fruit that rarely need incisor preparation prior to mastication. With a preference for small ripe soft skinned multi-seeded fruits, such as figs, *Hylobates lar* easily places whole fruit within the mouth to be crushed by the molars, thus forgoing the use of the anterior dentition. Although there is little preference to incisor manipulation, the nipping of food items by *Hylobates* is more common in comparison to folivores, such as *Presbytis* (Ungar, 1993; Gittens and Raemaekars, 1980). Although these frugivores tend to prefer the use of the molars, there is more use of the incisors relative to the use of incisors by folivores.

There are, however, more frugivores that do prefer some degree of incisal preparation prior to mastication and which relates to the degree of incisor heteromorphy found. For example, *Chiropotes* and *Pithecia* have preferences for seeds and soft pericarp contained within hard coated fruits. Instead of straight mastication by the molars, the fruit is prepared by the incisors. There is a tendancy for the incisors to be used to peel the skin and gouge out the contents (Kinzey, 1990; Anapol and Lee, 1990). Although the fruit is processed in similar ways, *Pithecia* and *Chiropotes* have very different amounts of incisor heteromorphy. This difference can be put down to the varying degrees of fruit hardness and the amount of incsial preparation require. In general *Pithecia*, who has a larger amount of incisor heteromorphy, consumes harder skinned fruit than *Chiropotes*.

Food properties, such as the abrasive quality of hard fruits, and opportunistic diets are important elements in understanding incisor heteromorphy. Hylander (1975)

pointed out that the increased frequency and duration of incisal preparation of frugivore diets caused more attrition and abrasion than folivore diets. The adaptive reponse is for enlarged incisors to delay dental obsolescence; the more incisal preparation undertaken, and the more abrasive the diet, the larger the incisors.

In the case of *Macaca*, more extensive incisal preparation is undertaken. The broad non-specific diet of *Macaca* requires a repertoire of incisor manipulation, which includes incising and nipping; tough skinned fruits and insects tend to be incised whilst smaller softer fruits are nipped (Ungar, 1994). Like *Macaca*, *Papio* also has a non-specific broad diet and similar incisal manipulation. According to de Vore and Washburn (1963: 360) "the incisors were used in biting and tearing the flesh" of fruit and animal prey. Also when eating grasses and tubers, *Papio* tends to either use the hands, similar to *Theropithecus*, or the incisors. These two anthropoids, *Macaca* and *Papio*, show an increased use of the incisors, relative to *Cebus* and *Hylobates*, during the inital stages of mastication coupled with broad opportunistic diets. Both genera also show higher degrees of incisor heteromorphy relative to *Cebus* and *Hylobates*.

Where *Macaca* and *Papio* undertake a few types of incisor preparation, *Pongo* has the most extensive use of the anterior dentition in ingestive behaviour of all the anthropoids sampled, as well as the most opportunistic diet. Orang-utans use their front teeth and lips on all the different types of food that they consumed (not just fruit) more frequently during ingestion than any other anthropoid (Ungar, 1994). The orang-utan repertoire of incisal preparation includes incising, crushing, scraping and stripping. In general, small to moderate fruit tends to be nipped several times prior to further mastication. Medium and harder husked fruit are either crushed or incised open with a lot of manipulation by the incisors. Large edible skinned fruit is generally incised open. Other food items, such as bark, are either stripped or scraped. The

abrasive diet and extensive ingestion behaviour of *Pongo* indicates the presence of enlarged incisors (especially the central incisors) and, therefore, a large amount of incisor heteromorphy.

With food preference comes various ingestion behaviours along with attrition and abrasion. Folivores, soft fruit eaters and a few hard fruit eaters tend to use only their molars for ingestion, whilst seed eaters, the majority of hard fruit eaters, faunivores (*Saimiri*), and opportunistic frugivores (broad, non-specific diet) use their incisors to prepare food prior to mastication. Incisor proportionality is a by product of adaptations to food preferences, ingestion behaviour and the subsequent abrasive quality of that food (Table 12). If the trends above are true then assumptions concerning other anthropoids in the spectrum and fossil hominoids could be made. For example, *Saimiri* shows a large amount of incisor hetromorphy, much more than many frugivores, but has a diet solely of insects and small prey. If tentatively applied then *Saimiri* probably undertakes a great deal of incisal prepartion. This is possible with the hard nature of its preferred food. The comparison between *Gorilla* and *Theropithecus* also points towards differing incisal preparation. Although both are highly folivorous *Gorilla*, owing to its size, must extensively ingest and masticate foliage. *Theropithecus*, however, probably depends solely on the use of its molars rather than incisors for ingestion. Another reason for the differences between *Theropithecus* and *Gorilla*, however, may be due to an underestimation of the percentage of fruit consumed by *Gorilla*. As stated earlier, different subspecies of *Gorilla* may consume differing quantities of fruit.

Diet, Incision Behaviour and Fossils

Using the published incisor heteromorphy ratios from Table 10, some inferences concerning the diet and ingestion behaviour can be made about Miocene fossil hominoids. According to Ungar (1996) incisal preparation was a regular part of the ingestive behaviour of most fossil Miocene hominoids. The extent of incisal preparation was probably more than seen with *Alouatta* and *Hylobates lar*. Perhaps the only exception to this is *Rangwapithecus*, as the majority of fossil hominoids do show relatively high incisor heteromorphy. *Rangwapithecus*' degree of incisor heteromorphy would seem to indicate a folivorous diet with very little, if any, incisal preparation. This dietary adaptation is also supported by the presence of long and narrow molars with numerous shearing crests in this genus (Fleagle, 1988). The molar morphology of *Proconsul nyanzae* seems to suggest a frugivorous diet (Fleagle, 1988). This is supported by its placement close to *Ateles* and *Cercocebus*, who are both predominantly frugivorous and undertake a reasonable degree of incisal preparation. It is possible that *Proconsul nynanze* could also have undertaken some ingestion behaviour similar to *Ateles* and *Cercocebus*. The relatively large incisors of *Micropithecus* and the robust, procumbent incisors of *Afropithecus* would seem to suggest a high degree of incisal preparation (Fleagle, 1988). Both were probably frugivorous, with the small cheek teeth of *Micropithecus* suggesting even more reliance on incision prior to mastication.

Kenyapithecus and *Ouranopithecus* show very similar degrees of incisor heteromorphy. Microwear analysis of the incisor of *Ouranopithecus* has indicated a high degree of ingestive behaviour similar to *Pongo* (Ungar, 1996). This, coupled with thick enamel on the cheek teeth and a thick mandible (Fleagle, 1988; Ungar,

1996), would suggest adaptations to a non-specific broad diet similar to *Pongo* and *Mandrillus*. Although the incisor heteromorphy value for *Kenyapithecus* is based on isolated incisors, the thicker molar enamel and robust mandible (Fleagle, 1988) would also indicate adaptation to a non-specific broad diet. The high values of incisor heteromorphy displayed by *Kenyapithecus*, *Ouranopithecus* and *Pongo*, coupled with the similarities in dental and mandibular morphology, would indicate similar diets and ingestive behaviours.

Hyper Incisor Heteromorphy

The fossil record and the analysis of extant taxa seems to support a correlation between incisor heteromorphy and incisal preparation. When considering assumptions concerning the diet and ingestive behaviour for those primates with hyper-incisor heteromorphy, such as *Sivapithecus* and *Ankarapithecus*, however, comparisons with extant genera can be complicated. *Cercopithecus* could be used for such comparisons. The incisor heteromorphy value for *Cercopithecus* indicates extreme enlargement of the central incisor, more than any other extant anthropoid. The diet of *Cercopithecus*, frugivory (78% for *C.campbelli*, 76% for *C.diana* and 78% for *C.cephus*) supplemented by insectivory, appears constant across the species present in the sample (Fleagle, 1988; Gautier-Hion, 1988b). Assuming that enlarged incisors are also indicative of incisal preparation, it is possible that *Cercopithecus* undertakes similar amounts of incisal preparation behaviour as *Pongo*. This probably accounts for the high incisor heteromorphy values seen within the *Cercopithecus* sample. The diet of the guenons is reflective of their relatively small size and any comparison with the larger hominoids of the Miocene will be problematic. Comparisons between extant

anthropoids and Miocene hominoids should be made with a larger sized anthropoid, such as *Pongo*, to avoid such difficulties.

Hyper - heteromorphy, as seen with *Ankarapithecus*, *Sivapithecus indicus* and *Sivapithecus parvada*, would seem to indicate a very abrasive diet, a high degree of incisal manipulation and a broad diet. Other characteristics, such as the thickness of the molar enamel for these genera, would also seem to suggest hard fruit mastication similar to *Cebus* (Kay, 1981; Teaford and Walker, 1984; Dumont, 1995). Although comparable to the general observations concerning the duet and food preparation behaviour of Pongo, the higher incisor heteromorphy values would seem to indicate a broader diet and greater incisal behaviour. If this is the case, then the ingestion behaviour of these fossil hominoids was very extensive, with a broad range of objects being incised, stripped, nipped or crushed by the incisors and then pulped by broad molars.

Dietary niches and fossil hominoid habitats

The evidence for the palaeo-habitats of *Sivapithecus* and *Ankarapithecus* supports the correlation between dietary adaptations (feeding behaviours and the diet) of these extinct anthropoids and hyper-incisor heteromorphy. Although there are some regional differences in the faunal and floral assemblages of the Siwaliks, India (*Sivapithecus*) and Pasalar, Turkey (*Ankarapithecus*), both appear to be indicative of seasonal environments (Andrews, 1983; Viranta and Andrews, 1995). Seasonality, with periods of fruit scarcity and abundance, could have forced woodland species with frugivorous diets, such as *Sivapithecus* and *Ankarapithecus*, to exploit alternative sources of food (Andrews, 1983). A mixed, broad diet may have been an adaptation to seasonal shortages, which required the dental adaptations, such as enlarged central

incisors and thick enamel, seen in those extinct anthropoid species with hyper-incisor heteromorphy.

Conclusions

The analysis of 25 extant anthropoid genera has indicated a widespread presence of incisor heteromorphy within anthropoids, with nearly every anthropoid genus sampled appearing to have a unique value. It is, therefore, hardly surprising to discern, from the phylogenetic analysis of this characteristic, that incisor heteromorphy is homoplastic for the majority of anthropoids. It would appear that the condition was acquired independently by each genus after the last common ancestor. Incisor heteromorphy seems to be highly susceptible to the niche occupied by a primate There are two exceptions to this. First, there is a recognised primitive as represented by *Cacajao*, *Callicebus* and *Macaca*. The use of two recognised phylogenies (Ford, 1986; Kay, 1990), based on skeletal evidence, would seem to support this inference. It is interesting to note that an above-average-value of incisor heteromorphy appears to be primitive for anthropoids. The other anthropoids show either a derived decrease or a derived increase relative to the primitive condition in incisor heteromorphy. Secondly, the only groups that share derived conditions are colobines and atelines. The widespread homoplasy, however, indicates the susceptibility of this characteristic to the environment.

Analysis and comparison would seem to indicate that incisor heteromorphy is predominantly an adaptive response to a frugivorous (including abrasive quality) diet and ingestive behaviour. The majority of folivores have very little incisor heteromorphy whilst the majority of frugivores have varying degrees of incisor heteromorphy. The harder and broader a frugivore diet, the more abrasive the material included, and the more likelihood of constant incisal preparation (ingestive behaviour)

the greater the incisor heteromorphy. In response to such pressures, frugivorous primates can have either thickened enamel on the molars or increased central incisors. If the diet is extremely abrasive, with constant incisal preparation, as in the case of *Pongo*, then both adapations can easily be seen. The enlargement of the central incisor, as with the thickening of the enamel on the molars, is an attempt to decrease the rate of attrition and dental obsolescence (Hylander, 1975; Kay, 1981).

These dietary trends can also be used to discern the diet of extinct anthropoids. Incisor heteromorphy has played a unique part in inferences concerning the *Sivapithecus - Pongo* clade and fossil hominoids in general. There is no evidence for the primitive condition, with perhaps the exception of *Dendropithecus*, amongst Miocene hominoids. This does not mean, however, that the degree of incisor heteromorphy within the clade is a shared derived characteristic. The widespread homoplasy would seem to indicate the independent acquisition of this character by not just extant anthropoids but also extinct anthropoids. This would explain the differing values seen in *Ankarapithecus*, *Sivapithecus* and *Pongo* and subsequent problems associated with phylogenetic homoplasy. The independently acquisition of incisor heteromorphy may explain the reduction seen in *Pongo* in comparison to *Sivapithecus* and *Ankarapithecus*. Incisor heteromorphy would then appear to be of little use when trying to discern phylogeny.

The implications of diet and ingestion behaviour, although tentatively applied, would seem to suggest a variety of incisal preparation associated with frugivorous and broad, non-specific diets amongst the majority of fossil primates, with the exception of *Rangwapithecus*. This is especially the case for those fossil anthropoids (*Sivapithecus* and *Ankarapithecus*) with hyper-heteromorphy. Hyper-heteromorphy is probably due to a very abrasive diet, a high degree of incisal manipulation and a very

broad non-specific diet, similar in some extent to *Pongo* but showing more extreme pressures.

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Appendix 1: Raw data

The following measurements were collected at the Natural History Museum (London) and are representative of 25 anthropoid genera. There are **89** incidences were antimeres were used.

TAXON	NUMBER	SEX	RI1MD	RI2MD	LI1MD	LI2MD
Gorilla	1939.942	M	11.98	8.11	12.35	8.13
Gorilla	1939.946	M	12.38	8.7	11.68	11.66
Gorilla	1939.944	M	12.2	**8.96**	**12.2**	8.96
Gorilla	1939.94	M	13.32	**8.14**	13.62	8.14
Gorilla	1939.964	M	13.83	10.25	12.57	10.11
Gorilla	49.603	M	12.72	7.97	13.09	**7.97**
Gorilla	78.1314	M	**13.01**	**8.31**	13.01	8.31
Gorilla	1965.3.3.12	M	14.55	9.19	14.2	10.25
Gorilla	20.4.13.4	M	11.98	**9.6**	12.69	9.6
Gorilla	1961.4.5.1	M	14.55	10.45	14.08	12.34
Gorilla	29.1.1.1	M	12.26	8.46	12.92	8.29
Gorilla	86.536	M	14.17	8.6	14.42	9.26
Gorilla	86.535	M	12.22	8.48	11.61	10.01
Gorilla	86.534	M	11.02	9.87	15.56	9.01
Gorilla	1.06.25.157.	M	14.23	11.99	14.17	**11.99**
Gorilla	1948.5.4.1	M	12.96	10.2	13.1	9.28
Gorilla	1939.923	M	12.92	9.19	13.61	9.03
Gorilla	49.663	M	13.5	10.12	13.85	10.17
Gorilla	1939.921	M	13.3	10.51	**13.3**	9.88
Gorilla	1939.92	M	13.2	**8.27**	12.99	8.27
Gorilla	23.11.29.6	M	11.54	8.99	11.51	8.04
Gorilla	23.11.29.5	M	10.93	7.15	10.33	7.35
Gorilla	23.11.29.7	M	12.9	**7.18**	12.23	7.18
Gorilla	25.1.4.3	M	**15.14**	9.65	15.14	8.98
Gorilla	23.11.29.4.	M	12.41	**9.2**	12.89	9.2
Gorilla	23.11.29.3	M	13.64	9.85	14.11	9.99
Gorilla	1939.93	M	11.88	**7.34**	**11.88**	7.34
Gorilla	1939.938	M	13.31	11.09	12.59	11.01
Gorilla	1939.932	M	13.99	9.01	13.65	9.16
Gorilla	1939.926	M	12.81	**10.4**	12.91	10.4
Gorilla	86.768	M	14.84	9.72	16.06	**9.72**
Gorilla	86.765	M	10.25	7.58	10.36	6.86
Gorilla	1948.3.3.2	M	**11.8**	8.07	11.8	7.22
Gorilla	1939.952	M	14.17	10.4	13.49	10.9
Gorilla	1939.912	M	10.93	**9.23**	11.72	9.23
Gorilla	1939.914	M	13.56	9.15	13.44	9.87
Gorilla	48.436	M	**13.28**	8.73	13.28	8.8
Gorilla	36.7.14.1	M	15.91	10.55	**15.91**	10.28
Gorilla	1939.913	M	12.38	8.38	12.01	8.64
Gorilla	49.664	F	11.61	9.22	11.8	**9.22**
Gorilla	64.12.1.5	F	**14.28**	8.42	14.28	**8.42**
Gorilla	28.4.1919	F	**8.78**	5.65	8.78	5.63
Gorilla	1939.922	F	12.25	8.29	12.37	8.59
Gorilla	1989.749	F	**13.81**	8.78	13.81	10.13
Gorilla	1939.927	F	12.78	8.63	12.16	8.37
Gorilla	1948.12.20.2	F	12.73	8.22	12.44	8.69
Gorilla	1948.5.4.2	F	11.72	8.53	**11.72**	8.03
Gorilla	23.11.29.8	F	11.05	7.63	11.5	8.09
Gorilla	1857.11.2.3	F	8.4	7.32	9.54	**7.32**

Gorilla	1939.936	F	**12.09**	**8.51**	12.09	8.51
Gorilla	1939.925	F	13.2	9.45	12.94	8.6
Gorilla	1857.11.2.2	F	12.87	10.14	12.95	10.16
Gorilla	1948.3.31.2	F	12.21	**8.28**	11.89	8.28
Gorilla	86.758	F	8.93	6.38	9.3	8.17
Gorilla	1951.9.27.17	F	13.68	9.11	12.49	9.04
Gorilla	1939.956	F	12.5	9.52	**12.5**	9.06
Gorilla	1948.3.31.1	F	11.35	8.33	11.04	8.26
Gorilla	7.1.8.4	F	11.19	7.37	11.4	7.72
Gorilla	7.1.8.3	F	10.92	7.62	10.03	7.37
Pan	86.214	M	12.25	9.52	12.32	9.3
Pan	1968.9.5.1	M	12.09	8.47	12.35	9.45
Pan	1939.3385	M	11.46	8.77	11.59	9.05
Pan	1939.3386	M	**11.03**	7.77	11.03	9.54
Pan	1948.10.25.2	M	11.62	8.64	10.58	8.55
Pan	1939.3375	M	12.18	8.73	11.87	8.22
Pan	1939.3376	M	11.47	8.72	10.76	8.98
Pan	1939.908	M	11.91	9.05	12.63	9.39
Pan	1939.951	M	13.01	**8.48**	12.49	8.48
Pan	1882.9.18.1	M	9.51	6.03	9.31	**6.03**
Pan	55.58	M	13.58	9.79	13.72	10.45
Pan	1.8.9.10	M	11.23	**7.93**	10.71	7.93
Pan	22.12.19.2	M	11.57	8.92	11.07	8.54
Pan	22.12.19.1	M	11.23	9.27	11.4	9.04
Pan	87.12.1.1.	M	12.63	10.21	**12.63**	9.06
Pan	1939.3365	M	11.62	9.27	11.49	10.12
Pan	1939.3364	M	10.62	9.24	11.19	9.24
Pan	1939.3369	M	11.7	9.14	11.13	8.82
Pan	1924.8.6.1	M	11.18	7.73	11.35	7.73
Pan	94.7.25.1	M	**9.97**	6.37	9.97	7.02
Pan	1917.12.16.1	M	7.31	6.12	7.49	5.34
Pan	1989.326	F	13.53	10.2	11.68	8.99
Pan	1939.3373	F	**12.26**	8.63	12.26	8.75
Pan	1939.3382	F	10.3	7.99	10.24	8.89
Pan	80.345	F	10.65	8.98	11.98	9.07
Pan	1939.3384	F	8.61	6.24	7.97	6.65
Pan	1939.992	F	11.24	**8.13**	10.75	8.13
Pan	1939.3383	F	11.81	**9.22**	**11.81**	9.22
Pan	27.1.4.1	F	9.66	7.58	10.47	**7.58**
Pan	20.4.13.2	F	10.71	8.78	10.47	**8.78**
Pan	20.10.21.4	F	**10.2**	7.18	10.2	7.37
Pan	1.8.9.9	F	11.96	7.88	11.64	7.38
Pan	2.3.3.1.1	F	**9.36**	8.4	9.36	**8.4**
Pan	1883.7.28.18	F	11.38	**8.21**	11.28	8.21
Pan	7.7.8.19	F	9.3	7.76	9.19	6.14
Pan	87.12.1.3	F	12.71	8.42	12.63	10.07
Pan	1939.3367	F	11.08	8.01	11.05	8.05
Pan	1939.3366	F	10.35	8.82	10.68	7.88
Pan	1864.12.1.7	F	11.74	8.7	12.32	8.26
Pan	1968.7.5.11	F	11.63	9.05	10.66	8.94
Pan	1968.7.5.5	F	11.94	9.08	11.12	8.97
Pan	1968.7.5.10	F	10.04	7.23	10.87	8.06
Pan	1939.3379	F	11.13	9.64	10.79	**9.64**
Pan	86.22	F	10.6	7.32	**10.6**	7.43
Pongo	1948.9.9.2	M	14.12	7.36	12.72	7.19

Pongo	72.167	M	15.16	7.22	14.25	7.26
Pongo	1948.7.6.3	M	15.41	9.19	15.11	8.04
Pongo	1948.10.25.1	M	14.73	9.06	15.1	9.12
Pongo	1939.1019	M	15.1	9.39	14.64	9.71
Pongo	1939.1017	M	14.31	**7.06**	13.87	7.06
Pongo	1939.1018	M	11.3	7.3	12.25	7.29
Pongo	18.5.23.1	M	**12.18**	7.26	12.18	6.67
Pongo	1939.1008	M	13.73	7.76	14.11	8.86
Pongo	1948.8.10.30.1	M	14.18	8.23	14.81	7.99
Pongo	1986.1118	M	14.14	8.11	**14.14**	7.97
Pongo	1986.111	M	**11.54**	7.63	11.54	8.03
Pongo	1898.8.28.11	M	13.29	8.03	11.86	7.51
Pongo	1939.1006	M	12.83	**7.91**	13.22	7.91
Pongo	68.16.4.2	M	13.88	9.67	15.03	8.92
Pongo	1939.1007	M	12.52	8.03	13.89	8.06
Pongo	1976.1431	M	14.23	7.54	13.6	7.82
Pongo	1976.1428	M	12.86	**7.68**	13.71	7.68
Pongo	1976.1429	M	13.49	8.18	13.38	8.31
Pongo	1976.1424	M	12.81	6.65	12.34	8.4
Pongo	1976.1426	M	14.34	8.78	13.61	8.9
Pongo	1976.1442	M	14.28	8.18	13.9	8.35
Pongo	1976.1443	M	13.28	7.76	13.27	7.13
Pongo	1976.1445	M	14.28	8.48	14.27	8.24
Pongo	1976.1439	M	13.87	9.02	**13.87**	8.42
Pongo	1976.144	M	**12.47**	7.11	12.47	6.89
Pongo	1976.1434	M	14.74	9	14.77	8.6
Pongo	1976.1435	M	13.86	8.91	13.82	8.81
Pongo	1892.11.5.5	M	12.18	9.33	12.84	12.84
Pongo	1856.11.8.2	M	13.61	8.89	14.32	8.37
Pongo	1879.11.21.213	M	11.07	7.15	11.87	8.81
Pongo	92.11.5.3	M	**13.76**	10.12	13.76	9.75
Pongo	1844.3.30.18	M	13.74	**7.59**	14.35	7.59
Pongo	80.346	F	13.6	8.09	12.31	7.95
Pongo	1948.11.23.1	F	13.66	8.24	13.88	6.94
Pongo	1948.7.6.1	F	**12.28**	8.27	12.28	6.75
Pongo	1179c	F	13.48	**8.04**	15.05	8.04
Pongo	1986.1113	F	12.78	8.4	12.77	7.96
Pongo	1986.1115	F	9.88	6.5	9.85	6.6
Pongo	1976.142	F	12.97	8.09	**12.97**	**8.09**
Pongo	1976.1422	F	12.7	6.86	12.06	6.93
Pongo	1976.1421	F	12.84	6.74	12.9	8.33
Pongo	1976.1423	F	10.83	6.55	10.91	6.88
Pongo	1976.1419	F	10.82	**6.14**	11.02	6.14
Pongo	1976.143	F	**14.9**	8.59	14.9	8.21
Pongo	1976.1427	F	12.24	6.69	**12.24**	7.25
Pongo	1986.11	F	12.29	8.3	12.39	8.28
Pongo	1986.1098	F	13.24	7.98	13.2	7.53
Hylobates						
H. hoolock	43.63	M	5.29	4.13	5.28	3.91
H. hoolock	1937.3.24.4	M	5.33	4.39	5.26	4.32
H. hoolock	21.7.9.1	M	5.04	4.17	5.18	3.82
H. hoolock	1937.3.24.5	M	4.82	4.08	5.11	4.17
H. hoolock	15.5.5.2	M	4.88	4.15	5.31	3.78
H. hoolock	1937.3.24.2	M	5.12	3.85	5.13	3.69
H. hoolock	1891.10.7.2	F	4.28	4.21	4.41	3.76

H. hoolock	1937.3.24.6	F	4.18	3.88	4.3	3.63
H. hoolock	21.7.9.2	F	5.22	4.39	5.45	4.52
H. hoolock	50.392	F	4.95	3.76	5.2	3.72
H. hoolock	1937.3.24.3	F	5.15	3.78	5.42	3.69
H.lar.entelloides	14.12.8.2	M	4.1	3.65	4.07	3.81
H.lar.entelloides	14.12.8.10	M	4.06	3.63	3.78	3.69
H.lar.entelloides	24.9.2.1	M	4.55	3.85	4.19	3.98
H.lar.entelloides	14.12.8.1	M	4.8	3.77	4.7	3.78
H.lar.entelloides	14.12.8.3	M	4.8	4.28	4.91	4.19
H.lar.entelloides	14.12.8.8	F	3.83	4.11	3.81	4.06
H.lar.entelloides	14.12.8.7	F	4.34	3.67	4.48	3.82
H.lar.entelloides	24.9.2.6	F	4.52	3.47	4.76	3.81
H.lar.entelloides	55.15	F	**5.29**	4.13	5.29	4.09
H.lar.entelloides	24.9.2.7	F	4.42	3.67	4.46	3.52
H.lar lar	55.1496	M	4.1	3.78	4.31	3.78
H.lar lar	55.1494	M	4.58	4.52	4.84	**4.52**
H.lar lar	10.10.1.6	M	5.39	3.37	5.32	3.64
H.lar lar	55.1492	M	5.52	4.45	5.54	4.15
H.lar lar	10.10.1.7	F	4.68	3.91	4.51	3.74
H.lar lar	10.10.1.8	F	4.57	3.59	4.95	2.99
H.lar lar	55.1498	F	3.94	3.68	3.93	3.49
H.lar lar	55.1493	F	4.55	3.89	4.41	4.09
H.pileatus	15.11.4.1	M	5.38	4.07	5.18	3.79
H.pileatus	15.11.4.4	F	4.81	3.57	4.5	3.4
H.agilis	60.5.4.47	M	4.76	3.72	4.87	3.61
H.agilis	55.1458	M	4.61	3.51	4.64	3.79
H.agilis	1892.9.4.14	M	5.19	3.68	5.41	3.78
H.agilis	20.12.4.5	M	5.33	4.23	5.8	4.12
H.agilis	33.6.6.1	M	**5.44**	4.15	5.44	3.95
H.agilis	34.7.18.10	F	3.64	2.96	3.37	2.98
H.agilis	34.7.18.11	F	4.07	3.2	3.71	3.03
H.agilis	55.1486	F	4.9	3.95	4.99	3.5
H.moloch	54.5	M	5.07	3.8	5.1	3.94
H.moloch	1845.4.2.1	M	4.47	3.7	4.72	3.02
H.moloch	1938.11.30.1	M	4.93	4.13	4.94	3.8
H.moloch	1938.11.30.2	F	4	4	**4**	4.1
H.concolor	26.10.4.1	M	4.7	3.52	4.68	3.51
H.concolor	27.12.1.1	M	4.3	3.54	4.5	3.45
H.concolor	11.2.24.4	M	5.32	4.58	5.33	4.18
H.concolor	93.9.12.1	M	5.19	**2.98**	5.2	2.98
H.concolor	33.4.1.2	F	5.85	4.21	4.98	3.98
H.concolor	1.171655093	F	3.67	2.95	3.62	**2.95**
H.concolor	6.10.4.2	F	5.26	3.79	5.02	3.82
H.sundactylus	6.10.4.1	M	4.61	3.6	4.61	3.63
H.sundactylus	81.3.15.1	M	5.7	4.61	5.73	4.55
H.sundactylus	1920.1.26.1	M	5.13	4.36	5.04	3.81
H.sundactylus	2422.09	F	5.14	4.27	5.05	4.4
H.sundactylus	55.1483	F	4.89	4.19	4.32	4.01
H.sundactylus	19.11.12.2	F	5.91	4.4	5.79	4.1
H.sundactylus	19.11.12.3	F	5.01	4.16	4.67	4.04
H.sundactylus	1920.1.26.2	F	4.74	4.02	4.63	**4.02**
Colobus						
C.angolensis	27.12.21.1	M	4.69	**3.43**	4.55	3.43
C.angolensis	95.4.1.2	M	4.85	4.47	4.93	3.77
C.angolensis	27.3.1.2	M	5.18	4.76	5.11	4.65

C.angolensis	1926.7.6.1	F	5.21	4.65	4.92	4.53
C.angolensis	26.11.1.16	F	4.68	4.28	4.67	4.04
C.polykomos adolf-friedenici						
C.p.adolf-friedenici	38.8.1.13	M	4.51	4.07	4.34	3.58
C.p.adolf-friedenici	12.7.26.4	M	4.93	4.48	4.69	3.94
C.p.adolf-friedenici	29.5.14.21	F	4.13	3.25	4.15	3.27
C.p.adolf-friedenici	29.5.14.23	F	3.89	3.66	4.39	3.77
C.p.adolf-friedenici	29.5.14.22	F	4.41	3.6	4.16	3.21
C.p.ruwenzori	69.374	M	4.22	**2.95**	4.13	2.95
C.p.ruwenzori	49.711	M	4.13	**3.49**	4.09	3.49
C.p.ruwenzori	1912.7.26.5	M	4.79	4.26	5.07	3.84
C.p.ruwenzori	49.71	F	4.14	3.49	4.23	2.97
C.p.ruwenzori	69.373	F	4.24	4.22	4.2	4.11
C.cottoni	30.11.11.9	M	5.53	4.48	5.19	3.73
C.cottoni	1938.4.21.3	M	4.56	3.88	4.68	3.7
C.cottoni	1937.8.18.1	M	4.93	4.1	4.77	4.2
C.cottoni	64.2022	M	5.4	3.9	5.05	4.28
C.cottoni	30.11.11.10	F	4.91	3.51	4.98	3.64
C.cottoni	1907.7.8.9	F	4.94	4.11	4.53	4.06
C.cottoni	64.2023	F	4.92	4.05	5.41	4.04
C.cottoni	2.1.2.20	F	4.3	3.88	4.24	3.63
Presbytis						
P.rubicundus	55.728	M	3.81	3.24	3.99	3.3
P.rubicundus	1892.11.28.1	M	3.89	3.26	3.96	3.32
P.rubicundus	55.729	F	4.35	3.88	4.39	3.57
P.rubicundus	20.12.4.4	F	4.22	3.62	4.31	3.43
P.rubicundus	1955.73	F	4.61	3.58	4.54	3.58
P.frontata	10.4.5.12	M	4.19	3.41	4.29	3.5
P.frontata	10.4.5.16	M	4.12	3.55	4.18	3.46
P.frontata	10.4.5.13	F	4.35	3.75	4.16	3.87
P.frontata	10.4.5.14	F	4.26	3.97	4.29	3.9
Pygathrix	6.11.6.1	M	4.59	4.04	4.83	4.03
Pygathrix	8.11.1.2	M	4.96	4.12	4.88	3.72
Pygathrix	8.11.1.3	M	5.15	3.98	4.98	3.59
Pygathrix	26.10.4.5	F	4.81	4.19	4.97	3.98
Pygathrix	27.12.1.10	F	4.74	4.19	4.53	3.76
Nasalis	10.4.5.5	M	5.55	3.83	5.42	3.93
Nasalis	10.4.5.4	M	4.11	3.5	4.12	3.81
Nasalis	1867.4.12.34	M	5.67	4.38	5.99	3.97
Nasalis	10.4.5.9	F	5.82	4.4	5.56	4.36
Nasalis	10.4.5.7	F	5.53	4.09	5.22	3.92
Nasalis	1923.7.1.1	F	5.89	3.72	6.18	3.86
Macaca fuscata	39.105	M	6.76	5.18	**6.76**	5.08
Macaca fuscata	5.11.3.2	M	5.21	4.58	5.16	4.22
Macaca fuscata	5.11.3.5	F	5.93	4.39	6.04	**4.39**
Macaca fuscata	5.11.3.4	F	N\A	4.74	5.53	4.82
Macaca fuscata	50.8.15.2	F	6.11	5.22	5.92	4.48
Macaca fuscata	73.11.5.9	F	6.27	5.09	6.26	5.08
M. nigra	39.1057	M	7.13	4.55	7.1	4.92
M. nigra	34.1.1.1	M	5.7	4.1	6.25	3.92
M. nigra	45.4.2.5	M	6.5	4.79	6.29	4.78
M. nigra	39.1058	M	7.56	4.78	7.33	4.33
M. nigra	57.4.8.15	F	7.45	4.89	6.85	4.96
M. nigra	1966.5.18.1	F	7.62	4.43	7.42	4.38
Mandrillus	49.82	M	9.61	5.34	9.63	5.23

Mandrillus	1974.201	M	8.56	6.02	8.72	6.19
Mandrillus	1959.1.2.6	M	8.69	5.98	8.7	4.98
Mandrillus	49.87	M	9.7	6.24	9.8	**6.24**
Mandrillus	12.10.28.63	M	8.99	5.47	**8.99**	5.85
Mandrillus	49.89	F	6.01	4.13	6.08	4.24
Mandrillus	1975.195	F	8.87	4.81	8.44	4.61
Mandrillus	1974.2	F	8.89	5.9	8.19	5
Mandrillus	1974.22	F	9.88	6.1	9.83	5.71
Mandrillus	1974.216	F	8.36	5.29	8.74	**5.29**
Theropithecus	39.535	M	6.58	5.39	6.4	5.2
Theropithecus	25.12.21.1	M	6.25	5.39	6.11	5.14
Theropithecus	24.8.7.3	M	6.39	5.13	6.08	5.15
Theropithecus	21.11.25.1	M	7.17	5.26	7.25	5.66
Theropithecus	24.8.7.4	M	6.11	4.88	5.83	5.07
Theropithecus	1857.3.14.2	M	6.05	5.35	5.67	5.35
Theropithecus	24.8.7.5	F	5.01	4.11	4.72	4.35
Papio						
P. hamadryas	32.7.6.1	M	9.34	6.17	9.06	6.28
P. hamadryas	10.10.3.1	M	9.02	5.75	9.17	5.98
P. hamadryas	1900.6.28.1	M	8.91	6.51	8.7	6.14
P. hamadryas	1855.12.26.36	M	10.17	7.1	10.02	7.15
P. hamadryas	72.4494	M	9.51	6.67	9.74	6.15
P. amadryas	1939.1031	F	7.68	5.84	7.11	5.41
P. ursinus	4.5.1.1	M	9.48	7.15	9.82	6.92
P. ursinus	1862.6.26.1	M	10.25	7.13	10.31	7.06
P. ursinus	5.5.7.37	M	9.9	7.33	10.07	6.97
P. ursinus	8.7.19.1	M	10.81	7.16	10.83	7.47
P. ursinus	8.7.19.2	F	7.2	5.79	6.95	5.92
P. ursinus	1862.6.26.2	F	9.05	6.29	9	5.5
Cercopithecus						
C. diana	71.2328	M	5.65	**3.15**	5.59	3.15
C. diana	35.10.22.18	M	5.62	3.37	5.7	3.25
C. diana	75.4.30.1	M	5.55	**3.46**	6.02	3.46
C. diana	75.4.30.2	F	5.29	3.12	5.02	2.57
C. diana	1939.588	F	5.08	2.96	5.07	2.23
C. campbelli	56.31	M	4.97	3.38	4.92	2.61
C. campbelli	24.12.10.1	M	4.99	2.65	4.81	2.57
C. campbelli	56.322	M	5.46	2.78	5.22	2.81
C. campbelli	56.315	F	4.92	2.59	5.03	2.59
C. campbelli	35.10.22.9	F	4.7	2.89	5.16	2.39
C. campbelli	53.125	F	4.8	2.6	4.89	2.48
C. mitis	1961.8.9.5	M	5.65	3.02	5.58	2.87
C. mitis	16.2.26.1	M	5.75	3.69	5.88	3.32
C. mitis	1961.8.9.4	M	5.89	3.48	6.17	3.24
C. mitis	40.14	F	4.93	3.47	4.68	3.11
C. mitis	30.11.11.55	F	4.11	2.93	4.12	2.77
C. mitis	7.4.6.7	F	4.96	3.38	4.91	3.22
C. cephus	0.2.5.7	M	5.93	3.35	5.76	3.04
C. cephus	66.3624	M	5.4	2.98	5.37	2.93
C. cephus	1987.12.1.1	F	5.61	3.12	5.5	3.19
C. cephus	1855.12.26.30	F	5.53	3.32	5.56	**3.32**
C. cephus	1857.4.8.12	F	5.96	3.65	6.06	3.7
Cercocebus						
C. torquatus	30.12.15.8	M	7.75	5.04	7.45	4.73
C. torquatus	48.45	M	8.39	5.92	8.13	**5.92**

C. torquatus	3.2.4.2	M	7.42	5.83	7.72	5.44
C. torquatus	3.2.4.1	M	8.29	5.37	7.85	5.87
C. torquatus	1938.7.7.4	F	7.23	4.87	7.1	4.69
C. torquatus	5.5.23.3	F	6.71	4.12	6.85	4.15
C. albingena	30.12.16.6	M	6.87	4.44	7.35	4.65
C. albingena	32.8.1.18	M	7.03	4.11	6.99	4.33
C. albingena	61.7.29.15	M	6.88	4.33	6.7	4.41
C. albingena	57.8.3.2	F	**6.62**	**4.31**	6.62	4.31
C. albingena	32.8.1.19	F	6.82	3.71	6.61	3.88
C. albingena	32.8.1.20	F	7.13	3.96	6.62	3.7
Aotus	5.11.2.1	M	3.75	2.53	3.82	2.49
Aotus	28.5.2.63	M	3.65	2.3	3.57	2.24
Aotus	27.1.1.20	M	3.41	2.22	3.31	2.11
Aotus	22.5.31.1	F	2.98	1.99	3.02	1.92
Aotus	27.11.1.19	F	3.54	2.13	3.42	2.2
Aotus	94.3.6.4	F	3.43	1.88	3.23	1.89
Allouatta	39.1061	M	2.89	2.66	3	2.44
Allouatta	34.9.10.2	M	3.64	3.73	3.73	3.94
Allouatta	54.39	M	4.65	4.07	4.75	4.05
Allouatta	28.5.2.6	F	3.51	3.39	3.63	3.28
Allouatta	52.854	F	4.04	3.58	3.98	3.23
Allouatta	27.11.1.2	F	3.9	3.63	3.73	3.39
Cebus	3.9.4.18	M	4.65	3.55	4.67	3.38
Cebus	34.9.2.4	M	4.73	3.94	4.39	3.82
Cebus	26.11.4.1	M	4.28	3.3	4.19	3.15
Cebus	3.3.1.12	F	4.35	3.24	4.23	3.33
Cebus	2.3.5.18	F	4.59	3.64	3.94	3.66
Cebus	5.5.4.2	F	4.27	3.48	4.06	3.62
Simari	27.1.1.12	M	2.94	2.27	2.93	2.38
Simari	27.1.1.11	M	2.77	1.88	2.72	1.91
Simari	28.5.2.60	M	2.78	2.02	2.77	1.9
Simari	27.1.1.18	F	2.66	1.79	2.36	1.84
Simari	27.1.1.16	F	2.79	1.82	2.56	1.9
Simari	28.5.2.54	F	2.85	1.76	2.79	1.68
Ateles	28.4.27.1	M	5.58	3.7	5.42	3.78
Ateles	27.8.11.26	M	5.15	3.69	4.81	3.48
Ateles	13.6.13.3	M	5.6	3.78	5.46	3.44
Ateles	27.3.6.2	F	4.94	3.92	5.01	3.7
Ateles	28.5.2.2	F	5.3	3.32	5.3	3.51
Ateles	28.4.27.2	F	5.02	3.73	4.83	3.62
Brachyteles	3.9.4.3	M	4.04	4.21	4.17	3.98
Brachyteles	3.9.4.5	M	3.99	3.83	**3.99**	3.59
Brachyteles	70.1982	M	3.5	3.5	3.57	3.66
Brachyteles	1848.10.25.2	F	3.56	3.47	3.75	3.45
Lagothrix	28.5.2.32	M	4.39	3.8	4.42	3.34
Lagothrix	28.5.2.31	M	4.36	3.54	4.52	3.51
Lagothrix	0.7.7.1	M	4.09	3.88	4.17	3.83
Lagothrix	28.5.2.37	F	4.45	3.89	**4.45**	4.16
Lagothrix	28.5.2.33	F	4.38	3.92	3.99	3.73
Lagothrix	0.11.5.13	F	4.64	3.96	4.64	4.05
Callicebus	34.6.14.2	M	3.11	1.83	2.9	2.06
Callicebus	14.3.1.1	M	3	2.24	2.84	2.26
Callicebus	28.4.27.7	M	3.2	2.21	3.38	2.45
Callicebus	27.8.11.63	F	3.05	2.15	3.05	2.15
Callicebus	28.4.27.8	F	2.95	2.35	2.95	2.09

Callicebus	25.12.11.8	F	3.09	2.39	2.95	2.33
Cacajao	28.4.27.4	M	4.22	3.17	4.21	3.04
Cacajao	28.5.2.39	M	4.31	3	4.59	2.98
Cacajao	34.6.14.1	M	3.99	3.06	4.19	3.02
Cacajao	28.4.27.5	F	3.95	3.03	3.9	2.96
Cacajao	28.4.27.6	F	4.35	3.14	4.38	3.04
Cacajao	27.3.6.6	F	4.06	3.25	4.24	3.11
Chiropotes	4.7.4.7	M	3.48	2.47	3.48	2.46
Chiropotes	30.11.9.3	M	3.52	2.42	3.51	2.23
Chiropotes	4.7.4.103	M	3.32	2.59	3.16	2.54
Chiropotes	4.7.4.9	F	3.4	2.39	3.19	2.45
Chiropotes	4.7.4.10	F	3.04	2.5	2.79	2.44
Chiropotes	4.7.4.8	F	2.87	2.41	3.18	2.45
Pithecia	25.12.11.6	M	3.64	2.5	3.61	2.53
Pithecia	20.7.14.4	M	3.5	2.68	3.53	2.49
Pithecia	20.7.14.5	F	3.28	2.45	3.3	2.36
Pithecia	25.12.11.5	F	3.21	2.14	3.29	2.18