MORPHOLOGICAL EVOLUTION OF THE EXTANT HOMINOIDS AND PAPIONINS: IMPLICATIONS FOR PALAEOANTHROPOLOGICAL CLADISTICS

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Mark Collard

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Hominid Palaeontology Research group, Department of Human Anatomy and Cell Biology,

The University of Liverpool, PO Box 147, Liverpool, L69 3BX

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ABSTRACT

The main purpose of the present study was to test the assumption on which most recent cladistic analyses of the early hominids and other fossil primates have been based. Namely that standard cranial and dental characters are reliable for reconstructing the cladistic relationships between primate species and genera. Two secondary hypotheses were also examined. The first was that some regions of the primate cranium are more reliable than others for reconstructing the cladistic relationships between species and genera. The second was that male and female primate crania differ in their reliability for reconstructing the cladistic relationships between species and genera. To test these hypotheses, craniometric data sets for the extant large-bodied hominoid genera and the extant papionin genera were compiled from standard palaeoanthropological measurements. Character state data matrices were derived from these 'model fossil assemblages' using several widely used size-adjustment techniques and coding procedures. Thereafter, the matrices were analyzed with a number of cladistic techniques (e.g. parsimony, bootstrapping). The resulting phylogenetic hypotheses were compared with the consensus molecular cladograms for the hominoids and papionins, which, for several reasons, were assumed to be correct.

The hypothesis that standard cranial and dental characters are reliable for reconstructing the cladistic relationships between primate species and genera was not supported by the analyses incorporated in the study. Neither was the hypothesis that some regions of the primate cranium are more reliable than others for reconstructing the cladistic relationships between species and genera. However, the third hypothesis was supported by the analyses. Female crania were found to be more reliable for phylogenetic reconstruction than male crania when characters from all regions were analyzed together. The analyses also revealed some regional differences between the sexes. Males were more reliable for phylogenetic reconstruction when characters from the man-

dible and lower dentition were analyzed, whereas females were more reliable when characters from the face and the cranial vault and base were examined. Palate characters did not exhibit sex-related differences in their reliability for phylogeny estimation.

The lack of support among the analyses for the principal hypothesis suggests that we should not rely on any of the cladistic hypotheses for the early hominids and other fossil primates that have been based on craniodental evidence. Most probably, these hypotheses reflect the phylogenetically misleading effects of convergence, parallelism and/or reversal rather than the phyletic history of the taxa. Likewise, the lack of support for the second hypothesis challenges the approach to data set and cladogram selection which is based on the assumption that some regions of the primate cranium are more reliable than others for phylogeny estimation. Lastly, the tests of the third hypothesis suggest that, when specimens can be sexed (e.g. fossil papionins) and the cranium can be evenly sampled for characters, palaeoanthropological cladists should base their analyses on female specimens. Analyses should also be based on female specimens when characters are taken only from the face or the cranial vault and base. In contrast, when examining mandible and lower dentition characters, analyses should be based on male specimens. Only when analyzing characters from the palate and upper dentition can the sex of the specimens be disregarded.

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CHAPTER 1. INTRODUCTION

1.1. INTRODUCTION TO THE STUDY

1.1.1. HYPOTHESES AND APPROACH

The main purpose of the present study was to test the assumption on which all recent cladistic analyses of the early hominids and other fossil primates have been based. Namely, that standard cranial and dental characters are reliable for reconstructing the cladistic relationships between primate species and genera. Testing this hypothesis was a priority because it has become clear in the last few years that, contrary to expectation, the use of cladistics in palaeoanthropology has not significantly improved our understanding of fossil primate interrelationships (Corruccini, 1994; Wood, 1994b; Pilbeam, 1996). Despite an explosive increase in the rate of recovery of primate fossils and considerable improvements in cladistic techniques, most of the important phylogenetic problems that troubled the early palaeoanthropological proponents of cladistics in the mid-1970s have yet to be resolved. Indeed, for many groups, including the intensively studied Plio-Pleistocene hominids, the range of phylogenetic hypotheses put forward by those who study the fossils has actually increased since the pioneering efforts of Delson (1975; 1977a; 1977b), Delson and Andrews (1975) and Eldredge and Tattersall (1975) first appeared in print.

Two secondary hypotheses were also examined in the study. The first was that some regions of the primate cranium are more reliable than others for reconstructing the cladistic relationships between species and genera. This hypothesis is significant because palaeoanthropologists have often used arguments about the phylogenetic reliability of the different cranial regions to discriminate between different data sets and competing cladistic hypotheses. For example, Skelton

and McHenry (1992; see also McHenry, 1994a; 1996) argued that the alternative to their favoured cladogram was unreliable because it was based mainly on traits associated with mastication. Masticatory traits, they contended, are likely to reflect the ecological similarities between taxa more strongly than their phylogenetic relationships. This, they argued, is evidenced by the occurrence of traits relating to heavy chewing in distantly related taxa, such as *Hadropithecus*, *Paranthropus* and *Theropithecus*. Similarly, Wood (1988; 1994b; see also Turner and Wood, 1993) has suggested that phylogenetically misleading characters are common in the early hominid masticatory system, and Begun (1994a) has claimed that the hominoid mandible is an especially poor source of phylogenetically informative characters.

The third hypothesis examined in the study was that male and female primate crania differ in their reliability for reconstructing the cladistic relationships between species and genera. The main reason for testing this hypothesis was that some recent analyses have indicated that the sexual composition of samples affects phylogeny estimation, while others have suggested that it does not. Creel (1986), for example, found that cladograms generated from male hominoid craniometric data did not differ from those generated from female data, whereas Hartman's (1988) male data yielded cladograms that differed markedly from those recovered from his female data.

The approach used to test the three hypotheses was similar to the one employed by Hartman (1988) in his assessment of the utility of hominoid molar morphology for phylogenetic reconstruction (see also Baum and Estabrook, 1978; Baum, 1983). Craniometric data sets for the extant large bodied hominoid genera and the extant papionin genera were compiled from standard palaeoanthropological measurements. Character state data sets were then derived from these 'model fossil assemblages' using several size adjustment techniques and coding procedures. Thereafter, the matrices were analyzed with a number of cladistic techniques (e.g. parsimony,

compatibility, bootstrapping), and the resulting phylogenetic hypotheses judged against the consensus molecular estimates of interhominoid and interpapionin affinities (figures 1 and 2).

1.1.2. STRUCTURE OF THESIS

This thesis is presented in six chapters. In the remainder of this chapter, the concepts and techniques that are central to the study, including phylogeny, homology and cladistics, are introduced. Chapter 2 presents a review of early hominid cladistics in order to illustrate the problems currently facing palaeoanthropological cladists. Chapter 3 discusses the evidential support for the hominoid and papionin molecular phylogenies on which the study was based. The fourth chapter gives details of the skeletal materials and analytical methods used to generate the morphological cladograms, and explains how they were compared with the consensus molecular cladograms. The results of the hominoid and papionin analyses are reported in Chapter 5. In the final chapter, the reliability of the tests is appraised, and the implications of the results for palaeoanthropological cladistics discussed.

1.2. INTRODUCTION TO SOME CONCEPTS

1.2.1. PHYLOGENY

A phylogeny, or phylogenetic tree, is a representation of the genealogical relationships among a group of biological or cultural entities (e.g. genes, individuals, species, genera, language groups) (Stewart, 1993). Phylogenies play several important roles in evolutionary biology (Harvey and Pagel, 1991; Miles and Dunham, 1993; Smith, 1994; Powell and DeSalle, 1995; Huelsenbeck and Rannala, 1997). Most significantly, phylogenies form the basis of biological classification, which is a prerequisite of the scientific study of the diversity of life. Currently, classification in

biology entails arranging species into hierarchical groups according to their characteristics, placing them in the Linnaean system of categories (e.g. genus, family, order, class), and giving a name to each of the category groups (e.g. *Homo*, Hominidae, Primates, Mammalia) (Simpson, 1945). Phylogeny is central to this process as there is general agreement among evolutionists that classifications should be based on naturally occurring groups, and that the only groups in which species occur naturally are those that result from speciation (Forey, 1992). While there are problems with the classification of fossil taxa (Forey, 1992; Michelson, 1996), and some concern about the on-going adequacy of the Linnaean hierarchy as a system of classification (e.g. Ridley, 1993; Valentine and May, 1996), there is general agreement that to produce an acceptable classification it is first necessary to reconstruct the phylogeny of the taxa to be classified (Smith, 1994).

A second role for phylogenetic hypotheses involves testing evolutionary hypotheses that posit causal relationships between characters (Harvey and Pagel, 1991; Maddison and Maddison, 1992). As Maddison and Maddison (1992) explain, traditionally if a biologist found that two traits were positively correlated in a sample of species and the correlation was statistically significant, he or she probably would have hypothesized that species with large values for one of the traits had been selected to have large values in the other trait, or vice versa. Today, however, it is recognized that such hypotheses are only valid if the species behave effectively as independent data points. If, for example, the species with large values were found to be descended from an ancestor that was not also shared by the species with small values, there would be reason to doubt the hypothesis, since in the analysis the species would have acted as two data points, one with large values and one with small values. A concrete example of this form of phylogenetic test is provided by Donoghue (1989), who used a composite of previously published seed plant phylogenies to refute Givnish's (1980) hypothesis that the observed

correlation between dioecy (male and female reproductive structures on separate plants) and animal dispersal of fleshy propagules in gymnosperms is the result of natural selection.

A third role for phylogenetic hypotheses is essentially the obverse of the one just described. If it can be demonstrated that two characters are associated in a number of distantly related taxa, then there is a firm base on which to construct a hypothesis which links them causally (Brooks and McLennan, 1991; Sanderson, 1991). One such well founded hypothesis has recently been presented by Hunter and Jernvall (1995). Using previously published phylogenies, these authors carried out two analyses designed to elucidate the evolutionary potential of the hypocone (a cusp added to the primitive triangular upper molar teeth of therian mammals). In the first, they examined the correlation between hypocone possession, diversity at the level of the family and species, and diet in a sample of extant mammals. They discovered that among extant taxa there is a strong positive correlation between hypocone possession and taxic diversity. They also found that taxa with hypocones tend to be either herbivores or generalists; very few extant faunivores have hypocones. In their second analysis, Hunter and Jernvall investigated the correlation across time between hypocone possession and taxic diversity in a large sample of fossil mammals. This analysis suggested that hypocones evolved independently more than twenty times during the Cenozoic and are strongly correlated with high species diversity. Hunter and Jernvall suggested that hypocones allow species to process grasses and other fibrous plants which other mammals cannot exploit. Since these plants are rich in energy, they can sustain larger animal populations than other resources. As the probability of extinction is linked to population size, one consequence of this is to lower the extinction rate for herbivores. Lower extinction rates on an ecological time scale can be expected to appear as an increase in diversity on a palaeontological time scale, because persistence increases the probability that a taxon will be sampled in the fossil record. Hence, in the mammalian fossil record, there is a strong correlation between hypocone possession and taxic diversity. In recent years, studies similar to

Hunter and Jernvall's have examined the relationship between hypercarnivory and taxic diversity in the carnivore guild (Van Valkenburgh, 1991), the evolution of social traits among the primates (DiFiore and Rendall, 1994), and the influence of temperature variation on enzyme concentration in the American teleost fish (Pierce and Crawford, 1997). The same general approach has also been used to investigate whether a significant increase in diversification coincided with the origin of angiosperms and their evolutionarily novel features (Sanderson and Donoghue, 1994).

A fourth role for phylogenetic hypotheses is that they enable hypotheses about character state evolution to be evaluated (Coddington, 1988; Lauder, 1990; Baum and Larson, 1991; Winterbottom and McLennan, 1993; Anderson, 1994; Losos and Miles, 1994). Clearly any such hypothesis can be refuted by showing that the historical sequence of events was other than the one proposed. For example, Werdelin (1993) has recently used a consensus phylogeny for the cat family, Felidae, to refute Weigel's (1961) that felid coat patterns evolved through the breakdown of a primitively uniform coat color into large spots and, subsequently, rosettes and smaller spots, with sidelines leading to stripes. Werdelin demonstrated that when the distribution of coat patterns was mapped on to a consensus phylogeny for the felids, neither of the resulting simplest character state transformation series was in line with Weigel's hypothesis. Instead, the transformation series suggested that the primitive condition from which the other coat patterns are derived is either small spots or stripes. The approach adopted by Werdelin has also been used in recent years to investigate the evolution of different life history stages among extant Mexican ambystomatid salamanders (Shaffer, 1984) and post-Palaeozoic echinoids (Smith et al., 1996), the development of the sword-like caudal fin in the platyfish and swordtail genus *Xiphophorus* (Meyer et al., 1994) and the evolution of pelagic modes of life in the Antarctic fish family Nototheniidae (Klingenberg and Ekau, 1996).

A fifth use for phylogenetic hypotheses has recently been outlined by Werdelin (1993; see also Werdelin and Solounias 1991). This author demonstrated how, with the aid of a phylogeny and a method for reconstructing ancestral states, it is possible to determine whether the evolution of a metric trait has been a gradual process, or whether it has been marked by periods of stasis and other periods of rapid change. Werdelin focused on the relative width of the hyaenid P_3, but the approach he adopted can be used to examine the tempo and mode of evolution of many continuously varying characters. By reconstructing the relative width of the P_3 at each branching point in a phylogeny for the Hyaenidae, Werdelin was able to generate a plot of changes in relative width against cladogenic events, i.e. of change per speciation event. His analysis demonstrated that the evolution of the hyaenid P_3 has essentially been a gradual phenomenon without any marked punctuations and stasis. It also showed that when rapid morphological change has occurred, it has coincided with times of increased speciation.

1.2.2. HOMOLOGY

Homology is perhaps the most important concept for those involved in phylogenetic reconstruction, since it underlies the choice of characters from which phylogenies are reconstructed (Minelli, 1993; Quicke, 1993; Smith, 1994). While it has been treated in a number of different ways in recent years (e.g. Rieppel, 1980, 1988, 1992; 1993; Van Valen, 1982; Roth, 1984, 1988. 1991; Wagner, 1989a, 1989b; de Pinna, 1991; Hall, 1992, 1994, 1995), most phylogeneticists currently employ the so-called taxic view of homology (e.g. Eldredge and Cracraft, 1980; Wiley, 1975, 1981; Nelson and Platnick, 1981; Patterson, 1982, 1988; Stevens, 1984; MacPhee, 1993; Cartmill, 1994; Smith, 1994). This concept equates homology with 'synapomorphy'. Also referred to as a shared derived character state, a synapomorphy is a character state that is inferred to have been inherited by a group of taxa from their most recent common ancestor (Donoghue, 1992).

Patterson (1982) outlined three tests for homology as synapomorphy, which have since become widely accepted among evolutionists (Smith, 1994). In order of increasing ability to discriminate between homology and non-homology, these are similarity, conjunction and congruence. The similarity test simply holds that homologous character states should resemble one another in their form, topological position and ontogeny. The test of conjunction excludes an assumption of homology between the character states of two taxa if those character states co-exist in another taxon. The test of congruence states that, as homologies define phylogenetic relationships, character states thought to be homologous must be congruent with the phylogenetic relationships defined by other homologies. That is, they must define the same set of phylogenetic relationships as the other homologies, or a subset of those relationships, or a larger set that subsumes them.

1.2.3. HOMOPLASY

Homoplasy is defined by Wiley (1981: 12) as "characters that display structural (and thus ontogenetic) similarities but are thought to have originated independently of each other, either from two different pre-existing characters or from a single pre-existing character at two different times or in two different species." In other words, a resemblance between two or more taxa is considered to be homoplastic if, according to the most parsimonious phylogeny, it was not present in their last common ancestor (Wiley, 1981; Eaglen, 1983). As such, homoplasies only make sense in relation to a phylogeny; they cannot be objectively identified prior to a phylogenetic analysis being carried out (Eaglen, 1983; DeSalle, 1994; Sundberg and Svensson, 1994; Bowler, 1996).

It is widely accepted that there is more than one sort of homoplasy, but opinions vary as to how many kinds there are, and what distinguishes them (e.g. Simpson, 1961; Cain, 1982; 1983; Pat-

terson, 1982; Rieppel, 1989; Wake, 1991; Minelli, 1993; Quicke, 1993; Smith, 1994; Bowler, 1996; Lieberman et al., 1996). Here, three forms of homoplasy are recognized. These differ with respect to the role played by natural selection in their evolution. The first, convergence, involves the independent development of the same character states in two or more taxa as a result of the taxa experiencing similar selective forces (Simpson, 1961; Bowler, 1996; Lieberman et al., 1996). Convergent homoplasies are, in other words, a results of adaptation to similar habits in a similar environment (Bowler, 1996). Defined in this way, convergence includes the form of homoplasy that is conventionally referred to as 'analogy' (e.g. Simpson, 1961; Ridley, 1993; Lieberman et al., 1996).

The second form of homoplasy identified here, parallelism, differs from convergence in that natural selection plays no role in its evolution. Parallelism entails the development of similar character states in two or more closely related taxa through aspects of development that limit the range of patterns in the living world but have no necessary connection with the demands of the environment (e.g. segmentation) (Wake, 1991; Gould, 1995; Bowler, 1996; Goodwin, 1996). Parallelisms, in other words, are by-products of the developmental process; they are not adaptations.

The final kind of homoplastic change recognized here is the reversal of character states, where, for example, a change in coat pattern from striped to spotted is followed by a change from spotted to striped (Simpson, 1953; Minelli, 1993). Most cases of reversal are probably due to natural selection, but the authors of a recent assessment of silenced gene reactivation have suggested that reversal may also be adaptively neutral (Marshall et al., 1994).

Most commonly accepted examples of homoplastic similarity involve particular characters (e.g. the gnawing incisors of lagomorphs and rodents), organs (e.g. the eyes of vertebrates and cepha-

lopods) or general shape and proportions (e.g. the hydrodynamic form of fish and dolphins) (Mayr and Ashlock, 1991; Ridley, 1993; Graur et al., 1995; Bowler, 1996). In some cases, however, homoplasy is much more pervasive. For example, the monophyletic status of the hawk and eagle order Falconiformes is currently the subject of considerable debate as a result of homoplasy. Most of the morphological traits of the New World vultures resemble those of the African and Eurasian vultures. However, a number of morphological traits and DNA-DNA hybridization experiments suggest that the condors (*Vultur*, *Gymnogyps*) and other New World vultures are more closely related to the storks than they are to the Old World vultures (Sibley and Ahlquist, 1983; 1985; 1987b; 1990; Sibley et al., 1988). Significantly, both hypotheses imply the existence of a large amount of homoplasy. The phylogenetic relationships of the giant panda (*Ailuropoda*) are also confused as a result of homoplasy. Most anatomical, immunological and karyological analyses (Zhang and Shi, 1991; Wayne, 1993), as well as DNA-DNA hybridization and isozyme electrophoresis experiments, have suggested that *Ailuropoda* is a member of the bear family (Ursidae). However, evidence from the viscera, skull, dentition, haemoglobin and mtDNA, together with ethological observations, indicate that *Ailuropoda* should be grouped with the lesser panda (*Ailurus*) in the raccoon family Procynidae (Gregory, 1936; Raven, 1936; Zhang and Shi, 1991). Again, a large amount of homoplasy is implied whichever hypothesis is adopted. Other frequently cited examples of pervasive homoplasy include the resemblances between the extant placental wolf (*Canis lupus*) and the Miocene Tasmanian marsupial wolf (*Thylacinus cynocephalus*), the character states shared by the Pliocene South American sabre-toothed marsupial carnivore *Thylacosmilus* and the Pleistocene North American sabre-toothed placental carnivore *Smilodon* and the numerous similarities between the modern placental jerboas (e.g. *Dipus*, *Jaculus*, *Allactaga*) and the marsupial 'jerboa' kangaroo *Bettongia* (Simpson, 1945; Ridley, 1993).

1.2.4. CLADISTICS

First coherently formulated by Hennig (1950; 1965; 1966), cladistics is a method for reconstructing the phylogeny of a group of taxa from the distribution among them of evolutionarily novel character states (Eldredge and Cracraft, 1980; Wiley, 1981; Patterson, 1980; Ridley, 1986; Ax, 1987; Scott-Ram, 1990; Pankhurst, 1991; Wiley et al., 1991; Minelli, 1993; Quicke, 1993; Smith, 1994). Based on the assumption that all taxa belong to a single evolving lineage, cladistics defines phylogenetic relationship in terms of relative recency of common ancestry, such that a pair of taxa are more closely related to one another than either is to a third taxon if they share a common ancestor that is not also shared by the third taxon (Hennig, 1966; Eldredge and Cracraft, 1980; Ax, 1987). In the cladistic method, taxa that can be inferred to share a common ancestor to the exclusion of the others in the sample are referred to as a clade or monophyletic group. The aim of a cladistic analysis of any group of taxa is to identify their clade hierarchy (Forey, 1990; 1992).

In its simplest form, cladistic analysis proceeds via three steps (McHenry, 1996). First, the probable direction or 'polarity' of evolutionary change among the character states exhibited by the group of taxa is established (e.g. mental eminence absent → mental eminence present, small supraorbital tori → medium supraorbital tori → large supraorbital tori). Several methods have been developed for polarizing the states of a character, including communality (Crisci and Stuessy, 1980; Eldredge and Cracaft, 1980), ontogeny (Nelson, 1978; Nelson and Platnick, 1981; Patterson, 1982, 1983; de Queiroz, 1985; Wheeler, 1990) and stratigraphic sequence analysis (Szalay, 1977; Nelson and Platnick, 1981; Schoch, 1986; Fortey and Chatterton, 1988; Fortey, 1990). The method favoured by most evolutionists, especially those working with fossil material, is outgroup analysis (Arnold, 1981; Watrous and Wheeler, 1981; Farris, 1982; Maddison et al., 1984; Clark and Curren, 1986; Smith, 1994). Outgroup analysis entails examining a close

relative of the study group in order to ascertain the states of each character at more inclusive levels of the clade hierarchy (Wood, 1989b; Smith, 1994). When a character occurs in two states among the group under study, but only one of the states is found in the 'outgroup', it is assumed that the state found only in the study taxa is evolutionarily novel or 'derived' with respect to the outgroup state (Wiley, 1981; Wood, 1989b; Forey, 1990; Smith, 1994).

Having determined the probable direction of change for the character states, the next step in a cladistic analysis is to construct a branching diagram of relationships for each character (McHenry, 1996). As shown in Figure 3, this is done by joining the two most derived taxa by two intersecting lines, and then successively connecting each of the other taxa according to how derived they are (McHenry, 1996). Each group of taxa defined by a set of intersecting lines corresponds to a clade, and the diagram is referred to as a 'cladogram' or 'tree'.

The final step in a cladistic analysis is to compile an ensemble cladogram from the character cladograms (McHenry, 1996). Ideally, the distribution of the character states among the taxa will be such that all the character cladograms imply relationships among the taxa that are congruent with one another. Normally, however, a number of the character cladograms will suggest relationships that are incompatible. When such 'character conflict' occurs, it is presumed that some of the characters reflect the real clade hierarchy, and others reflect false ones. The most popular way of resolving character conflict is to generate an ensemble cladogram that is consistent with the largest number of characters and therefore requires the smallest number of *ad hoc* hypotheses of homoplasy, to account for the distribution of character states among the taxa (McHenry, 1996). Known as parsimony analysis, this technique is usually defended in relation to the principle of parsimony, a methodological injunction which states that scientific explanations should not be made more complicated than they need be (see Eldredge and Cracraft, 1980; Nelson and

Platnick, 1981; Wiley, 1981; Crisci, 1982; Farris, 1983; Kluge, 1984; Brady, 1985; Rieppel, 1989; Forey, 1990; 1992; Stewart, 1993).

Several methods of assaying the 'fit' between an ensemble cladogram and a character state data set have been developed (e.g. Farris, 1989a; 1989b; Kluge and Farris, 1969; Archie, 1989; Meier et al., 1991). The most popular among palaeoanthropologists is the consistency index or CI of Kluge and Farris (1969). A measure of how parsimonious evolution has been, the CI for a single character is calculated by dividing the minimum number of character state changes required by any conceivable cladogram (*m*) by the number of changes required by the focal cladogram (*s*) (Swofford, 1991b). The CI for two or more characters is computed as *M/S*, where *M* and *S* are the sums of the *m* and *s* values for the individual characters (Swofford, 1991b). A CI of 1 indicates that the data are perfectly congruent with the cladogram (i.e. the cladogram requires no homoplastic changes to be hypothesized), and homoplasy levels increase as the CI decreases (Swofford, 1991b).

A second method of assessing the congruence between a cladogram and a data set is the retention index (RI) of Farris (1989a; 1989b). Equivalent to Archie's (1989) homoplasy excess ratio maximum index (Farris, 1989b; 1991; Archie, 1989; Swofford, 1991b), the RI is a measure of the number of homoplastic changes a cladogram requires that are independent of its length (Farris, 1989b; 1989b). The RI of a single character is calculated by subtracting the number of character state changes required by the focal cladogram (*s*) from the maximum possible amount of change required by a completely unresolved cladogram, i.e. a cladogram in which all the taxa are equally closely related (*g*) (Swofford,1991b). The resulting figure is then divided by the product of subtracting the minimum amount of change required by any conceivable cladogram (*m*) from *g* (Swofford, 1991b). As with the ensemble consistency index, the RI of two or more characters is computed as $(G - S)/(G - M)$, where *G*, *S* and *M* are the sums of the *g*, *s* and *m* val-

ues for the individual characters (Swofford, 1991b). A maximum RI of 1 indicates that the cladogram requires no homoplastic change, and the level of homoplasy increases as the index approaches 0 (Swofford, 1991b).

Bootstrapping offers an alternative method of assessing cladogram reliability. The phylogenetic bootstrap was originally developed by Felsenstein (1985) as a way of estimating the statistical likelihood of a given clade being real. However, due to several recent critiques (e.g. Carpenter, 1992; Kluge and Wolf, 1993; Mishler, 1994) bootstrapping is now considered by many researchers to be a heuristic tool rather than a statistical test (Disotell, 1992). In bootstrap analysis, a large number of subsets of data (normally 50 to 1000) are randomly sampled with replacement from the character state data set (character state assignments are retained in each sample). Minimum length cladograms are then computed from these subsets of the data, and a list of the clades that comprise the cladograms is compiled. Lastly, the percentage of the resampling cladograms in which each clade was found is calculated. Currently there is no consensus as to the percentage of bootstrap cladograms in which a clade should occur for it to be considered reliable. Some workers favour Felsenstein's (1985) original ≥95% criterion, while others have suggested that clades can occur in 70% of bootstrap cladograms and still be real (e.g. Hillis and Bull, 1993).

CHAPTER 2. EARLY HOMINID CLADISTICS

As indicated in the previous chapter, the present study was prompted in large part by the realization that, contrary to expectation, the widespread adoption of cladistic methodology has not substantially improved our understanding of fossil primate phylogenetics. To illustrate this, in the present chapter the most intensively studied group of fossil primates, the early hominids, are introduced and the application of cladistics to the study of their phylogenetic relationships reviewed.

2.1. EARLY HOMINIDS

2.1.1. DEFINITION OF HOMINID

'Hominid' is the informal term for a member of the Linnaean taxon Hominidae, which is defined taxonomically as the family containing the genus *Homo* (Simpson, 1945). Cladistically, Hominidae is defined as the monophyletic group comprising all the species whose common ancestor is more closely related to *Homo sapiens* than to any other living primate (Chamberlain, 1987). In recent years, the increasing molecular evidence for a closer phylogenetic relationship between the African apes and humans than between the African apes and the orangutan (see Chapter 3) has led some authors to include the African ape genera, *Gorilla* and *Pan*, as a subfamily (Gorillinae or Paninae) within Hominidae (e.g. Andrews and Cronin, 1982; Andrews, 1985; 1992; 1995; Richard, 1985) and others to include *Homo*, *Pan* and *Gorilla* in the same subfamily Homininae (e.g. Goodman, 1986; Groves, 1986; 1989). Neither of these nomenclatural changes is adopted here, however, as they are based on an assumption about the relationship between the Linnaean hierarchy and cladistic hypotheses that is currently the subject of considerable debate

(e.g. Stevens, 1985; de Queiroz and Gauthier, 1990; 1992; Martin, 1990; Mayr and Ashlock, 1991; Forey, 1992; Panchen, 1992; Valentine and May, 1996).

2.1.2. HOMINID ORIGINS

Dating the first appearance of the hominid clade palaeontologically is difficult because the fossil record of the apes between 12 and 4 million years ago (Myr) is poor (Pilbeam, 1996; Wood, 1996a). With the advent of molecular biology, however, it has become possible to use differences in the proteins and the DNA of extant species to estimate how long their gene pools have been separate (e.g. Zukerkandl and Pauling, 1965; Sarich and Wilson, 1967; Wilson et al., 1987). As currently implemented, this 'molecular clock' approach is based on Kimura's (1968; 1983) hypothesis that many, if not most, of the mutations that occur naturally in an organism's DNA are neutral with respect to natural selection. If it is assumed that these mutations have been occurring at the same rate through time and across lineages, the number of differences between a pair of taxa can be used to estimate when they last shared a common ancestor (Wilson et al., 1987). Recent applications of this method to the problem of human origins indicate that the hominid lineage first appeared between 8 and 4.5 Myr (Hasegawa et al., 1987; Sibley and Ahlquist, 1987a; Bailey et al., 1992a; Horai et al., 1995; Takahata, 1995).

2.1.3. HOMINID CHARACTERISTICS

For many years, the hominid clade was thought to be distinguished from the living and extinct apes by three complexes of derived traits (Aiello and Dean, 1990). The first was associated with a reduction in the dentition, particularly in the anterior dentition, while the second related to brain size increase. The third complex comprised adaptations to bipedal posture and gait, including changes to the pelvis and lower limbs, and a foramen magnum that is centrally located

and horizontally oriented. However, as Aiello and Dean (1990) have observed, it is now doubtful that the dental and brain size related traits are synapomorphic for the hominid clade. Dental reduction does not clearly discriminate the hominids from the other hominoid species, since the teeth of the earliest hominid species are more similar to the teeth of the Miocene apes than they are to the teeth of *H. sapiens*. Likewise, even allowing for the uncertainties involved in predicting body masses for extinct species, it is clear that when controlled for body mass the brains of a number of the early hominids were little, if at all, larger than those of the great apes. Relative brain size among the hominids only exceeds the observed range of variation seen in living non human primates after around 2 Myr.

Of the three complexes that were traditionally thought to distinguish the hominids from other primates, only the adaptations to bipedal posture and gait appear to be synapomorphies (Aiello and Dean, 1990). Yet even these are more ambiguous than they were once thought to be. Evidence from the lower limb suggests that the bipedalism practiced by a number of the early hominid species may not have been the same as that exhibited by *H. sapiens*, while evidence from the upper limb suggests that terrestrial bipedalism may not been their only form of locomotion (McHenry, 1994a; 1994b). The first unambiguous evidence for modern human like bipedal locomotion is the nearly complete juvenile male skeleton from West Turkana, KNM WT 15000. This specimen is more than three million years younger than the earliest hominid fossils.

2.1.4. EARLY HOMINID TAXONOMY

The family Hominidae comprises four genera: *Australopithecus*, *Ardipithecus*, *Paranthropus* and *Homo* (Tattersall, 1996; Wood, 1996a). *Australopithecus* was proposed in the mid 1920s (Dart, 1925), but was not fully accepted as a taxon until the late 1940s (Tattersall, 1996). *Australopithecus* includes *Plesianthropus* Broom 1937 as a junior synonym, and has three

species assigned to it: *Australopithecus afarensis*, *Australopithecus africanus* and *Australopithecus anamensis*. The second genus, *Ardipithecus*, was proposed by White et al. (1995) for material they had previously assigned to *Australopithecus* (White et al., 1994). Currently, *Ardipithecus* has just one species referred to it: *Ardipithecus ramidus*. The genus *Paranthropus* was initially proposed in the late 1930s (Broom, 1938). However, it has been widely accepted as a valid taxon only in the last decade, following the studies of, among others, Olson (1978; 1985), Dean (1986), Wood and Chamberlain (1986), Chamberlain and Wood (1987) and Kimbel et al. (1988). Previously, *Paranthropus* was considered by the majority of workers to be a junior synonym of *Australopithecus*, with the species now assigned to it commonly being referred to as the 'robust' australopithecines (Simpson, 1945; Le Gros Clark, 1964; Howell, 1978). *Paranthropus* includes two sunk genera, *Zinjanthropus* Leakey 1959 and *Paraustralopithecus* Arambourg and Coppens 1967 (Chamberlain, 1987), and has three species assigned to it: *Paranthropus robustus*, *Paranthropus boisei* and *Paranthropus aethiopicus*. The fourth genus, *Homo*, is attributed to Linnaeus (1758). As the type genus of the family Hominidae, *Homo* incorporates several sunk generic nomina, including *Pithecanthropus* Dubois 1894, *Protanthropus* Haeckel 1895, *Sinanthropus* Black 1927, *Cyphanthropus* Pycraft 1928, *Meganthropus* Weidenreich 1945 and *Telanthropus* Broom and Robinson 1949 (Simpson, 1945; Chamberlain, 1987). *Homo* has four early hominid species assigned to it: *Homo erectus*, *Homo ergaster*, *Homo habilis sensu stricto* and *Homo rudolfensis*.

2.1.5. EARLY HOMINID SPECIES

2.1.5.1. *Australopithecus afarensis*

This species was proposed by Johanson et al. (1978) on the basis of dental, cranial and postcranial remains from the Pliocene site of Hadar, Ethiopia, some of which had previously

been attributed to *Homo* sp. indent. and some to *Australopithecus* aff. *africanus* (Johanson and Taieb, 1976). Johanson et al. (1978) also included in the hypodigm a sample of mandibles and teeth from the Pliocene site of Laetoli, Tanzania, which had been referred to *Homo* sp. indent. by M. D. Leakey et al. (1977). Subsequent to the publication of Johanson et al. (1978), specimens of *A. afarensis* have been identified at a number of African localities, including Fejej, Maka, Belohdelie, Koobi Fora and Bahr el Ghazal (Klein, 1989; Grine, 1993; White et al., 1993; Wood, 1994b; 1996a). Recently, Brunet et al. (1996) have suggested that material recovered at Bahr el Ghazal, Chad, should be recognized as a separate species. Most of the dated specimens indicate that *A. afarensis* was extant from about 4 Myr to about 2.8 Myr (Grine, 1993).

The *A. afarensis* hypodigm, which is now reasonably comprehensive, indicates that the average height of the species was c.130 cm, with males averaging c.150 cm and females averaging c.100 cm (McHenry, 1991). Analyses of the c.40% complete skeleton from Hadar, AL 288, indicate that the body proportions of *A. afarensis* differed from those of living humans in that its legs were relatively short (McHenry, 1992). Body mass estimates suggest that the species was highly dimorphic, ranging from about 12 kg for a small female to more than 50 kg for a large male (Aiello, 1994; but see Senut and Tardieu, 1985). The craniodental anatomy of *A. afarensis* approaches that of the living chimpanzee in many features. *A. afarensis* had a relatively prognathic face and a posterior sagittal crest (Fleagle, 1988). It also had relatively large canines and incisors, and a small brain (400-500 cc) (Wood, 1996a). Key differences between *A. afarensis* and *Pan* include the large size, thick enamel and low cusps of the former's cheek teeth, its limited canine dimorphism and its forwardly-placed and inferiorly-oriented foramen magnum (Fleagle, 1988; Wood, 1996a). The postcranial skeleton of *A. afarensis* suggests that it had a 'mixed' locomotor repertoire. A number of characteristics of the pelvis and lower limb indicate that *A. afarensis* was capable of bipedal walking, albeit with a gait that was probably somewhat different from that of modern humans (e.g. valgus knees, non-opposable big toes, forwardly-placed

and inferiorly-oriented foramen magnum) (Johanson et al., 1982; Lovejoy, 1979; 1981; 1988; Stern and Susman, 1983; Tague and Lovejoy, 1986; Abitbol, 1995). Another group of traits suggest that *A. afarensis* retained a significant arboreal capability (e.g. relatively long and markedly curved proximal phalanges, highly mobile hip, shoulder and wrist joints, high humerofemoral index, funnel-shaped thoracic cage) (Johanson and Taieb, 1976; Stern and Susman, 1983; Senut and Tardieu, 1985; Schmid, 1991).

2.1.5.2. *Australopithecus africanus*

Proposed by Dart (1925) on the basis of a juvenile cranium from the southern African karst cave site of Taung, *Australopithecus africanus* is the type species of *Australopithecus*. Subsequent work at Taung has failed to recover additional *A. africanus* material, but numerous specimens have been found in cave deposits at Gladysvale, Makapansgat (Members 3 and 4) and especially Sterkfontein (Member 4) (Day, 1986; Grine, 1993; Wood, 1996a). Faunal and palaeomagnetic dating of the *A. africanus*-bearing deposits suggests that the species lived from about 3.5 Mya to around 2.3 Mya (Vrba, 1982; Jones et al., 1986; Delson, 1988; Clarke and Tobias, 1995).

A recent estimate suggests that the average stature of a male *A. africanus* was c.140 cm, and that the average stature of a female was c.115cm (McHenry, 1991). Recent body mass estimates suggest that male *A. africanus* weighed around 40 kg and females around 30 kg (McHenry, 1992; 1994c). Some traits (e.g. canine size) suggest that *A. africanus* was less sexually dimorphic than *A. afarensis*, whereas others (e.g. facial structure, cranial base morphology) imply that it was more dimorphic (Kimbel and White, 1988). In its craniodental anatomy, *A. africanus* was less ape-like than *A. afarensis*. Its face was less prognathic, its cranial base was shorter and its foramen magnum was more centrally-located. The brain of *A. africanus* was larger than that of *A. afarensis*, but not substantially so when body mass is taken into account (Wood, 1996a).

Compared with *A. afarensis*, *A. africanus* had larger premolars and molars, but smaller canines and incisors (Fleagle, 1988; Wood, 1996a). The postcranial skeleton of *A. africanus* was similar to that of *A. afarensis*, suggesting that it too combined terrestrial bipedalism with tree climbing (McHenry, 1986). The hypothesis of a 'mixed' locomotor repertoire for *A. africanus* has also been supported by Clarke and Tobias (1995), who described four articulating bones from the left foot of an *A. africanus* individual (Stw 573). Found in deposits dated to between 3.0 Myr and 3.5 Myr at Sterkfontein, these bones suggest that the individual to which they belonged was capable of both bipedal locomotion and climbing. The foot has what Clarke and Tobias called a 'compromise morphology', with the proximal end, especially the talus, displaying a number of human-like traits, and the distal end resembling the highly mobile hallux of the common chimpanzee, *P. troglodytes*. Thus, Stw 573 suggests that *A. africanus* was a facultative biped and climber, rather than an obligate terrestrial biped.

2.1.5.3. *Australopithecus anamensis*

This species was put forward by M. G. Leakey et al. (1995) to identify recently discovered dental, cranial and postcranial remains from Kanapoi and Allia Bay, northern Kenya. A partial humerus that was recovered from the upper deposits at Kanapoi in the 1960s was also referred to the species by Leakey and colleagues. Radiometric dates indicate that *A. anamensis* was extant around 4.1-3.9 Myr ago (Leakey et al., 1995).

Andrews (1995) has observed that, if it is accepted that the material from Kanapoi and Allia Bay is derived from a single species, *A. anamensis* exhibits an unexpected combination of traits. Its palate and dentition have much in common with those of the Middle to Late Miocene apes (e.g. shallow palate, largish upper and lower canines with vertical roots, thick enamel), whereas its humerus and tibia are *Homo*-like in a number of respects (e.g. length). In other features, *A.*

anamensis resembles *A. afarensis* (M. G. Leakey et al., 1995). Estimates based on a partial tibia from Kanapoi suggest that *A. anamensis* had a body mass of around 47-58 kg, which makes it larger than *A. afarensis* (Andrews, 1995; M. G. Leakey et al., 1995). M. G. Leakey et al. (1995) observed that the Kanapoi tibia has a number of traits which indicate that *A. anamensis* was a biped, including a very straight shaft, a rectangular proximal surface with anteroposterior lengthening of the articular surfaces and expanded metaphyseal bone.

2.1.5.4. *Ardipithecus ramidus*

Proposed by White et al. (1995) for material they had previously referred to *Australopithecus ramidus* (White et al., 1994), *Ardipithecus ramidus* is the oldest hominid species currently known. The published hypodigm of *A. ramdius* comprises dental, cranial and postcranial remains from the site of Aramis, Ethiopia, which date to around 4.4. Myr (White et al., 1994; 1995; Woldegabriel et al., 1994; 1995; but see Kappelman and Fleagle, 1995). However, it has been suggested that the 5 Myr mandibular specimens from Lothagam and Tabarin, Kenya may belong to the same taxon (Wood, 1996a).

Although the anatomy of *Ardipithecus ramidus* is known only from incomplete specimens, it appears to be similar to that of living chimpanzees. The dimensions of its shoulder joint suggest that *A. ramidus* weighed about 40 kg (Wood, 1996a), which is within 4 kg of the average for *Pan* males recorded by Fleagle (1988). Also like *Pan*, *A. ramidus* had markedly pneumatized temporal squamae, and relatively small-crowned and thin-enamelled molars (White et al., 1994). The main traits *A. ramidus* shares with later hominids are its low, blunt, incisiform, upper canines, and its centrally-located foramen magnum (White et al., 1994). The latter is especially important, as it suggests that the posture and gait of *A. ramidus* were more upright and bipedal, respectively, than those of *Pan* (Wood, 1996a).

2.1.5.5. *Paranthropus boisei*

Specimens now assigned to *Paranthropus boisei* were first recovered in the late 1950s from Bed I of Olduvai Gorge, Tanzania (L. S. B. Leakey, 1959). Subsequently, specimens attributed to *P. boisei* have been found at a number of sites in Kenya and Ethiopia (Wood, 1991; Suwa et al., 1997). Radiometric dating indicates that *P. boisei* was extant between about 2.3 Myr and 1.4 Myr (Wood et al., 1994; Suwa et al., 1997).

Like *A. afarensis*, *P. boisei* appears to have been very sexually dimorphic. McHenry (1992; 1994c) estimated average male body mass to have been about 49 kg and average female body mass to have been about 34 kg. The high degree of sexual dimorphism is also reflected in the variation present in the mandibular sample for the species (Kimbel and White, 1988). One recent analysis of the stature of *P. boisei* suggested that males would have been c.140 cm and females c.125 cm (McHenry, 1991). Cranially, *P. boisei* appears to have been adapted for heavy chewing (Rak, 1983). Compared with the australopithecines, it had smaller incisors and canines, larger, more thickly enamelled cheek teeth and a thicker mandible. The skull had a very broad, short, orthognathic face with large temporal fossae and flaring zygomatic arches (Fleagle, 1988). Some individuals that are presumed to be males also had sagittal crests, which indicates that they had powerful masticatory muscles (Fleagle, 1988). The brain of *P. boisei* was larger than those of *A. afarensis* and *A. africanus* both in absolute terms (430-530 cc) and when controlled for body size (EQ 2.7) (Wood, 1996a). Few limb bones can be definitely attributed to *P. boisei*, but several very large forelimb bones from East African sites have been assigned to the species (Fleagle, 1988). These bones suggest that, like the australopithecines, *P. boisei* could move arboreally with relative ease (McHenry, 1973; Howell, 1978; Howell and Wood, 1974). Similarly, various indices taken on the reasonably complete skeleton KNM-ER 1500, which

some assign to *P. boisei* (e.g., Grausz et al., 1988, but see Wood, 1991), show that this fossil falls midway between modern humans and the great apes in its upper limb and lower limb proportions and in many ways is similar in these proportions to *A. afarensis* (Aiello and Dean, 1990). *P. boisei*, therefore, is also likely to have had a 'mixed' locomotor repertoire.

2.1.5.6. *Paranthropus robustus*

This species is the type species of *Paranthropus*. Put forward in the late 1930s by Broom on the basis of material recovered from Member 3 of the southern African cave site of Kromdraai (Broom, 1938), *P. robustus* has subsequently also been found in large numbers at another southern African cave site, Swartkrans (Members 1, 2 and 3) (Grine, 1993; Wood, 1996a). Some workers have argued that the differences between the *P. robustus* samples from Swartkrans and Kromdraai are sufficient to warrant assigning the Swartkrans specimens to a separate species, *P. crassidens* (Howell, 1978; Grine, 1988), but others have rejected this suggestion (e.g. Kimbel and White, 1988), and it has not been generally accepted. Palaeomagnetism and faunal comparisons with well-dated sites elsewhere in Africa suggest that the *P. robustus* spanned the time range 1.8 Myr to 1.0 Myr (Vrba, 1982; Jones et al.,1986; Brain, 1988; Delson, 1988).

Paranthropus robustus was shorter and less sexually dimorphic than *P. boisei*. McHenry (1991) estimated males of the species to have been c.130 cm and females to have been c.110 cm. Body mass estimates suggest that male *P. robustus* weighed c.40 kg and females of the species c.30 kg (McHenry, 1992, 1994c). Like *P. boisei*, *P. robustus* appears to have been adapted for prolonged and/or powerful mastication. It had relatively small anterior teeth, molarised premolars, and large, thick enamelled molars (Wood, 1996). It also had robust, flaring zygomatics, large temporal fossae and a broad, short, flat face that was hafted high on the

neurocranium (Fleagle, 1988). Some of the larger specimens possessed sagittal and nuchal crests (Fleagle, 1988). At around 500 cc, the brain of *P. robustus* was about the same size as that of *P. boisei* in absolute terms, but was slightly larger when body mass is taken into account (EQ 3.1) (Wood, 19096a). The postcranial skeleton of *P. robustus* is poorly known (Fleagle, 1988), and opinions differ over the functional interpretation of what material there is. For example, some hold that it was more modern human-like in both its hands and its feet than *A. afarensis*, with the hand bones showing evidence of *Homo*-like manipulative abilities, and the foot bones indicating that it was more bipedal and less arboreal than *A. afarensis* (e.g. Susman, 1988). However, a comparison of the distal humerus and the talus of the type specimen, TM 1517, with those of humans and apes indicates that the upper limbs of *P. robustus* were longer in relation to their lower limbs than is the case in modern humans (Aiello and Dean, 1990). This suggests that *P. robustus* was adapted, to some extent, for climbing. Overall, it would appear that even if *P. robustus* was not as arboreal as *A. afarensis*, it is likely that it did spend a substantial proportion of its time in trees.

2.1.5.7. *Paranthropus aethiopicus*

Originally proposed by Arambourg and Coppens (1968), the species name *Paranthropus aethiopicus* has been widely accepted among palaeoanthropologists only in the last ten years (e.g. Kimbel and White, 1988; Kimbel et al., 1988; Grine, 1993). Prior to that, the handful of specimens that are now assigned to it were included in the hypodigm of *P. boisei.* At the moment, *P. aethiopicus* is known from the East African sites of West Turkana and the Omo River, and is dated to around 2.6 to 2.3 Myr (Grine, 1993).

Like the other paranthropines, the cheek teeth and mandible of *P. aethiopicus* were relatively large (Walker et al., 1986). It also possessed large sagittal and nuchal crests, a 'dished' midface

with cheeks located anterior to the level of the pyriform aperture, a nasoalveolar clivus that passed smoothly into the floor of the nose and a vertically deep and mediolaterally concave tympanic plate (Walker et al., 1986; Grine, 1993). *P. aethiopicus* had a smaller endocranial capacity (400-500 cc) than *P. boisei*, a more prognathic face, and larger anterior dentition (Walker and Leakey, 1988; Grine, 1993). To date, nothing is known about the morphology of its postcranial skeleton.

2.1.5.8. *Homo habilis sensu stricto*

Material now assigned to *H. habilis s. s.* was first recovered from Beds I and II at Olduvai Gorge in the early 1960s (L. S. B. Leakey et al., 1964). Additional dental, cranial and postcranial specimens have been recovered from a number of other localities in eastern and southern Africa, including Koobi Fora, Kenya, and Sterkfontein, South Africa (Tobias, 1991; Wood, 1991; 1992; 1996b; but see Grine et al., 1996). Current dating evidence indicate that *H. habilis s. s.* was extant between about 2.0 Myr and about 1.6 Myr (Wood, 1996b).

Compared to the australopithecines, *H. habilis s. s.* exhibited a lower level of sexual dimorphism. McHenry's (1992; 1994c) body mass estimates suggested that males of the species weighed about 37 kg and females about 32 kg. Average male stature has been estimated as c.160 cm and average female stature as c.120 cm (McHenry, 1991). The post-canine teeth of *H. habilis s. s.* were smaller than those of *Australopithecus* in absolute terms, but were no different when scaled to body mass (Wood, 1996b). Its absolute (500-700 cc) and relative (EQ 4) brain size were higher than those of the australopithecines and paranthropines (Wood,1996a; 1996b). The foramen magnum of *H. habilis s. s.* was closer to the middle of the skull and more horizontally inclined than in *Australopithecus*. Its skull base was reduced in length and increased in width relative to *Australopithecus* (Wood, 1996a), and its face was more modern human-like in

its proportions than those of the australopithecines (e.g. the midface was not the broadest of the three facial components) (Wood, 1996b). The skeletal anatomy of *H. habilis s. s.* suggests that like *A. afarensis* and *A. africanus* it was capable of utilizing both terrestrial bipedalism and climbing/suspensory locomotion. The OH 8 foot suggests that *H. habilis s. s.* was a biped (Wood, 1996b), while the hand bones associated the type specimen of *H. habilis s. s.*, OH 7, have been interpreted by Susman and Stern (1979; 1982) as implying an ape-like ability for underbranch suspension. Similarly, the relatively long arms of OH 62 (Johanson et al., 1987) suggest that *H. habilis s. s.* retained the tree climbing ability of the australopithecines (Aiello and Dean, 1990). Although most of the OH62 postcranial material lacks epiphyseal ends (all except for the proximal ulna), comparisons with AL 288-1 indicate the humerus of OH 62 was longer than that of *A. afarensis*, while its femur was either shorter, or of equal size (Aiello and Dean, 1990; Hartwig-Scherer and Martin, 1991). This suggests that the intermembral proportions of *H. habilis s. s.* were even more ape-like than were those of *A. afarensis*.

2.1.5.9. *Homo rudolfensis*

Originally proposed by Alexeev (1986), *H. rudolfensis* did not receive widespread support as a taxon until the early 1990s, when after a long and heated debate (e.g. Walker and Leakey, 1978; Wood, 1985; 1991; 1992; Stringer, 1986; Chamberlain and Wood, 1987; Chamberlain, 1989; Lieberman et al., 1988; Miller, 1991; Tobias, 1991; Rightmire, 1993; Walker, 1993), it was generally accepted that part of the *H. habilis sensu lato* hypodigm should be removed and recognized as a second species. There is still some debate over the composition of the hypodigm of the species (e.g. Wood, 1991; 1992; Rightmire, 1993), but most authors now accept that it centres on the well preserved cranium from Koobi Fora KNM-ER 1470. So far, *H. rudolfensis* specimens have been found in deposits in Kenya and Malawi, and have been radiometrically dated to between c. 2.5 Myr and c. 1.8 Myr (Wood, 1991; 1992; 1996a).

Compared to *H. habilis s. s.*, *H. rudolfensis* was heavier, with an average body mass of around 55 kg (Aiello and Wood, 1994). The brain of *H. rudolfensis* was larger in absolute terms (700-800 cc) but smaller when body mass is taken into account (EQ 3.2) (Wood, 1996a). The face of *H. rudolfensis* was longer than that of *H. habilis s. s.*, and its cheek bones were higher (Rightmire, 1993). It also had larger orbits, a higher and less sharply defined nasal opening, a broader midface, and a deeper malar region (Bilsborough and Wood, 1988; Rightmire, 1993). At present, no postcranial material can be reliably linked to *H. rudolfensis*. Two femora from Koobi Fora have been tentatively suggested to be from this species (Wood, 1992), but it is possible that they belong to one of the other early *Homo* species.

2.1.5.10. *Homo erectus*

The first specimens of *H. erectus* to be recovered were found at the site of Trinil, Java, Indonesia, in the early 1890s (Dubois, 1892). Subsequently numerous morphologically similar remains have been located elsewhere in Indonesia (e.g. Sangiran, Modjokerto, Ngangdong, Sambungmachan), as well as in China (e.g. Zhoukoudian, Gongwangling, Chenjiawo), Georgia (Dmanisi) and Africa (e.g. Olduvai) (Rightmire, 1990; 1992; Wood, 1991; 1992; 1994b; Gabunia and Vekuna, 1995). The earliest *H. erectus* material may be c.1.8 Myr old (Modjokerto, Dmanisi), while the youngest reliably dated material is around 200 Kyr old (Zhoukoudian) (Swisher et al., 1994; Dean and Delson, 1995; Gabunia and Vekuna, 1995; Wood, 1996b).

Compared with the australopithecines, *H. erectus* had a considerably greater body mass and much lower level of sexual dimorphism (Larick and Ciochon, 1996). One recent estimate, based on African specimens, suggested that male *H. erectus* averaged around 63 kg and females

averaged around 53 kg (McHenry, 1994c). At 900-1100 cc, the brain of *H. erectus* was both absolutely and relatively larger than those of the australopithecines (Wood, 1996a). Its premolars and molars, in contrast, were absolutely and relatively smaller than those of *Australopithecus*, and its mandible was more gracile (Wood, 1996b). Also unlike the australopithecines, *H. erectus* was an obligatory rather than facultative biped (Wood, 1996b). Compared with modern humans, *H. erectus* had a broad, heavy face, and a large pyriform aperture (Fleagle, 1988; Larick and Ciochon, 1996). It had massive, projecting supraorbital tori, and a long, low cranial vault that was constructed from very thick bone (Fleagle, 1988). Also, its mandible lacked a mental eminence or chin (Aiello and Dean, 1990).

2.1.5.11. *Homo ergaster*

The nomen *H. ergaster* was first used in the mid 1970s (Groves and Mazak, 1975). However, it was not widely accepted until the late 1980s/early 1990s, after a number of authors demonstrated that the specimens which had been known as 'early African' *Homo erectus* were sufficiently distinct from *H. erectus* to be considered a different species (e.g. Andrews, 1984; Stringer, 1984; Wood, 1984; 1991; 1992; 1994a; Tattersall, 1986; Groves, 1989; but see Turner and Chamberlain, 1989; Brauer and Mbua, 1992; Rightmire, 1992; Walker, 1993; Dean and Delson, 1995). The best known specimens assigned to *H. ergaster* come from the sites of Koobi Fora (e.g. KNM-ER 3733 and KNM-ER 3883) and West Turkana (e.g. KNM-WT 15000) in Kenya, while another important specimen has been found at Swartkrans (SK 847) (Wood, 1994a; but see Grine et al., 1993). Huang et al. (1995) have recently reported the discovery of c.1.9 Myr old gnathic material from the Chinese site of Longgupo Cave, which they believe may represent *H. ergaster*. However, the specific attribution of the Longgupo specimens has yet to be confirmed. Radiometric and faunal dating indicates that *H. ergaster* was extant between about 1.9 Myr and about 1.5 Myr (Wood, 1992; 1993).

Like *H. erectus*, *H. ergaster* was considerably larger than the australopithecines and exhibited a much lower level of sexual dimorphism. McHenry (1994c) estimated average male body mass to have been around 63 kg and average female body mass to have been about 52 kg. Its brain size (800-900 cc) was also greater than that of *Australopithecus*, although when it is scaled to body mass the difference is marginal (EQ 3.5) (Wood, 1996b). The jaws and posterior teeth of this species were smaller than those of the australopithecines and paranthropines. When tooth size is scaled to body mass, the teeth of *H. ergaster* were no larger than those of modern humans from Africa and Australia (Wood, 1995; 1996b). The cranial anatomy of *H. ergaster* was more generalized and gracile than that of *H. erectus*. Its vault was higher, wider across the parietals and constructed from thinner bone (Wood, 1994a; Larick and Ciochon, 1996). *H. ergaster* was also distinguished from *H. erectus* by its shorter cranial base, the morphology of its face, especially its relatively weak brow ridges and broad nasal aperture, and the nature of its premolar roots (Wood, 1994a; Larick and Ciochon, 1996). The postcranial anatomy of *H. ergaster* is better known than that of any other early hominid. One individual fossil from West Turkana (KNM-WT 15000) comprises 80 percent of the skeleton of a juvenile male, including large portions of almost all long bones (Brown et al., 1985). This specimen indicates that *H. ergaster* had similar limb proportions to modern humans, and a modern human-like body shape (Ruff and Walker, 1993; Ruff, 1994). Its lower limb bones and pelvis suggest that it had a commitment to bipedal locomotion which was equivalent to that seen in modern humans, and there is no evidence in the upper limb bones for the sort of climbing abilities possessed by the australopithecines (Walker and Leakey, 1993). Furthermore, KNM-WT 15000 had a barrel-shaped thoracic cage and narrow waist which imply that it may have been an efficient runner and/or able to travel long distance (Schmid, 1991; Aiello and Wheeler, 1995). A relatively narrow waist helps stabilize the upper body during bipedal running by enabling the arms to swing free in the lowered position and allowing greater torsion in the abdominal region (Schmid,

1991). A barrel-shaped chest facilitates high levels of sustained activity by allowing the upper rib cage to be raised during inspiration, which enlarges the thorax and increases the efficiency of the respiratory system (Aiello and Wheeler, 1995).

2.2. EARLY HOMINID CLADISTICS

The reconstruction of the phylogenetic relationships of the early hominid species has a long history in palaeoanthropology (Brace, 1981; Tattersall, 1996). However, a cladistic approach to early hominid phylogeny was introduced only relatively recently, with the publication of Eldredge and Tattersall (1975). In the present section, the results of Eldredge and Tattersall's investigation and those of subsequent cladistic studies of the early hominids are described briefly in chronological order.

2.2.1. 1975 TO 1986

Eldredge and Tattersall's (1975) seminal cladistic analysis of the hominids was based on craniodental characters for six taxa, *A. africanus* (including specimens now assigned to *H. habilis s. s.* or *H. rudolfensis*), *H. erectus*, *H. neanderthalensis*, *H. sapiens*, *Paranthropus* (including *Paranthropus boisei* and *Paranthropus robustus*) and *Ramapithecus*. The latter was thought until the early 1980s to be a hominid (e.g. de Bonis, 1983; Kay and Simons, 1983; Oxnard, 1984), but is now considered to be more closely related to the Miocene ape *Sivapithecus* (Andrews, 1978; 1982; Andrews and Pilbeam, 1996). On their preferred cladogram (Figure 4), Eldredge and Tattersall positioned *Ramapithecus* as the sister taxon of the hominids, and suggested that the three *Homo* species formed a clade, within which *H. neanderthalensis* and *H. sapiens* were tentatively linked as sister taxa to the exclusion of *H. erectus*. They also showed the *Homo* clade as the sister taxon to *Paranthropus*, and *A. africanus* as the sister taxon of the

clade formed by *Homo* and *Paranthropus*. In the text, however, Eldredge and Tattersall explained that they were unable to resolve the relationships between *A. africanus*, *Homo* and the paranthropines. They justified the placement of *A. africanus* as the sister taxon of *Paranthropus* and *Homo* on the grounds that the morphology of *A. africanus* is primitive or 'morphotypic', rather than by the presence of any shared derived characters in *Paranthropus* and *Homo*.

In the following year, Bonde (1976; see also 1977) used cladistic techniques to analyze cranial, dental and pelvic data from nine taxa: *A. africanus*, *H. erectus*, *H. habilis sensu lato* (i.e. *H. habilis s. s.* and *H. rudolfensis*), *H. modjokertensis* (i.e. Javan *H. erectus* specimens), *H. pekinensis* (i.e. Chinese *H. erectus* specimens), *H. neanderthalensis*, *H. sapiens*, *P. robustus* and *Ramapithecus*. A simplified version of his 'best fit' cladogram that was drawn up by Chamberlain (1987) is presented in Figure 5. Like Eldredge and Tattersall (1975), Bonde placed *Ramapithecus* as the sister taxon of the hominids, and grouped the *Homo* species together as a monophyletic clade, in which *H. neanderthalensis* and *H. sapiens* were sister taxa. Also like Eldredge and Tattersall (1975), Bonde had difficulty positioning *A. africanus* on the cladogram as a consequence of its primitive morphology. Bonde (1976; 1977), however, opted for a different resolution of the relationships between *A. africanus*, *Homo* and *Paranthropus*, placing *A. africanus* and the *Homo* species in a monophyletic clade with *Paranthropus* as its sister taxon. It is possible that this difference was a consequence of the fact that Bonde treated *H. habilis s. l.* as a distinct taxon, whereas Eldredge and Tattersall (1975) included its hypodigm in that of *A. africanus*.

In 1977 Eldredge and Tattersall returned to the question of hominid relationships in a paper co-authored with Delson (Delson et al., 1977). This time they included postcranial characters in their data set, and expanded their sample to include several other hominoid species, including *Dryopithecus*, *Gigantopithecus*, *Gorilla*, *Limnopithecus*, *Pan* and *Pongo*. Also in contrast to

their previous analysis, they kept the *A. africanus* and *H. habilis s. l.* hypodigms separate. Delson and colleagues' preferred hypothesis of relationship (Figure 6) agreed with Eldredge and Tattersall's (1975) cladogram with respect to *Ramapithecus*, *H. erectus*, *H. neanderthalensis* and *H. sapiens*. The ramapithecines were positioned as the sister taxon of the hominids, and the *Homo* species formed a monophyletic group to the exclusion of *A. africanus* and *Paranthropus*. However, the results of Delson and colleagues' analysis differed from those of Eldredge and Tattersall (1975) with regard to the position of *A. africanus*. On their cladogram, Delson et al. indicated that the position of *A. africanus* was uncertain, but in their discussion they, like Bonde (1976; 1977), suggested that *A. africanus* and *Homo* should be placed in a clade to the exclusion of *Paranthropus*. This arrangement was supported, they argued, by three postcranial characters: relative femoral length, relative ischial length, and degree of lumbar curvature. Also like Bonde (1976; 1977), Delson and colleagues found *H. habilis s. l.* to be the sister taxon of the other *Homo* species.

Later in the same year, the Eldredge/Tattersall team published a third analysis of hominid relationships (Tattersall and Eldredge, 1977; see also Schwartz et al., 1978). Their preferred cladogram (Figure 7) differed from those presented by Eldredge and Tattersall (1975) and Delson, Eldredge and Tattersall (1977). *Ramapithecus* was positioned as the sister taxon of the hominids. Within the hominid clade, the first branching event separated the common ancestor of *A. africanus*, *P. boisei* and *P. robustus* from the common ancestor of *H. erectus*, *H. habilis s. l.*, *H. neanderthalensis* and *H. sapiens*. Within the (*A. africanus*, *P. boisei*, *P. robustus*) clade, *P. boisei* and *P. robustus* were linked together to the exclusion of *A. africanus*. Within the *Homo* clade, the first branching event separated *H. habilis s. l.* from the common ancestor of *H. erectus*, *H. neanderthalensis* and *H. sapiens*. The second phylogenetically significant branching event within the *Homo* clade separated *H. erectus* from the common ancestor of *H. neanderthalensis* and *H. sapiens*. This arrangement, Tattersall and Eldredge argued, was supported by a re-

analysis of the postcranial evidence considered by Delson et al. (1977) which indicated that *Australopithecus* and *Paranthropus* shared a locomotor complex that was derived relative to that of *Homo*, which appeared to have retained the primitive hominoid pattern. Specifically, Tattersall and Eldredge found that the gracile and robust australopithecines showed a derived form of femur head and length not shared by *Homo*.

In the following year, Olson (1978) included all the material previously attributed to *A. africanus*, *H. habilis s. l.* and the early *Homo* material from Swartkrans in a new taxon *Homo africanus*. Taking these taxonomic changes into account, the cladogram he presented (Figure 8) was similar to those favoured by Bonde (1976; 1977) and Delson et al. (1977). It suggested that the first branching event in the evolution of the hominids separated the *Paranthropus* lineage from the common ancestor of a clade containing *H. africanus*, *H. erectus*, *H. neanderthalensis* and *H. sapiens*. The next branching event separated *H. africanus* from the common ancestor of *H. erectus*, *H. neanderthalensis* and *H. sapiens*. The final cladistically significant branching event split *H. erectus* from the common ancestor of *H. neanderthalensis* and *H. sapiens*.

Johanson and White (1979) carried out a cladistic analysis of the Plio-Pleistocene hominids to determine the relationships of the recently recognized species *A. afarensis*. This cladogram (Figure 9) differed from those published previously in suggesting that the new species *A. afarensis* was the sister taxon of all other hominids rather than *Ramapithecus*. In other respects, Johanson and White's preferred hypothesis of relationship resembled that of Tattersall and Eldredge (1977). The 'robust' australopithecines and *A. africanus* were linked in a clade that was the sister taxon of *Homo*, and *H. habilis s. l.* was positioned as the sister taxon of a clade containing *H. erectus* and *H. sapiens*. It should be noted, however, that Johanson and White only provided details of the shared derived character states supporting the sister group relationship between *A. africanus* and *P. robustus*

In an effort to overcome what they considered to be the deficiencies of earlier studies with respect to character definition and morphoclinal variation, Corruccini and McHenry (1980) adopted a quantitative approach to the cladistic analysis of the hominids. These authors examined 41 metric characters on the lower teeth and mandibles of several ape and hominid species, as well as on a number of unattributed fossil specimens. They determined the polarity of the morphoclines using outgroup, ontogenetic and functional criteria, and, after standardizing each character for size, divided the metric variables into discrete character states that corresponded to a fixed proportion of the variance in the original linear measurements. The cladogram Corruccini and McHenry presented (Figure 10) suggested that the first split in the evolution of the hominids separated the common ancestor of a clade containing *A. afarensis*, *A. africanus* and *P. boisei* and *P. robustus*, from the common ancestor of a clade containing *H. habilis s. l.*, *H. erectus* and *H. sapiens*. Within the (*Australopithecus*, *Paranthropus*) clade, *A. afarensis* was positioned as the sister taxon of a clade containing *A. africanus*, *P. boisei* and *P. robustus*, and *A africanus* was positioned as the sister taxon of the paranthropines. Within the *Homo* clade, *H. habilis s. l.* was positioned as the sister taxon of a clade containing *H. erectus* and *H. sapiens*. However, Corruccini and McHenry noted in their discussion of the cladogram that a trichotomous relationship involving *A. afarensis*, *Homo* and the (*A. africanus*, *P. boisei*, *P. robustus*) clade was equally likely.

In 1981 Johanson and White re-examined the phylogenetic relationships of *A. afarensis*, *A. africanus*, *P. robustus*, *H. erectus*, *H. habilis s. l.* and *H. sapiens* in a paper co-authored with Kimbel (White et al., 1981). They did so because they believed Johanson and White's (1979) cladogram contained an error in its second branch. As can be seen in Figure 11, White et al. retained Johanson and White's (1979) *Homo* clade, but opted to group all the australopithecine species together in a clade that was the sister taxon of *Homo*. Like Johanson and White (1979),

White et al. only provided descriptions of derived characters of the face, mandible and dentition that were shared exclusively by *A. africanus* and the robust australopithecines; they did not discuss the synapomorphies supporting the arrangement of the other hominid taxa.

Olson (1981; see also 1985) also offered an alternative model of the phylogenetic affinities of *A. afarensis* to that suggested by Johanson and White (1979) (Figure 12). He examined cranial traits in *A. afarensis* and rejected sexual dimorphism as an explanation for size variation in the hypodigm of the species. He proposed instead that the *A. afarensis* hypodigm should be divided into two taxa on the basis of size. He named the taxon comprising the large specimens *Paranthropus africanus*, and linked it cladistically with the 'robust' australopithecines. He referred to the taxon based on the small specimens as *Homo aethiopicus*, and linked it cladistically to a clade containing Olson's (1978) taxon *H. africanus* (which comprised the material assigned to *A. africanus* and *H. habilis s. l.*, and the early *Homo* specimens from Swartkrans) and later *Homo*. This cladistic hypothesis effectively distributed the hypodigm of *A. afarensis* across his earlier cladogram Olson's (1978).

The Johanson, White and Kimbel team returned to the problem of the phylogenetic relationships of *A. afarensis*, *A. africanus*, *P. boisei*, *P. robustus* and *Homo* in 1984 with a quantitative analysis of cranial and dental characters (Kimbel et al., 1984). Kimbel et al. discussed a list of shared derived characters in hominids in relation to four competing cladistic arrangements. In the first, *A. africanus*, *P. boisei*, *P. robustus*, and *Homo* were hypothesized to be the sister group of *A. afarensis*. In the second, *A. africanus*, *P. boisei* and *P. robustus* were hypothesized to be the sister group of a (*A. afarensis*, *Homo*) clade. In the third cladogram, *A. afarensis*, *P. boisei* and *P. robustus* were hypothesized to be the sister group of a clade containing *A. africanus* and *Homo*. In the last cladogram, a clade consisting of *P. boisei*, *P. robustus* and *Homo* was hypothesized to be the sister group of a (*A. afarensis*, *A. africanus*) clade. Kimbel et al. (1984)

argued in favour of the second cladogram (Figure 13). However, a re-analysis of their data carried out by Chamberlain (1987) indicated that the most parsimonious arrangement of Kimbel and co-workers' data is one in which *A. afarensis* is the sister taxon to a (*Homo*, *A. africanus*, *P. boisei*, *P. robustus*) clade, *Homo* the sister taxon of a (*A. africanus*, *Paranthropus*) clade, and *A. africanus* the sister taxon of a (*P. boisei*, *P. robustus*) clade (Figure 14).

Dean (1986) carried out a cladistics-based analysis of characters from the cranial base and developing dentition in *A. africanus*, *Homo* and *Paranthropus*, using the great apes as an outgroup. He found that *A. africanus* retained primitive character states, similar to those found in great apes and other primates, and that *Homo* and *Paranthropus* shared a number of derived character states. Figure 15 presents Dean's findings in the form of a cladogram.

Skelton and colleagues (1986) presented an analysis designed to identify the phyletic relationships of *H. habilis sensu lato*. These authors culled the states of 69 discrete characters from the literature for *A. afarensis*, *A. africanus*, *Paranthropus*, *H. habilis s. l.*, and then polarized the resulting morphoclines with a combination of outgroup analysis and the stratigraphic position of the taxa. Following this, Skeleton et al. established a series of 12 trait complexes, each of which consisted of the traits with identical morphoclines. From these trait complexes, Skeleton et al. (1986) derived four contradictory cladogram. Their 'best fit' cladogram (Figure 16), which was supported by the 45 of the 69 characters, suggested that the first branching event in the evolution of the hominids separated *A. afarensis* from the common ancestor of *A. africanus*, *H. habilis s. l.* and *Paranthropus*. The other phylogenetically significant branching event posited by the cladogram separated *A. africanus* from the common ancestor of a clade containing *H. habilis s. l.* and *Paranthropus*.

In the same year, Wood and Chamberlain (1986) attempted to determine whether the australopithecines and paranthropines constituted a grade, a clade, or both. They addressed the problem with a cladistic analysis of 39 size-corrected metric characters which had been recorded on the crania of seven fossil hominid species (*A. afarensis*, *A. africanus*, *P. robustus*, *P. boisei*, *H. erectus*, *H. habilis s. l.*, *H. sapiens*) and eight outgroup taxa. Wood and Chamberlain constructed cladograms for five cranial regions (vault, face, palate, cranial base, mandible). *Homo* was monophyletic in all the cladograms, as was *Paranthropus*. In contrast, the positions of *A. afarensis* and *A. africanus* were uncertain. The vault and face regional cladograms suggested that *A. africanus* was the sister taxon of *Homo*, and that *A. afarensis* the sister taxon of *Paranthropus* (Figure 17). The mandible and palate cladograms suggested that *A. africanus* is the sister taxon of *Paranthropus*, and that *A. afarensis* the sister taxon of the (*A. africanus*, *Paranthropus*) clade (Figure 18). The cranial base cladogram indicated that *A. africanus* is the sister taxon of *Paranthropus*, and that *A. afarensis* is the sister taxon of a clade comprising *Paranthopus*, *A. africanus* and *Homo*.

2.2.2. 1987 TO 1997

Cladistic analysis in human palaeontology entered a new phase in 1987 with the publication of the first computer aided cladistic analyses of the hominid clade (Stringer, 1987; Chamberlain and Wood, 1987). Stringer (1987) recorded 11 metric cranial and postcranial characters on an outgroup sample of apes and australopithecines and nine groups of specimens usually assigned to *Homo*: modern humans, early anatomically modern humans from Skhul and Qafzeh, Israel, African archaic *H. sapiens*, Neanderthals, early archaic *H. sapiens*, Asian *H. erectus*, early African *H. erectus*, Stringer's (1986) '1470 group' of *H. habilis s. l.* specimens and Stringer's (1986) '1813 group' of *H. habilis s. l.* specimens. He then ran two maximum parsimony analyses with the aid of a phylogenetic reconstruction program, one with the character states

ordered, and one with them free to change in any direction. Neither analysis produced a single most parsimonious tree. The analysis of the ordered data gave rise to three equally parsimonious trees, while the analysis of the unordered data produced seven trees of equal length. Although the unordered trees had higher consistency indices than those based on the ordered data (0.763 versus 0.744), Stringer opted to calculate a consensus cladogram from the ordered trees. This consensus hypothesis (Figure 19) positioned the Middle Palaeolithic-associated samples from Skhul-Qafzeh as the sister taxon of modern humans, and placed this clade within an unresolved trichotomous group along with African archaic *H. sapiens* and the Neanderthals. The sister group to this clade consisted of early African *H. erectus*, Asian *H. erectus*, and early archaic *H. sapiens*; the latter two taxa were found to be more closely related to one another than either was to early African *H. erectus*. The '1470 group' of *H. habilis s. l.* specimens was placed on the next branch, and the '1813 group' of *H. habilis s. l.* specimens appeared as the sister taxon of all the other *Homo* taxa.

In the same volume as Stringer (1987) gave details of his phylogenetic analysis of the genus *Homo*, Chamberlain and Wood (1987) reported the results of a computer aided analysis of a broad sample of early hominids. They examined size-corrected data from 90 cranial, mandibular and dental measurements recorded on seven hominid taxa: *A. afarensis*, *A. africanus*, *P. boisei*, *P. robustus*, *H. habilis s. l.*, *H. erectus* and *H. sapiens*. They carried out three maximum parsimony analyses. In the first, they used conventional definitions for all the hominid taxa. In the second, they divided the *H. habilis s. l.* hypodigm in line with Stringer's (1986) taxonomic scheme. In the third analysis, Chamberlain and Wood divided the *H. habilis s. l.* hypodigm in line with Chamberlain's (1987) morphometric study. Chamberlain and Wood's most parsimonious cladogram for the conventionally defined taxa (Figure 20) was consistent with that of Kimbel et al. (1984). Chamberlain and Wood's shortest arrangement using Stringer's (1986) subdivision of the *H. habilis s. l.* hypodigm (Figure 21) had essentially the same branching

pattern as last cladogram, with the two species of early *Homo*, *H. habilis s. s.* and *Homo* sp., placed as successive sister taxa to a clade comprising *H. erectus* and *H. sapiens*. Chamberlain and Wood's most parsimonious tree based on Chamberlain's (1987) subdivision of *H. habilis s. l.* implied a contrasting set of relationships for the two early *Homo* species (Figure 22). *H. erectus* and *H. sapiens* again formed a clade, as did the 'robust' australopithecine species. *A. afarensis* also retained its position as the sister taxon of all the other hominids. However, *H. habilis s. s.* was placed as the sister taxon of a (*A. africanus*, *P. boisei*, *P. robustus*, *H. erectus*, *H. sapiens*, *Homo* sp.) clade, and *Homo* sp. was hypothesized to be the sister taxon of the 'robust' australopithecines in a clade which also included *A. africanus*.

In the following year, Wood (1988) sought to determine whether the 'robust' australopithecines formed a monophyletic group by re-analyzing the data sets of Walker et al. (1986), Chamberlain and Wood (1986) and Chamberlain and Wood (1987). In the cladogram recovered from Walker and colleagues' (1986) data (Figure 23), *P. robustus* and *P. boisei* were grouped in a clade to the exclusion of the other hominid taxa, and that clade was positioned in a trichotomy with *Homo* and a clade comprising *A. africanus*, KNM-WT 17000, and *A. afarensis*. Within the latter clade, KNM-WT 17000 and *A. afarensis* were positioned as sister taxa. In the cladogram retrieved from Wood and Chamberlain's (1986) data (Figure 24), *P. boisei* and *P. robustus* were grouped in a clade, and that clade was positioned as the sister taxon of a clade containing *A. afarensis*, *A. africanus* and *Homo*. Three trees were recovered from the analysis of Chamberlain and Wood's (1987) data, all of which grouped *P. boisei* and *P. robustus* in a clade. The first (Figure 25) positioned the paranthropine clade as sister taxon of a clade containing *A. africanus*, *A. afarensis* and *Homo*, within which *Homo* and *A. africanus* were sister taxa. The second (Figure 26) positioned the 'robust' australopithecine clade as the sister taxon of an (*A. afarensis*, *A. africanus*, *Homo*) clade within which *A. afarensis* and *Homo* were sister taxon. The third tree (Figure 27) located the paranthropine clade in a trichotomy with *Homo* and a clade comprising

A. afarensis and *A. africanus*. As measured by the consistency index, none of the trees was substantially better than the shortest tree in which the 'robust' australopithecines, *P. boisei* and *P. robustus*, were more closely related to one of the other hominids than to each other.

Unhappy with what he perceived to be the low reliability of earlier analyses, Groves (1989) sought to overcome the problem by analyzing just three taxa: *Australopithecus*, *Paranthropus* and *Homo*. Working on the assumption that the membership of each taxon was generally agreed, Groves (1989) examined the level of support provided by 87 characters for each of the three possible cladograms for the taxa. His most parsimonious cladogram (supported by at least 18 and possibly as many as 20 characters) suggested that *Homo* and *Australopithecus* were more closely related to one another than either was to *Paranthropus* (Figure 28). Grove's next most parsimonious cladogram, which placed *Homo* and *Paranthropus* in a clade to the exclusion of *Australopithecus*, was supported by a maximum of six characters.

Following a quantitative review of the craniodental material from Koobi Fora, Kenya, Wood (1991) undertook a parsimony analysis to determine the effect of his taxonomic assignments on hominid phylogeny. Using the same measurements, size-adjustment techniques, coding procedures and polarization method as Chamberlain and Wood (1987), Wood examined nine hominid taxa: *A. afarensis*, *A. africanus*, *Homo* aff. *erectus* (= *H. ergaster*), *H. erectus*, *H. habilis s. s.*, *Homo* sp. nov. (= *H. rudolfensis*), *H. sapiens*, *P. boisei* and *P. robustus*. The hypodigms of *Homo* aff. *erectus*, *H. erectus*, *H. habilis*, *Homo* sp. nov. and *P. boisei* were based on the taxonomic review carried out earlier in the monograph. The hypodigms of *A. afarensis*, *A. africanus* and *P. robustus* were those used by Chamberlain and Wood (1987). The most parsimonious tree (Figure 29) suggested that the first branching event in the evolution of the ingroup separated *A. afarensis* from the common ancestor of *A. africanus*, *H.* aff. *erectus*, *H. erectus*, *H. habilis s. s.*, *H.* sp. nov., *H. sapiens*, *P. boisei* and *P. robustus*. The second branching

event isolated the common ancestor of the paranthropines from the common ancestor of *A. africanus* and the *Homo* taxa. The third branching event separated *A. africanus* from the common ancestor of the *Homo* taxa. The fourth branching event separated the common ancestor of *H. habilis s. s.* and *Homo* sp. nov. from the common ancestor of *H. erectus*, *H.* aff. *erectus* and *H. sapiens*. The last phylogenetically significant branching event separated *H. erectus* and the common ancestor of *Homo* aff. *erectus* and *H. sapiens*.

Skelton and McHenry (1992) presented a computer aided analysis of 77 discrete traits recorded on the crania of six early hominid taxa: *A. afarensis*, *A. africanus*, *P. aethiopicus*, *P. robustus*, *P. boisei* and early *Homo*. Aiming to overcome the problems of character correlation and character bias, Skelton and McHenry analyzed their data in three different ways with the aid a great ape outgroup. First, they constructed a maximum parsimony cladogram for all 77 characters. Next, they produced trees for subsets of the characters that were derived from different anatomical regions, as well as a consensus cladogram for the regional trees. Lastly, they grouped the traits into functional complexes and calculated a cladogram for each complex, along with a consensus tree for all the functional cladograms. Of the resulting hypotheses of relationship, the most persistent, and therefore Skelton and McHenry's preferred cladogram, positioned *Homo* and a (*P. boisei*, *P. robustus*) clade as sister taxa, *A. africanus* as the sister taxon to the (*Homo*, *P. boisei*, *P. robustus*) clade, *P. aethiopicus* as the sister group to the (*Homo*, *P. boisei*, *P. robustus*, *A. africanus*) clade, and *A. afarensis* as the sister group to all other hominids (Figure 30).

As part of an assessment of the relationships of *H. habilis s. s.* and *H. rudolfensis*, Lieberman and colleagues (1996) conducted a maximum parsimony analysis of 48 frequently used cranial, mandibular and dental characters recorded on eight early hominid taxa: *A. afarensis*, *A. africanus*, *P. aethiopicus*, *P. boisei*, *P. robustus*, early African *H. erectus* (= *H. ergaster*), *H. habilis s. s.* and *H. rudolfensis*. The character states for these taxa were taken from previously

published cladistic and taxonomic studies. The analysis yielded a single most parsimonious tree that differed from Skelton and McHenry's (1992) preferred tree with respect to the relationships of *A. africanus* (Figure 31). It suggested that the first branching event in the evolution of the hominids separated *A. afarensis* and the common ancestor of the other hominid species. The second branching event isolated *P. aethiopicus* and the common ancestor of *A. africanus*, *P. boisei*, *P. robustus*, *H. erectus*, *H. habilis s. s.* and *H. rudolfensis*. The third branching event separated the common ancestor of *P. boisei* and *P. robustus* from the common ancestor of *A. africanus*, *H. erectus*, *H. habilis s. s.* and *H. rudolfensis*. Within the latter clade, *H. rudolfensis* was positioned as the basal taxon, *A. africanus* occupied the next branch, and *H. habilis s. s.* and *H. erectus* appeared as sister taxa.

Strait and associates (1997) analyzed previously published character state data for 60 characters recorded on nine hominid taxa (*A. afarensis*, *A. africanus*, *H. ergaster*, *H. habilis s. s.*, *H. rudolfensis*, *H. sapiens*, *P. aethiopicus*, *P. boisei*, *P. robustus*) and a non-human primate outgroup. The data set was analyzed a number of times to examine the effects of different assumptions about character state evolution. The tree Strait et al. favoured was recovered in two analyses (VARIABLE = INTERMEDIATE and IRREVERSIBLE), and differed from Lieberman and colleagues' (1996) most parsimonious tree with respect to the position of *A. africanus* and *P. aethiopicus* (Figure 32). It suggested that *A. afarensis* was the sister taxon of all other hominids, and that *A. africanus* was the sister taxon of a (*Homo*, *Paranthropus*) clade. Within the (*Homo*, *Paranthropus*) clade, the paranthropine species formed a monophyletic group and the *Homo* species formed another. Within the *Paranthropus* clade, *P. boisei* and *P. robustus* were linked as sister taxa to the exclusion of *P. aethiopicus*. Within the *Homo* clade, *H. habilis s. s.* was positioned as the basal taxon, and *H. rudolfensis* was positioned as the sister taxon of *H. ergaster* and *H. sapiens*.

2.2.3. RELIABLE EARLY HOMINID RELATIONSHIPS

Among the early hominids only one clade has been consistently supported in the numerous cladistic analyses that have been carried out, and that clade, which comprises *P. boisei* and *P. robustus*, was widely accepted long before Eldredge and Tattersall's (1975) seminal cladistic analysis of the hominids appeared. The relationships between the (*P. boisei*, *P. robustus*) clade and the other Plio-Pleistocene hominid species, and the relationships among the other species, are as uncertain now as they have ever been. A similar result was obtained by Corruccini (1994) in his recent assessment of the confidence intervals associated with palaeoanthropological phylogenetic hypotheses published prior to 1993, including a number which dealt with the early hominid species. Corruccini (1994) found that very few hominid relationships could be resolved to any degree of statistical significance. The only consistent result he found was that *P. boisei* and *P. robustus* formed a clade separate from the other hominids.

CHAPTER 3. HOMINOID AND PAPIONIN CONSENSUS MOLECULAR CLADOGRAMS

The present study was designed to take advantage of the growing agreement among molecular anthropologists over the genus level phylogenetic relationships within the human and ape superfamily Hominoidea (Figure 1) and within the Old World monkey tribe Papionini (Figure 2). In this chapter, the hominoids are introduced and the evidential support for their consensus molecular cladogram outlined. Thereafter, the same is done for the papionins and their consensus molecular cladogram.

3.1. HOMINOIDEA

3.1.1. TAXONOMY, DISTRIBUTION AND CHARACTERISTICS OF THE EXTANT HOMINOIDEA

The superfamily Hominoidea comprises five extant genera: *Gorilla*, *Homo*, *Hylobates*, *Pan* and *Pongo*. Conventionally, 14 extant species are assigned to these genera (Fleagle, 1988; Nowak, 1991), although recent genetic work has suggested that this figure may need to be increased in the future (Morin et al., 1994). The gorilla genus contains one extant species: *Gorilla gorilla*. The human genus, *Homo*, also has just one living species assigned to it: *Homo sapiens*. The gibbon genus, *Hylobates*, has nine living species referred to it: *Hylobates agilis* (agile gibbon), *Hylobates concolor* (crested gibbon), *Hylobates hoolock* (hoolock gibbon), *Hylobates klossi* (Kloss' gibbon), *Hylobates lar* (white-handed gibbon), *Hylobates moloch* (silvery gibbon), *Hylobates muelleri* (Mueller's gibbon), *Hylobates pileatus* (pileated gibbon) and *Hylobates syndactylus* (siamang) (Fleagle, 1988; Nowak, 1991). *Pan*, the chimpanzee genus, comprises

two extant species: *Pan troglodytes* (common chimpanzee) and *Pan paniscus* (pygmy chimpanzee or bonobo). The orangutan genus, *Pongo*, has one living species assigned to it, *Pongo pygmaeus*.

With the exception of *Homo*, the hominoids are restricted in their distribution. *Pongo* is limited to Java and Sumatra, while *Hylobates* is found on mainland Southeast Asia from eastern India to southern China, and on Borneo, Java, Sumatra, and some of the Sunda shelf islands. *Gorilla* and *Pan* are found only in central Africa, the former's distribution being considerably smaller than the latter's (Fleagle, 1988; Nowak, 1991). In terms of habitat, *Hylobates*, *Gorilla* and *Pongo* occupy exclusively evergreen tropical forest, while *Pan* has been observed in rain forest, woodland and areas of dry savanna with very few trees (Goodall, 1986; Fleagle, 1988; Boesch and Boesch, 1989).

Although the hominoid genera are heterogeneous in body size (4 kg to 200 kg), sexual dimorphism patterns (none to extreme) and locomotor and dietary adaptations (terrestrial omnivory to arboreal frugivory), morphologists have long considered them to be a monophyletic group (e.g. Simpson, 1945; Le Gros Clark, 1949; 1964). The monophyly of Hominoidea has also been supported by various molecular analyses (e.g. Goodman, 1962; 1963; Sarich, 1971; Sarich and Wilson, 1967; Sibley and Ahlquist, 1984; Ruvolo et al., 1991; Bailey et al., 1992a; 1992b; Marks, 1992b; Sibley, 1992; Porter et al., 1995). Character states which have recently been argued to be synapomorphic for the hominoids include: (1) broad spatulate central incisors, (2) low crowned premolars with less honing on P_3, (3) relatively broad molars with rounded cusps, (4) presence of a vermiform appendix, (5) interstitial placental implantation, (6) sperm mitochondria with few gyres, (7) differential usage of the forelimb, including increased potential for raising arm above the head, for extending the forelimb at the elbow joint and for rotation of the forelimb, (8) greater flexibility of the wrist and opposable thumb, (9) more erect posture

during locomotion and feeding with broadening of thorax and loss of tail and (10) greater mobility at the hip and ankle joints (Groves, 1989; Andrews, 1992).

3.1.2. PHYLOGENETIC RELATIONSHIPS AMONG THE EXTANT HOMINOID GENERA

The molecular phylogeny for the Hominoidea used in the present study (Figure 1) contains three ingroup clades. The first groups together the great apes and *Homo* to the exclusion of *Hylobates*. The second, which is nested within the first, groups together the African apes and *Homo* to the exclusion of *Pongo*. The third clade, which is nested within the (*Gorilla*, *Homo*, *Pan*) clade, links together *Homo* and *Pan* to the exclusion of *Gorilla*. Evidence supporting each of these clades will now be summarized.

3.1.2.1. Great ape and human clade

The hypothesis that the first branching event in the evolution of the extant Hominoidea separated *Hylobates* from the common ancestor of *Gorilla*, *Homo*, *Pan* and *Pongo* has been explicitly or implicitly supported by nearly all recent morphological analyses (e.g. Ciochon, 1983; Groves, 1986; 1987; 1989; Andrews, 1985; 1987; 1992; Andrews and Martin, 1987; Pilbeam, 1996; Gebo et al., 1997; Rae, 1997). Although earlier authors, such as Simpson (1945) and Le Gros Clark (1949), did not agree with this arrangement, lately only the phenetic analyses of Creel and Preuschoft (1971) and Oxnard (1984) have failed to support it unequivocally.

Gross morphology-based cladistic analyses published in the past few years have highlighted numerous cranial, mandibular, dental, postcranial and soft tissue resemblances which separate *Gorilla*, *Homo*, *Pan* and *Pongo* from *Hylobates*. These include: (1) enlarged maxillary sinuses, (2)

orbits higher than broad, (3) increased alveolar prognathism with elongated premaxilla, (4) facial lengthening with elongation of nasal bones and narrow incisive foramen, (5) mandible robust with large inferior transverse sulcus, shortened but robust canines, (6) great increase in size of incisors relative to molar size, (7) robust and enlarged premolars relative to molars, (8) reduced upper premolar heteromorphy, (9) reduced molar cingula, (10) carpal reorganization, (11) reduced body hair, (12) loss of ischial callosities and (13) distal humerus with deep sulci either side of lateral trochlear keel (Groves, 1989; Andrews, 1992).

The basal position of *Hylobates* among the extant Hominoidea has also been supported by most of the molecular analyses carried out in the last 35 years. These include the 'albumin clock' work of Sarich and Wilson (Sarich and Wilson, 1967; Sarich 1971) and the single copy DNA-DNA hybridization studies of Sibley and Ahlquist (1984; 1987a), Caccone and Powell (1989) and Sibley et al. (1990). The (*Gorilla*, *Homo*, *Pan*, *Pongo*) clade was also found by Bailey and co-workers (1992a; 1992b) in their parsimony analyses of ε-globin gene sequences and non-coding sequences associated with the γ-globin and φη-globin loci. More recently, Goodman and colleagues (1994) recovered a great ape and human clade in a maximum likelihood analysis of an extended sequence alignment compiled from the γ-globin and φη-globin data sets of Bailey et al. (1992a).

Some molecular data-based studies have failed to support the (*Gorilla*, *Homo*, *Pan*, *Pongo*) clade (e.g. Goodman, 1962; 1963; Corruccini, 1992; 1994). However, none of them have contradicted it; rather, they have been unable to resolve one or more of the relationships. Goodman's (1962; 1963) serological analyses, for example, arrived at an unresolvable trichotomy comprising *Hylobates*, *Pongo* and an African ape and human clade.

3.1.2.2. African ape and human clade

Since the late nineteenth century, many morphologists have supported the hypothesis that *Gorilla*, *Homo* and *Pan* are more closely related to one another than any of them is to *Pongo*. Some of the earliest proponents of this arrangement were Darwin (1871), Huxley (1863; 1894), Elliot Smith (1924) and Gregory (1934). More recently, the African great ape and human clade has been favoured by both phenetic (e.g. Oxnard, 1989) and cladistic studies (e.g. Ciochon, 1983; Groves, 1986; 1987; 1989; Groves and Paterson, 1991; Andrews, 1985; 1987; 1988; 1992; Andrews and Martin, 1987; Begun, 1992; 1994b; Shoshani et al., 1996). Morphological resemblances among *Gorilla*, *Homo* and *Pan* which have lately been suggested to be synapomorphic include: (1) presence of a frontal sinus, (2) prominent continuous, bar-like supraorbital torus, (3) developed postorbital sulcus, (4) greater middle ear depth, (5) elongated nasoalveolar clivus of the premaxilla with narrowing of the incisive foramen, (6) increased klinorhynchy, (7) straight humeral shaft, (8) fusion of *os centrale* to scaphoid in the wrist, (9) robust metatarsal shafts, (10) large middle phalanges, (11) subdivision of the prostrate, (12) apocrine glands sparsely distributed over body, (13) eccrine glands abundant over body, (14) large axillary organ, (15) low proportion (3-21%) of type I aorta and (16) large uterus (Andrews, 1987; 1992; Begun, 1994b).

A large number of biomolecular and karyological analyses have also supported a (*Gorilla*, *Homo*, *Pan*) clade within the Hominoidea. Early examples include Zuckerkandl and associates' (1960) study of the primary structure of adult haemoglobin from a number of animals, and Goodman's (1962; 1963) and Sarich and Wilson's (Sarich and Wilson, 1967; Sarich, 1971) serological analyses. Closer to the present, the single copy DNA-DNA hybridization studies of Sibley and colleagues (Sibley and Ahlquist, 1984; 1987a; Sibley et al., 1990) and Caccone and Powell (1989) have favoured a (*Gorilla*, *Homo*, *Pan*) clade, as have most of the nuclear and mi-

tochondrial DNA sequence analyses, which have dominated the field since the mid-1980s. Recent examples of the latter include the analyses of ε-globin gene sequences and non-coding sequences associated with the γ-globin and φη-globin loci carried out by Goodman and colleagues (Bailey et al., 1992a; 1992b; Goodman et al., 1994), the analysis of a 4759 bp region of mtDNA encompassing genes for 11 transfer RNAs and six proteins performed by Horai et al. (1992), and Ruvolo and coworkers' (1991; 1994) analyses of hominoid mtDNA COII gene sequences. Additionally, Chaline and colleagues (1991) have recently given details of a karyological analysis in which the (*Gorilla*, *Homo*, *Pan*) clade was supported by mutations on chromosomes 2q, 3, 7, 10, 11, 17 and 20.

Although the (*Gorilla*, *Homo*, *Pan*) clade is now, in Oxnard's (1989:61) words, "accepted by almost everyone", the consensus is relatively new. Until recently, two alternative arrangements were also discussed in the literature. One of these, the Ponginae Hypothesis, grouped the African and Asian great apes together to the exclusion of *Homo* (Kluge, 1983). The other arrangement, the Red Ape Hypothesis, divided the large-bodied hominoids into two groups, one containing *Gorilla* and *Pan*, and the other containing *Homo* and *Pongo* (Schwartz, 1984; 1986; 1988). These hypotheses have been rejected by evolutionists largely because of the sheer weight of molecular evidence contradicting them. However, they have also been shown to be ill-supported by the available morphological data (e.g. Ciochon, 1983; Groves, 1986; Groves and Paterson, 1991; Andrews, 1987; 1992; Andrews and Martin, 1987). For example, Andrews (1987) demonstrated that most of the 11 character states claimed by Kluge (1983) to support the Ponginae Hypothesis were in fact either primitive retentions, parallelisms or allometric correlates of body size. Andrews (1987) was willing to accept only three of Kluge's (1983) resemblances as possible synapomorphies, and these were considerably outnumbered by the character states supporting a (*Gorilla*, *Homo*, *Pan*) clade (N = 12). In the same paper, Andrews (1987) showed that the Red Ape Hypothesis was less well supported than Schwartz (1984) claimed, and that it

was a less parsimonious solution than the African ape and human clade. Schwartz listed 15 resemblances between *Homo* and *Pongo*, which he interpreted as shared derived characters, including thick enamel, low-cusped cheek teeth, widespread mammary glands, female genitalia lacking tumescence, the longest hair and the longest copulation bouts. Andrews (1987) demonstrated that only four of these resemblances could be accepted as potential synapomorphies; the rest were either symplesiomorphic, poorly characterized, or, for other reasons, of questionable phylogenetic value. Again, the revised total was heavily outnumbered by the probable synapomorphic resemblances linking the African apes and *Homo*.

3.1.2.3. Chimpanzee and human clade

Of the clades which make up the hominoid tree depicted in Figure 1, the one linking *Pan* and *Homo* is the most contentious. Generally, morphologists explicitly or implicitly favour a sister group relationship between *Gorilla* and *Pan*, regardless of whether that clade is part of a great ape monophylum or an African ape plus human clade (e.g. Keith, 1902; 1912; Tuttle, 1969; Groves, 1970; Schwartz et al., 1978; Oxnard, 1984; 1989; Andrews, 1987; 1988; Andrews and Martin, 1987; Susman and Stern, 1991; Latimer and Ward, 1993; Hunt, 1994). According to one of the most widely cited papers on this subject (Andrews, 1987), the most important of the proposed synapomorphies of the (*Gorilla*, *Pan*) clade are features of the forelimb which are linked to the form of locomotion known as knuckle-walking, and patterns of enamel thickness, prism type and accretion rate which Martin (1983; 1985) found to be uniquely shared by the extant African apes.

A few analyses of phenotypic characters have failed to support a (*Gorilla*, *Pan*) clade. However, most of these have simply found the relationships between *Gorilla*, *Homo* and *Pan* impossible to resolve, rather than supporting the (*Homo*, *Pan*) clade (e.g. Groves, 1986; 1989; Groves and

Paterson, 1991). It appears that recently only Shoshani et al. (1996) have favoured a (*Homo*, *Pan*) clade in the light of an analysis of soft tissue and skeletal evidence.

In contrast to the situation in physical anthropology, the majority of analyses undertaken by molecular evolutionists in the last fifteen years have supported the (*Homo*, *Pan*) clade, albeit some more strongly than others. The amino acid sequence analyses carried out by Goodman et al. (1983; 1989) fall at the weak end of the spectrum, as do the analyses of the ψη-globin gene performed by Koop et al. (1986) and Miyamoto et al. (1987). Other studies which have only weakly supported a (*Homo*, *Pan*) clade include Koop and colleagues' (1989) sequence analysis of a 10.8 kb-long stretch of nuclear DNA containing the η-globin pseudogene, and Ueda and associates' (1989) sequence analysis of the immunoglobin ε pseudogene. At the other end of the spectrum, a sister group relationship between *Homo* and *Pan* was strongly supported by Sibley and Ahlquist's (1984) single copy nuclear DNA hybridization analysis, criticisms of which (Marks et al., 1988; Sarich et al., 1989) have been rebutted by subsequent hybridization analyses using different experimental protocols (Sibley et al., 1990; Sibley, 1992). The (*Homo*, *Pan*) clade was also strongly supported by Holmquist and colleagues' (1988) investigation of nucleotide sequence divergence in coding and non-coding regions of nuclear and mitochondrial DNA, and by Gonzalez and coworkers' (1990) sequence analysis of the 28S rRNA gene and ribosomal internal transcribed spacer region. Other analyses in which the same phylogenetic conclusion was clearly favoured include Bailey and associates' (1992b) analysis of long stretches of nuclear non-coding sequence associated with the ψη-globin and γ-globin loci, Ruvolo and co-workers' (1991) cladistic analysis of mtDNA COII gene sequences, and Horai et al.'s (1992) analysis of an extensive mtDNA region encompassing genes for 11 transfer RNAs and six proteins.

More recently published studies have clearly shown humans and chimpanzees to be most similar genetically. For example, Horai et al. (1995) sequenced the entire mitochondrial genome in hominoids and demonstrated strong support for a (*Homo*, *Pan*) monophylum. A similar pattern was identified in Takahata's (1995) likelihood analysis of a number of autosomal gene sequences, and in Goodman and colleagues' (1994) likelihood analysis of sequences from the non-converted γ and φη regions of the β-globin gene cluster. In two important papers Ruvolo (1994; Ruvolo et al., 1994) has shown that the (*Homo*, *Pan*) clade recovered from the mtDNA COII gene by Ruvolo et al. (1991) is unlikely to be a consequence of the 'gene tree/species tree' effect, in which ancestral polymorphism may lead to gene trees to differ from species trees (Nei, 1987; Pamilo and Nei, 1988; Rogers, 1994). Lastly, Ruvolo (1995; 1997) has demonstrated that when independence of data sets is taken into account, all the available nuclear and mitochondrial DNA data indicate that a human/chimp grouping is considerably more likely than any other relationship.

While a number of biomolecular analyses have been unable to resolve the relationships between *Gorilla*, *Homo* and *Pan* (e.g. Goodman, 1962; 1963; Sarich and Wilson, 1967; Benveniste and Todaro, 1976), genetic and karyological support for a (*Gorilla*, *Pan*) clade is limited. Bianchi and colleagues' (1985) chromosome analysis gave some support to an African ape clade, as did Stanyon and Chiarelli's (1982) cytogenetic analysis and two early DNA sequencing studies (Brown et al., 1982; Templeton, 1983). However, in recent years only one chromosome analysis (Marks, 1993) and one DNA sequence analysis (Djian and Green, 1989) have favoured this arrangement. Significantly, because Djian and Green's (1989) conclusion was based solely on sequence information in a tandemly-duplicated repeat region of the involucrin gene, and involucrin has been found to be polymorphic in a number of primate species, there is reason to believe that this incongruent molecular finding may be an example of the gene tree/species tree effect rather than a reflection of phylogenetic history (Ruvolo, 1994; Ruvolo et al., 1991).

How is the apparent conflict between the morphological and molecular data with respect to the relationships among *Gorilla*, *Homo* and *Pan* to be resolved? Some authors have argued that we are not yet in a position to decide, and that we need to remain open minded until more work has been done (e.g. Marks, 1988; 1992a; 1994; Marks et al., 1988; Miyamoto and Goodman, 1990; Andrews, 1992; Rogers, 1994). Others have contended that the conflict is a false one, and that *Gorilla*, *Homo* and *Pan* diverged from the same species, thereby forming a trichotomous cladistic pattern (e.g. Hasegawa et al., 1989; Groves, 1989; Van Valen, 1989; Corruccini, 1992; Chaline et al., 1996). However, the majority of evolutionary biologists have opted, with differing degrees of enthusiasm, to accept the consensus molecular tree over the tree favoured by the majority of morphological analyses (e.g. Diamond, 1988a; 1988b; 1991; Wood, 1989a; 1996a; Patterson et al., 1993; Foley, 1995; Pilbeam, 1996; Messier and Stewart, 1997). Although the relative merits of molecular, morphological and 'total evidence' analyses are currently the subject of considerable debate (e.g. Patterson, 1987; Donoghue et al., 1989; Swofford, 1991a; DeSalle and Grimaldi, 1991; de Queiroz, 1993; Eernisse and Kluge, 1993; Honeycutt and Adkins, 1993; Patterson et al., 1993; DeSalle, 1994; Larson, 1994; Mishler, 1994; Smith and Littlewood, 1994; de Queiroz et al., 1995; Hedges and Maxson, 1996; Givnish and Sytsma, 1997; Lee, 1997), the latter position can be defended on two counts.

First, the synapomorph status of the enamel and knuckle-walking character states, which authors like Andrews (1987; 1988) have suggested support a (*Gorilla*, *Pan*) clade, is far from certain. Begun (1992), for example, has noted that we do not know enough about dental enamel ultrastructure to be sure that Martin's (1983; 1985) findings have been correctly interpreted by those researchers who favour an African ape clade. Likewise, Beynon et al. (1991) have recently argued that the enamel depositional features of *Gorilla* and *Pan* claimed to be synapomorphic by Martin (1983; 1985), are not in fact present, and that the depositional processes of *Gorilla* and

Pan are no different from those seen in other hominoids, despite differences in enamel thickness. With respect to knuckle-walking, a number of authors have suggested that a knuckle-walking phase in hominid evolution cannot be ruled out, and that the complex of forelimb characters associated with this form of locomotion in *Gorilla* and *Pan* should therefore be viewed as symplesiomorphic. For instance, Begun (1992; 1994b) has argued that the shared loss by *Pan*, *Gorilla* and *Homo* of the *os centrale* and other traits relating to increased stability in the wrist may be indicative of a common ancestry of proto-knuckle-walking, from which the living apes have diverged minimally. Other workers who have suggested that humans have a knuckle-walking ancestry include Zhilman and Lowenstein (1983; see also Zihlman, 1989), Sarich (1985), Miyashiro (1985), Lewis (1989), Shea and Inouye (1993) and, most recently, Pilbeam (1996). An alternative thesis has been put forward by Larson (1992), who suggested that the morphological resemblances between the forelimbs of *Gorilla* and *Pan* may be convergent.

The second reason for favouring the (*Homo*, *Pan*) clade of the molecular analyses over the (*Gorilla*, *Pan*) clade of the morphological analyses is that the techniques of molecular systematics have been successfully tested on groups of taxa whose phylogenetic relationships are known, whereas those of morphological systematics have not. The earliest of these tests compared the results of molecular and morphological phylogenetic analyses based on inbred strains of laboratory mice whose actual phylogeny was known, and demonstrated that molecular data were considerably better than morphological data at approximating the phylogeny (Fitch and Atchley, 1987). More recently, Atchley and Fitch (1991) used the same approach to assess the reliability of analyses based on individual and multiple independent genetic loci. They found that while some individual loci failed to give the correct tree, when multiple independent loci were used they were able to accurately reconstruct the phylogenetic relationships of the mice. An even more thoroughly controlled experiment was carried out by Hillis and colleagues (1992). Having created a phylogeny for a bacteriophage through propagation, they produced a high resolution

restriction-site map for each ancestral taxon and all the descendants, and subjected these to a variety of phenetic and cladistic analyses. All the methods they used yielded the correct tree topology; the closest fit to the actual branch lengths was given by the maximum parsimony analysis, which correctly reconstructed 98.6 per cent of the ancestral restriction-site maps.

3.2. PAPIONINI

3.2.1. TAXONOMY, DISTRIBUTION AND CHARACTERISTICS OF THE EXTANT PAPIONINI

Papionini is one of several tribes in the Old World monkey family Cercopithecoidea (Kuhn, 1967; Strasser and Delson, 1987; Disotell, 1992; 1996; in press). It is composed of six living genera: *Cercocebus*, *Lophocebus*, *Macaca*, *Mandrillus*, *Papio* and *Theropithecus* (Disotell, 1992; 1994; 1996). *Cercocebus*, *Macaca*, *Papio* and *Theropithecus* are long established genera, whereas the generic status of *Lophocebus* and *Mandrillus* is relatively recent (Groves, 1978; 1989; Disotell, 1996; in press). For much of this century, the grey-cheeked and black mangabeys which comprise *Lophocebus* were included with the other mangabeys in *Cercocebus*, while the forest dwelling *Mandrillus* baboons were considered members of *Papio* (e.g. Buettner-Janusch, 1966; Szalay and Delson, 1979). It has been argued that an additional genus, *Allenopithecus*, should be included in the Papionini (Groves, 1989). However, this suggestion has been rejected on the grounds that *Allenopithecus* does not share several key derived features with the other six papionin genera (Disotell, 1992; 1994; Groves, in press).

Among the six papionin genera there are 27 widely recognized species. *Cercocebus* contains two extant species: *Cercocebus galeritus* (Tana River mangabey) and *Cercocebus torquatus* (white-collared mangabey) (Fleagle, 1988; Disotell, 1992; 1994). *Lophocebus* also has two ex-

tant species referred to it: *Lophocebus albigena* (grey-cheeked mangabey) and *Lophocebus aterrimus* (black mangabey) (Fleagle, 1988; Disotell, 1992; 1994). The macaque genus, *Macaca*, has 19 living species assigned to it: *Macaca arctoides* (bear macaque), *Macaca assamensis* (Assamese macaque), *Macaca brunescens* (Muna-Butung macaque), *Macaca cyclopes* (Taiwan macaque), *Macaca fascicularis* (crab-eating macaque), *Macaca fuscata* (Japanese macaque), *Macaca hecki* (Heck's macaque), *Macaca nemestrina* (pig-tailed macaque), *Macaca maura* (moor macaque), *Macaca mulatta* (rhesus macaque), *Macaca nigra* (Celebes black macaque), *Macaca nigriscens* (Gorontalo macaque), *Macaca ochreata* (ochre macaque), *Macaca radiata* (bonnet macaque), *Macaca silenus* (lion-tailed macaque), *Macaca sinica* (Toque macaque), *Macaca sylvanus* (barbary macaque), *Macaca thibetana* (Thibetan macaque) and *Macaca tonkeana* (Tonkean macaque) (Fooden, 1976). *Mandrillus*, the forest baboon genus, contains two extant species: *Mandrillus leucophaeus* (drill) and *Mandrillus sphinx* (mandrill) (Fleagle, 1988). Systematists have long agreed that there are five distinct morphs within the savanna baboon genus *Papio*, but there have been differences of opinion over the status of the morphs. Some have considered the morphs to be separate species, while others have argued that the extensive interbreeding between the morphs indicates that they are subspecies. The current consensus is that *Papio* comprises one species, *Papio hamadryas*, within which there are five subspecies: *Papio hamadryas anubis* (olive baboon), *Papio hamadryas cynocephalus* (yellow baboon), *Papio hamadryas hamadryas* (hamadryas or sacred baboon), *Papio hamadryas papio* (Guinea or Western baboon) and *Papio hamadryas ursinus* (chacma baboon) (Groves, 1989; Williams-Blangero et al., 1989; Disotell, 1992; 1996; in press; Jolly, 1993). There is only one extant species of *Theropithecus*, *Theropithecus gelada* (Fleagle, 1988).

Compared to its sister tribe Cercopithecini, Papionini has an extensive distribution and occupies a wide range of habitats (Fleagle, 1988; Nowak, 1991). *Cercocebus* is found in many of the forests of central and western Africa, as is *Lophocebus*. *Mandrillus* is a forest dweller as well, but

is restricted to West Africa. The range of *Theropithecus* is limited to the savanna of the Ethiopian highlands. *Papio* is also primarily a monkey of the African savanna; its representation outside that continent is limited to a small population of *P. h. hamadryas* in southern Arabia (Jolly, 1966). Unlike the other papionins, *Macaca* is found throughout much of temperate and tropical central and eastern Eurasia, as well as in parts of North Africa and on Gibraltar. In line with this wide distribution, *Macaca* occupies a broad range of habitats from lowland, secondary forests to upland, hilly environments.

Although the papionin genera are heterogeneous in body size (4.5 kg to 30 kg), sexual dimorphism patterns (moderate to extreme), and locomotor and dietary adaptations (terrestrial omnivory to arboreal frugivory), they are generally considered to form a monophyletic group (Jolly, 1966; 1967; 1970; Delson, 1975; Szalay and Delson, 1979; Groves, 1989; in press; Disotell et al., 1992; Disotell, 1994) Among the suite of character states which have lately been argued to distinguish Papionini from its sister taxon, Cercopithecini, are: (1) wider nasal aperture, (2) facial elongation, (3) lower incisors lacking enamel on lingual surfaces, (4) incisiform female canines, (5) 'flared' molars, i.e. convexity of the buccal and lingual surfaces, (6) wide range of facial gestures, (7) ischial callosities of males fused across midline, (8) female sexual skin, incorporating vagina, perineum, and anus, undergoes cyclical enlargement, being maximally swollen around time of ovulation and (10) preference for terrestrial substrate (Szalay and Delson, 1979; Strasser and Delson, 1987; Groves, 1989).

The papionins have also been found to be a monophyletic group in analyses of several lines of molecular evidence, including immunological distance statistics (Sarich and Cronin, 1976), amino acid sequences (Hewett-Emmett et al., 1976), single copy DNA-DNA hybridization temperatures (Benveniste and Todaro, 1976b), fast-repeat high t_m DNA sequences (Gillespie, 1977) and mtDNA sequences (Disotell, 1992; Disotell et al., 1992; Van der Kuyl et al., 1995). Addi-

tionally, several studies have demonstrated that the papionin genera share a diploid complement of 42 chromosomes (e.g. Darlington and Hague, 1955; Chiarelli, 1962; Guisto and Margulis, 1981), which Groves (1989) and Disotell (1992; 1994; 1996; in press) have argued is a derived character state relative to the cercopithecines.

Although most morphologists and molecular biologists now agree that the papionin genera form a monophyletic group, several studies have failed to support this hypothesis. The most prominent of these are those of Goodman and Moore (1971) and Dene et al. (1976). In their assessment of primate immunodiffusion statistics, Goodman and Moore (1971) found the phylogenetic status of Papionini to be equivocal. When they used anti-*Erythrocebus* serum, they found the mangabeys to be more closely related to the non-papionin taxa (*Erythrocebus*, *Cercopithecus*) than to *Macaca*, *Papio* (including *Mandrillus*) and *Theropithecus*. In contrast, when anti-*Papio* serum was used, *Cercocebus* grouped with the other papionins. In a follow-up to Goodman and Moore's (1971) study, Dene et al. (1976) found that both *Mandrillus* and the mangabeys grouped with *Erythrocebus* and *Cercopithecus* rather than with the other papionin taxa, *Macaca*, *Papio* and *Theropithecus*. To date, no convincing explanation of the anomalous results obtained by Goodman and Moore (1971) and Dene et al. (1976) has been offered.

3.2.2. PHYLOGENETIC RELATIONSHIPS AMONG THE EXTANT PAPIONIN GENERA

The phylogeny for papionins used in this study (Figure 2) contains four clades. The largest of these links *Cercocebus*, *Lophocebus*, *Mandrillus*, *Papio* and *Theropithecus* together to the exclusion of *Macaca*. The next largest clade links *Lophocebus*, *Papio* and *Theropithecus* together to the exclusion of *Cercocebus* and *Mandrillus*. One of the remaining clades is nested within the (*Lophocebus*, *Papio*, *Theropithecus*) clade and contains *Papio* and *Theropithecus*, while the other is the sister taxon of the (*Lophocebus*, *Papio*, *Theropithecus*) clade and comprises *Cercocebus* and *Mandrillus*. In this section, the evidential support for each of these clades will be outlined, beginning with the mangabey and baboon clade *Cercocebus*, *Lophocebus*, *Mandrillus*, *Papio* and *Theropithecus*.

3.2.2.1. Mangabey and baboon clade

The hypothesis that the first branching event in the evolution of the extant papionins separated *Macaca* from the common ancestor of the mangabeys and baboons has been supported by analyses of both morphological and molecular data. Among the most comprehensive of the morphological studies is Delson's (1975) review of the taxonomy and phylogeny of the extant and fossil Old World monkeys. In this study, Delson recognized three lineages among the papionins: one comprised *Macaca* and its extinct relatives, another *Theropithecus* and its extinct relatives, and the third *Papio* (including *Mandrillus*) and *Cercocebus* (including *Lophocebus*) and their extinct relatives. While advocating caution over the phylogenetic relationships between the lineages, Delson hypothesized that the common ancestor of the papionins was macaque-like in its cranial and dental morphology, and nominated a fossil hypodigm tentatively assigned to *Macaca* as the sister taxon of the other papionins on his cladogram. Later, Strasser

and Delson (1987) reached the same phylogenetic conclusion following a cladistic analysis of morphological and behavioural characters recorded for representatives of all the main Old World monkey subfamilies and tribes. They argued that living and fossil *Macaca* can be separated from the other papionins on the grounds that it is symplesiomorphic for anteorbital drop (shallow), facial fossae (absent) and substrate preference (semi-terrestrial). According to Disotell (1994), almost all morphologists now agree that the macaques are the sister group to the rest of the papionins.

Among the molecular analyses which have supported a mangabey and baboon clade within Papionini are Hewett-Emmett and co-workers' (1976) analysis of Old World monkey haemoglobin α-chain and β-chain amino acid sequences, Benveniste and Todaro's (1976b) single copy DNA-DNA hybridization analysis of primate genomic DNA, Sarich and Cronin's (1976; Cronin and Sarich, 1976) microcomplement fixation (MC'F) analyses of primate albumins and transferrins, and Disotell and colleagues' (1992) cladistic analysis of cercopithecoid mtDNA COII sequences. More recently, a mangabey and baboon clade was found in the most parsimonious tree obtained by Van der Kuyl and associates (1995) from c.390-bp segments of the mitochondrial 12s rRNA gene belonging to 26 catarrhine species (although they did not include *Theropithecus* in their sample), and in the minimum length tree recovered by Disotell's research team from sequences of the nDNA CD4 and α→1,3-galactosyltransferase loci (Disotell, personal communication).

While some studies have been unable to resolve the relationships between *Macaca* and the other papionin taxa (e.g. Sarich, 1970; Szalay and Delson, 1979; Dutrillaux, 1979; Dutrillaux et al., 1981; 1982; Stanyon et al., 1988), the only major authorities to have contradicted the mangabey and baboon clade in the last 30 years are Jolly (1966; 1967; 1970) and Hill (1974). Jolly (1966) posited a basal split between *Theropithecus* and a clade linking the mangabeys, *Macaca*,

Mandrillus and *Papio*. Jolly (1967; 1970) positioned *Theropithecus* as the basal papionin and *Macaca* as the sister taxon of a clade containing *Mandrillus*, *Papio* and the mangabeys. He defended this arrangement on the grounds that the lineage to which *Theropithecus* belongs appears relatively early in the fossil record, and has a large number of derived morphological features. Today, neither of these lines of evidence is considered valid for establishing phylogenetic relationships. Hill (1974) linked the mangabeys and *Macaca* in a clade that was the sister group of a clade containing *Mandrillus*, *Papio* and *Theropithecus*.

It should also be noted that Groves (1989; in press) has recently questioned whether *Macaca* is monophyletic. In a cladistic analysis of morphological data for several cercopithecid species (including *Cercocebus*, *Lophocebus*, *Macaca*, *Mandrillus*, *Papio* and *Theropithecus*), he found that one macaque species (*M. nemestrina*) was (weakly) associated with the other papionins, while the other (*M. sylvanus*) was most closely associated with a non-papionin taxon (Groves, in press).

3.2.2.2. *Lophocebus*, *Papio* and *Theropithecus* clade

The clade comprising *Lophocebus*, *Papio* and *Theropithecus* has been supported by analyses of a number of lines of molecular evidence, including haemoglobin α- and β-chain amino acid sequences (Hewett-Emmett et al., 1976), immunological distance statistics (Sarich and Cronin, 1976; Cronin and Sarich, 1976), single copy DNA-DNA hybridization temperatures (Benveniste and Todaro, 1976) and mtDNA nucleotide sequences (Disotell et al., 1992). A recently completed cladistic analysis of sequences of the nDNA CD4 and α→1,3-galactosyltransferase loci has also supported a (*Lophocebus*, *Papio*, *Theropithecus*) clade (Disotell, personal communication). Additionally, Van der Kuyl and colleagues' (1995) analysis of the mitochondrial 12s rRNA gene from 26 catarrhine species (including *Cercocebus*, *Lophocebus*, *Macaca*, *Mandrillus*

and *Papio*) suggested that *Lophocebus* and *Papio* share a common ancestor not shared by the other taxa in the sample.

None of the morphology-based phylogenetic analyses of the papionins published to date has favoured a (*Lophocebus*, *Papio*, *Theropithecus*) clade. For example, the phylogenetic trees presented by Delson (1975) and Szalay and Delson (1979) positioned *Papio* and *Mandrillus* as a clade, the mangabeys as the sister group of the (*Mandrillus*, *Papio*) clade, and *Theropithecus* as the closest relative of the *Cercocebus/Lophocebus*, *Mandrillus* and *Papio* clade. Strasser and Delson (1987) presented a cladogram in which *Theropithecus* was the sister taxon of a clade comprising *Cercocebus*, *Lophocebus*, *Mandrillus* and *Papio*, and *Lophocebus* was either the sister taxon of *Cercocebus* or part of a clade with *Mandrillus* and *Papio*. Groves (in press) found no evidence for *Lophocebus* being part of the papionin group.

However, in an earlier paper Groves (1978) suggested that *Lophocebus* approaches the condition in *Papio* in a number of character states. Based on these, Groves suggested that of the two mangabey genera, *Lophocebus* is more closely related to *Papio*. Additionally, Disotell (1994) has argued that the catamenial swelling of *L. albigena* is most similar to that of *Papio* among the papionins.

3.2.2.3. *Papio* and *Theropithecus* clade

The hypothesis that *Papio* and *Theropithecus* are more closely related to one another than either is to any other living papionin genus was supported by several early molecular analyses, such as Barnicot and Wade's (1970) electrophoresis examination of the adenylate kinase and haemoglobin α- and β-chains from a sample of Old World monkeys (including *Macaca*, *Papio*, *Mandrillus* and *Theropithecus*), Hewett-Emmett and co-workers' (1970) analysis of

cercopithecoid hemoglobin α-chain and β- chain amino acid sequences, and Sarich and colleagues' MC'F analyses of primate albumin and transferrin (Sarich, 1970; Sarich and Cronin, 1976; Cronin and Sarich, 1976). Among the recent biomolecular and karyological studies to have identified a (*Papio*, *Theropithecus*) clade are Stanyon and colleagues' (1988) high-resolution chromosome banding pattern analysis, Disotell and colleagues' (1992) cladistic analysis of eight cercopithecoid mtDNA COII sequences, and Disotell's (1994) maximum parsimony analysis of Nelkin and co-workers' (1980) restriction map data for the nuclearly-encoded ribosomal DNA region containing the 18S and 28S ribosomal RNA sequences. Additionally, a closer relationship between *Papio* and *Theropithecus* than between *Papio* and its traditional congener, *Mandrillus*, has been supported by Benveniste and Todaro's (1976) single copy DNA-DNA hybridization experiments, Dene and colleagues' (1976) immunodiffusion study, and Gillespie's (1977) thermal stability experiments with hybrids of papionin fast-repeat high t_m DNA sequences. Disotell (1996) has recently observed that all protein electromorph, DNA-DNA hybridization value, immunological distance, nuclear restriction map, amino acid sequence, and mtDNA sequence analyses point to a sister group relationship between *Papio* and *Theropithecus* to the exclusion of *Mandrillus*, the traditional sister taxon of *Papio*.

Traditionally, morphologists have grouped *Papio* with *Mandrillus* and suggested that this clade is more closely related to the mangabeys than it is to *Theropithecus*. However, in the last two decades support for a (*Papio*, *Theropithecus*) clade has grown. Jolly (1970) recognized several *Theropithecus*-like traits in *P. h. hamadryas*, including (1) relative incisor and molar size, (2) temporal crest position and shape, (3) degree of postorbital constriction, and (4) facial profile concavity. Following an analysis of morphological, molecular and palaeontological data, Cronin and Meikle (1979) suggested that *Theropithecus* may be a rapidly evolved offshoot from a *Papio*-like stock, but it was not clear whether they included *Mandrillus* in *Papio*. Strasser and Delson (1987), while positioning *Theropithecus* as the sister group of a (mangabey, *Mandrillus*,

Papio) clade on their preferred cladogram, indicated in the text that they were open to the possibility that *Theropithecus* is the sister taxon of a clade comprising *Mandrillus* and *Papio*.

More recently, Delson (1991a; 1991b; see also Delson and Dean, 1993) has argued that the similarities between *Papio baringensis*, a fossil papionin from the Turkana Basin, and *Theropithecus* are such that *Papio* and *Theropithecus* must be more closely related than morphologists had previously been willing to accept, although he still considered *Mandrillus* and *Papio* to be congeners. Jablonski (1993) also suggested that *Papio* and *Theropithecus* are sister taxa, but did not indicate how she thought *Papio* and *Theropithecus* were related to *Mandrillus*. Disotell (1994) has noted that male *Papio* and *Theropithecus* have a glans penis that contains a lateral notch while the meatus is relatively short, which is distinct from the condition of the glans penis seen in *Mandrillus* and *Cercocebus* (semi-lunate lateral border and a long urinary meatus that nearly reaches the dorsal border of the glans). One of these conditions is obviously synapomorphic, but this evidence has yet to be fully analyzed. Groves' (in press) recent cladistic analysis of several cercopithecoid genera was unable to clarify the relationships of *Papio* and *Theropithecus*, but did indicate that the closest relative of *Mandrillus* is *Cercocebus* rather than *Papio*.

3.2.2.4. *Cercocebus* and *Mandrillus* clade

Disotell (1996) has recently noted that most methodologically valid chromosomal and molecular studies have found the mangabeys to be paraphyletic, with *Cercocebus* most closely related to *Mandrillus*. For example, Dutrillaux et al. (1981) found that *Mandrillus* and *Cercocebus* share a complex (three-break) re-arrangement of chromosome 10, while the other papionins (except for *Macaca fascicularis*) are chromosomally conservative and cannot be differentiated, and Stanyon et al. (1988) found evidence for a (*Cercocebus*, *Mandrillus*) clade in their high-resolution

chromosome banding pattern analysis. More recently, a sister group relationship between *Cercocebus* and *Mandrillus* has been favoured in Disotell and co-workers' maximum parsimony analyses of mtDNA COII gene sequences and sequences of the nDNA CD4 and α→1,3-galactosyltransferase loci (Disotell et al., 1992; Disotell, personal communication). Additionally, Van der Kuyl and associates' (1995) cladistic analysis of segments of the mitochondrial 12s rRNA gene belonging to 26 catarrhine species (including *Cercocebus*, *Lophocebus*, *Macaca*, *Mandrillus* and *Papio*) suggested that *Cercocebus* and *Mandrillus* share a common ancestor that is not shared by any of the other taxa in the sample.

As noted above, most of the morphological analyses performed to date group *Mandrillus* with *Papio* rather than with *Cercocebus* (e.g. Delson, 1975; Szalay and Delson, 1979; Strasser and Delson, 1987). Indeed, Szalay and Delson (1979) suggested that *C. torquatus* shares a number of traits with *Papio*, while *L. albigena* is unlike *Papio* cranially. However, in a recent cladistic analysis of morphological evidence from a number of Old World monkey genera, Groves (in press) found a sister group relationship between *Cercocebus* and *Mandrillus* to be the only resolvable relationship within the Papionini. Additionally, Disotell (1994) has noted that *Cercocebus* has a long hallux like *Mandrillus*, which contrasts with the moderate sized hallux of *Papio* and the relatively short hallux of *Theropithecus*. Disotell also highlighted the fact that the female sexual swellings of *Cercocebus* and *Mandrillus* are similar in the extent to which the anus is incorporated into the swelling itself, and that the catamenial swellings of *Mandrillus* and *Papio* are very different. As mentioned in the preceding section, the morphology of glans penis is similar in *Cercocebus* and *Mandrillus*, and contrasts with that seen in *Papio*, the traditional congener of the forest baboon genus.

CHAPTER 4. MATERIALS, METHODS AND TESTS OF THE HYPOTHESES

This chapter is divided into three main sections. The first gives details of the craniodental material from which the study data were collected, and the instruments and techniques that were used to collect the data. The second describes the size-adjustment techniques and coding procedures with which the data were transformed for cladistic analysis. It also introduces the computer programs that were used to analyze the transformed data. The third section outlines the tests of the three hypotheses that were carried out using the craniodental data.

4.1. MATERIALS

4.1.1. DATASET A

Dataset A comprised values for 129 craniodental measurements recorded on mixed-sex samples of four extant hominoid taxa and two outgroups. The measurements are listed in Table 1. The hominoid taxa were *Gorilla gorilla*, *Homo sapiens*, *Pan troglodytes*, and *Pongo pygmaeus*. The outgroups were *Colobus guereza* and *Papio hamadryas anubis/cynocephalus*. Data for 77 of the measurements (P1-P23, M1-M33, F1-F10, C1-C10, C24) were taken from Wood (1975) and Wood et al. (1991). The former measured 24 *C. guereza* (12 males, 12 females), 37 *G. gorilla* (20 males, 17 females), 75 *H. sapiens* (40 males, 35 females), 35 *P. troglodytes* (13 males, 22 females), and 31 *P. h. anubis/cynocephalus* (14 males, 17 females). Wood et al. (1991) measured 41 *P. pygmaeus* specimens (20 males, 21 females). Data for the remaining 52 measurements (P24-P31, M34-M40, F11-F24, C11-C23, C25-C34) were taken from Chamberlain (1987). Chamberlain measured 20 *C. guereza* (ten males, ten females), 20 *G. gorilla* (ten males,

ten females), 20 *H. sapiens* (ten males, ten females), *P. troglodytes* (ten males, ten females), and 20 *P. pygmaeus* (ten males, ten females). Where necessary, cranial and mandibular values were rounded up to the nearest millimetre, and dental values to the nearest 0.1 mm. The raw data from Dataset A are presented in Appendix 1.

4.1.2. DATASET B

Dataset B consisted mainly of values for 62 cranial measurements recorded on mixed-sex samples of six extant papionin taxa and four outgroups. These data were collected by the author. The papionin taxa sampled were *Cercocebus galeritus/torquatus* (13 males, 13 females), *Lophocebus albigena/aterrimus* (20 males, 20 females), *Macaca fascicularis/mulatta* (20 males, 20 females), *Mandrillus leucophaeus/sphinx* (42 males, 20 females), *Papio hamadryas anubis/cynocephalus* (20 males, 19 females), and *Theropithecus gelada* (22 males, 22 females). The outgroup taxa were *Cercopithecus aethiops* (five males, five females), *Colobus badius* (three males, four females), *Erythrocebus patas* (five males, five females), and *Pan troglodytes* (ten males, seven females).

The skulls were measured at the Anthropologisches Institut und Museum, Universität Zürich-Irchel, Switzerland (*C. galeritus/torquatus*, *C. aethiops*, *C. badius*, *E. patas*, *M. fascicularis/mulatta*, *P. h. anubis/cynocephalus*, *T. gelada*, *P. troglodytes*), the Department of Human Anatomy and Cell Biology, The University of Liverpool, UK (*T. gelada*, *P. troglodytes*), the Muséum d'Histoire Naturelle, Genève, Switzerland (*E. patas*, *T. gelada*, *P. troglodytes*), the Muséum d'Histoire Naturelle, Paris, France (*E. patas*, *P. h. anubis/cynocephalus*, *T. gelada*, *P. troglodytes*, *C. aethiops*), the Museum für Naturkunde, Humboldt-Universitat zu Berlin, Germany (*C. galeritus/torquatus*, *L. albigena/aterrimus*, *M. fascicularis/mulatta*, *T. gelada*) and the Natural History Museum, London, UK (*C. galeritus/torquatus*, *C. badius*, *L. albigena/aterrimus*,

M. fascicularis/mulatta, *M. leucophaeus/sphinx*, *P. h. anubis/cynocephalus*, *T. gelada*, *P. troglodytes*). Only adult specimens were measured; a specimen was judged to be adult if its third molars had erupted. The sex of the specimens was determined from museum records, most of which were based on observations of soft tissue anatomy. The majority of the crania and mandibles had been obtained from animals living in the wild, but a few of the specimens held by the Natural History Museum, London, and most of those held by the Department of Human Anatomy and Cell Biology, The University of Liverpool, were obtained from captive animals.

The measurements are listed in Table 2, along with the landmarks on which they were based. Fifty-seven of the measurements were selected from those employed by Wood (1991) (P1-P15, M1-M14, F1-F14, C1-C13). They were selected in order to sample as evenly as possible the different aspects of cranial, mandibular and dental morphology, and thereby avoid bias towards particular anatomical regions (cf. Wood and Chamberlain, 1986; Chamberlain and Wood, 1987). It was also hoped that the dental measurements would reflect changing function along the tooth row. In line with Chamberlain (1987), alveolar tooth row chords were included as measurements of mandibular and palatal morphology which overlapped rather than duplicated the corresponding dental measurements. The remaining five measurements (P16, F15, F16, C15, C16) were selected from those employed by Chamberlain (1987) in order to fill the gaps in the anatomical coverage provided by the measurements from Wood (1991).

In line with Wood and Chamberlain (1986), the cranial and mandibular measurements were taken to the nearest 1 mm, while the dental measurements were recorded to the nearest 0.1 mm. The measurements were taken with Sylvac digital needle-point vernier calipers, GPM spreading calipers, or GPM co-ordinate calipers. The type of calipers used for each measurement is noted in Table 2. Where ectocranial crests obscured a landmark, the measurement was taken on the plane of the vault next to landmark. Bilateral measurements were averaged. The measurement

values were recorded on data sheets, together with a note of each specimen's sex, acquisition locality and museum catalogue number. The collated information was subsequently transferred to a Macintosh Powerbook 5300 microcomputer running the spreadsheet program Excel 5. Printouts of the computer files were visually checked against the original data sheets in order to eliminate transcription errors.

The measurement landmarks were checked against casts of some of the early *Homo* specimens measured by Wood (1991) and some of the specimens of *P. troglodytes* measured by Chamberlain (1987). To provide an estimate of intra-observer error, specimens of *E. patas* and *T. gelada* were re-measured on separate occasions. Tables 3 and 4 present the original values for these specimens, together with the values derived from the second round of measurements, and the difference between them. With the *E. patas* cranium and mandible the mean difference between the measurements amounted to 0.7% of the average measurement value. The mean difference between the original and replicated measurements on the *T. gelada* specimen amounted to 0.5% of the average measurement value. These figures compared favourably with those obtained by Chamberlain and Wood (1987) in a similar exercise.

The remainder of Dataset B comprised values for 55 of the measurements listed in Table 2 recorded on seven *C. torquatus* males, seven *C. torquatus* females, seven *C. badius* males, seven *C. badius* females, five *P. troglodytes* males, and seven *P. troglodytes* females. These data were taken from Chamberlain et al. (in preparation) and were collected by the lead author at the American Museum of Natural History, New York. The measurements are given in Table 5. Before Chamberlain and colleagues' data were incorporated into Dataset B, they were compared with those recorded by the candidate using Student's two-tailed t-test. Some significant differences between the variable means of the data sets were found (Table 6). However, as none of the variable means was significantly different in all the taxa, those differences were assumed to

reflect morphological dissimilarities between the samples rather than differences in the measurement landmarks used. All the raw data from Dataset B are presented in Appendix 2.

4.2. METHODS

4.2.1. SIZE-ADJUSTMENT TECHNIQUES

In order to control for the confounding effects of body size, three methods of size-adjustment were used, all of which belong to the Mosimann family of shape ratios (Jungers et al., 1995). In the first method (BMS), taxon averages were calculated for each variable and then divided by the cube root of the body mass of the appropriate taxon (Sneath and Sokal, 1973; Jungers, 1985; Wood, 1995). In the second method (AVE), the values for each specimen were divided by the average of all the specimen's values. In the third method (LSG), the natural log of each specimen value was divided by the natural log of the geometric mean of all the specimen's values. The geometric mean is computed as the *n*th root of the product of *n* measurements (Jungers et al., 1995). All of these methods equalize the volumes of the specimens or taxa while maintaining their original shapes.

4.2.2. CODING METHODS

Three methods of converting continuous data into discrete character states were employed, segment coding, Baum's coding procedure and divergence coding. Segment coding (Simon, 1983; Thorpe, 1984; Chappill, 1989) proceeds by dividing the range between the lowest and highest taxic means into a series of equal size segments (e.g. 0.1 to 1.1, 1.2 to 2.2, 2.3 to 3.3). Each segment is given a code (e.g. A, B, C), and the taxa are assigned codes according to where their means lie in the range. The same segment size is applied to all the characters in order to pre-

serve the proportionate differences in their ranges. Characters with larger ranges are therefore allocated more character states than characters with smaller ranges.

The coding procedure outlined by Baum (1988) involves ranking the minimum, mean and maximum values for the taxa in ascending order. If there are no ties among the minimum values, the ranks of the minimum values are used as the codes for the taxa. Where the ranks of the minimum values are the same for two or more taxa, the ranks of the mean values are used as the taxon codes. If the ranks of the mean values are also the same, the ranks of maximum values are used as the character states for the taxa. In the event that the minimum, mean and maximum values for two or more taxa are all equal, the taxa are assigned the same code.

In divergence coding (Thorpe, 1984) the mean values for the taxa are calculated, and the differences between them tested for statistical significance. The means are then ranked in ascending order, and a taxon-by-taxon matrix compiled. Each cell in the top row of the matrix is filled with a taxon name such that the rank of the taxa decreases from left to right. The cells of the first column of the matrix are also filled with the names of the taxa on the basis of their rank, with the highest ranked taxon being placed in the top cell and the lowest ranked taxon in the bottom cell. Thereafter, each column of the matrix is filled with -1s, +1s and 0s. A cell is filled with a -1 if the mean of the taxon in the column is greater than the mean of the taxon in the row and the difference between the means is significant. A cell is filled with a +1 if the mean of the column taxon is significantly lower than the mean of the row taxon. If the difference between the means of the column and row taxa is not significant, the cell is filled with 0. Once the matrix is completely filled, the total of 0s, -1s and +1s for each column is calculated. Lastly, an integer is added to each taxon total to make them positive figures and therefore suitable for use in computer-based phylogenetics programs.

4.2.3. PHYLOGENETICS PROGRAMS

Two phylogenetics programs were employed in the analyses: Phylogenetic Analysis Using Parsimony Version 3.0s (Swofford, 1991b) and MacClade Version 3 (Maddison and Maddison, 1992). The former, which is usually referred to as PAUP, is a cladistics-based phylogeny reconstruction program, whereas the latter allows the effects of different cladistic hypotheses to be explored within a parsimony framework.. In both programs, the parsimoniousness of a cladogram is assessed in relation to the sum of the lengths of its branches. The length of a branch connecting a pair of taxa on a cladogram is computed as the sum of the character state differences between the taxa under a given model of character state evolution (e.g. ordered, unordered, irreversible). Minimum length cladograms correspond to traditional most parsimonious cladograms, because minimizing the total number of character state changes is equivalent to minimizing the number of 'extra' steps needed to explain the evolution of the characters on the cladogram (Gooder, 1991).

4.3. TESTS OF THE HYPOTHESES

4.3.1. HYPOTHESIS 1 TESTS

Standard cranial and dental characters are reliable for reconstructing the cladistic relationships between primate species and genera

Six tests of Hypothesis 1 were performed. Two were based on parsimony analysis (Farris, 1970; Kluge, 1984), two on compatibility analysis (Le Quesne, 1969; 1974, 1982; Estabrook et al., 1977; Brooks and McLennan, 1991) and two on the bootstrap procedure (Felsenstein, 1985). As

there is currently no agreement about how best to conduct a cladistic analysis of morphometric data, the tests comprised several analyses, each of which used a different combination of taxa, size-adjustment technique and coding procedure.

4.3.1.1. Parsimony-based test of Hypothesis 1 using characters from all Dataset A regions

The test comprised eleven analyses (A-K). The first eight, analyses A through H, were based on the 77 variables used by Wood et al. (1991). The remainder, analyses I through K, were based on all 129 measurements used to compile Dataset A. Five of the 77 variable analyses (A, D, E, F, G) and the three 129 variable analyses included *C. guereza* as the outgroup to the four hominoid taxa (*G. gorilla*, *H. sapiens*, *P. troglodytes*, *P. pygmaeus*). Two of the other 77 variable analyses (B, H) incorporated *P. h. anubis/cynocephalus* as the outgroup. The remaining 77 variable analysis (C) included both *C. guereza* and *P. h. anubis/cynocephalus* as outgroups.

In analyses A, B and C the data were adjusted to account for body size using the BMS method. The body masses used are presented in Table 7. In analyses D and I, the AVE method of size adjustment was applied to the data. Size-adjustment was accomplished in analyses E, F, G, H, J using the LSG method. Due to limitations on the available memory of the Macintosh Powerbook 5300 microcomputer on which the analyses were performed, the data from Wood (1975) and Wood et al. (1991) were size-adjusted separately from Chamberlain's (1987) data in analyses I, J and K.

Once adjusted for the effects of size, the data in analyses A, B, C and G were converted into discrete characters for phylogenetic analysis using segment coding. The data used in analyses A, B and C were coded together, and a segment size of 2 was applied to all characters. In Analysis G, a segment size of 0.1 was applied to all characters. In analyses D, F, H, I and K, the size-

adjusted data were coded using the procedure outlined by Baum (1988). In Analysis D the values were set to two decimal places before coding. In analyses F, H, I and K the default setting for Excel 5 was used. The data were coded in analyses E and J with divergence coding (Thorpe, 1984). In both analyses, Student's t-test (two-tailed) was used to test for statistical significance ($P \leq 0.05$), and 10 was added to each taxon total to make them positive.

After coding, the matrices (tables 8-18) was subjected to parsimony analysis using PAUP's Branch and Bound routine, which is guaranteed to find the shortest length cladogram (Swofford, 1991b). Because all the characters were metrical and their states could therefore be assumed to have evolved serially, the characters were always treated as freely-reversing, linearly-ordered variables (Chamberlain and Wood, 1987; Baum, 1988; Slowinski, 1993; Rae, 1997). The characters were also always given equal weight. Subsequently, the data matrices were transferred to MacClade. A cladogram with the same ingroup topology as the most parsimonious cladogram was set up in the program's Tree Window and rooted by positioning the outgroup as the sister group of the hominoid taxa. Characters that were uninformative with respect to the most parsimonious cladogram were excluded from the data matrix, and the length, consistency index (CI) and retention index (RI) recorded. Lastly, the cladogram was compared with the consensus molecular cladogram for the hominoid genera (Figure 1).

The hypothesis was considered supported if the analyses consistently favoured cladograms that were compatible with the hominoid consensus molecular cladogram. The condition 'consistently favoured' was attached to the tests because cladistic programs can generate cladograms from random data (Smith, 1994). As the merits or otherwise of the size-adjustment and coding procedures have yet to be assessed, recovering the consensus molecular cladogram from one or even a few of the analyses would thus not have been a convincing demonstration that cladistic techniques work on primate craniodental data. Additionally, it is reasonable to assume that if a data

set contains a strong phylogenetic signal, the signal should be identified regardless of which out-groups, size-adjustment techniques and coding procedures are used (see Sokal, 1985).

4.3.1.2. Parsimony-based test of Hypothesis 1 using characters from all Dataset B regions

The test consisted of nine analyses (1-9). Analyses 1 through 6 were based on values for all 62 measurements from *C. galeritus/torquatus*, *L. albigena/aterrimus*, *M. fascicularis/mulatta*, *M. leucophaeus/sphinx*, *P. troglodytes*, *P. h. anubis/cynocephalus* and *T. gelada*. In Analysis 7, *Pan* was replaced as the outgroup by *C. aethiops*. In Analysis 8, a composite taxon comprising *C. aethiops*, *C. badius*, *E. patas*, and *P. troglodytes* was included as an outgroup. In Analysis 9, the *Mandrillus* sample was adjusted to account for the imbalance between the number of males and females by deleting the data for every other male specimen (N = 21), and *P. troglodytes* was included as the outgroup.

The effects of body size differences between the taxa were controlled in analyses 1 and 2 using the BMS method. The body masses used are listed in Table 19. Size adjustment was accomplished in analyses 3 and 4 via the AVE method. In analyses 5, 6, 7, 8 and 9 the data were size adjusted using the LSG method. In the first three analyses segment coding was used to convert the continuous data into discrete character states. Segment sizes of 10, 5 and 0.1 were applied to all characters in analyses 1, 2, and 3, respectively. Baum's coding procedure was used to carry out the continuous-to-discrete conversion in analyses 4 and 5. In Analyses 6, 7, 8 and 9, the data were transformed using divergence coding. Again, Student's t-test (two-tailed) was used to test for statistical significance ($P \leq 0.05$), and 10 was added to each taxon total to make them positive.

In all the analyses, the matrices (tables 20-28) were subjected to parsimony analysis using PAUP (branch and bound and ordered characters options). Each matrix was then transferred to MacClade. A cladogram with the same ingroup branching pattern as the most parsimonious cladogram was set up in the program's Tree Window and rooted by placing the outgroup as the sister taxon of the papionins. Characters that were uninformative with respect to the cladogram were then excluded, and the descriptive statistics recorded. In the last part of the analysis, the cladogram was compared with the papionin consensus molecular cladogram (Figure 2). As with the Dataset A test, the hypothesis was considered supported if the analyses consistently favoured cladograms that were compatible with the papionin consensus molecular cladogram.

4.3.1.3. Compatibility-based test of Hypothesis 1 using characters from all Dataset A regions

Two analyses formed this test (L and M). Analysis L was based on the character state data matrix prepared for Analysis I. Analysis M was based on the data matrix used in Analysis J. In both analyses, the data for each character were subjected to parsimony analysis using PAUP (branch and bound and ordered characters options). Next, the character cladograms were compared by hand to identify the minimum number of fully- and partially-resolved topologies. Each clique of characters was tested for compatibility by generating a minimum length cladogram and calculating its CI. The number of characters supporting each cladogram was then calculated and the size of the largest clique of characters compared with the size of the clique of characters supporting the consensus molecular cladogram for the hominoids. The hypothesis was considered supported if both analyses favoured cladograms that were compatible with the hominoid consensus molecular cladogram.

4.3.1.4. Compatibility-based test of Hypothesis 1 using characters from all Dataset B regions

This test consisted of two analyses (10-11). The analyses were based, respectively, on the character state data matrices from analyses 6 and 7. In both analyses, the data for each character were subjected to parsimony analysis using PAUP (branch and bound and ordered characters options). Next, the character cladograms were compared to identify the minimum number of fully- and partially-resolved topologies. The cliques of characters were tested for compatibility by calculating minimum length cladograms and CIs from them using PAUP. The number of characters supporting each cladogram was then calculated, and the size of the largest clique of characters compared with the size of the clique of characters supporting the papionin consensus molecular cladogram. The hypothesis was considered supported if both analyses favoured cladograms that were compatible with the papionin consensus molecular cladogram.

4.3.1.5. Bootstrap-based test of Hypothesis 1 using characters from all Dataset A regions

This test consisted of 11 analyses (N-X). The analyses were based, respectively, on the character state data matrices prepared for analyses A-K. In each analysis, PAUP (branch and bound and ordered characters options) was used to generate a 50% majority-rule consensus cladogram from 1000 subsets of the data matrix. The clades that were by the bootstrap cladograms were then compared with the clades of the consensus molecular cladogram for the hominoid genera. The hypothesis was judged supported if clades of the hominoid consensus molecular cladogram were consistently favoured by the analyses. A molecular clade was considered favoured if it was supported by 70% or more of the bootstrap replications and there was no better supported non-molecular clade. The first condition was imposed on the test because Hillis and Bull (1993) have suggested that clades which occur in ≥70% of the resampling cladograms in a bootstrap

analysis can be considered 'real'. The second condition was attached to the test because in a palaeontological analysis a 'false' clade that was supported by 95% of the bootstrap replications would be considered more reliable than a 'true' clade that was supported by 75% of the replications, even though such a conclusion would be misleading.

4.3.1.6. Bootstrap-based test of Hypothesis 1 using characters from all Dataset B regions

This test consisted of nine analyses (12-20). The analyses were based on the character state data matrices used in analyses 1-9. In each analysis, a 50% majority-rule consensus cladogram was derived from 1000 subsets of the data matrix using PAUP (branch and bound and ordered characters options). The clades that were supported by the bootstrap cladograms were then compared with the clades that form the consensus molecular cladogram for the papionins. The hypothesis was judged supported if clades of the papionin consensus molecular cladogram were consistently favoured by the analyses. Again, a molecular clade was considered favoured if it was supported by 70% or more of the bootstrap replications and there was no better supported non-molecular clade.

4.3.2. HYPOTHESIS 2 TESTS

Some regions of the primate cranium are more reliable than others for reconstructing the cladistic relationships between species and genera

The second hypothesis was subjected to six tests in which the characters were grouped into regions that are thought to be anatomically and/or functionally integrated (cf. Bilsborough, 1976; Wood and Chamberlain, 1986; Chamberlain and Wood, 1987). Four regional character groups were recognized: palate and upper dentition, mandible and lower dentition, face, and cranial

vault and base. Two tests were based on parsimony analysis, two on the bootstrap procedure and two on the consistency index.

4.3.2.1. Parsimony-based test of Hypothesis 2 using regional character groups from Dataset A

This test comprised three analyses (Y-AA). The analyses were based, respectively, on the data matrices used in analyses I, J and K. In each analysis, 31 variables were assigned to the palate and upper dentition character group, 40 to the mandible and lower dentition character group, 24 to the face character group, and 34 to the cranial vault and base character group. Each of the regional groups was then subjected to parsimony analysis using PAUP (branch and bound and ordered characters options). Thereafter, the regional data files were transferred to MacClade. The most parsimonious cladograms for the region were set up in the program's Tree Window and rooted by placing the outgroup as the sister taxon of the hominoids. The uninformative characters were then excluded from the data sets, and the descriptive statistics recorded. Lastly, the regional cladograms were checked for congruence with the hominoid consensus molecular cladogram (Figure 1). The hypothesis was considered supported if the regions consistently favoured different cladograms and one of the favoured cladograms was compatible with the hominoid consensus molecular cladogram.

4.3.2.2. Parsimony-based test of Hypothesis 2 using regional character groups from Dataset B

This test consisted of five analyses (21-25). The analyses were based, respectively, on the character state data matrices used in analyses 2, 3, 4, 6 and 7. In each analysis, 16 characters were assigned to the palate and upper dentition character group, 14 to the mandible and lower denti-

tion character group, 16 to the face character group, and 16 to the cranial vault and base character group. PAUP was then used to calculate a minimum length cladogram for each of the regional data sets. Thereafter, the four regional data files were transferred to MacClade. The most parsimonious cladograms were set up in the program's Tree Window and rooted by placing the outgroup as the sister taxon of the papionins. The characters that were uninformative with respect to the cladograms were excluded from each of the regional data sets, and the length, CI and RI recorded. In the last part of the analysis, the regional cladograms were compared with the consensus molecular cladogram for the papionin genera (Figure 2). The hypothesis was considered supported if the regions consistently favoured different cladograms and one of the favoured cladograms was compatible with the papionin consensus molecular cladogram.

4.3.2.3. Bootstrap-based test of Hypothesis 2 using regional character groups from Dataset A

This test comprised three analyses (BB, CC, DD). The analyses were based on the data matrices used in analysis I, J and K. In each analysis the character state data were divided into regional character groups as per the parsimony-based test of Hypothesis 2 using MacClade. Thereafter, a 1000 replication 50% majority-rule bootstrap cladogram was generated for each of the regional groups using PAUP. Lastly, the clades that were supported by the bootstrap cladograms were compared with the clades that comprise the hominoid consensus molecular cladogram. The hypothesis was judged supported if some but not all the regions consistently favoured clades of the hominoid consensus molecular cladogram. As with the bootstrap-based tests of Hypothesis 1, molecular clades were considered favoured only if they appeared in 70% or more of the bootstrap replications and if there was no better supported non-molecular clade.

4.3.2.4. Bootstrap-based test of Hypothesis 2 using regional character groups from Dataset B

This test comprised five analyses (26-30). These were based on the data matrices compiled in analyses 2, 3, 4, 6 and 7. In each analysis, MacClade was used to divide the character state data into the four cranial regions, as per the parsimony-based test of Hypothesis 2. The resulting regional matrices were transferred to PAUP and that program was used to generate a 1000 replication 50% majority-rule bootstrap cladogram for each regional group. Lastly, the clades that were supported by the bootstrap cladograms were compared with the clades that make up the papionin consensus molecular cladogram. The hypothesis was judged supported if some but not all the regions consistently favoured clades of the papionin consensus molecular cladogram. Again, molecular clades were considered favoured only if they appeared in 70% or more of the bootstrap replications and if there was no better supported non-molecular clade.

4.3.2.5. Consistency index-based test of Hypothesis 2 regional character groups from Dataset A

This test comprised three analyses (EE-GG). The first was based on the data matrix used in Analysis I, while the second and third employed the matrices generated in analysis J and K, respectively. In each analysis, the character state data were divided into the four cranial regions in MacClade's Data Editor. Thereafter, the regional matrices were examined in the program's Tree Window (ordered characters option). For each region, a cladogram with the same ingroup branching pattern as the hominoid consensus molecular cladogram was set up and rooted by placing the outgroup as the sister taxon of the hominoid taxa. The uninformative characters were excluded from the data matrix and the consistency index recorded. In the last part of the analysis, the CIs of the four regional cladograms were compared to establish their rank order and

a comparison made with the rank orders obtained in the other analyses. The hypothesis was judged supported if the analyses consistently favoured the same rank order of regional CIs for the hominoid consensus molecular cladogram.

4.3.2.6. Consistency index-based test of Hypothesis 2 regional character groups from Data-set B

This test comprised five analyses. Analysis 31 was based on the data matrix used in Analysis 2 and Analysis 32 on the one used in Analysis 3. Analysis 33 on the Analysis 4 matrix and Analysis 34 was based on the matrix used in Analysis 6. Analysis 35 was based on the Analysis 7. In each analysis the character state data were divided into the four cranial regions in MacClade's Data Editor. The regional matrices were then examined in the program's Tree Window (ordered characters option). For each region, a cladogram with the same ingroup branching pattern as the papionin consensus molecular cladogram was set up and rooted by placing the outgroup as the sister taxon of the ingroup. The uninformative characters were excluded from the data matrix and the CI recorded. Lastly, the rank order of the CIs of the four regional cladograms was determined and a comparison made with the rank orders obtained in the other analyses. The hypothesis was deemed supported if the analyses consistently favoured the same rank order of regional CIs for the papionin consensus molecular cladogram.

4.3.3. HYPOTHESIS 3 TESTS

Male and female primate crania differ in their reliability for reconstructing the cladistic relationships between species and genera

This hypothesis was subjected to six tests in which the males and females were treated as separate taxa and characters from all the cranial regions were analyzed together. Two tests were based on parsimony analysis, two on the bootstrap procedure, and two on the consistency index. The third hypothesis was also subjected to 24 tests in which the males and females were treated as separate taxa and characters from just one of the cranial regions were analyzed. Eight of the tests were based on parsimony analysis, eight on bootstrapping, and eight on the consistency index. The test criteria for these tests were the same as those for the tests in which characters from all the cranial regions were analyzed together.

4.3.3.1. Parsimony-based test of Hypothesis 3 using characters from all Dataset A regions

This test consisted of four analyses (HH-KK). All the analyses utilized the 129 characters on which Dataset A was based, and all included *Colobus* males and *Colobus* females as outgroup taxa. In Analysis HH, the data were adjusted to negate the effects of body size by dividing the specimen values by the specimen geometric means (the SGM method). In analyses II, JJ and KK, the data were size-adjusted by dividing the natural log of the specimen value by the natural log of the specimen geometric mean (the LSG method). Again, data from Wood (1975) and Wood et al. (1991) were size-adjusted separately from Chamberlain's (1987) data. Following size adjustment, in Analysis HH the data were converted into discrete characters using Baum's coding procedure. In analyses II and JJ the data were coded using segment coding with a segment size of 0.15 and 0.08, respectively. In Analysis KK divergence coding was used to carry

out the conversion. Thereafter, in each analysis, the male and female taxa were placed in separate data files. The matrices are presented in tables 29 through 32.

The male and female characters were separately subjected to parsimony analysis using PAUP. As with the tests of hypotheses 1 and 2, the most parsimonious cladograms were calculated using the branch and bound, and the characters were treated as freely-reversing, linearly-ordered variables of equal weight. Next, the male and female files were transferred to MacClade. For each file, the most parsimonious cladogram was set up in the program's Tree Window and rooted by placing the outgroup as the sister taxon of the hominoids. The uninformative characters were excluded, and the lengths, CIs and RIs recorded. Lastly, the male and female cladograms were checked for congruence with the consensus molecular cladogram for the hominoid genera (Figure 1). The hypothesis was considered supported if the analyses favoured cladograms that were compatible with the hominoid consensus molecular cladogram for one sex but not the other.

4.3.3.2. Parsimony-based test of Hypothesis 3 using characters from all Dataset B regions

This test comprised two analyses (36, 37). Both analyses utilized all 62 characters on which Dataset B was based, and included *Pan* males and *Pan* females as outgroup taxa. In Analysis 36, the data were adjusted to negate the effects of body size by dividing the specimen values by the specimen averages (the AVE method). In Analysis 37, the data were size-adjusted using the GEM method. Following size-adjustment, in both analyses the data were converted into discrete characters using Baum's coding procedure. The matrices are presented in tables 33 and 34.

The male and female data files were separately subjected to parsimony analysis using PAUP (branch and bound and ordered characters options). Next, the male and female files were trans-

ferred to MacClade. For each file, the most parsimonious cladogram was set up in the Tree Window and rooted by placing the outgroup as the sister taxon of the papionins. The uninformative characters were excluded, and the lengths, CIs and RIs for the male and female cladograms recorded. In the last part of the analysis, the male and female cladograms were compared with the papionin consensus molecular cladogram (Figure 2). The hypothesis was considered supported if both analyses favoured cladograms that were compatible with the papionin consensus molecular cladogram for one sex but not the other.

4.3.3.3. Bootstrap-based test of Hypothesis 3 using characters from all Dataset A regions

This test comprised four analyses (LL-OO). The first two analyses (LL and MM) were based on the data matrices generated in analyses HH and II, respectively. The second two (NN and OO) were based on the data matrices used in analyses JJ and KK. In each analysis, the male and female taxa were placed in separate data files. A 1000 replication 50% majority-rule bootstrap cladogram was then generated for each file using PAUP (branch and bound and ordered characters options). Lastly, the clades that were supported by the bootstrap cladograms were compared with the clades of the hominoid consensus molecular cladogram. The hypothesis was considered supported if the analyses consistently favoured clades of the hominoid consensus molecular cladogram for one sex but not the other. A molecular clade was considered favoured if it was supported by 70% or more of the bootstrap replications and there was no better supported nonmolecular clade.

4.3.3.4. Bootstrap-based test of Hypothesis 3 using characters from all Dataset B regions

This test comprised two analyses (38 and 39). Analysis 38 was based on the data matrix used in Analysis 36, while Analysis 39 was based on the data matrix used in Analysis 37. In each analy-

sis, the male and female taxa were placed in separate data files. Next, PAUP (branch and bound and ordered characters options) was used to generate a 1000 replication 50% majority-rule bootstrap cladogram for each file. In the last part of the analysis, the clades supported the bootstrap cladograms were compared with the clades of the consensus molecular cladogram for the papionin genera. The hypothesis was considered supported if both analyses favoured clades of the papionin consensus molecular cladogram for one sex but not the other. Again, molecular clade was considered favoured if it was supported by 70% or more of the bootstrap replications and there was no better supported non-molecular clade.

4.3.3.5. Consistency index-based test of Hypothesis 3 using characters from all Dataset A regions

This test comprised four analyses (PP-SS). The first, Analysis PP, was based on the data matrix used in Analysis HH. The second, Analysis QQ, was based on the data matrix used in Analysis II. The third analysis, Analysis RR, was based on the data matrix used in Analysis JJ. The fourth, Analysis SS, was based on the data matrix prepared for Analysis KK. In each analysis, the male and female taxa were placed in separate data files. These files were then examined in the Tree Window of MacClade. For each file, a cladogram with the same ingroup branching pattern as the hominoid consensus molecular cladogram was set up and rooted by placing the outgroup as the sister taxon of the ingroup. The uninformative characters were excluded from the data matrix, and the consistency index recorded. Lastly, the CIs of the male and female cladograms were ranked and a comparison made with the rank orders obtained in the other analyses. The hypothesis was judged supported if the CIs of the hominoid consensus molecular cladograms for one sex were consistently higher than the CIs of the consensus molecular cladograms for the other sex.

4.3.3.6. Consistency index-based test of Hypothesis 3 using characters from all Dataset B regions

This test consisted of two analyses, 40 and 41, which employed the data matrices prepared for analyses 36 and 37, respectively. In each analysis, the male and female taxa were placed in separate data files. These files were then examined in MacClade's Tree Window. For each file, a cladogram with the same ingroup branching pattern as the papionin consensus molecular cladogram was set up and rooted by placing the outgroup as the sister taxon of the ingroup. The uninformative characters were excluded from the data matrix and the consistency index recorded. Lastly, the male and female CIs were ranked and a comparison made with the rank orders obtained in the other analyses. The hypothesis was judged supported if the CIs of the consensus molecular cladograms for one sex were both higher than the CIs of the consensus molecular cladograms for the other sex.

4.3.3.7. Parsimony-based test of Hypothesis 3 using palate and upper dentition characters from Dataset A

This test consisted of four analyses. Analyses TT, UU and VV were based on the data matrices used in analyses HH, II and JJ, respectively. The other analysis, UU, was based on the data matrix prepared for Analysis KK. In each analysis, the characters from the mandible and lower dentition (M1-M40), the face (F1-F24), and the cranial vault and base (C1-C34) were deleted, and the male and female taxa placed in separate data files. These files were then subjected to parsimony analysis using PAUP. Thereafter, the male and female files were then transferred to MacClade. The most parsimonious cladogram was set up in the program's Tree Window and rooted by placing the outgroup as the sister taxon of the hominoids. The uninformative charac-

ters were excluded and the descriptive statistics recorded. Lastly, the male and female cladograms were compared with the consensus molecular cladogram for the ape and human superfamily. The hypothesis was considered supported if the analyses favoured cladograms that were compatible with the hominoid consensus molecular cladogram for one sex but not the other.

4.3.3.8. Parsimony-based test of Hypothesis 3 using palate and upper dentition characters from Dataset B

This test comprised two analyses (42, 43). Analysis 42 was based on the data matrix used in Analysis 36. Analysis 43 was based on the data matrix used in Analysis 37. In each analysis, the characters from the mandible and lower dentition (M1-M14), the face (F1-F16), and the cranial vault and base (C1-C16) were deleted, and the male and female taxa placed in separate data files. These files were then subjected to parsimony analysis using PAUP. The male and female files were then transferred to MacClade, and the most parsimonious cladogram was set up in the Tree Window of the program. The cladogram was rooted by placing the outgroup as the sister taxon of the papionins, and the uninformative characters were excluded. Lastly, the descriptive statistics were recorded, and the male and female cladograms were checked for congruence with the papionin consensus molecular cladogram. The hypothesis was deemed supported if both analyses favoured cladograms that were compatible with the papionin consensus molecular cladogram for one sex but not the other.

4.3.3.9. Bootstrap-based test of Hypothesis 3 using palate and upper dentition characters from Dataset A

This test comprised four analyses (XX, YY, ZZ, AAAA). These were based on the character state data matrices compiled in analyses HH, II, JJ and KK, respectively. In each analysis, the

characters from the mandible and lower dentition, the face, and the cranial vault and base were deleted, and the male and female taxa placed in separate data files. A 1000 replication 505 majority-rule bootstrap cladogram was then generated for each file using PAUP. Lastly, the clades supported by the bootstrap cladograms identified were compared with the clades that comprise the hominoid consensus molecular cladogram. The hypothesis was considered supported if the analyses consistently favoured clades of the hominoid consensus molecular cladogram for one sex but not the other. A molecular clade was considered favoured if it was supported by 70% or more of the bootstrap replications and there was no better supported non-molecular clade.

4.3.3.10. Bootstrap-based test of Hypothesis 3 using palate and upper dentition characters from Dataset B

This test comprised two analyses. The first, Analysis 44, was based on the data matrix that was compiled in Analysis 36. The second, Analysis 45, was employed the data matrix used in Analysis 37. In each analysis, the characters from the mandible and lower dentition, the face, and the cranial vault and base were deleted, and the male and female taxa placed in separate data files. PAUP was then used to generate a 1000 replication 50% majority-rule bootstrap cladogram. Lastly, the clades supported by the bootstrap cladograms were compared with the clades of the consensus molecular cladogram for the baboon, mangabey and macaque tribe. The hypothesis was considered supported if both analyses favoured clades of the papionin consensus molecular cladogram for one sex but not the other. Again, a molecular clade was considered favoured if it was supported by 70% or more of the bootstrap replications and there was no better supported non-molecular clade.

4.3.3.11. Consistency index-based test of Hypothesis 3 using palate and upper dentition characters from Dataset A

This test comprised four analyses (BBB, CCC, DDD, EEE), which employed the data matrices generated in analyses HH, II, JJ and KK, respectively. In each analysis, the characters from the mandible and lower dentition, the face, and the cranial vault and base were deleted, and the male and female taxa placed in separate data files. These files were then examined in MacClade's Tree Window. For each file, a cladogram with the same ingroup branching pattern as the hominoid consensus molecular cladogram was set up and rooted by placing the outgroup as the sister taxon of the ingroup. The uninformative characters were excluded from the data matrix and the consistency index recorded. In the last part of each analysis, the CIs of the male and female cladograms were ranked and a comparison made with the rank orders obtained in the other analyses. The hypothesis was judged supported if the CIs of the hominoid consensus molecular cladograms for one sex were consistently higher than the CIs of the consensus molecular cladograms for the other sex.

4.3.3.12. Consistency index-based test of Hypothesis 3 using palate and upper dentition characters from Dataset B

This test consisted of two analyses. The first, Analysis 46, was based on the data matrix used in Analysis 36. The second, Analysis 47, used the data matrix that was compiled in Analysis 37. In each analysis, the characters from the mandible and lower dentition, the face, and the cranial vault and base were deleted, and the male and female taxa placed in separate data files. These files were then examined in MacClade's Tree Window. For each file, a cladogram with the same ingroup branching pattern as the consensus molecular cladogram for the papionins was set up and rooted by placing the outgroup as the sister taxon of the ingroup. The uninformative char-

acters were excluded from the data matrix and the consistency index recorded. Lastly, the CIs for the male and female cladograms were ranked and a comparison made with the rank orders obtained in the other analyses. The hypothesis was judged supported if the CIs of the papionin consensus molecular cladograms for one sex were both higher than the CIs of the consensus molecular cladograms for the other sex.

4.3.3.13. Parsimony-based test of Hypothesis 3 using mandible and lower dentition characters from Dataset A

This test consisted of four analyses (FFF, GGG, HHH, III). These were based on the character state data matrices generated in analyses HH, II, JJ and KK, respectively. In each analysis, the characters from the palate and upper dentition (P1-P31), the face (F1-F24), and the cranial vault and base (C1-C34) were deleted, and the male and female taxa placed in separate data files. These files were then subjected to parsimony analysis using PAUP. Thereafter, the male and female files were transferred to MacClade. For each file, the most parsimonious topology was set up in the Tree Window of the program and rooted by placing the outgroup as the sister taxon of the hominoids. The uninformative characters were excluded, and the descriptive statistics recorded. Lastly, the male and female cladograms were compared with the consensus molecular cladogram for the hominoid genera. The hypothesis was deemed supported if the analyses favoured cladograms that were compatible with the hominoid consensus molecular cladogram for one sex but not the other.

4.3.3.14. Parsimony-based test of Hypothesis 3 using mandible and lower dentition characters from Dataset B

This test comprised two analyses (48, 49). The first was based on the data matrix generated in Analysis 36, while the second employed the data matrix used in Analysis 37. In each analysis, the characters from the palate and upper dentition (P1-P16), the face (F1-F16), and the cranial vault and base (C1-C16) were deleted, and the male and female taxa placed in separate data files. These files were then subjected to parsimony analysis using PAUP. Thereafter, the male and female files were transferred to MacClade. For each file, the most parsimonious cladogram was set up in the program's Tree Window and rooted by placing the outgroup as the sister taxon of the papionins. The uninformative characters were excluded, and the lengths, CIs and RIs recorded. Lastly, the topologies of the male and female cladograms were compared with the consensus molecular cladogram for the papionins. The hypothesis was deemed supported if both analyses favoured cladograms that were compatible with the papionin consensus molecular cladogram for one sex but not the other.

4.3.3.15. Bootstrap-based test of Hypothesis 3 using mandible and lower dentition characters from Dataset A

This test comprised four analyses, KKK, LLL, MMM and NNN, which were based on the character state data matrices created in analyses HH, II, JJ and KK, respectively. In each analysis, the characters from the palate and upper dentition, the face, and the cranial vault and base were deleted, and the male and female taxa placed in separate data files. PAUP was then used to generate a 1000 replication 50% majority-rule bootstrap cladogram. Lastly, the clades supported by the bootstrap cladogram were compared with the clades that form the hominoid consensus molecular cladogram. The hypothesis was considered supported if the analyses consistently fa-

voured clades of the hominoid consensus molecular cladogram for one sex but not the other. A molecular clade was considered favoured if it was supported by 70% or more of the bootstrap replications and there was no better supported non-molecular clade.

4.3.3.16. Bootstrap-based test of Hypothesis 3 using mandible and lower dentition characters from Dataset B

This test comprised two analyses. The first, Analysis 50, was based on the data matrix used in Analysis 36, while the second, Analysis 51, was based on the data matrix used in Analysis 37. In each analysis, the characters from the palate and upper dentition, the face, and the cranial vault and base were deleted, and the male and female taxa placed in separate data files. A 1000 replication 50% majority-rule bootstrap cladogram was then generated for each file using PAUP. In the last part of the analysis, the clades supported by the bootstrap cladograms were compared with the clades that make up the papionin consensus molecular cladogram. The hypothesis was considered supported if both analyses favoured clades of the papionin consensus molecular cladogram for one sex but not the other. Again, molecular clade was considered favoured if it was supported by 70% or more of the bootstrap replications and there was no better supported non-molecular clade.

4.3.3.17. Consistency index-based test of Hypothesis 3 using mandible and lower dentition characters from Dataset A

This test comprised four analyses, OOO, PPP, QQQ and RRR, which were based on the character state data matrices prepared in analyses HH, II, JJ and KK, respectively. In each analysis, the characters from the palate and upper dentition, the face, and the cranial vault and base were deleted, and the male and female taxa placed in separate data files. These files were then examined

in MacClade's Tree Window. For each file, a cladogram with the same ingroup branching pattern as the hominoid consensus molecular cladogram was set up. This was rooted by placing the outgroup as the sister taxon of the ingroup, and the uninformative characters were then excluded from the character state data matrix. Lastly, the consistency indices for the male and female cladograms were ranked and a comparison made with the rank orders obtained in the other analyses. The hypothesis was judged supported if the CIs of the hominoid consensus molecular cladograms for one sex were consistently higher than the CIs of the consensus molecular cladograms for the other sex.

4.3.3.18. Consistency index-based test of Hypothesis 3 using mandible and lower dentition characters from Dataset B

This test comprised two analyses. The first, Analysis 52, was based on the data matrix that was compiled in Analysis 36. The second, Analysis 53, employed the data matrix that was used in Analysis 37. In each analysis, the characters from the palate and upper dentition, the face, and the cranial vault and base were deleted, and the male and female taxa placed in separate data files. These files were then examined in MacClade's Tree Window. For each file, a cladogram with the same ingroup branching pattern as the papionin consensus molecular cladogram was set up. This was rooted by placing the outgroup as the sister taxon of the ingroup, and the uninformative characters were then excluded from the data matrix. Lastly, the consistency indices for the male and female cladograms were ranked and a comparison made with the rank orders obtained in the other analyses. The hypothesis was judged supported if the CIs of the papionin consensus molecular cladograms for one sex were both higher than the CIs of the consensus molecular cladograms for the other sex.

4.3.3.19. Parsimony-based test of Hypothesis 3 using face characters from Dataset A

This test consisted of four analyses, SSS, TTT, UUU and VVV, which employed the data matrices prepared in analyses HH, II, JJ and KK, respectively. In each analysis, the characters from the palate and upper dentition (P1-31), the mandible and lower dentition (M1-M40), and the cranial vault and base (C1-C34) were deleted, and the male and female taxa placed in separate data files. These files were subjected to parsimony analysis using PAUP. The male and female files were then transferred to MacClade. For each file, a cladogram with same ingroup topology as the most parsimonious cladogram was set up in the Tree Window and rooted by placing the outgroup as the sister taxon of the hominoids. The uninformative characters were excluded, and the lengths, CIs and RIs recorded. Lastly, the male and female cladograms were compared with the consensus molecular cladogram for the Hominoidea. The hypothesis was deemed supported if the analyses favoured cladograms that were compatible with the hominoid consensus molecular cladogram for one sex but not the other.

4.3.3.20. Parsimony-based test of Hypothesis 3 using face characters from Dataset B

This test comprised two analyses (54, 55), which were based on the data matrices used in analyses 36 and 37, respectively. In each analysis, the characters from the palate and upper dentition (P1-P16), the mandible and lower dentition (M1-M14), the cranial vault and base (C1-C16) were deleted, and the males and females placed in separate data matrices. PAUP was then used to identify the most parsimonious cladograms for the matrices. Thereafter, the male and female matrices were transferred to MacClade. For each matrix, a cladogram with the same ingroup topology as the most parsimonious cladogram was set up in the Tree Window of the program and rooted by placing the outgroup as the sister taxon of the papionins. Characters that were uninformative with respect to the most parsimonious topology were excluded, and the lengths, CIs

and RIs recorded. Lastly, the male and female cladograms were checked for congruence with the papionin consensus molecular cladogram. The hypothesis was deemed supported if both analyses favoured cladograms that were compatible with the papionin consensus molecular cladogram for one sex but not the other.

4.3.3.21. Bootstrap-based test of Hypothesis 3 using face characters from Dataset A

This test comprised four analyses. The first three, analyses WWW, XXX and YYY, were based on the data matrices used in analyses HH, II and JJ, respectively. The fourth, Analysis XXX, employed the data matrix used in Analysis KK. In each analysis, the characters from the palate and upper dentition, the mandible and lower dentition, and the cranial vault and base were deleted, and the male and female taxa placed in separate data files. A 1000 replication bootstrap cladogram was then generated for each file using PAUP. Lastly, the clades supported by the bootstrap cladograms were compared with the clades of the consensus molecular cladogram for the hominoid genera. The hypothesis was considered supported if the analyses consistently favoured clades of the hominoid consensus molecular cladogram for one sex but not the other. A molecular clade was considered favoured if it was supported by 70% or more of the bootstrap replications and there was no better supported non-molecular clade.

4.3.3.22. Bootstrap-based test of Hypothesis 3 using face characters from Dataset B

This test consisted of two analyses. The first, Analysis 56, was based on the data matrix used in Analysis 36, while the second, Analysis 57, was based on the data matrix used in Analysis 37. In each analysis, the characters from the palate and upper dentition, the mandible and lower dentition, and the cranial vault and base were deleted, and the male and female taxa placed in separate data files. A 1000 replication bootstrap cladogram was then generated for each file using PAUP.

Lastly, the clades supported by the bootstrap cladograms were compared with the clades that comprise the papionin molecular cladogram. The hypothesis was considered supported if both analyses favoured clades of the papionin consensus molecular cladogram for one sex but not the other. Again, a molecular clade was considered favoured if it was supported by 70% or more of the bootstrap replications and there was no better supported non-molecular clade.

4.3.3.23. Consistency index-based test of Hypothesis 3 using face characters from Dataset A

This test comprised four analyses. The first, Analysis AAAA, was based on the data matrix used in Analysis HH. The second, Analysis BBBB, was based on the data matrix used in Analysis II. The third analysis, Analysis CCCC, was based on the data matrix used in Analysis JJ. The fourth, Analysis DDDD, was based on the data matrix prepared for Analysis KK. In each analysis, the characters from the palate and upper dentition, the mandible and lower dentition, and the cranial vault and base were deleted, and the male and female taxa placed in separate data files. These files were then examined in MacClade's Tree window. For each file, a cladogram with the same ingroup branching pattern as the hominoid consensus molecular cladogram was set up and rooted by placing the outgroup as the sister taxon of the ingroup. The uninformative characters were excluded from the data matrix and the consistency index recorded. In the last part of the analysis, the CIs of the male and female cladograms were ranked and a comparison made with the rank orders obtained in the other analyses. The hypothesis was judged supported if the CIs of the consensus molecular cladograms for one sex were consistently higher than the CIs of the consensus molecular cladograms for the other sex.

4.3.3.24. Consistency index-based test of Hypothesis 3 using face characters from Dataset B

This test comprised two analyses. The first, Analysis 58, was based on the data matrix used in Analysis 36. The second, Analysis 59, was based on the data matrix used in Analysis 37. In each analysis, the characters from the palate and upper dentition, the mandible and lower dentition, and the cranial vault and base were deleted, and the male and female taxa placed in separate data files. These files were then examined in MacClade's Tree window. For each file, a cladogram with the same ingroup branching pattern as the consensus molecular cladogram for the Papionini was set up and rooted by placing the outgroup as the sister taxon of the ingroup. The uninformative characters were excluded from the data matrix and the consistency index recorded. Lastly, the consistency indices for the male and female cladograms were ranked and a comparison made with the rank orders obtained in the other analyses. The hypothesis was judged supported if the CIs of the papionin consensus molecular cladograms for one sex were both higher than the CIs of the consensus molecular cladograms for the other sex.

4.3.3.25. Parsimony-based test of Hypothesis 3 using cranial vault and base characters from Dataset A

This test consisted of four analyses, EEEE, FFFF, GGGG and HHHH, which were based on the data matrices compiled in analyses HH, II, JJ and KK, respectively. In each analysis, the characters from the palate and upper dentition (P1-P31), the mandible and lower dentition (M1-M40), and the face (F1-F24) were deleted, and the male and female taxa placed in separate data files. These files were subjected to parsimony analysis using PAUP. The male and female files were then transferred to MacClade. The most parsimonious topology was set up in the program's Tree Window and rooted by placing the outgroup as the sister taxon of the hominoids. The uninformative characters were excluded, and the lengths, CIs and RIs recorded. Lastly, the

male and female cladograms were compared with the hominoid consensus molecular cladogram. The hypothesis was deemed supported if the analyses favoured cladograms that were compatible with the hominoid consensus molecular cladogram for one sex but not the other.

4.3.3.26. Parsimony-based test of Hypothesis 3 using cranial vault and base characters from Dataset B

This test comprised two analyses (60, 61). Analysis 60 was based on the data matrix used in Analysis 36. Analysis 61 was based on the data matrix used in Analysis 37. In each analysis, the characters from the palate and upper dentition (P1-P16), the mandible and lower dentition (M1-M14), and the face (F1-F16) were deleted, and the male and female taxa placed in separate data files. These files were then subjected to parsimony analysis using PAUP. Thereafter, the male and female files were transferred to MacClade. The most parsimonious cladogram was set up in the Tree Window and rooted by placing the outgroup as the sister taxon of the papionins. The uninformative characters were excluded, and the lengths, CIs and RIs recorded. In the last part of the analysis, the male and female cladograms were checked for congruence with the consensus molecular cladogram for the papionin genera. The hypothesis was deemed supported if both analyses favoured cladograms that were compatible with the papionin consensus molecular cladogram for one sex but not the other.

4.3.3.27. Bootstrap-based test of Hypothesis 3 using cranial vault and base characters from Dataset A

This test comprised four analyses. The first two, analyses IIII and JJJJ, were based on the data matrices used in analyses HH and II, respectively. The other two, analyses KKKK and LLLL, employed the data matrices used in analyses JJ and KK. In each analysis, the characters from the

palate and upper dentition, the mandible and lower dentition, and the face were deleted, and the male and female taxa placed in separate data files. A 1000 replication 50% majority-rule bootstrap cladogram was then generated for each file using PAUP. The clades supported by the bootstrap cladograms were then compared with the clades that form the consensus molecular cladogram for the ape and human superfamily. The hypothesis was considered supported if the analyses consistently favoured clades of the hominoid consensus molecular cladogram for one sex but not the other. A molecular clade was considered favoured if it was supported by 70% or more of the bootstrap replications and there was no better supported non-molecular clade.

4.3.3.28. Bootstrap-based test of Hypothesis 3 using cranial vault and base characters from Dataset B

This test consisted of two analyses (62, 63). Analysis 62 was based on the data matrix used in Analysis 36. Analysis 63 was based on the data matrix prepared in Analysis 37. In each analysis, the characters from the palate and upper dentition, the mandible and lower dentition, and the face were deleted, and the male and female taxa placed in separate data files. A 1000 replication 50% majority-rule bootstrap cladogram was then generated for each file using PAUP. Lastly, the clades supported by the bootstrap cladograms were compared with those that comprise the consensus molecular cladogram for the papionin genera. The hypothesis was considered supported if both analyses favoured clades of the papionin consensus molecular cladogram for one sex but not the other. Again, a molecular clade was considered favoured if it was supported by 70% or more of the bootstrap replications and there was no better supported non-molecular clade.

4.3.3.29. Consistency index-based test of Hypothesis 3 using cranial vault and base characters from Dataset A

This test comprised four analyses. The first three, analyses MMMM, NNNN and OOOO, were based on the data matrices used in analyses HH, II and JJ, respectively. The fourth, Analysis PPPP, was based on the data matrix prepared for Analysis KK. In each analysis, the characters from the palate and upper dentition, the mandible and lower dentition, and the face were deleted, and the male and female taxa placed in separate data files. These files were then examined in MacClade's Tree Window. For each file, a cladogram with the same ingroup branching pattern as the hominoid consensus molecular cladogram was set up and rooted by placing the outgroup as the sister taxon of the ingroup. Next, characters that were uninformative with respect to the cladogram were excluded from the data matrix. Lastly, the consistency indices for the male and female cladograms were ranked and a comparison made with the rank orders obtained in the other analyses. The hypothesis was judged supported if the CIs of the hominoid consensus molecular cladograms for one sex were consistently higher than the CIs of the consensus molecular cladograms for the other sex.

4.3.3.30. Consistency index-based test of Hypothesis 3 using cranial vault and base characters from Dataset B

This test consisted of two analyses (64, 65). The first, Analysis 64, was based on the data matrix generated in Analysis 36, while the second, Analysis 65 employed the data matrix used in Analysis 37. In each analysis, the characters from the palate and upper dentition, the mandible and lower dentition, and the face were deleted, and the male and female taxa placed in separate data files. These files were then examined in MacClade's Tree Window. For each file, a cladogram with the same ingroup branching pattern as the papionin consensus molecular cladogram was set

up and rooted by placing the outgroup as the sister taxon of the ingroup. The uninformative characters were excluded from the data matrix and the consistency index recorded. In the last part of the analysis, the CIs of the male and female cladograms were ranked and a comparison made with the rank orders obtained in the other analyses. The hypothesis was judged supported if the CIs of the papionin consensus molecular cladograms for one sex were both higher than the CIs of the consensus molecular cladograms for the other sex.

CHAPTER 5. RESULTS

This chapter is divided into three main sections. The first reports the results of the tests of the hypothesis that standard cranial and dental characters are reliable for reconstructing the cladistic relationships between primate species and genera. The results of the tests of the hypothesis that some regions of the primate cranium are more reliable than others for reconstructing the cladistic relationships between species and genera are summarized in the second section. The third section reports the results of the tests of the hypothesis that male and female primate crania differ in their reliability for reconstructing the cladistic relationships between species and genera.

5.1. TESTS OF HYPOTHESIS 1

Standard cranial and dental characters are reliable for reconstructing the cladistic relationships between primate species and genera.

Six tests of this hypothesis were performed. The first two were based on parsimony analysis, the second two on compatibility analysis and the last two on the bootstrap.

5.1.1. PARSIMONY-BASED TEST OF HYPOTHESIS 1 USING CHARACTERS FROM ALL DATASET A REGIONS

This test consisted of 11 analyses (A-K). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 35. The cladograms fa-

voured in the analyses are presented in figures 33-35. The descriptive statistics associated with the cladograms are given in Table 36. The hypothesis was considered supported if the analyses consistently favoured cladograms that were compatible with the hominoid consensus molecular cladogram (Figure 1).

5.1.1.1. Analysis A

Analysis A identified a single most parsimonious cladogram for the taxa (Figure 33). This cladogram was in no way compatible with the hominoid consensus molecular cladogram. It suggested that the first branching event in the evolution of the ingroup separated *Homo* from the common ancestor of *Gorilla*, *Pan* and *Pongo*. The other cladistically significant branching event posited by the cladogram isolated *Pan* from the common ancestor of *Gorilla* and *Pongo*.

5.1.1.2. Analysis B

Three equally parsimonious arrangements for the taxa were recovered in Analysis B (figures 33-35). The first had the same branching pattern as the consensus molecular cladogram for the Hominoidea. The other two were incompatible with the consensus molecular cladogram. One was topologically identical to the cladogram favoured in Analysis A. The other posited a single phylogenetically significant branching event that separated the common ancestor of *Gorilla* and *Pongo* from the common ancestor of *Homo* and *Pan*. The strict consensus of the three cladograms had no ingroup structure.

5.1.1.3. Analysis C

Analysis C yielded two equally parsimonious arrangements for the taxa (figures 33 and 35). Neither cladogram agreed with the consensus molecular cladogram for the hominoids. One had the same branching pattern as the most parsimonious cladogram recovered in Analysis A and the second of the three cladograms favoured in Analysis B. The other was topologically identical to the third of the cladograms recovered in Analysis B. The strict consensus of the two cladograms recognized one clade, which comprised *Gorilla* and *Pongo*.

5.1.1.4. Analysis D

Two equally parsimonious arrangements for the taxa were also retrieved in Analysis D (figures 33 and 35). Again, neither of the cladograms was compatible with the consensus molecular cladogram for the hominoids. One matched the most parsimonious cladogram recovered in Analysis A, the second of the Analysis B cladograms and the first of the cladograms retrieved in Analysis C. The other had the same topology as the third of the Analysis B cladograms and the second of the cladograms favoured in Analysis C. The strict consensus of the cladograms contained one clade, which linked *Gorilla* and *Pongo* to the exclusion of *Homo* and *Pan*.

5.1.1.5. Analysis E

A single cladogram was obtained in Analysis E (Figure 33). It was not compatible with the hominoid consensus molecular cladogram, having the same branching pattern as the most parsimonious

cladogram recovered in Analysis A, the second of the three cladograms favoured in Analysis B and the first of cladograms favoured in analyses C and D.

5.1.1.6. Analysis F

A single most parsimonious cladogram was favoured in Analysis F (Figure 33). This cladogram was incompatible with the consensus molecular cladogram for the hominoid genera. It had the same branching pattern as the most parsimonious cladograms recovered in analyses A and E, the second of the three most parsimonious cladogram retrieved in Analysis B and the first of the cladograms favoured in analyses C and D.

5.1.1.7. Analysis G

A single most parsimonious cladogram was obtained in Analysis G (Figure 33). This cladogram did not agree with the hominoid consensus molecular cladogram. It had the same branching pattern as the cladograms favoured in analyses A, E and F, the second of cladograms retrieved in Analysis B and the first of the cladograms identified in analyses C and D.

5.1.1.8 Analysis H

A single most parsimonious cladogram was recovered in Analysis H (Figure 35). This cladogram was not compatible with the hominoid consensus molecular cladogram. It was topologically identical to the third of the three most parsimonious cladograms obtained in Analysis B.

5.1.1.9. Analysis I

A single most parsimonious cladogram was identified in Analysis I (Figure 33). This cladogram was incompatible with the consensus molecular cladogram for the hominoids, having the same branching pattern as the most parsimonious cladograms recovered in analyses A, E, F and G, the second of the cladograms favoured in Analysis B and the first of the cladograms obtained in analyses C and D.

5.1.1.10. Analysis J

Analysis J favoured a single most parsimonious cladogram (Figure 33). It did not agree with the consensus molecular cladogram for the hominoids. Rather it had the same branching pattern as the most parsimonious cladograms identified in analyses A, E, F, G and I, the second of the cladograms retrieved in Analysis B and the first of the cladograms recovered in analyses C and D.

5.1.1.11. Analysis K

A single most parsimonious cladogram was obtained in Analysis K (Figure 33). It was incompatible with the consensus molecular cladogram for the hominoid genera. Like the cladograms favoured in analyses A, E, F, G, I and J, the second of the cladograms retrieved in Analysis B, and the first of cladograms recovered in analyses C and D, this cladogram suggested that *Homo* is the sister taxon of *Gorilla*, *Pan* and *Pongo*, and *Pan* the sister taxon of *Gorilla* and *Pongo*.

5.1.1.12. Test result

The test did not support the hypothesis. The criterion that the analyses should consistently favour cladograms that are compatible with the hominoid consensus molecular cladogram, was not fulfilled. None of the single most parsimonious cladograms had the same branching pattern as the consensus molecular cladogram for the hominoids, and none of the strict consensus cladograms was compatible with it.

5.1.2. PARSIMONY-BASED TEST OF HYPOTHESIS 1 USING CHARACTERS FROM ALL DATASET B REGIONS

This test comprised nine analyses (1-9). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 37. The cladograms favoured in the analyses are presented in figures 36-43 The descriptive statistics associated with the cladograms are presented in Table 38. The hypothesis was considered supported if the analyses consistently favoured cladograms that were compatible with the papionin consensus molecular cladogram (Figure 2).

5.1.2.1. Analysis 1

Three equally parsimonious cladograms were recovered in Analysis 1 (figures 36-38). None of these cladograms concurred with the consensus molecular estimate of the affinities of the papionin genera. In the first cladogram, *Lophocebus* was positioned as the sister taxon of the other papionin taxa, and *Cercocebus* was located as the sister taxon of a macaque and baboon clade. Within the macaque and

baboon clade, *Macaca* and *Theropithecus* appeared as one monophyletic group, and *Mandrillus* and *Papio* appeared as another. The second cladogram had the same branching pattern as the first except that the positions of *Cercocebus* and *Lophocebus* were reversed. In the third cladogram, *Cercocebus* was located as the sister group of the other papionin taxa, and *Lophocebus* was placed as the sister group of the macaque and baboon clade. Within the macaque and baboon clade, *Mandrillus* and *Papio* again formed a monophyletic group. The relationships between *Macaca*, *Theropithecus* and the (*Mandrillus*, *Papio*) clade were unresolved. The strict consensus of the cladograms was not compatible with the papionin consensus molecular cladogram, since it grouped together *Macaca*, *Mandrillus*, *Papio* and *Theropithecus* to the exclusion of *Cercocebus* and *Lophocebus*. It also differed from the consensus molecular cladogram in recognizing *Mandrillus* and *Papio* as sister taxa.

5.1.2.2. Analysis 2

Analysis 2 produced a single most parsimonious cladogram (Figure 39). It did not agree with the consensus molecular cladogram for the Papionini. Instead it located *Lophocebus* as the sister taxon of a (*Cercocebus*, *Macaca*, *Mandrillus*, *Papio*, *Theropithecus*) clade, and *Cercocebus* as the sister taxon of a (*Macaca*, *Mandrillus*, *Papio*, *Theropithecus*) clade. Within the (*Macaca*, *Mandrillus*, *Papio*, *Theropithecus*) clade, *Papio* was positioned as the sister taxon of a (*Macaca*, *Mandrillus*, *Theropithecus*) clade, and *Theropithecus* was placed as the sister taxon of a (*Macaca*, *Mandrillus*) clade.

5.1.2.3. Analysis 3

Analysis 3 favoured a single most parsimonious arrangement for the taxa (Figure 40). This arrangement was not compatible with the papionin consensus molecular cladogram. It suggested instead that *Lophocebus* is the sister group of a (*Cercocebus*, *Macaca*, *Mandrillus*, *Papio*, *Theropithecus*) clade, and *Macaca* the sister group of a (*Cercocebus*, *Mandrillus*, *Papio*, *Theropithecus*) clade. It also suggested that *Cercocebus* is the sister group of a (*Mandrillus*, *Papio*, *Theropithecus*) clade, and *Theropithecus* the sister group of a (*Mandrillus*, *Papio*) clade.

5.1.2.4. Analysis 4

A single most parsimonious cladogram was obtained in Analysis 4 (Figure 41). It did not agree with the papionin consensus molecular cladogram. Rather, it positioned *Lophocebus* as the sister taxon of a (*Cercocebus*, *Macaca*, *Mandrillus*, *Papio*, *Theropithecus*) clade, and *Cercocebus* as the sister taxon of a (*Macaca*, *Mandrillus*, *Papio*, *Theropithecus*) clade. Within the latter clade, *Macaca* was positioned as the sister taxon of a (*Mandrillus*, *Papio*, *Theropithecus*) clade, and *Theropithecus* was located as the sister taxon of a (*Mandrillus*, *Papio*) clade.

5.1.2.5. Analysis 5

A single most parsimonious cladogram was identified in Analysis 5 (Figure 42). This cladogram was incompatible with the papionin consensus molecular cladogram. It divided the taxa into two main subgroups. One consisted of the baboon taxa, *Mandrillus*, *Papio* and *Theropithecus*. The other comprised *Cercocebus*, *Lophocebus* and *Macaca*. Within the baboon subgroup, *Mandrillus*

and *Papio* were united in a clade to the exclusion of *Theropithecus*. Within the (*Cercocebus*, *Lophocebus*, *Macaca*) clade, *Lophocebus* and *Macaca* were paired as sister taxa.

5.1.2.6. Analysis 6

A single most parsimonious cladogram was retrieved in Analysis 6 (Figure 43). This cladogram was incompatible with the consensus molecular cladogram for the papionins. It had two main branches. The first linked together the three baboon genera, *Mandrillus*, *Papio* and *Theropithecus*. The second comprised the mangabey and macaque genera, *Cercocebus*, *Macaca* and *Lophocebus*. Within the baboon group, *Mandrillus* and *Theropithecus* appeared as sister taxa. In the mangabey and macaque group, *Lophocebus* and *Macaca* formed a monophyletic assemblage.

5.1.2.7. Analysis 7

Analysis 7 favoured a single most parsimonious cladogram (Figure 40). It was in no way compatible with the consensus molecular cladogram for the Papionini, having the same branching pattern as the most parsimonious cladogram recovered in the third analysis.

5.1.2.8. Analysis 8

A single most parsimonious cladogram was obtained in Analysis 8 (Figure 40). It was incompatible with the consensus molecular cladogram for the papionins, having the same branching pattern as the most parsimonious cladograms retrieved in analyses 3 and 7.

5.1.2.9. Analysis 9

Analysis 9 yielded a single most parsimonious cladogram (Figure 43). It did not agree with the consensus molecular estimate of interpapionin relationships, having the same topology as the cladogram favoured in Analysis 6.

5.1.2.10. Test result

The test did not support the hypothesis. The criterion that the analyses should consistently favour cladograms that are compatible with the papionin consensus molecular cladogram, was not met. None of the single most parsimonious cladograms had the same branching pattern as the papionin consensus molecular cladogram. The strict consensus cladogram favoured in Analysis 1 was also not compatible with the consensus molecular cladogram.

5.1.3. COMPATIBILITY-BASED TEST OF HYPOTHESIS 1 USING CHARACTERS FROM ALL DATASET A REGIONS

This test comprised two analyses (L and M). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 39. The hypothesis was considered supported if both analyses favoured cladograms that were compatible with the hominoid consensus molecular cladogram.

5.1.3.1. Analysis L

Analysis L yielded 15 cladograms (Table 40). The best supported cladogram was based on 19 characters (15%). It was in no way compatible with the consensus molecular cladogram for the hominoid genera. Rather, it suggested that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo*, and that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Pan*. The molecular cladogram was supported by eight characters (6%). There were six fully resolved cladograms that were better supported than the consensus molecular cladogram. These were supported by between nine and 19 characters.

5.1.3.2. Analysis M

Analysis M yielded 12 cladograms (Table 41). The largest clique of characters (46 or 38%) again suggested that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo*, and that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Pan*. The molecular cladogram was supported by 11 characters (9%). There were eight fully resolved cladograms that were better supported than the consensus molecular cladogram. These were supported by between 12 and 46 characters.

5.1.3.3. Test result

Hypothesis 1 was not supported by the test. The criterion that both analyses should favour cladograms that are compatible with the hominoid consensus molecular cladogram, was not satisfied.

Neither of the favoured cladograms were compatible with the consensus molecular cladogram for the hominoids.

5.1.4. COMPATIBILITY-BASED TEST OF HYPOTHESIS 1 USING CHARACTERS FROM ALL DATASET B REGIONS

This test comprised two analyses (10 and 11). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 42. The hypothesis was considered supported if both analyses favoured cladograms that were compatible with the papionin consensus molecular cladogram.

5.1.4.1. Analysis 10

Analysis 10 produced 22 fully resolved and 13 partially resolved cladograms (Table 43). None of the cladograms had the same topology as the molecular cladogram for the Papionini. The best supported cladogram was based on 11 characters (18%). This cladogram suggested that *Mandrillus* is the sister taxon of a (*Cercocebus*, *Lophocebus*, *Macaca*, *Papio*, *Theropithecus*) clade, and that *Papio* the sister taxon of a (*Cercocebus*, *Lophocebus*, *Macaca*, *Theropithecus*) clade. It also suggested that *Theropithecus* the sister taxon of a (*Cercocebus*, *Lophocebus*, *Macaca*), and that *Cercocebus* the sister taxon of (*Lophocebus*, *Macaca*) clade.

5.1.4.2. Analysis 11

Analysis 11 yielded 23 fully resolved and 14 partially resolved cladograms (Table 44). None of the cladograms had the same branching pattern as the consensus molecular cladogram for the papionin genera. The best supported cladogram was based on 15 characters (24%). This cladogram agreed with the consensus molecular cladogram for the Papionini on the basal position of *Macaca* among the ingroup taxa, but was otherwise incompatible with it. *Lophocebus* was located as the sister taxon of a (*Cercocebus*, *Mandrillus*, *Papio*, *Theropithecus*) clade, *Cercocebus* appeared as the sister taxon of a (*Mandrillus*, *Papio*, *Theropithecus*) clade, and *Theropithecus* was positioned as the sister taxon of a (*Mandrillus*, *Papio*) clade.

5.1.4.3. Test result

The test did not support Hypothesis 1. The criterion that both analyses should favour cladograms that are compatible with the papionin consensus molecular cladogram, was not satisfied. Neither of the favoured cladograms was compatible with the consensus molecular cladogram for the papionin genera.

5.1.5. BOOTSTRAP-BASED TEST OF HYPOTHESIS 1 USING CHARACTERS FROM ALL DATASET A REGIONS

This test consisted of 11 analyses (N-X). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 45. The hypothesis was judged supported if clades of the hominoid consensus molecular cladogram were consistently fa-

voured by the analyses. A molecular clade was considered favoured if it was supported by 70% or more of the bootstrap replications and there was no better supported non-molecular clade.

5.1.5.1. Analysis N

Analysis N yielded one clade, which was incompatible with the molecular cladogram. Identified in 83% of the bootstrap cladogram, it suggested that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Homo* or *Pan*.

5.1.5.2. Analysis O

No clades were supported at or above 70% in Analysis O.

5.1.5.3. Analysis P

One non-molecular clade was retrieved from Analysis P. It suggested that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Homo* or *Pan* (80%).

5.1.5.4. Analysis Q

No clades were supported at or above 70% in Analysis Q.

5.1.5.5. Analysis R

Two clades were recovered from Analysis R, neither of which was compatible with the hominoid consensus molecular cladogram. One suggested that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Homo* or *Pan* (100%). The other indicated that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (100%).

5.1.5.6. Analysis S

Two clades were found in 70%, or more, of the bootstrap cladograms in Analysis S. Both clades differed for those that comprise the consensus molecular cladogram for the Hominoidea. One suggested that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Homo* or *Pan* (100%). The other indicated that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (100%).

5.1.5.7. Analysis T

Two clades were supported by 70%, or more, of the bootstrap cladograms in Analysis T, neither of which was compatible with the hominoid consensus molecular cladogram. One suggested that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Homo* or *Pan* (93%). The other indicated that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (100%).

5.1.5.8. Analysis U

One clade was supported by 70%, or more, of the bootstrap cladograms in Analysis U. It was incompatible with the consensus molecular cladogram for the hominoids, suggesting instead that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Homo* or *Pan* (91%).

5.1.5.9. Analysis V

No clades were supported at or above 70% in Analysis V.

5.1.5.10. Analysis W

Two clades were recovered in Analysis W, neither of which was compatible with the consensus molecular cladogram for the hominoids. One suggested that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Homo* or *Pan* (100%). The other indicated that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (100%).

5.1.5.11. Analysis X

Two clades were retrieved in Analysis X. Both clades differed from those that comprise the hominoid consensus molecular cladogram. One suggested that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Homo* or *Pan* (100%). The other indicated that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (100%).

5.1.5.12. Test result

The test did not support Hypothesis 1. The criterion that the analyses should consistently favour clades of the hominoid consensus molecular cladogram, was not met. None of the 13 clades recovered was compatible with the hominoid relationships suggested by the majority of the molecular evidence.

5.1.6. BOOTSTRAP-BASED TEST OF HYPOTHESIS 1 USING CHARACTERS FROM ALL DATASET B REGIONS

This test consisted of nine analyses (12-20). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 46. The hypothesis was judged supported if clades of the papionin consensus molecular cladogram were consistently favoured by the analyses. Again, a molecular clade was considered favoured if it was supported by 70% or more of the bootstrap replications and there was no better supported non-molecular clade.

5.1.6.1. Analysis 12

One clade was recovered from Analysis 12. It was incompatible with the papionin molecular cladogram, suggesting instead that *Macaca*, *Mandrillus*, *Papio* and *Theropithecus* are more closely related to one another than any of them is to *Cercocebus* or *Lophocebus* (81%).

5.1.6.2. Analysis 13

Two clades were retrieved from Analysis 13, neither of which agreed with the biomolecular cladogram for the papionins. One indicated that *Cercocebus*, *Macaca*, *Mandrillus*, *Papio* and *Theropithecus* are more closely related to one another than any of them is to *Lophocebus* or the outgroup (74%). The other implied that *Macaca*, *Mandrillus*, *Papio* and *Theropithecus* are more closely related to one another than any of them is to *Cercocebus* or *Lophocebus* (99%).

5.1.6.3. Analysis 14

Three clades were obtained in Analysis 14. None of them was compatible with the papionin molecular cladogram. The first suggested that *Cercocebus*, *Macaca*, *Mandrillus*, *Papio* and *Theropithecus* are more closely related to one another than any of them is to *Lophocebus* (76%). The second implied that *Mandrillus*, *Papio* and *Theropithecus* are more closely related to one another than any of them is to *Cercocebus*, *Lophocebus* or *Macaca* (99%). The third indicated that *Mandrillus* and *Papio* are more closely related to one another than either is to *Cercocebus*, *Lophocebus*, *Macaca* or *Theropithecus* (79%).

5.1.6.4. Analysis 15

Analysis 15 identified three clades, none of which was compatible with the consensus molecular cladogram for the papionin genera. According to the first clade, *Cercocebus*, *Macaca*, *Mandrillus*, *Papio* and *Theropithecus* are more closely related to one another than any of them is to *Lophocebus* (97%). The second clade indicated that *Macaca*, *Mandrillus*, *Papio* and *Theropithecus* are more

closely related to one another than any of them is to *Cercocebus* or *Lophocebus* (79%). The third clade suggested that *Mandrillus*, *Papio* and *Theropithecus* are more closely related to one another than any of them is to *Cercocebus*, *Lophocebus* or *Macaca* (95%).

5.1.6.5. Analysis 16

Two clades were recovered in Analysis 16. Both clades differed from those supported by the majority of the biomolecular data. One suggested that *Cercocebus*, *Lophocebus* and *Macaca* are more closely related to one another than any of them is to *Mandrillus*, *Papio* or *Theropithecus* (84%). The other indicated that *Lophocebus* and *Macaca* are more closely related to one another than either is to *Cercocebus*, *Mandrillus*, *Papio* or *Theropithecus* (71%).

5.1.6.6. Analysis 17

Analysis 17 identified two clades, neither of which was compatible with the consensus molecular cladogram for the papionins. The first indicated that *Cercocebus*, *Lophocebus* and *Macaca* are more closely related to one another than any of them is to *Mandrillus*, *Papio* or *Theropithecus* (100%). The second suggested that *Lophocebus* and *Macaca* are more closely related to one another than either is to *Cercocebus*, *Mandrillus*, *Papio* or *Theropithecus* (100%).

5.1.6.7. Analysis 18

Three clades were identified in Analysis 18, none of which was compatible with the consensus molecular cladogram for the Papionini. According to the first, *Cercocebus*, *Mandrillus*, *Papio* and

Theropithecus are more closely related to one another than any of them is to *Lophocebus* or *Macaca* (100%). The second clade indicated that *Mandrillus*, *Papio* and *Theropithecus* are more closely related to one another than any of them is to *Cercocebus*, *Lophocebus* or *Macaca* (100%). The third clade suggested that *Mandrillus* and *Papio* are more closely related to one another than either is to *Cercocebus*, *Lophocebus*, *Macaca* or *Theropithecus* (91%).

5.1.6.8. Analysis 19

Analysis 19 identified three clades. The clades were all incompatible with the consensus molecular cladogram for the Papionini. The first suggested that *Cercocebus*, *Mandrillus*, *Papio* and *Theropithecus* are more closely related to one another than any of them is to *Lophocebus* or *Macaca* (96%). The second indicated that *Mandrillus*, *Papio* and *Theropithecus* are more closely related to one another than any of them is to *Cercocebus*, *Lophocebus* or *Macaca* (100%). The third implied that *Mandrillus* and *Papio* are more closely related to one another than either is to *Cercocebus*, *Lophocebus*, *Macaca* or *Theropithecus* (94%).

5.1.6.9. Analysis 20

Three clades were recovered in Analysis 20, none of which agreed with the consensus molecular cladogram for the Papionini. The first suggested that *Cercocebus*, *Lophocebus* and *Macaca* are more closely related to one another than any of them is to *Mandrillus*, *Papio* or *Theropithecus* (100%). The second indicated that *Mandrillus*, *Papio* and *Theropithecus* are more closely related to one another than any of them is to *Cercocebus*, *Lophocebus* or *Macaca* (72%). The third implied

that *Lophocebus* and *Macaca* are more closely related to one another than either is to *Cercocebus*, *Mandrillus*, *Papio* or *Theropithecus* (100%).

5.1.6.10. Test result

The test did not support Hypothesis 1. The criterion that the analyses should consistently favour clades of the papionin consensus molecular cladogram, was not fulfilled. None of the 22 clade recovered was compatible with the papionin relationships suggested by the majority of the molecular evidence.

5.2. HYPOTHESIS 2 TESTS

Some regions of the primate cranium are more reliable than others for reconstructing the cladistic relationships between species and genera

The second hypothesis was subjected to six tests in which the variables were grouped into anatomically- and functionally-integrated regions. Two were based on parsimony analysis, two on bootstrapping and two on the consistency index.

5.2.1. PARSIMONY-BASED TEST OF HYPOTHESIS 2 USING REGIONALLY-GROUPED CHARACTERS FROM DATASET A

This test comprised three analyses (Y-AA). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 47. The cladograms

favoured in the analyses are presented in figures 44-46. The descriptive statistics associated with the cladograms are given in Table 48. The hypothesis was deemed supported if the regions consistently favoured different cladograms and one of the favoured cladograms was compatible with the hominoid consensus molecular cladogram.

5.2.1.1. Analysis Y

Single most parsimonious cladograms were retrieved from all four regional character groups in Analysis Y (figures 44-46). None of the cladograms was compatible with the hominoid consensus molecular cladogram. The palate and upper dentition cladogram suggested that *Gorilla* is the sister taxon of a (*Pongo*, *Homo*, *Pan*) clade, and that *Pongo* is the sister taxon of a (*Homo*, *Pan*) clade. The mandible and lower dentition cladogram posited a basal split between *Gorilla* and *Pongo*, on the one hand, and *Homo* and *Pan*, on the other. The cladograms favoured by the face and vault character groups positioned *Homo* as the sister taxon of a (*Gorilla*, *Pan*, *Pongo*) clade, and *Pan* as the sister taxon of a (*Gorilla*, *Pongo*) clade.

5.2.1.2. Analysis Z

Analysis Z identified single most parsimonious cladograms for each of the four regional character groups. None of the cladograms was compatible with the hominoid consensus molecular cladogram. They all suggested that *Homo* is the sister taxon of a (*Gorilla*, *Pan*, *Pongo*) clade, and that *Pan* is the sister taxon of a (*Gorilla*, *Pongo*) clade(Figure 46).

5.2.1.3. Analysis AA

Analysis AA identified a single most parsimonious cladograms for each of the four regional character groups. They were all incompatible with the consensus molecular cladogram for the hominoid genera, suggesting instead that *Homo* is the sister taxon of a (*Gorilla*, *Pan*, *Pongo*) clade, and that *Pan* is the sister taxon of a (*Gorilla*, *Pongo*) clade (Figure 46).

5.2.1.4. Test results

The Dataset A parsimony-based test did not support Hypothesis 2. The criterion that the regions should consistently favour different cladograms and one of the favoured cladograms should be compatible with the hominoid consensus molecular cladogram, was not fulfilled. None of the favoured cladograms was compatible with the hominoid consensus molecular cladogram.

5.2.2. PARSIMONY-BASED TEST OF HYPOTHESIS 2 USING REGIONALLY-GROUPED CHARACTERS FROM DATASET B

This test consisted of five analyses (21-25). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 49. The cladograms favoured in the analyses are presented in figures 47-75. The descriptive statistics associated with the cladograms are given in Table 50. The hypothesis was considered supported if the regions consistently favoured different cladograms and one of the favoured cladograms was compatible with the papionin consensus molecular cladogram.

5.2.2.1. Analysis 21

A single most parsimonious cladogram, which was incompatible with the papionin consensus molecular cladogram, was identified for the palate and upper dentition character group in Analysis 21 (Figure 47). It positioned *Cercocebus* as the sister taxon of a (*Lophocebus*, *Macaca*, *Mandrillus*, *Papio*, *Theropithecus*) clade, and *Lophocebus* as the sister taxon of a (*Macaca*, *Mandrillus*, *Papio*, *Theropithecus*) clade. The relationships within the latter clade were unresolved.

Five equally parsimonious arrangements for the taxa were retrieved from the mandible and lower dentition data in Analysis 21 (figures 48-52). None of the cladograms was compatible with the papionin consensus molecular cladogram. The first posited a trichotomy between *Cercocebus*, *Papio* and a clade containing *Lophocebus*, *Macaca*, *Mandrillus* and *Theropithecus*. Within the latter clade, *Lophocebus* was positioned as the basal taxon, and *Mandrillus* appeared as the sister taxon of *Macaca* and *Theropithecus*. The second suggested that the initial branching event in the evolution of the ingroup taxa separated the common ancestor of *Cercocebus* and *Papio* from the common ancestor of *Lophocebus*, *Macaca*, *Mandrillus* and *Theropithecus*. Within the (*Lophocebus*, *Macaca*, *Mandrillus*, *Theropithecus*) clade, *Lophocebus* was located as the basal taxon, and *Mandrillus* was positioned as the sister group of *Macaca* and *Theropithecus*. The third placed *Lophocebus* as the sister taxon of a (*Cercocebus*, *Macaca*, *Mandrillus*, *Papio*, *Theropithecus*) clade. Within the (*Cercocebus*, *Macaca*, *Mandrillus*, *Papio*, *Theropithecus*), a trichotomy was posited between *Cercocebus*, *Papio* and a (*Macaca*, *Mandrillus*, *Theropithecus*) clade. Within the (*Macaca*, *Mandrillus*, *Theropithecus*) clade, *Mandrillus* appeared as the sister taxon of *Macaca* and *Theropithecus*. The fourth cladogram was identical to the third cladogram except that the positions of *Mandrillus* and

Theropithecus were reversed. The fifth cladogram suggested that the initial branching event in the evolution of the ingroup separated *Lophocebus* from the common ancestor of the other papionin taxa. The next branching event separated the common ancestor of *Cercocebus* and *Papio* from the common ancestor of *Macaca*, *Mandrillus* and *Theropithecus*. The final cladistically significant branching event separated *Theropithecus* from the common ancestor of *Macaca* and *Mandrillus*. The strict consensus of the five cladograms was incompatible with the consensus molecular cladogram for the papionins, since it linked *Macaca*, *Mandrillus* and *Theropithecus* in a clade to the exclusion of *Papio*, *Cercocebus* and *Lophocebus*.

A single most parsimonious cladogram, which was incompatible with the papionin consensus molecular cladogram, was identified for the face characters in Analysis 21 (Figure 53). It suggested that the first branching event in the evolution of the extant papionin genera separated *Lophocebus* from the common ancestor of *Cercocebus*, *Macaca*, *Mandrillus*, *Papio* and *Theropithecus*. The second branching event split *Cercocebus* from the common ancestor of *Macaca*, *Mandrillus*, *Papio*, and *Theropithecus*. *Theropithecus* and the common ancestor of *Macaca*, *Mandrillus* and *Papio* were isolated from one another by the third branching event. The final cladistically meaningful branching event separated *Macaca* from the common ancestor of *Mandrillus* and *Papio*.

Two equally parsimonious arrangements for the taxa were retrieved from the cranial vault and base character group in Analysis 21 (figures 54 and 55). Neither cladogram was compatible with the papionin consensus molecular cladogram. The first positioned *Theropithecus* as the sister taxon of a (*Cercocebus*, *Lophocebus*, *Macaca*, *Mandrillus*, *Papio*) clade, and posited a trichotomy between *Papio*, a (*Cercocebus*, *Mandrillus*) clade and a (*Lophocebus*, *Macaca*) clade. The second located *Theropithecus* as the sister taxon of a monophyletic group comprising *Cercocebus*, *Lophocebus*,

Macaca, *Mandrillus* and *Papio*, and *Papio* as the sister taxon of a (*Cercocebus*, *Lophocebus*, *Macaca*, *Mandrillus*) clade. Within the latter clade, *Cercocebus* and *Mandrillus* appeared as a monophyletic assemblage, and *Lophocebus* and *Macaca* as another. The strict consensus of the cladograms was incompatible with the consensus molecular cladogram for the papionins. It positioned *Theropithecus* as the basal papionin, and posited a trichotomous relationship between *Papio*, a (*Cercocebus*, *Mandrillus*) clade and a (*Lophocebus*, *Macaca*) clade.

5.2.2.2. Analysis 22

A single most parsimonious cladogram was identified for the palate and upper dentition data in Analysis 22 (Figure 56). It was not compatible with the papionin consensus molecular cladogram, since it united *Mandrillus* and *Theropithecus* in a clade separate from the other ingroup taxa, and positioned *Papio* as the sister taxa the (*Mandrillus*, *Theropithecus*) clade. It also suggested that the (*Mandrillus*, *Papio*, *Theropithecus*) clade was the sister taxon of a clade containing *Cercocebus* and *Macaca*, and positioned *Lophocebus* as the sister group of the (*Cercocebus*, *Macaca*, *Mandrillus*, *Papio*, *Theropithecus*) clade.

Three equally parsimonious arrangements for the taxa were retrieved from the mandible and lower dentition characters in Analysis 22 (figures 57-59). None of the cladograms was congruent with the papionin consensus molecular cladogram. The first positioned *Macaca* as the sister taxon of the other papionin taxa, *Papio* as the sister taxon of a (*Cercocebus*, *Lophocebus*, *Mandrillus*, *Theropithecus*) clade, *Cercocebus* as the sister taxon of a (*Lophocebus*, *Mandrillus*, *Theropithecus*) clade, and *Lophocebus* as the sister taxon of *Mandrillus* and *Theropithecus*. The second was identical to the first cladogram except that the positions of *Cercocebus* and *Lophocebus* were reversed. The third

located *Macaca* as the sister taxon of the other papionin taxa, and *Papio* as the sister taxon of a (*Cercocebus*, *Lophocebus*, *Mandrillus*, *Theropithecus*) clade. Within the (*Cercocebus*, *Lophocebus*, *Mandrillus*, *Theropithecus*) clade, *Cercocebus* and *Lophocebus* appeared as a monophylum, and *Mandrillus* and *Theropithecus* appeared as another. The strict consensus of the three cladograms was incompatible with the consensus molecular cladogram for the papionins. It positioned *Macaca* as the basal papionin, and *Papio* as the sister taxon of a clade comprising *Mandrillus*, *Cercocebus*, *Lophocebus* and *Theropithecus*. Within the latter clade, *Mandrillus* and *Theropithecus* were linked as sister taxa.

Four equally parsimonious solutions were identified for the face data in Analysis 22 (figures 60-63). None of the cladograms had the same branching pattern as the papionin consensus molecular cladogram. The first cladogram suggested that *Lophocebus* is the sister taxon of the other papionin taxa, and that *Cercocebus* is the sister taxon of a (*Macaca*, *Mandrillus*, *Papio*, *Theropithecus*) clade. Within the latter clade, *Macaca* appeared as the sister taxon of *Mandrillus*, *Papio* and *Theropithecus*, and *Theropithecus* appeared as the sister taxon of *Mandrillus* and *Papio*. The second positioned *Cercocebus* as the sister group of the other papionins, *Macaca* as the sister group of a (*Lophocebus*, *Mandrillus*, *Papio*, *Theropithecus*) clade, and *Lophocebus* as the sister group of a (*Mandrillus*, *Papio*, *Theropithecus*) clade. The relationships within the latter clade were the same as those suggested by the first cladogram. The third cladogram located *Lophocebus* as the sister taxon of a (*Cercocebus*, *Macaca*, *Mandrillus*, *Papio*, *Theropithecus*) clade. Within that clade, a trichotomy was posited between *Cercocebus*, *Macaca* and a clade comprising *Mandrillus*, *Papio* and *Theropithecus*. Within the latter clade, *Theropithecus* appeared as the sister taxon of *Mandrillus* and *Papio*. The fourth cladogram positioned *Lophocebus* as the sister taxon of a (*Cercocebus*, *Macaca*, *Mandrillus*, *Papio*, *Theropithecus*) clade. Within that clade, *Cercocebus* and *Macaca* formed a

clade, and baboon taxa, *Mandrillus*, *Papio* and *Theropithecus*, formed another. Within the baboon clade, *Theropithecus* appeared as the sister group of *Mandrillus* and *Papio*. The strict consensus of the four cladograms was not congruent with the papionin consensus molecular cladogram. It contained two clades, one comprising *Papio*, *Theropithecus* and *Mandrillus*, and the other consisting of *Mandrillus* and *Papio*.

One most parsimonious cladogram, which was incompatible with the papionin consensus molecular cladogram, was identified for the cranial vault and base characters in Analysis 22 (Figure 64). This cladogram suggested that the initial branching event in the evolution of the extant papionin genera separated *Lophocebus* from the common ancestor of the other ingroup taxa, and that the second branching event isolated *Macaca* from the common ancestor of *Cercocebus*, *Mandrillus*, *Papio* and *Theropithecus*. The third branching event posited by the cladogram separated *Cercocebus* from the common ancestor of the three baboon taxa, *Mandrillus*, *Papio* and *Theropithecus*. The final cladistically significant split isolated *Theropithecus* from the common ancestor of *Mandrillus* and *Papio*.

5.2.2.3. Analysis 23

A single cladogram was favoured for the palate and upper dentition characters in Analysis 23 (Figure 65). Incompatible with the papionin consensus molecular cladogram, this cladogram suggested that the initial branching event in the evolution of the ingroup taxa separated *Lophocebus* from the common ancestor of the other papionin genera. The second branching event divided *Papio* from the common ancestor of *Cercocebus*, *Macaca*, *Mandrillus* and *Theropithecus*. The third separated *Macaca* from the common ancestor of *Cercocebus*, *Mandrillus* and *Theropithecus*. The final phylo-

genetically significant branching event separated *Cercocebus* from the common ancestor of *Mandrillus* and *Theropithecus*.

One most parsimonious cladogram was identified for the mandible and lower dentition character group in Analysis 23 (Figure 66). It posited a sister group relationship between *Lophocebus* and *Mandrillus*. To this clade it connected successively *Papio*, *Macaca*, *Theropithecus*, and lastly *Cercocebus*.

Two equally parsimonious arrangements for the taxa were retrieved from the face character group in Analysis 23 (figures 60 and 63). Neither cladogram was compatible with the papionin consensus molecular cladogram. The first located *Lophocebus* as the sister group of the other papionin taxa, and *Cercocebus* as the sister group of a (*Macaca*, *Mandrillus*, *Papio*, *Theropithecus*) clade. Within the latter clade, *Macaca* appeared as the sister group of the three baboon genera, *Mandrillus*, *Papio* and *Theropithecus*. Within the baboon clade, *Theropithecus* was positioned as the sister taxon of *Papio* and *Theropithecus*. The second cladogram had the same topology as the first cladogram except that *Cercocebus* and *Macaca* formed a clade that was a sister taxon of a (*Mandrillus*, *Papio*, *Theropithecus*) clade. The strict consensus of the cladograms was not congruent with the consensus molecular cladogram for the papionins. It suggested that *Lophocebus* is the basal papionin, and posited a trichotomous relationship between *Cercocebus*, *Macaca* and a clade comprising the three baboon genera. Within the latter, *Mandrillus* and *Papio* were located as sister taxa.

Two equally parsimonious arrangements for the taxa were also recovered from the cranial vault and base character group in Analysis 23 (figures 60 and 67). Neither cladogram was compatible with the papionin consensus molecular cladogram. The first suggested that the earliest branching event in the

evolution of the extant papionin genera separated *Lophocebus* from the common ancestor of *Cercocebus*, *Macaca*, *Mandrillus*, *Papio* and *Theropithecus*. The second branching event separated *Cercocebus* from the common ancestor *Macaca*, *Mandrillus*, *Papio* and *Theropithecus*. The third separated *Macaca* from the common ancestor of *Mandrillus*, *Papio* and *Theropithecus*. The final cladistically significant split separated *Theropithecus* from the common ancestor of *Mandrillus* and *Papio*. The second cladogram was identical to the first except that the initial branching event separated the common ancestor of *Lophocebus* and *Cercocebus* from the common ancestor of *Macaca*, *Mandrillus*, *Papio* and *Theropithecus*. The strict consensus of cladograms was incompatible with the papionin consensus molecular cladogram. It contained three clades. One comprised *Macaca* and the three baboon genera. The second consisted of *Mandrillus*, *Theropithecus* and *Papio*. The third comprised *Mandrillus* and *Papio*.

5.2.2.4. Analysis 24

Three equally parsimonious solutions were identified for the palate and upper dentition data in Analysis 24 (figures 68-70). None of the cladograms was compatible with the papionin consensus molecular cladogram. The first divided the taxa into two main subgroups. One contained *Cercocebus*, *Lophocebus* and *Macaca*. The other contained *Mandrillus*, *Papio* and *Theropithecus*. Within the (*Cercocebus*, *Lophocebus*, *Macaca*) clade, *Cercocebus* appeared as the sister taxon of *Lophocebus* and *Macaca*. Within the (*Mandrillus Papio*, *Theropithecus*) clade, *Papio* was positioned as the sister group of *Mandrillus* and *Theropithecus*. The second cladogram also divided the taxa into two subgroups. One comprised *Mandrillus* and *Theropithecus*. The other comprised *Cercocebus*, *Lophocebus*, *Macaca* and *Papio*. Within the latter clade, *Papio* appeared as the basal taxon, and *Cercocebus* appeared as the sister taxon of *Lophocebus* and *Macaca*. The third cladogram had the same

branching pattern as the second except that *Papio* appeared as the basal papionin rather than as the sister taxon of the mangabeys and macaques. The strict consensus of the cladograms was not congruent with the consensus molecular cladogram for the papionins. It contained three clades. One consisted of *Mandrillus* and *Papio*. Another comprised the mangabeys and macaques. The other clade comprised *Macaca* and *Lophocebus*.

Analysis 24 identified a single most parsimonious cladogram for the mandible and lower dentition characters (Figure 68). It was not compatible with the papionin consensus molecular cladogram. It divided the ingroup taxa into two subgroups. One of these contained the mangabeys and macaques, while the other contained the three baboon taxa. Within the former clade, the cladogram suggested that *Lophocebus* and *Macaca* are more closely related to each other than either is to *Cercocebus*. Within the baboon clade, *Mandrillus* and *Theropithecus* were positioned as sister taxa to the exclusion of *Papio*.

One most parsimonious cladogram was obtained for the face character group in Analysis 24 (Figure 71). This cladogram was not compatible with the papionin consensus molecular cladogram. It suggested an early division between *Mandrillus* and *Papio* on the one hand, and *Cercocebus*, *Lophocebus*, *Macaca*, and *Theropithecus* on the other. Within the latter clade, the first genus to diverge was *Theropithecus*. Thereafter, *Cercocebus* split off, leaving *Lophocebus* and *Macaca* as sister taxa.

A single most parsimonious cladogram was obtained for the cranial vault and base data in Analysis 24 (Figure 72). This cladogram was not compatible with the papionin consensus molecular cladogram. It posited a basal split between a clade comprising *Lophocebus*, *Cercocebus*, and *Macaca*, and one consisting of *Theropithecus*, *Papio* and *Mandrillus*. Within the former clade, the cladogram

indicated that *Cercocebus* was the first taxon to diverge, while within the baboon clade, it suggested that *Theropithecus* was the first to diverge.

5.2.2.5. Analysis 25

Analysis 25 identified one most parsimonious cladogram for the palate and upper dentition characters (Figure 73). It was not compatible with the papionin consensus molecular cladogram, suggesting instead that the first branching event in the evolution of the ingroup taxa separated *Macaca* from the common ancestor of the other papionin genera. The second branching event posited by the cladogram separated *Lophocebus* from the common ancestor of *Cercocebus*, *Mandrillus*, *Papio* and *Theropithecus*. The third separated *Cercocebus* from the common ancestor of the three baboon taxa. The final cladistically meaningful split isolated *Papio* from the common ancestor of *Mandrillus* and *Theropithecus*.

A single cladogram was identified for the mandible and lower dentition character group in Analysis 25 (Figure 74). This cladogram was not compatible with the papionin consensus molecular cladogram. Rather it suggested that the first branching event in the evolution of the ingroup taxa separated *Lophocebus* from the common ancestor of a clade containing *Cercocebus*, *Macaca*, *Mandrillus*, *Papio* and *Theropithecus*. The second branching event separated *Macaca* from the common ancestor of *Cercocebus* and the baboons. The third isolated *Cercocebus* from the common ancestor of the baboons. The final phylogenetically informative split separated *Papio* from the common ancestor of *Mandrillus* and *Theropithecus*.

One most parsimonious cladogram was identified for the face characters in Analysis 25 (Figure 75). It was not compatible with the papionin consensus molecular cladogram. It positioned *Macaca* as the basal ingroup, *Lophocebus* as the sister group of a (*Cercocebus*, *Mandrillus*, *Papio*, *Theropithecus*) clade, *Cercocebus* as the sister taxon of a baboon clade, and *Theropithecus* as the sister group of a clade comprising *Mandrillus* and *Papio*.

A single most parsimonious cladogram was identified for the cranial vault and base character group in Analysis 25 (Figure 64). This cladogram was not compatible with the papionin consensus molecular cladogram. Instead, it suggested that the first branching event in the evolution of the extant papionin genera separated *Lophocebus* from the common ancestor of the other ingroup taxa. The second split separated *Macaca* from the common ancestor of *Cercocebus*, *Mandrillus*, *Papio* and *Theropithecus*. The third separated *Cercocebus* from the common ancestor of the three baboon genera. The final cladistically informative branching event separated *Theropithecus* from the common ancestor of *Mandrillus* and *Papio*.

5.2.2.6. Test results

The Dataset B parsimony-based test did not support Hypothesis 2. The criterion that the regions should consistently favour different cladograms and one of the favoured cladograms should be compatible with the papionin consensus molecular cladogram, was not fulfilled. None of the favoured cladograms was compatible with the papionin consensus molecular cladogram.

5.2.3. BOOTSTRAP-BASED TEST OF HYPOTHESIS 2 USING REGIONALLY-GROUPED CHARACTERS FROM DATASET A

This test comprised three analyses (BB-DD). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 51. The hypothesis was judged supported if some but not all the regions consistently favoured clades of the hominoid consensus molecular cladogram. As with the bootstrap-based tests of Hypothesis 1, molecular clades were considered favoured only if they appeared in 70% or more of the bootstrap replications and if there was no better supported non-molecular clade. The condition 'consistently favoured' was attached to the tests because cladistic programs can generate clades from random data (Smith, 1994), and because it is reasonable to assume that if a data set contains a strong phylogenetic signal, the signal should be identified regardless of which outgroups, size-adjustment techniques and coding procedures are used (see Sokal, 1985).

5.2.3.1. Analysis BB

Two clades were recovered from the palate and upper dentition characters in Analysis BB. The first, which was compatible with the hominoid consensus molecular cladogram, suggested that *Homo* and *Pan* are more closely related to one another than either is to *Gorilla* or *Pongo* (89%). The other, which was not compatible with the consensus molecular cladogram, suggested that *Homo*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Gorilla* (94%).

Two clades were retrieved from the mandible and lower dentition character group in Analysis BB. The first, which was compatible with the hominoid consensus molecular cladogram, suggested that

Homo and *Pan* are more closely related to one another than either is to *Gorilla* or *Pongo* (71%). The second clade, which was not compatible with the hominoid consensus molecular cladogram, indicated a closer relationship between *Gorilla* and *Pongo* than between either of them and *Homo* or *Pan* (73%).

Two clades were recovered from the face characters in Analysis BB, neither of which was compatible with the hominoid consensus molecular cladogram. The first suggested that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (82%). The other indicated that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Homo* or *Pan* (80%).

Two clades were retrieved from the cranial vault and base character data in Analysis BB, neither of which was compatible with the hominoid consensus molecular cladogram. The first indicated that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (74%). The other clade suggested that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Homo* or *Pan* (74%).

5.2.3.2. Analysis CC

Two clades were recovered for the palate and upper dentition characters in Analysis CC, neither of which was compatible with the hominoid consensus molecular cladogram. One clade suggested that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (77%). The other clade implied that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Homo* or *Pan* (97%).

Analysis CC also yielded two clades for the mandible and lower dentition data. Again, neither agreed with the hominoid consensus molecular cladogram. One suggested instead that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (90%). The other clade implied that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Homo* or *Pan* (73%).

Two clades were obtained from the face character group in Analysis CC. One was identical to the first of the two clades recovered from the palate and mandible characters (100%), and the other was the same as the second of the two clades retrieved from the palate and mandible character groups (96%).

Two clades were favoured for the cranial vault and base data in Analysis CC, neither of which was compatible with the hominoid consensus molecular cladogram. The first was identical to the first of the two clades recovered from the other regional character groups (99%). The second was the same as the second of the two clades obtained from the other character groups (99%).

5.2.3.3. Analysis DD

One clade was recovered from the palate and upper dentition character group in Analysis DD. It was not compatible with the hominoid consensus molecular cladogram. It suggested that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Homo* or *Pan* (87%).

Analysis DD yielded two clades for the mandible and lower dentition data, neither of which was compatible with the consensus molecular cladogram for the hominoid genera. One indicated that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (85%). The other implied that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Homo* or *Pan* (89%).

Two clades were also obtained from the face character group in Analysis DD. Again, neither was compatible with the hominoid consensus molecular cladogram. One indicated that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (99%). The other implied that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Homo* or *Pan* (84%).

Two clades were favoured for the cranial vault and base characters in Analysis DD. Neither clade was compatible with the hominoid consensus molecular cladogram. The first was identical to the first of the two clades recovered from the mandible and lower dentition, and face character groups (98%). The second was the same as the clade recovered from the palate and upper dentition characters, and as the second of the two clades obtained from the mandible and lower dentition, and face character groups (98%).

5.2.3.4. Test result

The Dataset A bootstrap-based test did not support Hypothesis 2. The criterion that some but not all the regions consistently favoured clades of the hominoid consensus molecular cladogram, was not met. The (*Homo*, *Pan*) clade of the consensus molecular cladogram was recovered from the palate

and mandible character groups in one analysis, but better supported non-molecular clades were also recovered from those character groups. None of the other analyses recovered clades that were compatible with the consensus molecular cladogram for the hominoids.

5.2.4. BOOTSTRAP-BASED TEST OF HYPOTHESIS 2 USING REGIONALLY-GROUPED CHARACTERS FROM DATASET B

This test consisted of five analyses (26-30). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 52. The hypothesis was judged supported if some but not all the regions consistently favoured clades of the papionin consensus molecular cladogram. A molecular clades were considered favoured only if they appeared in 70% or more of the bootstrap replications and if there was no better supported non-molecular clade.

5.2.4.1. Analysis 26

No ≥70% clades were recovered from the mandible and lower dentition character group in Analysis 26, and none were retrieved from the cranial vault and base character group.

One clade was recovered from the palate and upper dentition characters in Analysis 26. It was not compatible with the papionin consensus molecular cladogram. It suggested instead that *Macaca*, *Mandrillus*, *Papio* and *Theropithecus* are more closely related to one another than any of them is to *Cercocebus* or *Lophocebus* (89%).

Two clades were retrieved from the face characters in Analysis 26. Neither clade was compatible with the papionin consensus molecular cladogram. One clade was identical to the clade recovered from the palate characters (95%). The other clade suggested that *Cercocebus*, *Macaca*, *Mandrillus*, *Papio* and *Theropithecus* are more closely related to one another than any of them is to *Lophocebus* (89%).

5.2.4.2. Analysis 27

Three clades were retrieved from the palate and upper dentition characters in Analysis 27. None of the clades was compatible with the papionin consensus molecular cladogram. The first comprised *Cercocebus*, *Macaca*, *Mandrillus*, *Papio* and *Theropithecus*, and appeared in 77% of the bootstrap cladograms. The second comprised *Mandrillus*, *Papio* and *Theropithecus*, and appeared in 85% of the bootstrap cladograms. The third comprised *Mandrillus* and *Theropithecus*, and appeared in 84% of the bootstrap cladograms.

One clade was recovered from the mandible and lower dentition data in Analysis 27. It was not compatible with the papionin consensus molecular cladogram. It comprised *Mandrillus* and *Theropithecus*, and was supported by 84% of the bootstrap cladograms

Two clades were obtained from the face characters in Analysis 27, neither of which was compatible with the papionin consensus molecular cladogram. One was identical to the second clade recovered from the palate characters, and appeared in 85% of the bootstrap cladograms. The other was the

same as the third clade retrieved from the palate data, and was supported by 95% of the bootstrap cladograms.

Two clades were also identified for the cranial vault and base variables in Analysis 27. Neither was compatible with the papionin consensus molecular cladogram. One was identical to the second clade recovered from the palate and upper dentition characters. The other was the same as the third clade retrieved from the palate and upper dentition data. The first clade was supported by 88% of the bootstrap cladograms, the second by 86% of them.

5.2.4.3. Analysis 28

No ≥70% clades were obtained from the mandible and lower dentition data in Analysis 28.

Two clades were recovered from the palate and upper dentition characters in Analysis 28. Neither was compatible with the papionin consensus molecular cladogram. One comprised *Cercocebus*, *Macaca*, *Mandrillus*, *Papio* and *Theropithecus*. The other comprised *Mandrillus* and *Theropithecus*. The former clade appeared in 75% of the bootstrap cladograms, the latter in 95% of them.

Analysis 28 yielded three non-molecular clades for the face variables. The first was identical to the second clade recovered from the palate characters. The second contained *Mandrillus*, *Papio* and *Theropithecus*, while the third contained *Mandrillus* and *Papio*. The first clade appeared in 71% of the bootstrap cladograms, the second in 75%, and the third in 81%.

Two clades were recovered from the cranial vault and base traits in Analysis 28, neither of which was compatible with the papionin consensus molecular cladogram. One was identical to the second clade recovered from the face characters (98%). The other was identical to the third clade retrieved from the face data (98%).

5.2.4.4. Analysis 29

No ≥70% clades were recovered from the palate and upper dentition measurements in Analysis 29.

Three clades were obtained from the mandible and lower dentition data in Analysis 29, none of which was compatible with the papionin consensus molecular cladogram. The first comprised *Mandrillus*, *Papio* and *Theropithecus*. The second comprised *Mandrillus* and *Theropithecus*. The third comprised *Lophocebus* and *Macaca*. The first clade was supported by 77% of the bootstrap cladograms, the second by 73%, and the third by 89%.

Three clades were identified for the face character group in Analysis 29. None of the clades were compatible with the papionin consensus molecular cladogram. The first contained *Cercocebus*, *Lophocebus*, *Macaca* and *Theropithecus* (78%). The second contained *Cercocebus*, *Lophocebus* and *Macaca* (97%). The third was identical to the last clade recovered from the mandible data (98%).

Analysis 29 yielded three clades for the cranial vault and base variables, none of which were compatible with the papionin consensus molecular cladogram. The first was identical to the first clade recovered from the mandible and lower dentition data. The second was the same as the second clade retrieved from the face characters. The third was identical to the third clade recovered from the

mandible and lower dentition data, and the third clade retrieved from the face character set. The first clade was supported by 85% of the bootstrap cladograms, the second by 92%, and the third by 90%.

5.2.4.5. Analysis 30

No ≥70% clades were recovered from the palate and upper dentition traits in Analysis 30.

Two clades were obtained from the mandible and lower dentition character group in Analysis 30; neither was compatible with the papionin consensus molecular cladogram. One comprised *Cercocebus*, *Macaca*, *Mandrillus*, *Papio* and *Theropithecus*. The other comprised *Cercocebus*, *Mandrillus*, *Papio* and *Theropithecus*. The first clade appeared in 83% of the bootstrap cladograms, the second appeared in 85%.

Three non-molecular clades were retrieved from the face character group in Analysis 30. The first was identical to the second clade recovered from the mandible characters (94%). The second contained *Mandrillus*, *Papio* and *Theropithecus* (96%), and the third contained *Mandrillus* and *Papio* (90%).

Three clades were also retrieved from the cranial vault and base measurements in Analysis 30, none of which matched those that make up the papionin molecular cladogram. Again, the first was the same as the second clade obtained from the mandible characters (94%), the second contained *Mandrillus*, *Papio* and *Theropithecus* (99%), and the third comprised *Mandrillus* and *Papio* (90%).

5.2.4.6. Test result

The Dataset B bootstrap-based test did not support Hypothesis 2. The criterion that some but not all the regions should consistently favour clades of the papionin consensus molecular cladogram, was not fulfilled. None of the 35 clades recovered was compatible with the consensus molecular estimate of the affinities of the papionin genera.

5.2.5. CONSISTENCY INDEX-BASED TEST OF HYPOTHESIS 2 USING REGIONALLY-GROUPED CHARACTERS FROM DATASET A

This test comprised three analyses (EE-GG). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 53. The hypothesis was judged supported if the analyses all favoured the same rank order of regional CIs for the hominoid consensus molecular cladogram.

5.2.5.1. Analysis EE

In Analysis EE, the palate and anterior dentition character group had the highest CI (0.734), the mandible and lower dentition character group the second highest (0.728), the cranial vault and base character group the third highest (0.712), and the face character group the lowest (0.706).

5.2.5.2. Analysis FF

In Analysis FF, the face measurements had the highest CI (0.711), the mandible and lower dentition character group the second highest (0.700), the cranial vault and base traits the third highest (0.679), and the palate and upper dentition character group the lowest CI (0.667).

5.2.5.3. Analysis GG

In Analysis GG, the mandible and lower dentition character group had the highest consistency index (0.723), the palate and upper dentition characters the second highest (0.709), the cranial vault and base character group the third highest (0.697) and the face data the lowest CI (0.696).

5.2.5.4. Test result

The Dataset A consistency index-based test did not support Hypothesis 2. The criterion that the analyses should all support the same order among the CIs of the regional cladograms was not fulfilled. Each of the analyses suggested a different regional order.

5.2.6. CONSISTENCY INDEX-BASED TEST OF HYPOTHESIS 2 USING REGIONALLY-GROUPED CHARACTERS FROM DATASET B

This test comprised five analyses (31-35). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 54. The hypothesis was

judged supported if the analyses all favoured the same rank order of regional CIs for the papionin consensus molecular cladogram.

5.2.6.1. Analysis 31

In Analysis 31, the face characters had the highest CI (0.524), the palate and upper dentition character group and the cranial vault and base variables had the equal-second highest (0.500), and the mandible and lower dentition character group had the lowest CI (0.400).

5.2.6.2. Analysis 32

In Analysis 32, the face character group had the highest CI (0.604), the palate and upper dentition character group had the second highest (0.591), the cranial vault and base traits had the third highest (0.533), and the mandible and lower dentition character group had the lowest CI (0.462).

5.2.6.3. Analysis 33

In Analysis 33, the face traits and the cranial vault and base variables had the joint highest CIs (0.555), the palate and upper dentition character group the next highest (0.545) and the mandible and lower dentition characters had the lowest CI (0.528).

5.2.6.4. Analysis 34

In Analysis 34, the palate and upper dentition characters had the highest CI (0.559), the mandible and lower dentition character group had the second highest (0.553), the cranial vault and base variables had the third highest (0.533), and the face character group had the lowest CI (0.521).

5.2.6.5. Analysis 35

In Analysis 35, the palate and upper dentition measurements had the highest CI (0.566), the cranial vault and base character group had the second highest (0.537), the face data had the third highest (0.521), and the mandible and lower dentition character group had the lowest CI (0.510).

5.2.6.6. Test result

The Dataset B consistency index-based test did not support Hypothesis 2. The criterion that the analyses should all support the same order among the consistency indices of the regional cladograms was not fulfilled. Each analysis supported a different order among the regional CIs.

5.3. HYPOTHESIS 3 TESTS

Male and female primate crania differ in their reliability for reconstructing the cladistic relationships between species and genera

The third hypothesis was subjected to six tests in which the males and females were treated as separate taxa, and characters from all the cranial regions were analyzed together. Two of the tests were based on parsimony analysis, two on the bootstrap and two on the consistency index. The third hypothesis was also subjected to 24 tests in which the males and females were treated as separate taxa, and characters from just one of the cranial regions (palate and upper dentition, mandible and lower dentition, face, cranial vault and base) were analyzed. Eight of the tests were based on parsimony analysis and eight on bootstrapping. The remaining eight were based on the consistency index.

5.3.1. PARSIMONY-BASED TEST OF HYPOTHESIS 3 USING CHARACTERS FROM ALL DATASET A REGIONS

This test comprised four analyses (HH-KK). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 55. The cladograms favoured in the analyses are presented in figures 76 and 77. The descriptive statistics associated with the cladograms are given in Table 56. The hypothesis was considered supported if the analyses consistently favoured cladograms that were compatible with the hominoid consensus molecular cladogram for one sex but not the other.

5.3.1.1. Analysis HH

A single cladogram was recovered from the male taxa in Analysis HH (Figure 76). It positioned *Homo* as the sister taxon of a (*Gorilla*, *Pan*, *Pongo*) clade, and *Pan* as the sister taxon of a (*Gorilla*, *Pongo*) clade. A single cladogram was also obtained for the female taxa in Analysis HH. Again, *Homo* appeared as the sister group of a (*Gorilla*, *Pan*, *Pongo*) clade, and *Pan* as the sister group of a (*Gorilla*, *Pongo*) clade (Figure 77).

5.3.1.2. Analysis II

A single cladogram was identified for the male taxa in Analysis II. It suggested that *Homo* is the sister taxon of a *Gorilla*, *Pan* and *Pongo*, and that *Pan* is the sister taxon of a *Gorilla* and *Pongo* (Figure 76). In Analysis II, the female character state data yielded a single cladogram with the same branching pattern as the male cladogram (Figure 77).

5.3.1.3. Analysis JJ

A single cladogram was obtained for the male taxa in Analysis JJ. It located *Homo* as the sister taxon of a (*Gorilla*, *Pan*, *Pongo*) clade, and *Pan* as the sister taxon of a (*Gorilla*, *Pongo*) clade (Figure 76). A single cladogram was also retrieved for the female taxa in Analysis JJ. It was topologically identical to the male cladogram (Figure 77).

5.3.1.4. Analysis KK

A single cladogram was favoured for the male character state data in Analysis KK. It indicated that *Homo* is the sister taxon of a (*Gorilla*, *Pan*, *Pongo*) clade, and that *Pan* is the sister taxon of a (*Gorilla*, *Pongo*) clade (Figure 76). Analysis KK identified a single most parsimonious cladogram for the female taxa, which had the same branching pattern as the male cladogram (Figure 77).

5.3.1.5. Test result

Hypothesis 3 was not supported by the test. The criterion that the analyses should consistently favour cladograms that are compatible with the hominoid consensus molecular cladogram for one sex but not the other, was not fulfilled. None of the most parsimonious cladograms recovered from Dataset A had the same branching pattern as the consensus molecular cladogram for the hominoids.

5.3.2. PARSIMONY-BASED TEST OF HYPOTHESIS 3 USING CHARACTERS FROM ALL DATASET B REGIONS

This test consisted of two analyses (36 and 37). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 57. The cladograms favoured in the analyses are presented in figures 78-82. The descriptive statistics associated with the cladograms are given in Table 58. The hypothesis was considered supported if both analyses favoured cladograms that were compatible with the papionin consensus molecular cladogram for one sex but not the other.

5.3.2.1. Analysis 36

A single cladogram was recovered for the male taxa in Analysis 36. As shown in Figure 78, it suggested that the first branching event to take place in the evolution of the extant papionin genera separated *Lophocebus* from the common ancestor of *Cercocebus*, *Macaca*, *Mandrillus*, *Papio* and *Theropithecus*. The next branching event split *Cercocebus* from the common ancestor of *Macaca*, *Mandrillus*, *Papio* and *Theropithecus*. *Macaca* and the common ancestor of *Mandrillus*, *Papio* and *Theropithecus* separated in the third branching event. The final cladistically significant branching event split *Theropithecus* from the common ancestor of *Mandrillus* and *Papio*.

A single most parsimonious cladogram was also obtained for the female character state data in Analysis 36. It had the same branching pattern as the male cladogram except that within the baboon it supported a sister group relationship between *Theropithecus* and *Papio* rather than one between *Mandrillus* and *Papio* (Figure 79).

5.3.2.2. Analysis 37

Two equally parsimonious cladograms were recovered for the male taxa in Analysis 37, neither of which was compatible with the consensus molecular cladogram for the papionins. As shown in Figure 80, the first cladogram had two main branches, one comprising *Cercocebus*, *Lophocebus* and *Macaca*, and the other comprising *Mandrillus*, *Papio* and *Theropithecus*. Within the former group, *Cercocebus* appeared as the sister group of *Lophocebus* and *Macaca*. Within the latter clade, *Mandrillus* was positioned as the sister taxon of *Papio* and *Theropithecus*.

The second cladogram recovered from the male data had the same branching pattern as the first except that the positions of *Mandrillus* and *Theropithecus* were reversed (Figure 81). The strict consensus of the cladograms also was not compatible with the papionin consensus molecular cladogram. It had two main branches, one consisting of the mangabeys and macaques, and the other comprising *Mandrillus*, *Papio* and *Theropithecus*. Within the former group, *Cercocebus* appeared as the sister group of *Lophocebus* and *Macaca*. The relationships within the latter group were unresolved.

One most parsimonious cladogram was obtained for the female data in Analysis 37. As shown in Figure 82, it suggested that the first branching event in the evolution of the ingroup taxa separated the common ancestor of *Papio* and *Theropithecus* from the common ancestor of *Cercocebus*, *Lophocebus*, *Macaca*, *Mandrillus* and *Theropithecus*. The second isolated *Mandrillus* from the common ancestor of *Cercocebus*, *Lophocebus* and *Macaca*. The final cladistically significant split separated *Cercocebus* from the common ancestor of *Lophocebus* and *Macaca*.

5.3.2.3. Test result

Hypothesis 3 was not supported by the test. The criterion that both analyses should favour cladograms that are compatible with the papionin consensus molecular cladogram for one sex but not the other, was not met. None of the favoured Dataset B cladograms was compatible with the papionin consensus molecular cladogram.

5.3.3. BOOTSTRAP-BASED TEST OF HYPOTHESIS 3 USING CHARACTERS FROM ALL DATASET A REGIONS

This test comprised four analyses (LL-OO). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 59. The hypothesis was considered supported if the analyses consistently favoured clades of the hominoid consensus molecular cladogram for one sex but not the other. A molecular clade was considered favoured if it was supported by 70% or more of the bootstrap replications and there was no better supported non-molecular clade.

5.3.3.1. Analysis LL

Two clades were recovered from the male data in Analysis LL. One suggested that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (100%). The other implied that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Homo* or *Pan* (100%).

Two clades were also obtained from the female data in Analysis LL. Again, one suggested that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (100%), and the other implied that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Homo* or *Pan* (100%).

5.3.3.2. Analysis MM

Two clades were recovered from the male data in Analysis MM. According to the first, *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (100%). The other indicated that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Homo* or *Pan* (93%). One clade was obtained from the female data in Analysis MM. It indicated that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (90%).

5.3.3.3. Analysis NN

Two clades were recovered from the male data in Analysis NN. The first suggested that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (100%). The second implied that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Homo* or *Pan* (95%). Two clades were also obtained from the female data in Analysis NN. Again, one suggested that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (100%), and the other implied that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Homo* or *Pan* (95%).

5.3.3.4. Analysis OO

Analysis OO identified two clades for the male data. One indicated that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (100%). The other implied that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Homo* or *Pan*

(100%). Two clades were also recovered from the female data in Analysis OO. Again, one suggested that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (100%), and the other implied that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Homo* or *Pan* (98%).

5.3.3.5. Test result

The test did not support Hypothesis 3. The criterion that the analyses should consistently favour clades of the hominoid consensus molecular cladogram for one sex but not the other, was not fulfilled. None of the 15 clades recovered was compatible with the consensus molecular cladogram for the hominoid genera.

5.3.4. BOOTSTRAP-BASED TEST OF HYPOTHESIS 3 USING CHARACTERS FROM ALL DATASET B REGIONS

This test consisted of two analyses (38 and 39). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 60. The hypothesis was considered supported if both analyses favoured clades of the papionin consensus molecular cladogram for one sex but not the other. A molecular clade was considered favoured if it was supported by 70% or more of the bootstrap replications and there was no better supported non-molecular clade. The condition 'both analyses' was attached to the tests because cladistic programs can generate clades from random data (Smith, 1994), and because it is reasonable to assume that if a data set contains a strong phylogenetic signal, the signal should be identified regardless of which outgroups, size-adjustment techniques and coding procedures are used (see Sokal, 1985).

5.3.4.1. Analysis 38

Three clades were recovered from the male data in Analysis 38. None of them were compatible with the papionin consensus molecular cladogram. The first contained *Cercocebus*, *Macaca*, *Mandrillus*, *Papio* and *Theropithecus* (98%). The second contained *Mandrillus*, *Papio* and *Theropithecus* (97%). The third contained *Mandrillus* and *Papio* (81%). Two clades were retrieved from the female data in Analysis 38, neither of which was compatible with the consensus molecular cladogram. One was identical to the first clade recovered from the male data (99%). The other contained *Macaca*, *Mandrillus*, *Papio* and *Theropithecus* (87%).

5.3.4.2. Analysis 39

Three clades were retrieved from the male characters in Analysis 39. The first clade contained *Mandrillus*, *Papio* and *Theropithecus* (73%). The clade contained *Cercocebus*, *Lophocebus* and *Macaca* (88%). The third clade contained *Lophocebus* and *Macaca* (80%). Four clades were obtained from the female characters in Analysis 39, three of which were incompatible with the papionin molecular cladogram. The first clade comprised *Cercocebus*, *Lophocebus*, *Macaca* and *Mandrillus* (80%). The second consisted of *Cercocebus*, *Lophocebus* and *Macaca* (89%), and the third comprised *Lophocebus* and *Macaca* (91%). The fourth clade was compatible with the molecular cladogram, and comprised *Papio* and *Theropithecus* (84%).

5.3.4.3. Test result

The test did not support Hypothesis 3. The criterion that both analyses should favour clades of the papionin consensus molecular cladogram for one sex but not the other, was not fulfilled. The (*Papio*, *Theropithecus*) clade of the consensus molecular cladogram was recovered from the female data in one analysis, but the other analysis did not yield a consensus molecular clade for the female data. Neither analysis produced a consensus molecular clade for the male data.

5.3.5. CONSISTENCY INDEX-BASED TEST OF HYPOTHESIS 3 USING CHARACTERS FROM ALL DATASET A REGIONS

This test comprised four analyses (PP-SS). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 61. The hypothesis was judged supported if the CIs of the hominoid consensus molecular cladograms for one sex were consistently higher than the CIs of the consensus molecular cladograms for the other sex.

5.3.5.1. Analysis PP

In Analysis PP, the female consensus molecular cladogram had a higher consistency index (0.707) than the male consensus molecular cladogram (0.683).

5.3.5.2. Analysis QQ

In Analysis QQ, the CI for the female consensus molecular cladogram was higher (0.631) than the CI for the male consensus molecular cladogram (0.585).

5.3.5.3. Analysis RR

In Analysis RR, the consensus molecular cladogram for the female taxa had a higher CI (0.712) than the consensus molecular cladogram for the male taxa (0.650).

5.3.5.4. Analysis SS

In Analysis SS, the female consensus molecular cladogram had a higher CI (0.709) than the male consensus molecular cladogram (0.704).

5.3.5.5. Test result

Hypothesis 3 was supported by the test. The criterion that the CIs of the consensus molecular cladograms of one sex should be consistently higher than the CIs of the consensus molecular cladograms for the other sex, was fulfilled. The female cladograms all had higher consistency indices than the male cladograms.

5.3.6. CONSISTENCY INDEX-BASED TEST OF HYPOTHESIS 3 USING CHARACTERS FROM ALL DATASET B REGIONS

This test consisted of two analyses (40 and 41). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 62. The hypothesis was judged supported if the CIs of the papionin consensus molecular cladograms for one sex were both higher than the CIs of the consensus molecular cladograms for the other sex.

5.3.6.1. Analysis 40

In Analysis 40, the CI of the female consensus molecular cladogram was higher (0.579) than the CI of the male consensus molecular cladogram (0.574).

5.3.6.2. Analysis 41

In Analysis 41, the female consensus molecular cladogram had a higher CI (0.574) than the male consensus molecular cladogram (0.562).

5.3.6.3. Test result

Hypothesis 3 was supported by the test. The criterion that the CIs of the consensus molecular cladograms for one sex should both be higher than the CIs of the consensus molecular cladograms for the other sex, was fulfilled. In both analyses, the female cladogram had a higher CI than the male cladogram.

5.3.7. PARSIMONY-BASED TEST OF HYPOTHESIS 3 USING PALATE AND UPPER DENTITION CHARACTERS FROM DATASET A

This test comprised four analyses (TT-WW). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 63. The cladograms favoured in the analyses are presented in figures 83-85. The descriptive statistics associated with the cladograms are given in Table 64. The hypothesis was deemed supported if the analyses consistently favoured cladograms that were compatible with the hominoid consensus molecular cladogram for one sex but not the other.

5.3.7.1. Analysis TT

A single most parsimonious cladogram was identified for the male characters in Analysis TT. It located *Homo* as the sister taxon of a (*Gorilla*, *Pan*, *Pongo*) clade, and *Pan* as the sister taxon of a (*Gorilla*, *Pongo*) clade (Figure 83). One most parsimonious cladograms was identified for the female characters in Analysis TT. It had the same branching pattern as the male cladogram (Figure 84).

5.3.7.2. Analysis UU

A single most parsimonious cladogram was identified for the male data in Analysis UU. It positioned *Homo* as the sister taxon of a (*Gorilla*, *Pan*, *Pongo*) clade, and *Pan* as the sister taxon of a (*Gorilla*, *Pongo*) clade (Figure 83). A single most parsimonious cladogram was recovered from the

female data in Analysis UU. It was topologically identical with the most parsimonious cladogram recovered from the male characters (Figure 84).

5.3.7.3. Analysis VV

A single cladogram was identified for the male palate characters in Analysis VV. It positioned *Homo* as the sister taxon of a (*Gorilla*, *Pan*, *Pongo*) clade, and *Pan* as the sister taxon of a (*Gorilla*, *Pongo*) clade (Figure 83). Two equally parsimonious solutions were obtained for the female palate characters in Analysis VV. One had the same branching pattern as the male cladogram (Figure 84). The other located *Homo* as the sister group of a (*Gorilla*, *Pan*, *Pongo*) clade, and *Gorilla* as the sister group of a (*Pan*, *Pongo*) clade (Figure 85). The strict consensus of the cladograms was not compatible with the hominoid consensus molecular cladogram, since it contained one clade comprising *Gorilla*, *Pan* and *Pongo*.

5.3.7.4. Analysis WW

One cladogram was recovered from the male characters in Analysis WW. It positioned *Homo* as the sister taxon of a (*Gorilla*, *Pan*, *Pongo*) clade, and *Pan* as the sister taxon of a (*Gorilla*, *Pongo*) clade (Figure 83). A single cladogram was identified for the female palate characters in Analysis WW. It had the same branching pattern as the male most parsimonious cladogram (Figure 84).

5.3.7.5. Test result

Hypothesis 3 was not supported by the test. The criterion that the analyses should consistently favour cladograms that are compatible with the hominoid consensus molecular cladogram for one sex but not the other, was not fulfilled. None of the favoured cladograms were compatible with the consensus molecular cladogram for the Hominoidea.

5.3.8. PARSIMONY-BASED TEST OF HYPOTHESIS 3 USING PALATE AND UPPER DENTITION CHARACTERS FROM DATASET B

This test consisted of two analyses (42 and 43). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 65. The cladograms favoured in the analyses are presented in figures 86-88. The descriptive statistics associated with the cladograms are given in Table 66. The hypothesis was deemed supported if both analyses favoured cladograms that were compatible with the papionin consensus molecular cladogram for one sex but not the other.

5.3.8.1. Analysis 42

One most parsimonious cladogram was recovered for the male taxa in Analysis 42 (Figure 86). It suggested that *Lophocebus* was the first papionin to diverge. It then divided the other taxa into two subgroups. One of these subgroups contained *Macaca* and *Papio*; the other contained *Cercocebus*, *Mandrillus*, and *Theropithecus*. Within the latter clade, the male cladogram posited a sister group relationship between the two baboon taxa.

One most parsimonious cladogram was recovered from the female data in Analysis 42 (Figure 87). It suggested that the first branching event in the evolution of the ingroup separated *Lophocebus* from the common ancestor of the other papionin genera. The second branching event separated *Papio* from the common ancestor of *Cercocebus*, *Macaca*, *Mandrillus* and *Theropithecus*. The last phylogenetically significant branching event isolated the common ancestor of *Cercocebus* and *Mandrillus* from the common ancestor of *Macaca* and *Theropithecus*.

5.3.8.2. Analysis 43

A single most parsimonious cladogram was recovered from the male characters in Analysis 43 (Figure 88). It positioned *Lophocebus* as the sister taxon of a (*Cercocebus*, *Macaca*, *Mandrillus*, *Papio*, *Theropithecus*) clade, *Papio* as the sister taxon of a (*Cercocebus*, *Macaca*, *Mandrillus*, *Theropithecus*) clade, *Macaca* as the sister taxon of a (*Cercocebus*, *Mandrillus*, *Theropithecus*) clade, and *Theropithecus* as the sister taxon of a (*Cercocebus*, *Mandrillus*) clade. A single cladogram was also favoured for the female data in Analysis 43 (Figure 87). It had the same branching pattern as the male cladogram except that it linked *Macaca* and *Theropithecus* together as a monophyletic assemblage whose sister taxon was the (*Cercocebus*, *Mandrillus*) clade.

5.3.8.3. Test result

Hypothesis 3 was not supported by the test. The criterion that both analyses should favour cladograms that are compatible with the papionin consensus molecular cladogram for one sex but not the

other, was not fulfilled. None of favoured cladograms were compatible with papionin consensus molecular cladogram.

5.3.9. BOOTSTRAP-BASED TEST OF HYPOTHESIS 3 USING PALATE AND UPPER DENTITION CHARACTERS FROM DATASET A

This test comprised four analyses (XX-ZZ). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 67. The hypothesis was considered supported if the analyses consistently favoured clades of the hominoid consensus molecular cladogram for one sex but not the other. A molecular clade was considered favoured if it was supported by 70% or more of the bootstrap replications and there was no better supported non-molecular clade.

5.3.9.1. Analysis XX

Two clades were recovered from the male palate data in Analysis XXX. One suggested that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (100%). The other implied that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Homo* or *Pan* (100%). Two clades were also recovered from the female palate characters in Analysis XXX. Again, one suggested that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (100%). The other indicated that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Homo* or *Pan* (100%).

5.3.9.2. Analysis YY

Two clades were recovered from the male palate data in Analysis YY. According to the first, *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (87%). The other clade implied that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Homo* or *Pan* (85%). One clade was recovered from the female palate characters in Analysis YY. It suggested that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Homo* or *Pan* (76%).

5.3.9.3. Analysis ZZ

One clade was recovered from the male palate data in Analysis ZZ. It suggested that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (91%). A single clade was also retrieved from the female palate characters in Analysis ZZ. It too implied that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (99%).

5.3.9.4. Analysis AAA

Two clades were recovered from the male palate characters in Analysis AAA. One suggested that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (92%). The other indicated that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Homo*, *Pan* (91%). Two clades were recovered from the female data in Analysis AAA. According to the first, *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of

them is to *Homo* (89%). The second clade implied that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Homo* or *Pan* (98%).

5.3.9.5. Test result

The test did not uphold Hypothesis 3. The criterion that the analyses should consistently favour clades of the hominoid consensus molecular cladogram for one sex but not the other, was not fulfilled. None of the clades recovered was compatible with the consensus molecular estimate of interhominoid affinities.

5.3.10. BOOTSTRAP-BASED TEST OF HYPOTHESIS 3 USING PALATE AND UPPER DENTITION CHARACTERS FROM DATASET B

This test comprised two analyses (44 and 45). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 68. The hypothesis was considered supported if both analyses consistently favoured clades of the hominoid consensus molecular cladogram for one sex but not the other. As in the previous analysis, a molecular clade was considered favoured if it was supported by 70% or more of the bootstrap replications and there was no better supported non-molecular clade.

5.3.10.1 Analysis 44

Three clades were recovered from the male palate characters in Analysis 44. The first indicated that *Cercocebus*, *Macaca*, *Mandrillus*, *Papio* and *Theropithecus* are more closely related to one another

than any of them is to *Lophocebus* (83%). The second suggested that *Cercocebus*, *Mandrillus* and *Theropithecus* share a common ancestor not shared by *Lophocebus*, *Macaca* and *Papio* (78%). The third clade implied that *Mandrillus* and *Theropithecus* form a clade to the exclusion of the other papionin genera (97%). Analysis 44 identified one clade for the female palate and upper dentition character group, which suggested that *Cercocebus*, *Macaca*, and the three baboon genera, *Mandrillus*, *Papio* and *Theropithecus*, are more closely related to one another than any of them is to *Lophocebus* (87%).

5.3.10.2 Analysis 45

Three clades were retrieved from the male palate characters in Analysis 45, none of which was compatible with the biomolecular estimate of interpapionin affinities. The first indicated that *Cercocebus*, *Macaca*, *Mandrillus*, *Papio* and *Theropithecus* share a common ancestor that is not shared by *Lophocebus* (79%). The second implied that *Cercocebus*, *Macaca*, *Mandrillus* and *Theropithecus* are more closely related to one anther than any of them is to *Lophocebus*, *Papio* (85%). The third clade suggested that *Cercocebus*, *Mandrillus* and *Theropithecus* form a clade to the exclusion of *Lophocebus*, *Macaca*, *Papio* (85%). No clades were recovered from the female palate character group in Analysis 45.

5.3.10.3. Test result

The test did not uphold Hypothesis 3. The criterion that both analyses should favour clades of the papionin consensus molecular cladogram for one sex but not the other, was not fulfilled. None of

the clades recovered was compatible with the consensus molecular estimate of interpapionin relationships.

5.3.11. CONSISTENCY INDEX-BASED TEST OF HYPOTHESIS 3 USING PALATE AND UPPER DENTITION CHARACTERS FROM DATASET A

This test comprised four analyses (BBB-EEE). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 69. The hypothesis was considered supported if the CIs of the consensus molecular cladograms for one sex were consistently higher than the CIs of the consensus molecular cladograms for the other sex.

5.3.11.1. Analysis BBB

In Analysis BBB, the consensus molecular cladogram for the female data had a higher consistency index (0.694) than the male consensus molecular cladogram (0.665).

5.3.11.2. Analysis CCC

In Analysis CCC, the female consensus molecular cladogram had a higher consistency index (0.593) than the male consensus molecular cladogram (0.556).

5.3.11.3. Analysis DDD

In Analysis DDD, the consistency index for the male consensus molecular cladogram (0.657) was higher than consistency index for the female consensus molecular cladogram (0.649).

5.3.11.4. Analysis EEE

In Analysis EEE, the male consensus molecular cladogram had a higher consistency index (0.704) than the female consensus molecular cladogram (0.694).

5.3.11.5. Test result

The test did not support Hypothesis 3. The criterion that the CIs of the consensus molecular cladograms for one sex should be consistently higher than the CIs of the consensus molecular cladograms for the other sex, was not fulfilled. The female cladogram had a higher consistency index than the male cladogram in two analyses, and the male cladogram had a higher CI than the female cladogram in the other analyses.

5.3.12. CONSISTENCY INDEX-BASED TEST OF HYPOTHESIS 3 USING PALATE AND UPPER DENTITION CHARACTERS FROM DATASET B

This test comprised two analyses (46 and 47). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 70. The hypothesis

was considered supported if the CIs of the consensus molecular cladograms for one sex were both higher than the CIs of the consensus molecular cladograms for the other sex.

5.3.12.1. Analysis 46

In Analysis 46, the male consensus molecular cladogram had a higher consistency index (0.569) than the female consensus molecular cladogram (0.560).

5.3.12.2. Analysis 47

In Analysis 47, the female consensus molecular cladogram had a higher consistency index (0.597) than the male consensus molecular cladogram (0.545).

5.3.12.3. Test result

The test did not support Hypothesis 3. The criterion that the CIs of the consensus molecular cladograms for one sex should both be higher than the CIs of the consensus molecular cladograms for the other sex, was not fulfilled. The female cladogram had a higher consistency index than the male cladogram in one analysis, while the male cladogram had a higher CI than the female cladogram in the other analysis.

5.3.13. PARSIMONY-BASED TEST OF HYPOTHESIS 3 USING MANDIBLE AND LOWER DENTITION CHARACTERS FROM DATASET A

The test comprised four analyses (FFF-III). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 71. The cladograms favoured in the analyses are presented in figures 83-85 and 89. The descriptive statistics associated with the cladograms are given in Table 72. The hypothesis was considered supported if the analyses consistently favoured cladograms that were compatible with the hominoid consensus molecular cladogram for one sex but not the other.

5.3.13.1. Analysis FFF

A single most parsimonious was recovered from the male data in Analysis FFF (Figure 83). It positioned *Homo* as the sister taxon of a (*Gorilla*, *Pan*, *Pongo*) clade, and *Pan* as the sister taxon of a (*Gorilla*, *Pongo*) clade. A single cladogram was also favoured for the female data in Analysis FFF (Figure 84). Again, *Homo* was located as the sister taxon of a (*Gorilla*, *Pan*, *Pongo*) clade, and *Pan* as the sister taxon of a (*Gorilla*, *Pongo*) clade.

5.3.13.2. Analysis GGG

Analysis GGG favoured a single cladogram for the male characters (Figure 89). *Homo* was hypothesized to be the sister group of a (*Gorilla*, *Pan*, *Pongo*) clade, and *Gorilla* the sister taxon of a (*Pan*, *Pongo*) clade. A single most parsimonious cladogram was also recovered from the female data in

Analysis GGG (Figure 85). It too suggested that *Homo* is the sister taxon of *Gorilla*, *Pan* and *Pongo*, and *Gorilla* the sister taxon of *Pan* and *Pongo*.

5.3.13.3. Analysis HHH

In Analysis HHH, a single cladogram was favoured for the male mandible character group (Figure 89). It positioned *Homo* as the sister taxon of a (*Gorilla*, *Pan*, *Pongo*) clade, and *Gorilla* as the sister taxon of a (*Pan*, *Pongo*) clade. A single most parsimonious cladogram was recovered from the female taxa in Analysis HHH (Figure 85). It located *Homo* as the sister taxon of a (*Gorilla*, *Pan*, *Pongo*) clade, and *Gorilla* as the sister taxon of a (*Pan*, *Pongo*) clade.

5.3.13.4. Analysis III

A single most parsimonious cladogram was recovered from the male mandible characters in Analysis III (Figure 83). It positioned *Homo* as the sister taxon of a (*Gorilla*, *Pan*, *Pongo*) clade, and *Pan* as the sister taxon of a (*Gorilla*, *Pongo*) clade. A single most parsimonious cladogram was also obtained from the female data in Analysis III (Figure 85). It located *Homo* as the sister taxon of a (*Gorilla*, *Pan*, *Pongo*) clade, and *Gorilla* as the sister taxon of a (*Pan*, *Pongo*) clade.

5.3.13.5. Test result

Hypothesis 3 was not supported by the test. The criterion that the analyses should consistently favour cladograms that are compatible with the hominoid consensus molecular cladogram for one sex

but not the other, was not fulfilled. None of the favoured cladograms recovered was compatible with the molecular cladogram for the Hominoidea.

5.3.14. PARSIMONY-BASED TEST OF HYPOTHESIS 3 USING MANDIBLE AND LOWER DENTITION CHARACTERS FROM DATASET B

This test comprised two analyses (48 and 49). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 73. The cladograms favoured in the analyses are presented in figures 90-95. The descriptive statistics associated with the cladograms are given in Table 74. The hypothesis was deemed supported if both analyses favoured cladograms that were compatible with the papionin consensus molecular cladogram for one sex but not the other.

5.3.14.1. Analysis 48

Analysis 48 yielded a single most parsimonious cladogram for the male data (Figure 90). It linked *Mandrillus* and *Lophocebus* together in a clade, and positioned *Papio* as their sister taxon. It also suggested that the sister taxon of the (*Lophocebus*, *Mandrillus*, *Papio*) clade was a clade containing *Cercocebus* and *Theropithecus*, and that *Macaca* was the basal ingroup taxon.

Three equally parsimonious cladograms were obtained from the female data in Analysis 48 (figures 91-93). None of the cladograms had the same branching pattern as the papionin molecular cladogram. The first suggested that the initial branching event in the evolution of the ingroup separated *Cercocebus* from the common ancestor of *Lophocebus*, *Macaca*, *Mandrillus*, *Papio* and *Theropith-*

ecus, and that the next branching event isolated *Theropithecus* from the common ancestor of *Lophocebus*, *Macaca*, *Mandrillus* and *Papio*. *Mandrillus* was isolated from the common ancestor of *Lophocebus*, *Macaca* and *Papio* in the third branching event, and then *Macaca* was separated from the common ancestor of *Lophocebus* and Papio. The second cladogram had two main branches. One comprised *Cercocebus*, *Mandrillus* and *Theropithecus*; the other comprised *Lophocebus*, *Macaca* and *Papio*. Within the former group, *Mandrillus* and *Theropithecus* appeared as a monophylum. Within the latter group, *Macaca* and *Papio* were positioned as sister taxa. In the third cladogram, *Cercocebus* was positioned as the sister taxon of *Lophocebus*, *Macaca*, *Mandrillus*, *Papio* and *Theropithecus*, and *Papio* was positioned as the sister group of a clade comprising *Lophocebus*, *Macaca*, *Mandrillus* and *Theropithecus*. Within the (*Lophocebus*, *Macaca*, *Mandrillus*, *Theropithecus*) clade, *Lophocebus* appeared as the sister taxon of *Macaca*, *Mandrillus* and *Theropithecus*, and *Macaca* as the sister group of *Mandrillus* and *Theropithecus*. The strict consensus of the cladograms had no ingroup structure.

5.3.14.2. Analysis 49

A single most parsimonious cladogram was retrieved from the male data in Analysis 49, which was incompatible with the molecular cladogram for the Papionini (Figure 94). It had two main branches, one comprising *Cercocebus*, *Lophocebus* and *Macaca*, and the other comprising the three baboon genera, *Mandrillus*, *Papio* and *Theropithecus*. Monophyletic assemblages were formed by *Lophocebus* and *Macaca* within the (*Cercocebus*, *Lophocebus*, *Macaca*) clade, and by *Mandrillus* and *Theropithecus* in the baboon clade. A single cladogram was also favoured for the female data in Analysis 49 (Figure 95). It divided the ingroup taxa into a (*Mandrillus*, *Theropithecus*) clade and a (*Cercocebus*, *Lophocebus*, *Macaca*, *Papio*) clade. Within the latter clade, *Cercocebus* was posi-

tioned as the sister taxon of *Lophocebus*, *Macaca* and *Papio, and Papio* as the sister taxon of *Lophocebus* and *Macaca*.

5.3.14.3. Test result

Hypothesis 3 was not supported by the test. The criterion that both analyses should favour cladograms that are compatible with the papionin consensus molecular cladogram for one sex but not the other, was not fulfilled. None of the favoured cladograms was compatible with the papionin consensus molecular cladogram.

5.3.15. BOOTSTRAP-BASED TEST OF HYPOTHESIS 3 USING MANDIBLE AND LOWER DENTITION CHARACTERS FROM DATASET A

This test comprised four analyses (KKK-NNN). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 75. The hypothesis was considered supported if the analyses consistently favoured clades of the hominoid consensus molecular cladogram for one sex but not the other. A molecular clade was considered favoured if it was supported by 70% or more of the bootstrap replications and there was no better supported non-molecular clade.

5.2.15.1. Analysis KKK

Two clades were recovered from the male mandible data in Analysis KKK. One suggested that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (100%),

and the other implied that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Homo* or *Pan* (100%). Two clades were also recovered from the female mandible data in Analysis KKK. Again, one indicated that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (100%), and the other indicated that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Homo* or *Pan* (100%).

5.2.15.2. Analysis LLL

One clade was recovered from the male mandible data in Analysis LLL. It suggested that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (89%). One clade was also recovered from the female mandible data in Analysis LLL. Again, it indicated that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (92%).

5.2.15.3. Analysis MMM

One clade was recovered from the male mandible and lower dentition data in Analysis MMM. It suggested that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (97%). Analysis MMM identified two clades for the female mandible and lower dentition characters. One suggested that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (99%), and the other indicated that *Pan* and *Pongo* are more closely related to one another than either of them is to *Gorilla* or *Homo* (94%).

5.2.15.4. Analysis NNN

One clade was retrieved from the male taxa in Analysis NNN. It suggested that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (85%). Analysis NNN identified two clades for the female mandible characters. One implied that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (96%); the other suggested that *Pan* and *Pongo* are more closely related to one another than either of them is to *Gorilla* or *Homo* (84%).

5.2.15.5. Test result

The test did not support Hypothesis 3. The criterion that the analyses should consistently favour clades of the hominoid consensus molecular cladogram for one sex but not the other, was not met. None of the clades recovered was compatible with the consensus molecular assessment of inter-hominoid affinities.

5.3.16. BOOTSTRAP-BASED TEST OF HYPOTHESIS 3 USING MANDIBLE AND LOWER DENTITION CHARACTERS FROM DATASET B

The test comprised two analyses (50 and 51). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 76. The hypothesis was considered supported if both analyses favoured clades of the papionin consensus molecular cladogram for one sex but not the other. A molecular clade was considered favoured if it was sup-

ported by 70% or more of the bootstrap replications and there was no better supported non-molecular clade.

5.3.16.1 Analysis 50

Two clades were obtained from the male mandible and lower dentition characters in Analysis 50, neither of which was among those that comprise the papionin molecular cladogram. One suggested that *Lophocebus*, *Mandrillus* and *Papio* are more closely related to one another than any of them is to *Cercocebus*, *Macaca* or *Theropithecus* (77%), and the other indicated that *Lophocebus* and *Mandrillus* are more closely related to one another than either of them is to *Cercocebus*, *Macaca*, *Papio* or *Theropithecus* (70%). No clades were recovered from the female mandible and lower dentition character group in Analysis 50.

5.3.16.2 Analysis 51

No clades were recovered from the male mandible and lower dentition character group in Analysis 51. One clade was retrieved from the female mandible and lower dentition characters in Analysis 51. It grouped *Lophocebus* and *Macaca* together to the exclusion of *Cercocebus*, *Mandrillus*, *Papio* and *Theropithecus* (94%).

5.3.16.3 Test result

The test did not support Hypothesis 3. The criterion that the analyses should both favour clades of the papionin consensus molecular cladogram for one sex but not from the other, was not met. None

of the clades recovered was compatible with the consensus molecular estimate of interpapionin relationships.

5.3.17. CONSISTENCY INDEX-BASED TEST OF HYPOTHESIS 3 USING MANDIBLE AND LOWER DENTITION CHARACTERS FROM DATASET A

This test consisted of four analyses (OOO-RRR). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 77. The hypothesis was considered supported if the CIs of the consensus molecular cladograms for one sex were consistently higher than the CIs of the consensus molecular cladograms for the other sex. The condition 'consistently favoured' was attached to the tests because cladistic programs can generate cladograms and clades from random data (Smith, 1994), and because it is reasonable to assume that if a data set contains a strong phylogenetic signal, the signal should be identified regardless of which outgroups, size-adjustment techniques and coding procedures are used (see Sokal, 1985).

5.3.17.1 Analysis OOO

In Analysis OOO, the female consensus molecular cladogram had a higher consistency index (0.680) than the male consensus molecular cladogram (0.673).

5.3.17.2 Analysis PPP

In Analysis PPP, the female consensus molecular cladogram had a higher consistency index (0.609) than the male consensus molecular cladogram (0.556).

5.3.17.3 Analysis QQQ

In Analysis QQQ, the consistency index of the female consensus molecular cladogram was higher (0.699) than the consistency index of the male consensus molecular cladogram (0.640).

5.3.17.4 Analysis RRR

In Analysis RRR, the male consensus molecular cladogram had a higher consistency index (0.713) than the female consensus molecular cladogram (0.685).

5.3.17.5 Test result

The test did not uphold Hypothesis 3. The criterion that the CIs of the consensus molecular cladograms for one sex should be consistently higher than the CIs of the consensus molecular cladograms for the other sex, was not fulfilled. The female cladogram had a higher consistency index than the male cladogram in three of the four analyses, but in the other analysis the male cladogram had a higher consistency index than the female cladogram.

5.3.18. CONSISTENCY INDEX-BASED TEST OF HYPOTHESIS 3 USING MANDIBLE AND LOWER DENTITION CHARACTERS FROM DATASET B

This test consisted of two analyses (52 and 53). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 78. The hypothesis

was considered supported if the CIs of the consensus molecular cladograms for one sex were both higher than the CIs of the consensus molecular cladograms for the other sex.

5.3.18.1 Analysis 52

In Analysis 52, the male consensus molecular cladogram had a higher consistency index (0.581) than the female consensus molecular cladogram (0.570).

5.3.18.2. Analysis 53

In Analysis 53, the male consensus molecular cladogram had a higher consistency index (0.595) than the female consensus molecular cladogram (0.520).

5.3.18.3. Test result

The test supported Hypothesis 3. The criterion that the CIs of the consensus molecular cladograms for one sex should both be higher than the CIs of the consensus molecular cladograms for the other sex, was fulfilled. The male cladogram had a higher consistency index than the female cladogram in both analyses.

5.3.19. PARSIMONY-BASED TEST OF HYPOTHESIS 3 USING FACE CHARACTERS FROM DATASET A

This test comprised four analyses (SSS-VVV). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 79. The cladograms favoured in the analyses are presented in figures 83-85 and 96-98. The descriptive statistics associated with the cladograms are given in Table 80. The hypothesis was deemed supported if the analyses consistently favoured cladograms that were compatible with the hominoid consensus molecular cladogram for one sex but not the other.

5.3.19.1. Analysis SSS

A single most parsimonious cladogram was recovered from the male data in Analysis SSS (Figure 83). It positioned *Homo* as the sister taxon of a (*Gorilla*, *Pan*, *Pongo*) clade, and *Pan* as the sister taxon of a (*Gorilla*, *Pongo*) clade. One most parsimonious cladogram was also retrieved from the female characters in Analysis SSS (Figure 96). It located *Homo* as the sister taxon of a (*Gorilla*, *Pan*, *Pongo*) clade, and *Pongo* as the sister taxon of a (*Gorilla*, *Pan*) clade.

5.3.19.2. Analysis TTT

A single most parsimonious cladogram was recovered from the male taxa in Analysis TTT (Figure 83). It positioned *Homo* as the sister taxon of a (*Gorilla*, *Pan*, *Pongo*) clade, and *Pongo* as the sister taxon of a (*Gorilla*, *Pan*) clade. Analysis TTT produced one most parsimonious arrangement for the female data (Figure 97). It had the same topology as the molecular cladogram.

5.3.19.3. Analysis UUU

One most parsimonious cladogram was recovered for the male taxa in Analysis UUU (Figure 83). It located *Homo* as the sister taxon of a (*Gorilla*, *Pan*, *Pongo*) clade, and *Pongo* as the sister taxon of a (*Gorilla*, *Pan*) clade. Three equally parsimonious solutions were retrieved for the female taxa in Analysis UUU. The first (Figure 84) had the same branching pattern as the male cladogram. The second positioned *Homo* as the sister taxon of a (*Gorilla*, *Pan*, *Pongo*) clade, and *Gorilla* as the sister taxon of a (*Pongo*, *Pan*) clade (Figure 85). The third cladogram located *Pongo* as the sister taxon of a (*Gorilla*, *Homo*, *Pan*) clade, and *Homo* as the sister taxon of a (*Gorilla*, *Pan*) clade (Figure 98). The strict consensus of the cladograms had no ingroup structure.

5.3.19.4. Analysis VVV

One most parsimonious cladogram was recovered from the male data in Analysis VVV (Figure 83). It located *Homo* as the sister taxon of a (*Gorilla*, *Pan*, *Pongo*) clade, and *Pongo* as the sister taxon of a (*Gorilla*, *Pan*) clade. A single cladogram was also recovered from the female data in Analysis VVV (Figures 96). Again, it was incompatible with the molecular cladogram, suggesting that *Homo* is the sister taxon of a (*Gorilla*, *Pan*, *Pongo*) clade, and *Pongo* the sister taxon of a (*Gorilla*, *Pan*) clade.

5.3.19.5. Test result

The test did not support Hypothesis 3. The criterion that the analyses should consistently favour cladograms that were compatible with the hominoid consensus molecular cladogram for one sex but not the other, was not fulfilled. None of the most parsimonious cladograms recovered had the same branching pattern as the hominoid consensus molecular cladogram.

5.3.20. PARSIMONY-BASED TEST OF HYPOTHESIS 3 USING FACE CHARACTERS FROM DATASET B

The test comprised two analyses (54 and 55). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 81. The cladograms favoured in the analyses are presented in figures 99-103. The descriptive statistics associated with the cladograms are given in Table 82. The hypothesis was deemed supported if both analyses favoured cladograms that were compatible with the papionin consensus molecular cladogram for one sex but not the other.

5.3.20.1. Analysis 54

A single most parsimonious cladogram was identified for the male taxa in Analysis 54 (Figure 99). It linked *Mandrillus* and *Papio* together in a clade, placed *Theropithecus* as their sister taxon, and positioned *Cercocebus* as the sister taxon of the (*Mandrillus*, *Papio*, *Theropithecus*) clade. It also suggested that *Macaca* is the sister taxon of the (*Cercocebus*, *Mandrillus*, *Papio*, *Theropithecus*) clade, and that *Lophocebus* is the basal papionin.

Two equally parsimonious cladograms were recovered from the female data in Analysis 54. The first (Figure 100) suggested that the initial branching event separated *Lophocebus* from the common ancestor of *Cercocebus*, *Macaca*, *Mandrillus*, *Papio* and *Theropithecus*. The next branching event isolated the common ancestor of a clade comprising *Cercocebus* and *Macaca* from the common ancestor of a clade comprising the three baboon taxa, *Mandrillus*, *Papio* and *Theropithecus*. The last cladistically-significant branching event separated *Theropithecus* from the common ancestor of *Mandrillus* and *Papio*. The second female cladogram (Figure 101) had the same branching pattern as the first cladogram except that *Macaca* appeared as the sister taxon of the baboon clade, and *Cercocebus* was positioned as the sister group of *Macaca* and the three baboon genera. The strict consensus of the cladograms was incompatible with the consensus molecular cladogram. It suggested that the initial branching event separated *Lophocebus* from the common ancestor of *Cercocebus*, *Macaca*, *Mandrillus*, *Papio* and *Theropithecus*. Thereafter, it posited a trichotomous relationship between *Cercocebus*, *Macaca* and a clade comprising the baboon genera.

5.3.20.2. Analysis 55

Analysis 55 yielded a single most parsimonious cladogram for the male taxa, which was not compatible with the papionin molecular cladogram (Figure 102). It positioned *Mandrillus* as the basal ingroup taxon, *Papio* as the sister taxon of a (*Cercocebus*, *Lophocebus*, *Macaca*, *Theropithecus*) clade, *Theropithecus* as the sister taxon of a (*Cercocebus*, *Lophocebus*, *Macaca*) clade, and *Cercocebus* as the sister taxon of a (*Lophocebus*, *Macaca*) clade. A single most parsimonious cladogram was also recovered from the female taxa in Analysis 55 (Figure 103). Its branching pattern differed from that of the molecular cladogram. *Theropithecus* was located as the basal ingroup taxon,

Papio as the sister taxon of a (*Cercocebus*, *Lophocebus*, *Macaca*, *Mandrillus*) clade, and *Mandrillus* as the sister taxon of a (*Cercocebus*, *Lophocebus*, *Macaca*) clade. Within the (*Cercocebus*, *Lophocebus*, *Macaca*) clade, *Lophocebus* appeared as the sister taxon of *Cercocebus* and *Macaca*.

5.3.20.3. Test result

The test did not support Hypothesis 3. The criterion that both analyses should favour cladograms that were compatible with the papionin consensus molecular cladogram for one sex but not the other, was not fulfilled. None of the favoured cladograms were compatible with the biomolecular cladogram for the Papionini.

5.3.21. BOOTSTRAP-BASED TEST OF HYPOTHESIS 3 USING FACE CHARACTERS FROM DATASET A

This test comprised four analyses (WWW-ZZZ). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 83. The hypothesis was considered supported if the analyses consistently favoured clades of the hominoid consensus molecular cladogram for one sex but not the other. A molecular clade was considered favoured if it was supported by 70% or more of the bootstrap replications and there was no better supported non-molecular clade.

5.3.21.1. Analysis WWW

Analysis WWW identified two clades for the male face characters, neither of which was compatible with the hominoid biomolecular cladogram. One suggested that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (87%), and the other indicated that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Gorilla* or *Homo* (87%). No ≥70% clades were recovered for the female face data in Analysis WWW.

5.3.21.2. Analysis XXX

Analysis XXX identified one clade for the male face characters. It suggested that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (94%). No ≥70% clades were recovered for the female face data in Analysis XXX.

5.3.21.3. Analysis YYY

Analysis YYY identified one clade for the male face characters, which was incompatible with the hominoid molecular cladogram. It suggested that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (99%). No clades were recovered for the female face data in Analysis YYY.

5.3.21.4. Analysis ZZZ

Two clades were identified for the male face characters in Analysis ZZZ. Neither clade was compatible with the molecular cladogram for the Hominoidea. One suggested that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (100%), while the other indicated that *Pan* and *Pongo* are more closely related to one another than either of them is to *Gorilla* or *Homo* (97%). No clades were recovered for the female face data in Analysis ZZZ.

5.3.21.5. Test result

Hypothesis 3 was not supported by the test. The criterion that the analyses should consistently favour clades of the hominoid consensus molecular cladogram for one sex but not the other, was not fulfilled. None of the clades recovered was compatible with the consensus molecular cladogram for the Hominoidea.

5.3.22. BOOTSTRAP-BASED TEST OF HYPOTHESIS 3 USING FACE CHARACTERS FROM DATATSET B

This test comprised two analyses (56 and 57). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 84. The hypothesis was considered supported if both analyses favoured clades of the papionin consensus molecular cladogram for one sex but not the other. As with the previous analysis, a molecular clade was considered favoured if it was supported by 70% or more of the bootstrap replications and there was no better supported non-molecular clade.

5.3.22.1. Analysis 56

Three clades were recovered from the male data in Analysis 56, none of which was compatible with the papionin molecular cladogram. The first suggested that *Cercocebus*, *Macaca* and the three baboon genera, *Mandrillus*, *Papio* and *Theropithecus*, are more closely related to one another than any of them is to *Lophocebus* (85%). The second indicated that the three baboon genera form clade to the exclusion of the other taxa in the sample (82%). The third implied that *Mandrillus* and *Papio* share a common ancestor not shared by *Cercocebus*, *Lophocebus*, *Macaca* or *Theropithecus* (94%). No clades were retrieved from the female characters in Analysis 56.

5.3.22.2. Analysis 57

Two clades were identified for the male face characters in Analysis 57, neither of which matched those that comprise the molecular cladogram. One suggested that *Cercocebus*, *Lophocebus* and *Macaca* are more closely related to one another than any of them is to *Mandrillus*, *Papio*, *Theropithecus* (94%). The other indicated that *Lophocebus* and *Macaca* are more closely related to one another than either of them is to *Cercocebus*, *Mandrillus*, *Papio* or *Theropithecus* (90%). Four clades were recovered from the female face character group in Analysis 57. None of them was compatible with the molecular cladogram. The first comprised *Cercocebus*, *Lophocebus*, *Macaca*, *Mandrillus* and *Papio* (72%), the second *Cercocebus*, *Lophocebus*, *Macaca* and *Mandrillus* (94%), the third *Cercocebus*, *Lophocebus* and *Macaca* (78%), and the fourth comprised *Cercocebus* and *Macaca* (86%).

5.3.22.3. Test result

Hypothesis 3 was not supported by the Dataset B 'face' bootstrap-based test. The criterion that the analyses should both favour clades of the papionin consensus molecular clade for one sex but not the other, was not fulfilled. None of the clades recovered was compatible with the molecular estimate of interpapionin affinities.

5.3.23. CONSISTENCY INDEX-TEST OF HYPOTHESIS 3 USING FACE CHARACTERS FROM DATASET A

This test comprised four analyses (AAAA-DDDD). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 85. The hypothesis was deemed supported if the CIs of the consensus molecular cladograms for one sex were consistently higher than the CIs of the consensus molecular cladograms for the other sex.

5,3.23.1. Analysis AAAA

In Analysis AAAA, the CI for the female consensus molecular cladogram was higher (0.744) than the CI of the male consensus molecular cladogram (0.707).

5,3.23.2. Analysis BBBB

In Analysis BBBB, the CI for the female consensus molecular cladogram (0.688) was higher than the CI for the male consensus molecular cladogram (0.609).

5,3.23.3. Analysis CCCC

In Analysis CCCC, the female consensus molecular cladogram had a higher CI (0.771) than the male consensus molecular cladogram (0.667).

5.3.23.4. Analysis DDDD

In Analysis DDDD, the female consensus molecular cladogram had a higher CI (0.755) than the male consensus molecular cladogram (0.667).

5.3.23.5. Test result

The test supported Hypothesis 3. The criterion that the CIs of the consensus molecular cladograms for one sex should be consistently higher than the CIs of the consensus molecular cladograms for other sex, was met. The female cladogram had a higher consistency index than the male cladogram in all the analyses.

5.3.24. CONSISTENCY INDEX-BASED TEST OF HYPOTHESIS 3 USING FACE CHARACTERS FROM DATASET B

This test comprised two analyses (58 and 59). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 86. The hypothesis was deemed supported if the CIs of the consensus molecular cladograms for one sex were both higher than the CIs of the consensus molecular cladograms for the other sex.

5.3.24.1. Analysis 58

In Analysis 58, the consistency index of the consensus molecular cladogram for the male taxa (0.584) was higher than the consistency index of the female consensus molecular cladogram (0.569).

5.3.24.2. Analysis 59

In Analysis 59, the CI of the female consensus molecular cladogram (0.585) was higher than that of the male consensus molecular cladogram (0.556).

5.3.24.3. Test result

The test did not support Hypothesis 3. The criterion that the CIs of the consensus molecular cladograms for one sex should both be higher than the CIs of the consensus molecular cladograms for the other sex, was not fulfilled. The male cladogram had a higher consistency index than the female

cladogram in one analysis, but the female cladogram had a higher consistency index than the male cladogram in the other analysis.

5.3.25. PARSIMONY-BASED TEST OF HYPOTHESIS 3 USING CRANIAL VAULT AND BASE CHARACTERS FROM DATASET A

The tests consisted of four analyses (EEEE-HHHH). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 87. The cladograms favoured in the analyses are presented in figures 83 and 104-107. The descriptive statistics associated with the cladograms are given in Table 88. The hypothesis was deemed supported if the analyses consistently favoured cladograms that were compatible with the hominoid consensus molecular cladogram for one sex but not the other. The condition 'consistently favoured' was attached to the tests because cladistic programs can generate cladograms from random data (Smith, 1994), and because it is reasonable to assume that if a data set contains a strong phylogenetic signal, the signal should be identified regardless of which outgroups, size-adjustment techniques and coding procedures are used (see Sokal, 1985).

5.3.25.1. Analysis EEEE

Analysis EEEE yielded one most parsimonious cladogram for the male data (Figure 104). The branching pattern of this cladogram differed from that of the molecular cladogram for the Hominoidea. It positioned *Pan* as the sister taxon of a (*Gorilla*, *Homo*, *Pongo*) clade, and *Pongo* as the sister taxon of a (*Gorilla*, *Homo*) clade. A single most parsimonious cladogram was also recovered from the female taxa in Analysis EEEE. This too was not compatible with the hominoid molecular clado-

gram (Figure 105). It located *Pongo* as the sister group of a (*Gorilla*, *Homo*, *Pan*) clade, and *Pan* as the sister taxon of a (*Gorilla*, *Homo*) clade.

5.3.25.2. Analysis FFFF

One most parsimonious cladogram was recovered from the male data in Analysis FFFF (Figure 83). This cladogram was not compatible with the molecular cladogram. It positioned *Homo* as the sister taxon of a (*Gorilla*, *Pan*, *Pongo*) clade, and *Pan* as the sister taxon of a (*Gorilla*, *Pongo*) clade. A single most parsimonious cladogram was identified for the female data in Analysis FFFF (Figure 106). This cladogram was not compatible with the molecular cladogram. It located *Gorilla* as the sister taxon of a (*Homo*, *Pan*, *Pongo*) clade, and *Pongo* as the sister taxon of a (*Homo*, *Pan*) clade.

5.3.25.3. Analysis GGGG

One most parsimonious cladogram was recovered from the male data in Analysis GGGG (Figure 83). The topology of this cladogram differed from that of the hominoid molecular cladogram. *Homo* was located as the sister taxon of a (*Gorilla*, *Pan*, *Pongo*) clade, and *Pan* as the sister taxon of a (*Gorilla*, *Pongo*) clade. Two equally parsimonious solutions were favoured for the female data in Analysis GGGG (figures 106 and 107). The branching patterns of these cladograms differed from that of the hominoid molecular cladogram. One suggested that the initial branching event in the evolution of the hominoid taxa separated *Gorilla* from the common ancestor of *Homo*, *Pan* and *Pongo*, and that the second branching event separated *Pongo* from the common ancestor of *Homo* and *Pan*. The other cladogram posited a single branching event that separated the common ancestor of *Gorilla* and *Pongo* from the common ancestor of *Homo* and *Pan*. The strict consensus of the cla-

dograms contained one clade that was compatible with the hominoid consensus molecular cladogram. This comprised *Homo* and *Pan*.

5.3.25.4. Analysis HHHH

One most parsimonious cladogram was obtained for the male data in Analysis HHHH (Figure 83). The topology of this cladogram differed from that of the hominoid molecular cladogram. *Homo* appeared as the sister taxon of a (*Gorilla*, *Pan*, *Pongo*) clade, and *Pan* was shown as the sister taxon of a (*Gorilla*, *Pongo*) clade. A single most parsimonious cladogram was also recovered for the female taxa in Analysis HHHH (Figure 84). Again, this cladogram was incompatible with the molecular cladogram, positioning *Homo* as the sister taxon of a (*Gorilla*, *Pan*, *Pongo*) clade and *Pan* as the sister taxon of a (*Gorilla*, *Pongo*) clade.

5.3.25.5. Test result

The parsimony-based test in which most parsimonious cladograms were identified for the cranial vault and base characters in Dataset A did not support Hypothesis 3. The criterion that the analyses should consistently favour cladograms that were compatible with the hominoid consensus molecular cladogram for one sex but not the other, was not fulfilled. One of the female cladograms was compatible with the consensus molecular cladogram for the hominoids, but the other female cladograms were incompatible with it. None of the male cladograms were compatible with the hominoid consensus molecular cladogram.

5.3.26. PARSIMONY-BASED TEST OF HYPOTHESIS 3 USING CRANIAL VAULT AND BASE CHARACTERS FROM DATASET B

This test comprised two analyses (60 and 61). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 89. The cladograms favoured in the analyses are presented in figures 108-110. The descriptive statistics associated with the cladograms are given in Table 90. The hypothesis was deemed supported if both analyses favoured cladograms that were compatible with the papionin consensus molecular cladogram for one sex but not the other.

5.3.26.1. Analysis 60

One most parsimonious cladogram was obtained for the male taxa in Analysis 60 (Figure 108). It linked *Cercocebus* and *Lophocebus* together as a monophyletic group, and suggested that they formed the sister taxon of a clade comprising *Macaca*, *Mandrillus*, *Papio*, and *Theropithecus*. Within the latter clade, the *Mandrillus*, *Papio*, and *Theropithecus* formed a clade separate from *Macaca*, and *Mandrillus* and *Papio* were hypothesized to be more closely related to one another than either is to *Theropithecus*. Analysis 60 also yielded a single most parsimonious cladogram for the female data (Figure 109). It was topologically identical to the male cladogram except that it posited a sister group relationship between *Papio* and *Theropithecus* within the baboon clade, rather than one between *Mandrillus* and *Papio*.

5.3.26.2. Analysis 61

One most parsimonious cladogram was obtained for the male taxa in Analysis 61 (Figure 108). It divided the ingroup taxa into a (*Cercocebus*, *Lophocebus*) clade, and a (*Macaca*, *Mandrillus*, *Papio*, *Theropithecus*) clade. Within the latter clade, *Macaca* was positioned as the sister group of the three baboon taxa, and *Theropithecus* as the sister group of *Mandrillus* and *Papio*. A single most parsimonious cladogram was also recovered for the female data in Analysis 61 (Figure 110). It divided the ingroup taxa into a (*Papio*, *Theropithecus*) clade, and a (*Cercocebus*, *Lophocebus*, *Macaca*, *Mandrillus*) clade. Within the latter clade, *Mandrillus* was positioned as the sister taxon of a (*Cercocebus*, *Lophocebus*, *Macaca*) clade, and *Cercocebus* as the sister taxon of a (*Lophocebus*, *Macaca*) clade.

5.3.26.3. Test result

Hypothesis 3 was not supported by the test. The criterion that both analyses should favour cladograms that were compatible with the papionin consensus molecular cladogram for one sex but not the other, was not fulfilled. All the favoured cladograms differed from the papionin consensus molecular cladogram.

5.3.27. BOOTSTRAP-BASED TEST OF HYPOTHESIS 3 USING CRANIAL VAULT AND BASE CHARACTERS FROM DATASET A

The test comprised four analyses (IIII-LLLL). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 91. The hypothesis

was considered supported if the analyses consistently favoured clades of the hominoid consensus molecular cladogram for one sex but not the other. A molecular clade was considered favoured if it was supported by 70% or more of the bootstrap replications and there was no better supported non-molecular clade.

5.3.27.1. Analysis IIII

Two clades were identified for the male vault characters in Analysis IIII. One suggested that *Gorilla*, *Homo* and *Pongo* are more closely related to one another than any of them is to *Pan* (73%), and the other indicated that *Gorilla* and *Homo* are more closely related to one another than either of them is to *Gorilla* or *Homo* (89%). One clade was recovered from the female vault data in Analysis IIII. This clade did not agree with the molecular cladogram for the hominoids. It suggested that *Gorilla* and *Homo* are more closely related to one another than any of them is to *Pan* or *Pongo* (83%).

5.3.27.2. Analysis JJJJ

Analysis JJJJ yielded two clades for the male vault characters. Both clades were incompatible with the hominoid molecular cladogram. One suggested that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (82%), and the other indicated that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Gorilla*, *Homo* (95%). No clades were recovered for the female vault data in Analysis JJJJ.

5.3.27.3. Analysis KKKK

Two clades were identified for the male vault characters in Analysis KKKK, neither of which was compatible with the molecular cladogram for the Hominoidea. One suggested that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (99%), and the other indicated that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Gorilla* or *Homo* (100%). No clades were recovered for the female vault data in Analysis KKKK.

5.3.27.4. Analysis LLLL

Two clades were identified for the male vault characters in Analysis LLLL. Neither of the clades matched those that comprise the hominoid molecular cladogram. One suggested that *Gorilla*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Homo* (100%), and the other indicated that *Gorilla* and *Pongo* are more closely related to one another than either of them is to *Gorilla* or *Homo*. No clades were recovered for the female vault data in Analysis LLLL.

5.3.27.5. Test result

The test did not support Hypothesis 3. The criterion that the analyses should consistently favour clades of the hominoid consensus molecular cladogram for one sex but not the other, was not fulfilled. None of the clades recovered was compatible with the consensus molecular estimate of interhominoid affinities.

5.3.28. BOOTSTRAP-BASED TEST OF HYPOTHESIS 3 USING CRANIAL VAULT AND BASE CHARACTERS FROM DATASET B

The test comprised two analyses (62 and 63). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 92. The hypothesis was considered supported if both analyses favoured clades of the papionin consensus molecular cladogram for one sex but not the other. A molecular clade was considered favoured if it was supported by 70% or more of the bootstrap replications and there was no better supported non-molecular clade.

5.3.28.1. Analysis 62

Analysis 62 identified three clades for the male vault data, none of which was compatible with the relationships suggested by the molecular evidence. The first suggested that *Macaca* and the three baboon genera, *Mandrillus*, *Papio* and *Theropithecus*, are more closely related to one another than any of them is to *Cercocebus* or *Lophocebus* (78%). The second indicated that the three baboon genera share a common ancestor not shared by the other taxa in the sample (98%). The third implied that *Mandrillus* and *Papio* form a clade to the exclusion of the *Cercocebus*, *Lophocebus*, *Macaca* or *Theropithecus* (98%). The female vault data yielded one clade in Analysis 62. This clade was compatible with the molecular cladogram for the Papionini. It suggested that *Papio* and *Theropithecus* are more closely related to one another than either is to any other taxon in the sample (93%).

5.3.28.2. Analysis 63

Two clades were recovered from the male vault characters in Analysis 63, neither of which was compatible with the biomolecular estimate of interpapionin affinities. One suggested that the three baboon genera, *Mandrillus*, *Papio* and *Theropithecus*, share a common ancestor not shared by the mangabeys and macaques (88%). The other indicated that *Mandrillus* and *Papio* are more closely related to one another than either of them is to *Cercocebus*, *Lophocebus*, *Macaca* or *Theropithecus* (89%).

The female vault data yielded four clades in Analysis 63. Three of the clades were incompatible with the papionin molecular cladogram. The first suggested that *Cercocebus*, *Lophocebus*, *Macaca* and *Mandrillus* are more closely related to one another than any of them is to *Papio* or *Theropithecus* (83%). The second indicated that *Cercocebus*, *Lophocebus* and *Macaca* share a common ancestor not shared by *Mandrillus*, *Papio* or *Theropithecus* (74%). The third suggested that *Lophocebus* and *Macaca* form a clade to the exclusion of the other taxa in the sample (76%). The fourth clade was compatible with the biomolecular cladogram, and indicated that *Papio* and *Theropithecus* are more closely related to one another than either is to *Cercocebus*, *Lophocebus*, *Macaca* or *Mandrillus* (93%).

5.3.28.3. Test result

The test supported Hypothesis 3. The criterion that both analyses should favour clades of the papionin consensus molecular cladogram for one sex but not the other, was fulfilled. The (*Papio*, *Theropithecus*) clade of the consensus molecular cladogram was recovered from the female vault

data in both analyses, while all the clades recovered from the male data were incompatible with the relationships suggested by the biomolecular evidence.

5.3.29. CONSISTENCY INDEX-BASED TEST OF HYPOTHESIS 3 USING DATASET A CRANIAL VAULT AND BASE CHARACTERS

This test consisted of four analyses (MMMM-QQQQ). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 93. The hypothesis was considered supported if the CIs of the consensus molecular cladograms for one sex were consistently higher than the CIs of the consensus molecular cladograms for the other sex, was fulfilled.

5.3.29.1. Analysis MMMM

In Analysis MMMM, the CI for the male consensus molecular cladogram (0.696) was lower than the CI for the female consensus molecular cladogram (0.725).

5.3.29.2. Analysis NNNN

In Analysis NNNN, the consistency index recorded for the female consensus molecular cladogram (0.667) was higher than the consistency index recorded for the male consensus molecular cladogram (0.615).

5.3.29.3. Analysis OOOO

In Analysis OOOO, the consistency index for the consensus molecular cladogram based on the female data (0.766) was higher than that (0.642) for the male consensus molecular cladogram.

5.3.29.4. Analysis PPPP

In Analysis PPPP, the consistency index recorded for the female consensus molecular cladogram was higher (0.725) than the consistency index (0.721) for the male consensus molecular cladogram.

5.3.29.5. Test result

Hypothesis 3 was supported by the test. The criterion that the CIs of the consensus molecular cladograms for one sex should be consistently higher than the CIs of the consensus molecular cladograms for the other sex, was fulfilled. The female cladogram had a higher consistency index than the male cladogram in all the analyses.

5.3.30. CONSISTENCY-INDEX TEST OF HYPOTHESIS 3 USING DATASET B CRANIAL VAULT AND BASE CHARACTERS

This test consisted of two analyses (64 and 65). The variables, ingroups, outgroups, size-adjustment techniques and coding procedures used in the analyses are summarized in Table 94. The hypothesis was considered supported if the CIs of the consensus molecular cladograms for one sex were both higher than the CIs of the consensus molecular cladograms for the other sex, was fulfilled.

5.3.30.1 Analysis 64

In Analysis 64, the consistency index for the consensus molecular cladogram based on the female data (0.620) was higher than the consistency index for the male consensus molecular cladogram (0.565).

5.3.30.2. Analysis 65

In Analysis 65, the consistency index for the female consensus molecular cladogram (0.593) was higher than the consistency index for the male consensus molecular cladogram (0.560).

5.3.30.3. Test result

The test supported Hypothesis 3. The criterion that the CIs of the consensus molecular cladograms for one sex should both be higher than the CIs of the consensus molecular cladograms for the other sex, was fulfilled. The female cladogram had a higher consistency index than the male cladogram in both analyses.

CHAPTER 6. DISCUSSION AND CONCLUSIONS

The present study tested the hypothesis that standard cranial and dental characters are reliable for reconstructing the cladistic relationships between primate species and genera. It also tested two secondary hypotheses. The first was that some regions of the primate cranium are more reliable than others for reconstructing the cladistic relationships between species and genera. The second was that male and female primate crania differ in their reliability for reconstructing the cladistic relationships between species and genera. In this chapter, the results of the tests of these hypotheses are summarized (see also tables 95-97). Thereafter, the reliability of the results is assessed, and the implications of the results for current understanding of the phylogenetic relationships of the early hominids and other fossil primates discussed. Lastly, the conclusions of the study of the study are set out.

6.1. SUMMARY OF RESULTS

6.1.1. Hypothesis 1 tests

Neither the Dataset A parsimony-based test nor the Dataset B parsimony-based test supported the hypothesis that standard cranial and dental characters are reliable for reconstructing the cladistic relationships between primate species and genera. The criterion that the analyses should consistently favour cladograms that are compatible with the relevant consensus molecular cladogram, was not fulfilled. None of the single most parsimonious or strict consensus cladograms favoured in the Dataset A parsimony analyses was compatible with the hominoid consensus molecular cladogram. Likewise, none of the most parsimonious or strict consensus cladograms recovered

from Dataset B was compatible with the cladogram supported by the majority of the papionin biomolecular data.

Hypothesis 1 was also not supported by either of the compatibility-based tests. The criterion that cladograms compatible with the relevant consensus molecular cladogram should be consistently favoured, was not fulfilled. Neither of the cladograms favoured in the Dataset A analyses had the same branching pattern as the molecular cladogram for the Hominoidea. Similarly. neither of the cladograms favoured in the Dataset B analyses was compatible with the consensus molecular cladogram for the papionins.

Lastly, neither of the bootstrap-based tests supported Hypothesis 1. The criterion that clades of the appropriate consensus molecular cladogram should be consistently favoured by 70% or more of the bootstrap replications and there should not be a better supported non-molecular clade, was not met. None of the clades recovered in the Dataset A analyses was compatible with the hominoid relationships suggested by the majority of the molecular evidence, and none of the clades recovered in the Dataset B analyses was compatible with the consensus molecular cladogram for the papionins.

6.1.2. Hypothesis 2 tests

The hypothesis that some regions of the primate cranium are more reliable than others for reconstructing the cladistic relationships between species and genera was not supported by either of the parsimony-based tests. The criterion that the analyses should favour the appropriate consensus molecular cladogram for some but not all the cranial regions, was not met. None of the cladograms supported by the Dataset A regional analyses had the same branching pattern as the

hominoid consensus molecular cladogram, and none of the cladograms recovered from the Data-set B regions had the same topology as the papionin consensus molecular cladogram.

The bootstrap-based tests also did not uphold Hypothesis 2. The criterion that, in all the analyses, some but not all of the regions should favour a clade of the appropriate consensus molecular cladogram and there should not be a better supported non-molecular clade, was not fulfilled. The (*Homo*, *Pan*) clade of the hominoid consensus molecular cladogram was recovered from the palate and mandible character groups in one analysis, but, in each case, there was a better supported non-molecular clade. None of the other hominoid analyses favoured molecular clades. None of the 35 clades recovered was compatible with the biomolecular estimate of interpapionin affinities.

Lastly, Hypothesis 2 was not supported by either of the consistency index-based tests. The criterion that the analyses should support a consistent order among the consistency indices of the regional cladograms, was not fulfilled. Neither the analyses of Dataset A nor the analyses of Data-set B consistently supported a rank order among the regional CIs when the branching pattern of the appropriate consensus molecular cladogram was imposed on them.

6.1.3. Hypothesis 3 tests

The hypothesis that male and female primate crania differ in their reliability for reconstructing the cladistic relationships between species and genera was supported by the two consistency index-based tests in which all the characters were analyzed together. These tests indicated that the crania of female primates are slightly more reliable for reconstructing genus- or species-level cladistic relationships than the crania of male primates.

Hypothesis 3 was also supported by Dataset B consistency index-based test in which the characters from the mandible and lower dentition were analyzed separately, the Dataset A consistency index-based test in which the characters from the face were analyzed separately and the Dataset B bootstrap-based test in which the characters from cranial vault and base were analyzed separately. The two consistency index-based tests in which the characters from the vault and cranial base were analyzed separately also supported the hypothesis. These tests suggested that the mandible of male primates is less prone to homoplasy than the mandible of female primates, that the face of female primates is less prone to homoplasy than the face of male primates, and that the cranial vault and base of female primates are less prone to homoplasy than the cranial vault and base of male primates.

Hypothesis 3 was not supported by the two parsimony-based tests in which all the characters were analyzed together, or by the parsimony-based tests in which most parsimonious cladograms were computed for each of the regional character groups. Hypothesis 3 was also not supported by the bootstrap-based tests in which all the characters were analyzed together, or by the 'palate', 'mandible' and 'face' bootstrap-based tests. Additionally, the hypothesis received no support from the 'palate' consistency index-based tests, the Dataset A 'mandible' consistency-index based test, the Dataset B 'face' consistency index-based test, or the Dataset A 'vault' bootstrap-based test.

6.2. RELIABILITY OF RESULTS

Before concluding that hypotheses 1 and 2 are incorrect and that Hypothesis 3 is correct, several potential problems with the results have to be discounted. These are (1) craniometric data are unsuitable for cladistic analysis, (2) the wrong options were exercised during the construction of

the character state data matrices, (3) the outgroup taxa used skewed the results, (4) the consensus molecular cladograms against which the craniometric cladograms were judged are incorrect and (5) the test results are reliable but only in relation to the extant Hominoidea and Papionini.

6.2.1. Craniometric data and cladistics

Many authors (e.g. Pimentel and Riggins, 1987; Crisp and Weston, 1987; Cranston and Humphries, 1988; Crowe, 1994; Disotell, 1994; Moore, 1994) contend that only discrete characters (e.g. either a 'sagittal crest', or 'no sagittal crest') can be used in cladistic analyses. Continuous data, including those obtained from measurements, are rejected because such data are thought to be incapable of providing valid cladistic information (Rae, in press). Alternatively, continuous data are discounted because it is believed that converting continuous data into discrete states as required by most computer-based phylogeny reconstruction programs is an arbitrary process (Rae, in press).

Neither of these objections is valid, however. First, as Maddison et al. (1984), Felsenstein (1988), Swofford and Olsen (1990), Lieberman (1995) and, most especially, Rae (1993; in press) have pointed out, there is no intrinsic difference between discrete character state data and continuous data as far as the cladistic methodology is concerned. The only criterion a character must fulfil for use in a cladistic analysis is that its states are homologous, and measurement-based characters can meet this criterion as easily as discrete morphological characters (Rae, in press). Second, a number of the methods that have been developed to convert continuously distributed characters into discrete character states are based on statistical tests, and are therefore non-arbitrary (Rae, 1993; in press).

There are, in fact, several reasons why those attempting to reconstruct the phylogenetic relationships of fossil primates should prefer morphometric data over discrete character state data. One of the most important is that many so-called discrete morphological characters are in fact arbitrarily chosen divisions of a continuum, either in terms of gross morphology or at the developmental level (Bilsborough, 1986; Baum, 1988; Chappill, 1989; Trinkaus, 1990; 1992; Stevens, 1991; Stuessy, 1990; Thiele, 1993). The concomitant of this is that the assessment of discrete character states can be highly subjective. As several recent discrete character-based analyses of the Miocene hominoid *Afropithecus turkanensis* have indicated, one researcher's 'weakly-developed' inferior mandibular torus is another researcher's 'well-developed' inferior torus (Leakey and Leakey, 1986; Andrews and Martin, 1987; Conroy, 1994). In contrast, the landmarks on which measurements are based can be defined in such a way that the same value can be obtained regardless of who is collecting the data. Thus, measurement data are likely to be more accurate and reproducible than discrete character state data.

Another reason for preferring measurement data over discrete data is that the assessment of discrete character states cannot deal with the confounding effects of body size differences between taxa, whereas metric data can be adjusted to take such differences into account. This point is exemplified by Wood and colleagues' (submitted) assessment of the likelihood of association between OH 8 and OH 35, the *Homo habilis* left talus and distal left tibia from Olduvai Gorge, Tanzania. When Wood et al. did not correct for body size, they obtained the same result as had been obtained in earlier discrete character assessments: the talus and the tibia appeared to have belonged to the same individual. However, when they controlled for differences in body size, they found that it was statistically unlikely that the two bones had come from animals belonging to the same species, let alone the same individual.

6.2.2. Data matrix construction options

One of the principal options exercised during the construction of the character state data matrices concerned size adjustment. At the moment, there are two main approaches to the problem of adjusting morphometric data for the confounding effects of body size (Preuschoft, 1989). In the first, the specimen values or taxon means of each variable are divided by the body mass of the taxon or some other proxy of body size, such as skull size or femoral circumference (Creel, 1986; Martin and MacLarnon, 1988; Ruliang et al., 1991; Moore and Cherverud, 1992; Albrecht et al., 1993; Anthony and Kay, 1993). This 'geometric' or 'isometric' adjustment equalizes the volumes of the specimens or taxa while maintaining their original shapes (Creel, 1986; Jungers et al., 1995). In the second approach, regression equations based on a proxy of body size are used to transform each specimen value or taxon mean to the value it would be expected to have if the specimen or taxon was the same size as the average of all the specimens or taxa in the regression sample (Creel, 1986; Simmons et al., 1991; Jungers and Cole, 1992; Kidder et al., 1992; Falsetti et al., 1993; Grine et al., 1993; Richmond and Jungers et al., 1995; Wood, 1995). This 'allometric' adjustment corrects for both the size differences between the specimens or taxa and the shape differences associated with the size differences (Creel, 1986; Jungers et al., 1995).

Given that the three size-adjustment techniques used in the present study are all variants of the geometric approach, would the results of the analyses have been different if an allometric method had been employed instead? Two recent studies suggest that the answer to this question is 'no', at least in relation to the hominoid analyses. The first is Creel's (1986) 'Hominoid size and phylogeny'. In the opening section of this paper, Creel discussed the results of several parsimony analyses of craniometric data from single-sex samples of the extant hominoid genera. One of these analyses was based on female data that had been adjusted for the effects of body size using a geometric technique, while another was based on female data that had been size-adjusted using

an allometric technique. According to Creel, the most parsimonious cladograms recovered in these analyses were "so similar that all conclusions apply equally well to either data set" (Creel, 1986: 85). The second study which suggests that the hominoid results would not have been different if an allometric method of size-adjustment had been used is Singleton's (1996) 'Quantitative character coding in hominoid phylogeny reconstruction'. Among other things, Singleton compared the effects of different size-adjustment and coding methods on the results of cladistic analyses of hominoid craniometric data. Like Creel (1986), she found that the cladograms favoured in the analyses in which the data were geometrically-adjusted were "roughly congruent" with the most parsimonious cladograms obtained in the analyses in which the data were adjusted allometrically (Singleton, 1996: 3).

It is possible that an allometric size-adjustment technique would have produced more accurate results in the papionin analyses. However, the large number of cladogram topologies favoured in the parsimony analyses of Dataset B that were carried out to test Hypothesis 1 suggest that this is unlikely. If size-related shape changes were responsible for the failure of nine analyses to support the papionin consensus molecular cladogram, one would have expected the analyses to have agreed on a branching pattern for *Cercocebus*, *Lophocebus*, *Macaca*, *Mandrillus*, *Papio* and *Theropithecus*, whereas the analyses actually yielded seven different most parsimonious branching patterns for the taxa.

The other main option exercised in the compilation of the matrices involved the discrete coding of the continuous characters. Currently, there are several alternatives to the three coding procedures used in the present study, the most popular of which are gap coding, homogeneous subset coding, generalized gap coding and gap weighting. There are, however, a number of reasons to doubt that the alternative methods would have given better results than those obtained using segment coding, Baum's method and divergence coding. First, divergence coding, homogeneous

subset coding and generalized gap coding determine character states in a similar manner (Quicke, 1993; Strait et al., 1996). As outlined in Chapter 4, divergence coding (Thorpe, 1984) arranges the mean character values for each taxon in rank order. A taxon by taxon matrix is then filled with either 1s, -1s or 0s depending on whether the means for each pair of taxa are significantly different (less than or greater) or not. Having completed this process, the total score of 1s, -1s and 0s is calculated for each taxon and that value used as the character state. Homogeneous subset coding (Simon, 1983; Archie, 1985) proceeds by dividing the study taxa into homogeneous subsets. A homogeneous subset is defined as a group of taxa whose sample means do not differ significantly from each other (Rae, 1997). Taxa are assigned the same character state if they have the same subset membership, i.e. if they are significantly different from the same sample of taxa (Rae, 1997). Generalized gap coding (Archie, 1985; Goldman, 1988) orders taxa according to their mean values, and then statistically compares pooled data for all possible groups of adjacent taxa with data for contiguous taxa or groups of contiguous taxa. If there is a statistically significant difference between the means, the boundary between the two groups is taken as a 'gap', and different character states are assigned to the taxa. All three methods, therefore, rely on tests of statistical significance to assign character states to taxa, and differ only in how those tests are applied. It is unlikely therefore that either homogeneous subset coding or generalized gap coding would have produced cladograms or clades that differed from those obtained using divergence coding.

The second reason for doubting that the alternative coding methods would have given better results is that segment coding, gap coding and gap weighting all determine character states arbitrarily. As discussed in Chapter 4, segment coding (Kendrick, 1964; Simon, 1983; Thorpe, 1984; Chappill, 1989) proceeds by dividing the range of each character into a number of equal-sized segments, with the same segment size being applied to all characters. Taxa are then assigned character states according to the segment in which their mean lies. Segment coding is arbitrary

since the number and distribution of the character states it yields, and their allocation to taxa, depends on the segment size chosen, and there is no defensible reason why one segment size should be preferred over another (Rae, in press). Gap coding (Mickevich and Johnson, 1976; Almeida and Bisby, 1984; Thorpe, 1984; Archie, 1985) arranges taxa in ascending order according to their sample means. It then assigns the same character state to contiguous taxa whose means differ by less than one gap length, which is conventionally a function of the within-group standard deviation (Rae, in press). Gap coding is arbitrary because there is no reason why the gap should correspond to a standard deviation unit of, say, 0.4 rather than one of 0.5, 1 or 1.5 (Rae, in press). Thiele's (1993) gap weighting proceeds by standardizing the range of each character. The ranges are then split into divisions of uniform size whose number matches the maximum number of character states allowable by a given parsimony algorithm, and the taxa are assigned character states according to the division in which their mean lies. Gap weighting is arbitrary since the character state assignments it yields are dependent on the parsimony algorithm employed, and algorithms vary in the maximum number of states they allow characters to have. Thus, while it is possible that gap coding or gap weighting might have yielded cladograms and/or clades that were compatible with the consensus molecular cladograms, the arbitrariness of the methods would have meant that the cladograms and/or clades could not be relied on.

The third reason for doubting that the alternative coding procedures would have produced better results is that the few published investigations of the merits or otherwise of the different approaches have not reached consistent conclusions. One study compared gap coding, segment coding and divergence coding, and concluded that gap coding is preferable to segment coding and divergence coding (Thorpe, 1984). Another compared homogeneous subset coding, gap coding and generalized gap coding, and concluded that homogeneous subset coding and generalized gap coding are better than gap coding (Archie, 1985). While a third compared gap coding,

generalized gap coding and segment coding, and concluded that segment coding is better than gap coding and generalized gap coding (Chappill, 1989).

Recently, Strait et al. (1996) have presented a new coding procedure called finite mixture coding. This procedure uses finite mixture analysis and maximum likelihood estimation to identify distinct statistical populations of taxa within the values recorded for a character. The number of states into which the range of each character is divided corresponds to the number of identifiable statistical populations, and taxa whose means are found within the same statistical population are assigned the same character state. Strait and colleagues' method appears to overcome many of the problems associated with the other coding methods. However, because it requires relatively large samples of either taxon means or individual specimens to identify a code, the applicability of finite mixture coding in analyses of fossil taxa is limited (Strait, personal communication). As such, it would not have been an appropriate coding procedure for the present study.

6.2.3. Outgroups

Choice of outgroup taxon or taxa can affect the success of outgroup polarization quite markedly (Smith, 1994). The sister group of the study taxa is considered to be the best outgroup, because it should share the greatest number of character states with the common ancestor of the ingroup, and will therefore correctly polarize the greatest number of character state transformation series (Maddison et al., 1984; Brooks and McLennan, 1991; Minelli, 1993). More distantly related taxa can be problematic because divergent evolution reduces the number of character states that can be recognized as homologous between the ingroup and outgroup (Smith, 1994). More distantly related taxa can also be problematic because convergent evolution tends to increase the number of homoplastic character states shared between the ingroup and outgroup (Chamberlain, personal communication).

Although the Dataset A outgroups, *Colobus* and *Papio*, are quite distant relatives of the Hominoidea (the last common ancestor of the apes and Old World monkeys is thought to have gone extinct around 28 Mya) it is unlikely that poor outgroup choice accounts for the lack of support for hypotheses 1 and 2 among the Dataset A tests, or their support for Hypothesis 3. Creel (1986) and Hartman (1988) included the closest living relative of the extant large-bodied hominoids, *Hylobates*, in their cladometric analyses, and neither analysis favoured a cladogram with the same branching pattern as the consensus molecular cladogram. Creel's (1986) cladograms all suggested that *Gorilla*, *Pan* and *Pongo* form a clade to the exclusion of *Homo* and *Hylobates*, and that within the (*Gorilla*, *Pan*, *Pongo*) clade, *Gorilla* and *Pongo* are more closely related to one another than either is to *Pan*. Most of Hartman's (1988) cladograms implied that *Homo*, *Pan* and *Pongo* are more closely related to one another than any of them is to *Gorilla* or *Hylobates*, and that within the (*Homo*, *Pan*, *Pongo*) clade, *Homo* and *Pongo* are more closely related to one another than either is to *Pongo*.

It is also unlikely that poor outgroup choice accounts for the lack of support for Hypothesis 1 among the Dataset B tests, as one of the taxa included as outgroups in Dataset B, *Cercopithecus*, is a member of the papionin's sister tribe, Cercopithecini. Moreover, Disotell (1992) found *Cercopithecus* to be the most effective outgroup in his investigation of papionin phylogeny using mtDNA COII gene sequences, the results of which support the consensus molecular cladogram that was used to judge the Dataset B cladograms and clades.

6.2.4. Consensus molecular cladograms

Clearly the results are dependent on the accuracy of the consensus molecular cladograms that were used to judge the craniometric cladograms and clades. If either of the consensus molecular

cladograms is incorrect, and the true phylogeny was among the cladograms favoured in the parsimony, compatibility and/or bootstrap analyses, the tests would have supported Hypothesis 1. Likewise, the tests may have supported Hypothesis 2 and given different results in relation to Hypothesis 3. Several observations suggest this possibility can be discounted, however. First, as discussed in Chapter 3, not only are both consensus molecular cladograms supported by multiple lines of independent molecular and karyological evidence, but, also, some of the methods that were used to generate them have been successfully tested on taxa of known phylogeny. Congruence of multiple lines of independent evidence is widely acknowledged to be the strongest support possible for a phylogenetic hypothesis (Quicke, 1993; Disotell, 1994), while success in replication studies has long been used in the historical sciences as a criterion for discriminating between methodologies that yield competing hypotheses (Trigger, 1989).

Second, the analyses did not favour the second-best estimates of interhominoid and interpapionin affinities. As discussed in Chapter 3, most of the analyses of hominoid phylogeny that do not support the cladogram used in the present study favour a cladogram in which *Pongo* is the sister taxon of a (*Gorilla*, *Homo*, *Pan*) clade, and *Homo* is the sister taxon of a (*Gorilla*, *Pan*) clade (Figure 111). This cladogram was not recovered as the sole most parsimonious arrangement in any of the Dataset A parsimony analyses, and none of its clades were obtained in the Dataset A bootstrap analyses. The (*Pongo* (*Homo* (*Gorilla*, *Pan*))) cladogram was among the cladograms supported in the compatibility analyses, but in both analyses it was less well supported than the hominoid consensus molecular cladogram. In Analysis L, the (*Pongo* (*Homo* (*Gorilla*, *Pan*))) cladogram was supported by three characters and the consensus molecular cladogram for the hominoids by eight characters. In Analysis M, it was supported by six characters and the consensus molecular cladogram by 11 characters. Currently, the consensus molecular cladogram for the Papionini used to evaluate the cladograms and clades recovered from Dataset B does not have a published competitor that withstands scrutiny. The cladograms put forward for the papionins

that differ from the consensus molecular cladogram are based on "non-explicit interpretations of intuitively analyzed data" (Brower et al., 1996: 431), or result from cladistic analyses that have subsequently been shown to underestimate the number of most parsimonious cladograms (Disotell, 1992; in press). Disotell (personal communication) has recently indicated that a maximum parsimony analysis of nDNA rejects the (*Papio*, *Theropithecus*) clade of the consensus molecular cladogram in favour of a (*Lophocebus*, *Theropithecus*) clade (Figure 112). However, this cladogram was not favoured in the Dataset B parsimony analyses. Neither was it supported in the compatibility analyses of Dataset B, nor were its clades recovered in the Dataset B bootstrap analyses.

Third, the results of the Hypothesis 1 tests are consistent with those of a recently completed study, in which the methods of palaeoanthropological cladistics were tested without reference to a specific phylogeny (Collard and Wood, in preparation a). In this investigation, which was modelled on that of Boyce (1969), Collard and Wood sought to determine whether current cladistic techniques can correctly group the sexes of the hominoid and papionin genera. This test assumed that if cladistics 'works', the males and females of each genus should form clades as they are undisputed sister taxa, regardless of the genus-level relationships. Two cladistic analyses, one for the hominoid data and one for the papionin data, in which the males and females were treated as separate taxa in the same phylogenetic analysis, were carried out.

The hominoid test was based on 129 metric variables recorded on *Gorilla*, *Homo*, *Pan* and *Pongo*. These were adjusted for the effects of size differences between the taxa by logging each specimen value and then dividing each one by the logged specimen geometric mean. Conversion into discrete character states was accomplished using divergence coding. One minimum length cladogram was recovered from the hominoid data. It correctly linked the sexes of *Homo* in a clade and the sexes of *Pan* in another, but failed to group the sexes of *Gorilla* and *Pongo* in ex-

clusive clades. The *Gorilla* males were positioned as the sister taxon of all the other taxa. The *Gorilla* females were located as the sister taxon of a clade containing the *Pongo* males, *Pongo* females, *Homo* males, *Homo* females, *Pan* males and *Pan* females. The *Pongo* males were positioned as the sister taxon of a clade containing *Pongo* females, *Homo* males, *Homo* females, *Pan* males and *Pan* females, and the *Pongo* females were positioned as the sister taxon of a clade containing the *Homo* males, *Homo* females, *Pan* males and *Pan* females.

The papionin test was based on 62 variables for *Cercocebus*, *Lophocebus*, *Macaca*, *Mandrillus*, *Papio* and *Theropithecus*. These were adjusted for the effects of size differences between the taxa by dividing each specimen value by the specimen average. Conversion into discrete character states was accomplished using Baum's coding procedure. One minimum length cladogram was also recovered from the branch-and-bound analysis of the papionin data set. It correctly grouped the sexes of *Theropithecus* as sister taxa, the sexes of *Lophocebus* and the sexes of *Macaca*. However, none of the other sexes were correctly linked. For example, *Mandrillus* females were positioned as the sister taxon of *Cercocebus* females, while *Mandrillus* males were shown as the sister group of the *Theropithecus* males and females.

6.2.5. Taxon-specific results

Is it legitimate to extrapolate from the results of the tests incorporated in the present study to cladistic studies of the early hominids and other fossil primates? Or is it possible, for example, that the Hypothesis 1 tests demonstrate that the cladistic relationships of the living hominoids and papionins cannot be reconstructed from cranial morphology using current palaeoanthropological techniques, but say nothing about how well the techniques work with craniodental data from the early hominids and other fossil primates? The tests of the hypotheses were undertaken on the assumption that their results would be biologically meaningful within the primate order, or

at the very least within other catarrhine groups such as the Miocene hominoids and Plio-Pleistocene hominids. This can be defended on two counts. First, the hominoids and papionins share with other primates a substantial biological baseline on which evolutionary processes, such as convergence and reversal, can operate. Thus, the problems encountered in the reconstruction of interhominoid and interpapionin cladistic relationships from cranial morphology can be expected to bedevil attempts to reconstruct the relationships of other primate taxa from craniodental data.

Second, comparison of the consistency indices recorded for the most parsimonious cladograms recovered from the 'best' data matrices with those recorded in morphology-based cladistic analyses of other primate taxa indicates that the hominoid and papionin data sets are not atypical with regard to the amount of homoplasy they contain. The most parsimonious cladogram recovered in Analysis J had a CI of 0.80, and the most parsimonious cladogram retrieved in Analysis 7 had a CI of 0.70. These index values compare favourably with those obtained in recent cladistic analyses of the early hominid species. For instance, the cladograms presented by Chamberlain and Wood (1987) had CI values between 0.69 and 0.71, Wood's (1988) re-analysis of Walker and associates' (1986) data set favoured a cladogram with a CI of 0.68, and Wood's (1991) most parsimonious cladograms had CIs of 0.65. Likewise, the most parsimonious cladogram obtained by Skelton and McHenry (1992) from their complete data set had a CI of 0.72, Lieberman and coworkers' (1996) most parsimonious cladogram had a CI of 0.68, and the two cladograms favoured by Strait et al. (1997) in the most recent cladistic analysis of the early hominids had CIs of 0.59 and 0.58.

The Analysis J and Analysis 7 index values are also similar to those obtained in several recent cladistic analyses of non-hominid primate taxa. For example, Groves and Eaglen's (1988) most parsimonious cladograms for the Lemuridae had CIs of 0.55, the most parsimonious cladograms

retrieved by Yoder (1994) from her morphological data set for the Strepsirhini had CIs of 0.40, and the most parsimonious cladograms recovered by Groves and Trueman (1995) from their re-analysis of Tattersall and Schwartz's (1991) lemurid data set had a CI of 0.55. More recently, the cladogram favoured by Stringer and colleagues (1997) in their analysis of *H. sapiens* interpopulation relationships had a CI of 0.68. Lastly, Gooder and Chamberlain's (submitted) most parsimonious cladogram for the mona monkey species group had a CI of 0.65.

6.3. IMPLICATIONS OF RESULTS

Given that it seems the findings of the study cannot be rejected on the grounds that the tests were flawed, what are their implications for palaeoanthropological cladistics?

6.3.1. Hypothesis 1 results

The lack of support for Hypothesis 1 among the tests strongly suggests that standard morphological characters from the primate cranium and dentition do not yield reliable species- and genus-level phylogenetic hypotheses. Convincing genus- and species-level cladistic hypotheses may be recoverable from molecular data (e.g. Ruvolo et al., 1991; 1994; Disotell, 1994; 1996; 1997; Yoder, 1994). They may also be recoverable from morphological data sets that are dominated by soft tissue characters (Shoshani et al., 1996). However, standard craniodental alone cannot be relied on to yield such hypotheses. More problematically, it is clear from the tests that the results of cladistic analyses of craniodental characters can be very misleading. For example, in the 'best' of the Hypothesis 1 parsimony analyses (i.e. those prepared using the geometric mean-based size-adjustment technique and divergence coding), the consensus molecular cladograms were less parsimonious than a substantial number of 'false' cladograms. PAUP/MacClade analyses of the data matrix from Analysis J indicated that, out of a total of fifteen possible cladograms,

seven were shorter than the hominoid consensus molecular cladogram. Comparable analyses of the data matrix from Analysis 7 indicated that, out of a total of 945 possible cladograms, 533 were shorter than the papionin consensus molecular cladogram. Likewise, the bootstrap-based tests of Hypothesis 1 indicated that cladistics can return impressive levels of what many would see as statistical support for phylogenetic relationships which are most likely incorrect. In a number of the Dataset A bootstrap analyses, the 'false' (*Gorilla*, *Pan*, *Pongo*) clade was identified in more than 70% of the bootstrap cladograms. In fact, in some analyses the (*Gorilla*, *Pan*, *Pongo*) clade appeared in 100% of the bootstrap cladograms. Likewise, the 'false' (*Mandrillus*, *Papio*) clade was supported by more than 70% of the bootstrap cladograms in several of the Dataset B bootstrap analyses. In other words, when used to reconstruct the phylogenetic relationships of primate genera or species from craniodental data alone, cladistic methods can yield not only 'false-positive' results or Type II errors, but 'false-positive' results that pass by a substantial margin the statistical test favoured by many palaeoanthropological cladists.

The obvious implication of the foregoing is that we cannot rely on the cladograms for the early hominids and other fossil primate genera and species that have been obtained from craniodental data. No matter how carefully the analyses have been conducted - and arguably the cladistic analyses carried out by palaeoanthropologists have been at least as rigorous as those carried out by cladists working in other areas of palaeontology - it is highly unlikely that the cladograms produced by, for example, Szalay and Delson (1979), Chamberlain and Wood (1987), Skelton and McHenry (1992) or Strait et al. (1997) correctly represent the phylogenetic relationships of the taxa. Rather, the cladistic hypotheses obtained by these authors, and the many others who have undertaken cladistic analyses of fossil primate craniodental remains, most probably reflect the phylogenetically misleading effects of convergence, parallelism and/or reversal among the taxa. This is the case even with those relationships that have been found to be reliable in bootstrap analyses of fossil primates. We cannot assume, for example, that the high level of boot-

strap support Corruccini (1994) found for a 'robust' australopithecine clade comprising *Paranthropus boisei* and *Paranthropus robustus* in his reassessment of previously published hominoid cranial data means that the clade is a real historical entity. Nor can we assume that the 89% support Cameron (1997) found for a (*Pongo*, *Sivapithecus*, Spanish Miocene hominoid) clade in his bootstrap analysis of craniodental data from several extant and fossil hominoid genera means that it is real. Both results could, like the high level of support for the (*Gorilla*, *Pan*, *Pongo*) clade in a number of the Dataset A analyses from the present study, be 'false-positives'.

Given that there is widespread agreement among palaeoanthropologists that cladistics is a better method of phylogenetic reconstruction than its two main competitors, phenetics and evolutionary systematics, the results of the present study also imply that we cannot rely on **any** phylogenetic hypothesis for the fossil primate genera and species, no matter how many workers accept it. It is possible, for example, that the traditional hypothesis which views the 'robust' australopithecines from East and southern Africa as a monophyletic group is incorrect. The resemblances shared by *Paranthropus boisei* and *Paranthropus robustus* may not have been inherited from a common ancestor; they may in fact have developed independently in response to similarities in their diets or other ecological factors (e.g. Wood, 1988). Likewise, it is feasible that, contrary to popular opinion, the early *Homo* specimens from southern Africa Stw 53 and SK 847 do not share a common ancestor with the early *Homo* specimens from East Africa to the exclusion of the other early hominid species. Stw 53 and SK 847 could in fact be more closely related to *Australopithecus africanus* or *Paranthropus robustus* than they are to the East African early *Homo* species, with the morphological similarities they share with the East African early *Homo* species resulting from convergent evolution. Indeed, we cannot ignore the possibility that the East and southern African early hominid species represent separate evolutionary radiations resulting from the division of an ancestral hominid species whose distribution included both East and southern Africa, and the subsequent evolution of similar morphological solutions to similar ecological conditions.

In short, the results of the tests of Hypothesis 1 imply that we can be sure of very little, if anything, about the genus-level and species-level phylogenetic relationships of the early hominids and other fossil primate species.

How can we improve our reconstructions of the phylogenetic relationships of fossil primate genera and species? Providing the correct size-adjustment method, coding procedure and polarization technique are used, a cladistic analysis will apparently fail to identify phylogenetic relationships as a consequence of correlation among resemblances resulting from convergence, parallelism and/or reversal. The challenge for those applying cladistics to fossil primate data therefore is to develop dependable criteria for distinguishing these phylogenetically misleading homoplastic resemblances from phylogenetically informative homologous resemblances.

One promising criterion has recently been outlined by Lieberman and colleagues (1996; see also Lieberman, 1995; 1996). These authors argued that the most reliable way of distinguishing homoplastic resemblances from homologous resemblances is to examine the ontogeny of the characters. Homologous resemblances, they averred, must arise through the same developmental mechanisms, whereas homoplastic resemblances can come about through the same or different developmental mechanisms. Thus if a resemblance between two or more taxa has arisen through different developmental pathways it has to be a consequence of convergence, parallelism or reversal. An example of such a resemblance cited by Lieberman et al. is facial orthognathism in early *Homo*. This character state is shared by *H. ergaster*, *H. habilis* and *H. rudolfensis*, and at first sight appears to be synapomorphy distinguishing *H. ergaster*, *H. habilis* and *H. rudolfensis* from the australopithecines and paranthropines. However, analyses by several authors (e.g. Rak, 1983; Bilsborough and Wood, 1988; Bromage, 1989; Wood, 1991) indicate that facial orthognathism in *H. ergaster* and *H. habilis* developed differently from that of *H. rudolfensis*. The facial orthognathism of the former seems to have been a consequence of premaxillary

reduction, whereas the latter's facial orthognathism seems to have been a consequence of anterior migration of the mid- and upper-face. Thus the resemblance in facial orthognathism between *H. ergaster* and *H. habilis* on the one hand, and *H. rudolfensis* on the other, is homoplasic.

Another criterion that may prove useful is congruence with the spatial distribution of fossil primate taxa. Most palaeoanthropological cladists ignore biogeography as a source of data with which to test their hypotheses. However, as Simpson's (1945: 7) discussion of the relationship between zoogeographic and phylogenetic theories indicates, biogeographic data can, given the right method, be used to eliminate competing cladistic hypotheses:

> "Similar animals living in adjacent areas are likely to be more closely related than animals, even equally similar animals, widely separated. Animals of similar immediate geographic origin are more likely to be related than animals whose immediate ancestors lived in different regions - in fact, animals clearly cannot have common ancestry without also having common geographic origin...Zoogeographic and phylogenetic theories must be concordant if both are true, and a stated phylogeny cannot be considered well established unless it can be reconciled, at least, with any equally probable zoogeographic deductions."

One method of using Simpson's "zoogeographic deductions" to choose between competing cladograms for the fossil primates is currently being developed by Collard and Wood (in preparation b). Adapted from the technique used by Ramskold and Werdelin (1991) to investigate the geographic distribution of phacopid trilobites through time, Collard and Wood's method proceeds by identifying the 50 most parsimonious cladograms for a group of primate taxa based on morphological evidence. Next, the geographic area across which the taxa are distributed (e.g. Eurasia) is divided into a series of equal size regions, each of which is given a name. Thereafter, the taxo-

nomic names at the termini of the cladograms are replaced by the regions where the taxa come from. The number of biogeographic episodes involving non-adjacent regions (e.g. migration between two regions separated by a third, habitat fragmentation resulting in a region-sized gap between the ranges of two taxa) implied by each cladogram is then calculated. Finally, the cladogram that implies the smallest number of biogeographic episodes is identified. This cladogram is considered to be the best representation of the phylogenetic relationships of the taxa on the grounds that it maximizes the congruence between the morphologic and biogeographic data. In the near future, Collard and Wood will apply this method to the anthropoid fossil record.

A third criterion that deserves further investigation is congruence with the stratigraphic ranges of the taxa. Cladograms predict the order in which fossil taxa appeared (Cracraft, 1981). Thus, if a cladogram is correct, the order in which the taxa appear in the fossil record should be congruent with that predicted by the cladogram (Paul, 1982). So far attempts to operationalize this criterion have focussed on long-lived groups with good fossil records, such as the echinoids and the Ordovician archaeogastropods Lophospiridae (Marshall, 1990; Wagner, 1995). However, there appears to be no good reason why the approach adopted by Marshall (1990) and Wagner (1995), which is based on the work of Strauss and Sadler (1989), cannot be adapted for use with the primate fossil record.

6.3.2. Implications of tests of hypotheses 2 and 3

The lack of support for Hypothesis 2 among the analyses suggests that the different regions of the primate cranium do not differ in their reliability for phylogenetic reconstruction; they are all equally prone to homoplasy. This in turn implies that recent arguments about the relative reliability of the cranial regions for phylogenetic reconstruction are suspect. For example, the finding that characters from the palate and upper teeth and mandible and lower teeth are no less

phylogenetically informative than those from the face or the cranial vault and base contradicts the assertion that homoplasies are particularly common in the primate masticatory system (Skelton and McHenry, 1992; Turner and Wood, 1993; McHenry, 1994; 1996, Wood, 1994). Likewise, the finding that characters from the mandible and lower teeth are no worse for phylogenetic reconstruction than those from the palate and upper teeth, face or cranial vault and base refutes Begun's (1994a) suggestion that the hominoid mandible is a particularly poor source of phylogenetically informative characters.

The results of the Hypothesis 3 tests indicate, *contra* Creel (1986), that the sexual composition of primate fossil samples can affect genus- and species-level phylogeny estimation. Specifically, the results suggest that when specimens can be reliably sexed (e.g. fossil papionins) and characters from all the cranial regions are analyzed together, better results are likely to be obtained by analyzing female specimens rather than males. Female specimens are also likely to be more informative when characters from the face or the cranial vault and base are examined. In contrast, when mandibular data are analyzed cladistically, male specimens are likely to be more informative than females. The sex of specimens is unlikely to affect the results of analyses based on palate characters. One possible explanation for the greater utility of female face and vault morphology for phylogenetic reconstruction is that the morphs of male and female primates differ mainly in characters that can be plausibly related to intermale bluff and aggression (e.g. ectocranial crests, canines) (McGown, 1978). Since primates exhibit a limited range of bluff and aggression behaviours, characters related to such behaviours can be expected to be prone to phylogeny-obscuring convergence. It is unclear why the mandibles and lower teeth of male primates are more phylogenetically informative than those of female primates, or why the palates and upper teeth of the sexes do not differ in their utility for phylogenetic reconstruction.

6.4. CONCLUSIONS

This study tested the hypothesis on which all recent cladistic analyses of the early hominids and other fossil primates have been based. Namely that standard cranial and dental characters are reliable for reconstructing the cladistic relationships between primate species and genera. The study indicated that this assumption is probably incorrect. Apparently, craniodental morphology cannot be relied on to reconstruct the phylogenetic relationships of the fossil primate genera and species. Instead, the results incorporated in this thesis suggest that such data yield cladograms that principally reflect the effects among the taxa of convergence, parallelism and/or reversal. Given this, it is very unlikely that any of the current cladistic hypotheses for early hominids and other fossil primate genera and species are accurate. Even those hypotheses that appear to be statistically reliable are probably phylogenetically misleading.

Two secondary hypotheses were also tested in this study. The first was that some regions of the primate cranium are more reliable than others for reconstructing the cladistic relationships between species and genera. The study did not support this hypothesis. Rather it indicated that the regions of the primate cranium do not differ in their reliability for phylogenetic reconstruction at the genus- or species-level. Contrary to current opinion, the regions most closely associated with mastication, the palate and upper dentition and mandible and lower dentition, are no less reliable as sources of phylogenetic informative characters than the face or the cranial vault and base; they are all equally poor sources of phylogenetic information. None of the regions can be relied on to estimate the phylogenetic relationships of primate species and genera.

The other secondary hypothesis tested in the study was that male and female primates differ in their reliability for reconstructing the cladistic relationships between species and genera. The study supported this hypothesis. It indicated that when characters from all regions of the cranium

are analyzed, females are more reliable than males. Females are also more reliable than males when characters from the face and the cranial vault and base are analyzed. In contrast, when analyses focus on characters from the mandible and lower dentition, males are more reliable than females. Palate characters do not exhibit sex-related differences in their reliability for phylogeny estimation.

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