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**GEOMETRIC MORPHOMETRIC ANALYSES OF EXTANT AND FOSSIL
HOMINOID CRANIOFACIAL MORPHOLOGY**

by

KIERAN P. McNULTY

**A dissertation submitted to the Graduate Faculty in Anthropology in partial fulfillment of
the requirements for the degree of Doctor of Philosophy.**

The City University of New York

2003

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This manuscript has been read and accepted for the Graduate Faculty in Anthropology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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THE CITY UNIVERSITY OF NEW YORK

ABSTRACT**GEOMETRIC MORPHOMETRIC ANALYSES OF EXTANT AND FOSSIL
HOMINOID CRANIOFACIAL MORPHOLOGY**

by

KIERAN P. McNULTY

Advisor: Professor Eric Delson

Phylogenetic relationships within the Hominoidea are largely controversial, with alternative hypotheses debated for nearly every fossil taxon. Such disagreement is due, in part, to reliance upon verbal description and traditional morphometric approaches to characterize variability in complex, three-dimensional morphologies. This study used geometric morphometric techniques to study hominoid affinities in pursuit of three objectives: 1) a quantitative analysis of craniofacial shape variation among extant hominoid specimens and taxa; 2) an assessment of similarities within and differences between the morphologies of anthropoid crown clades; and 3) an examination of the affinities of selected fossil specimens. These goals were pursued in three separate analytical units, examining the morphology of the whole cranium, the supraorbital region, and the palate. Based on a generalized Procrustes analysis, data were studied using standard multivariate statistical techniques: principal components analysis, canonical variates analysis, Mahalanobis distance clustering, and discriminant analysis. I also

introduced a new method (phylogenetic node discrimination) for testing the affinities of fossil specimens within an assumed phylogeny.

The methods used here also proved to be powerful tools for discerning subtle differences in shape, leading to new ideas about the affinities of extant hominoid morphologies. In analyses of the whole cranium, *Gorilla* was largely conservative among extant apes. Hominoid supraorbital morphology was shown to have three distinct states, corresponding to hylobatids, pongines, and hominines; cercopithecoid genera all shared one distinct morphology. Results from palatal morphology supported previous descriptive analyses, suggesting that *Hylobates* retains primitive catarrhine morphology, while hominids are more derived. Beyond this, platyrrhine palatal morphology was shown to be distinct from that of catarrhines.

Results from phylogenetic node discriminations provided new evidence regarding the affinities of fossil specimens. Among Early Miocene taxa, *Proconsul* and *Morotopithecus* could not be grouped conclusively with hominoids, while *Afropithecus* and *Turkanapithecus* demonstrated marked hominoid affinities; surprisingly, *Rangwapithecus* placed strongly with the hominids. Among Late Miocene taxa, *Dryopithecus* was found to group with hominids, but not hominines; *Graecopithecus* demonstrated strong hominine affinities, grouping closely with *Gorilla*. Of all these fossil taxa, only *Sivapithecus* demonstrated any affinity to the pongine lineage.

For the Kathleens, the Michaels, and Maureen

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CHAPTER 1: INTRODUCTION

It has recently been declared that the phylogenetic relationships among extant apes are now firmly resolved, owing largely to evidence from genetics (Pilbeam, 2002: 304). On the whole, this would seem to be an accurate assessment of the current state of affairs in the field of physical anthropology. With notably few exceptions (e.g., Andrews & Delson, 2000; Köhler *et al.*, 2001), most researchers today have explicitly or implicitly accepted the abundance of genetic (e.g., Goodman, 1963; Sarich & Wilson, 1967; Sarich, 1971; Caccone & Powell, 1989; Ruvolo, 1994, 1995, 1997; Goodman *et al.*, 1998) and somewhat scarcer morphological (e.g., Groves, 1986; Begun *et al.*, 1997; Strait *et al.*, 1997, in part; Gibbs *et al.*, 2000) evidence supporting a close link between humans and chimpanzees, followed by successive sister groups of *Gorilla*, *Pongo*, and *Hylobates*. The resolution of most of these relationships, however, substantially predates modern genetic and morphological analytical techniques. The position of hylobatids as the “sister taxon” to the great apes and humans was generally accepted well before such a term became vogue (e.g., Pilgrim, 1927; Simpson, 1945, 1949, 1953; Weidenreich, 1946). The monophyly of African apes and humans has been discussed for more than a century (e.g., Huxley, 1863; Darwin, 1872; Nuttall, 1904; Keith, 1911), but probably gained broad approval with the advent of early molecular phylogenetic techniques (e.g., Goodman, 1962, 1963; Sarich & Wilson, 1967; Sarich, 1971).

It is only more recently that the close evolutionary link between *Pan* and *Homo*—to the exclusion of *Gorilla*—has become widely accepted. Yet, regardless of whether or not one agrees with this hypothesis, it seems doubtful that such resolution will increase our understanding (read: agreement among researchers) of the evolutionary relationships

among fossil hominoids. The recognition of a distinct human-chimpanzee lineage is unlikely to reveal important morphological information about homoplasy and convergent evolution, as the vast majority of similarities between *Pan* and *Gorilla* are presumably symplesiomorphic. Nor does it offer much hope for improving our understanding of most fossil hominoids. The stem hominine morphology is still likely to be regarded as gorilla- or chimpanzee-like, leaving largely unaffected the relationships of taxa external to this node; non-human fossils that fit within the hominine clade are conspicuously absent (Pilbeam, 2002; but see Dean & Delson, 1992)—though very recent discoveries (Senut, 2001; Brunet *et al.*, 2002) may be interesting in this regard. Ironically, consensus about the close evolutionary relationship between *Pan* and *Homo* has dramatically underscored morphological differences found in latter genus.

If there is now agreement in the scientific community about the phylogeny of living apes, what can be said about that of fossil apes and putative hominoids? Relationships among hylobatids, pongines, and hominines, as well as the broader connections among hominoids, cercopithecoids, and platyrrhines are the most crucial for determining the placement of nearly all extinct hominoids and non-cercopithecoid catarrhines; these have been well established for the last few decades. Yet, is there a single extinct hominoid (*sensu lato*) genus whose phylogenetic relationships can be agreed upon by all workers?

The extinct ape *Dryopithecus* is an excellent example of the current situation in fossil hominoid systematics. Since its referral to the hominoid superfamily (Lartet, 1856), this genus has gone through a long series of taxonomic expansions and contractions as well as a number of phylogenetic revisions (see Szalay & Delson, 1979; Begun, 2002 for

reviews of this history). Currently, there are four outstanding hypotheses about how this genus relates to a phylogeny of modern taxa. Benefit & McCrossin (1995; McCrossin & Benefit, 1994, 1997) argue that *Dryopithecus* is an undifferentiated ape representing a primitive radiation of stem hominoids. A second view places *Dryopithecus* among great apes as a basal lineage (e.g. Andrews & Martin, 1987; Andrews, 1992; Begun, 1992; Andrews *et al.*, 1996; Rose, 1997; C. Ward, 1997). Begun (e.g., 1994, 2002) and colleagues (Begun & Kordos, 1997; Begun *et al.*, 1997; Kordos & Begun, 2001) suggest that this genus represents a stem hominine close to the ancestry of African apes and humans. Finally, Moyà Solà & Köhler (1993, 1995) and others (Cameron, 1997, in part; Köhler *et al.*, 2001) have placed *Dryopithecus* near the base of a pongine radiation. Ignoring modern humans for the moment, a fundamental agreement over relationships among African apes, *Pongo*, and *Hylobates* (compare, e.g., Andrews, 1992; Begun, 1994; McCrossin & Benefit, 1994; Moyà Solà & Köhler, 1995) has not brought resolution to the phylogenetic status of *Dryopithecus*. Thus, while arrival at a consensus is worthy of note in any scientific field, it is unclear that knowing the correct placement of *Homo* within a phylogeny of extant apes will bring about new clarity of the relationships among fossils.

This lack of concordance among researchers results from many factors, not least of which is sampling error: geographical, temporal, ecological, populational, anatomical, and phylogenetic. Yet, with regard to these factors, all workers deal with exactly the same set of biases—namely, the fossil record. The fact that so many ways have been found to disagree suggests a more fundamental disconnect: workers analyzing the same bits of evidence are drawing remarkably different conclusions. Debate over the

supraorbital morphology of *Dryopithecus* is directly to the point. Begun (1994) gives explicit descriptive criteria for his diagnosis of a supraorbital torus in this genus. Benefit & McCrossin (1995; see Cunningham, 1901, cited therein) offer an alternative definition of torus, however, and exclude *Dryopithecus* from this condition. Meanwhile, Köhler *et al.* (2001) argue a third position that *Dryopithecus* morphology shares derived features with the costae of *Pongo*. Yet, these mutually exclusive hypotheses are all founded upon the same set of fossil specimens.

Many incongruities between opposing phylogenetic hypotheses can be attributed in part to two related factors: verbally defined morphology and polymorphism. While precise quantitative definitions are easily accomplished for certain types of traits (e.g. the number of premolars), complex three-dimensional morphology is typically defined verbally: the more complex the feature (i.e., the more words required to precisely define it), the more degrees of interpretation that accompany the definition. Compounding this problem is the variability of structures within taxa. Methods have been developed to cope with variation in certain types of characters (e.g. discrete characters, linear dimensions), but there have been fewer attempts to capture and quantify the complex three-dimensional variations that characterize many anatomical features. Descriptive analysis is, and should be, an important part of paleoanthropological research. Yet, verbal description is generally inadequate to represent the range and significance of variability in some structures. Reliance on such methods, then, introduces a dimension of subjectivity into the analysis, along which multiple interpretations are easily accommodated.

The use of traditional morphometric techniques (see Marcus, 1990) represented a step towards quantitative treatment of morphological features and their variability. Such studies have long been used in the field of paleoanthropology (e.g., Le Gros Clark, 1950, 1955; Bronowski & Long, 1952; Howells, 1973, 1989; Stringer, 1974; Oxnard, 1975; Kay & Simons, 1983; Bilsborough & Wood, 1988; Albrecht & Miller, 1993) and continue to be widely employed today. These techniques are ideal for analyzing some types of structures (e.g., dental dimensions, orbit shape), but fail to capture the detailed anatomy of complex morphologies. Moreover, such methods extract shape from its biological and geometric context, reducing three-dimensional morphology to a set of disparate one-dimensional lines. Thus, use of traditional morphometrics has long been a trade-off between the anatomical detail available through descriptive analysis and the statistical rigor of quantitative approaches.

Recent advances in geometric morphometric analysis have enabled workers to incorporate the positive aspects of both approaches in their research. These methods utilize landmark coordinates as variables, rather than caliper measures, angles, and areas (Marcus, 1990). Thus, shape data are measured from within the biological and geometric framework of the original specimen. The addition of curvilinear (Dean, 1993; Rohlf & Marcus, 1993; Yaroeh, 1996; McNulty, 2001; Harvati, 2001; Mitteroecker *et al.*, 2003) and surface (e.g., Gunz *et al.*, 2002; Weber *et al.*, 2003; Delson *et al.*, 2003) data to landmark configurations allows such techniques to approach the level of detail available through careful descriptive analysis. Yet, as a statistical methodology, these data can be subjected to the same measures and analyses of variability that are applied to traditional morphometric data. In all of these respects, geometric morphometric analysis is better

able to capture and quantify shape than are multivariate analyses of traditional distance measures (Rohlf, 2000).

As of yet, few researchers (but see, e.g., Leakey *et al.*, 1991) have applied landmark-based morphometrics to analyses of non-human fossil hominoids. It is certainly true that the recovery of more fossils, from different geo-temporal and ecological spaces, is likely to shed much light on the evolutionary history of the Hominoidea (Pilbeam, 1997, 2002; Pilbeam & Young, 2001). Yet, the failure of researchers to agree over basic morphological assessments from the current record does not bode well for consensus over a much broader sample. It is the hope of this project that a quantitative analysis of hominoid craniofacial morphology can offer a better understanding of the morphological variation among extant apes and their fossil predecessors, a statistical assessment of competing hypotheses regarding the affinities of these taxa, and new alternatives for testing and exploring these morphological relationships. This text does not conclude with a declaration of consensus over the phylogenetic relationships among extant and fossil hominoids. Yet, the analyses offered herein comprise a new way of addressing some of the old problems and disagreements, thereby providing insights about hominoid craniofacial morphologies, as well as quantitative support for (and evidence against) the affinities of fossil specimens. In that manner, this project advances our understanding of the evolutionary history of the Hominoidea.

PROJECT GOALS AND DESIGN

This study set out to accomplish three specific objectives: 1) quantitatively assess craniofacial shape variation among extant hominoid specimens and taxa; 2) test for

similarities within and differences between the morphologies of anthropoid and hominoid crown clades; and 3) use models of extant shape variation to examine the affinities of fossil hominoids and non-cercopithecoid catarrhine specimens. In order to accomplish the latter goal, this project was specifically designed to accommodate the fragmentary nature of most fossils. First, many of the landmarks used here were chosen with regard to quantifying known specimens of extinct hominoids and non-cercopithecoid catarrhines. Even so, the maximum number of landmarks on the most incomplete specimen sets the limit on the morphology that can be analyzed. Therefore, the project goals outlined above were addressed in three separate analytical units. The first unit analyzed the entire set of cranial landmarks; none of the included fossil specimens preserves all of these, but several were analyzed using a slightly reduced cranial dataset. The second analytical unit examined only supraorbital morphology. This region is used frequently, often in purely qualitative terms, to distinguish among extant and fossil hominoid taxa; a number of fossil specimens preserve all or much of the brow ridge, without retaining much more of the cranial morphology. The third unit analyzed the inferior maxillary/premaxillary complex, referred to informally as palatal morphology. This is a commonly preserved anatomical element, with a number of fairly complete palates in the fossil record. By pursuing three separate analytical units, a broad examination of hominoid crania was possible, without sacrificing quantitative assessment of more fragmentary fossil specimens.

Each analytical unit is described in a separate chapter of this text. Statistical analyses in each are basically the same and can be divided into two types. Initial analyses are purely phenetic, designed to explore differences among specimens and taxa that are

emergent from the data. The second half of each chapter is also phenetic in origin, but underpinned by well-established phylogenetic relationships. Together, this battery of statistical tests provides a comprehensive, quantitative analysis of hominoid craniofacial morphology. Fossil specimens, though not appropriate for all analyses, are examined in light of these extant phenetic and phylophenetic models.

All of the extant hominoid genera were extensively sampled for this project. This included all species and subspecies of the hominids (great apes and humans). *Hylobates* is the only extant ape genus that comprises a complex infrageneric taxonomy of species and subspecies. As such, it was broadly, but not completely sampled. Smaller samples of cercopithecoid (*Cercopithecus*, *Papio*, *Procolobus*) and platyrrhine (*Ateles*, *Cebus*) genera were also studied in order to place the hominoid morphology in a broader anthropoid context. Extinct hominoids (*Australopithecus*, *Dryopithecus*, *Graecopithecus*, early *Homo*, *Paranthropus*, and *Sivapithecus*) and putative hominoids (*Afropithecus*, *Morotopithecus*, *Proconsul*, *Rangwapithecus*, and *Turkanapithecus*) were the focus of fossil analyses. Specimens of *Propliopithecus* were also included in this project, as almost all workers agree on their status as basal catarrhines. While this work was not aimed specifically at determining its affinities, *Propliopithecus* provided an important context against which Early Miocene putative hominoids were compared.

TAXONOMY AND ABBREVIATIONS

The taxonomic names used in this work reflect a modern understanding of the close relationship between humans and the African apes—particularly *Pan*. Primate taxa above the family level are referred to by their commonly accepted names: Anthroidea

(Mivart, 1864), anthropoids, for the suborder of New World monkeys, Old World monkeys, and apes; Platyrrhini (Geoffroy, 1812), platyrrhines, infraorder of New World monkeys; Catarrhini (Geoffroy, 1812), catarrhines, infraorder of Old World monkeys and apes; Cercopithecoidea (Gray, 1821), cercopithecoids, superfamily of Old World monkeys; Hominoidea (Gray, 1825), hominoids, superfamily of apes. There is no consensus among workers about the appropriate application of taxonomic names at the family level and below, however. The meanings attached to such terms in this text are defined below, and generally follow the taxonomy used by Delson *et al.* (2000: xxiii-xxvii). Appropriate designations for popularly disputed genus names (e.g., *Graecopithecus*, *Propliopithecus*) are discussed in Chapter 2.

Hylobatidae (Gray, 1870), hylobatids: one of two extant hominoid families, comprised of the lesser apes; currently known only from the genus *Hylobates*.

Hominidae (Gray, 1825), hominids: the other extant hominoid family, made up of all great apes and humans. Traditional usage of this name, restricted exclusively to the human lineage, is rejected here in favor of this broader definition.

Ponginae (Elliot, 1913), pongines: subfamily of Asian great apes.

Homininae (Gray, 1825), hominines: subfamily of African apes and humans.

Hominini (Gray, 1825), hominins: tribe composed of all taxa in the human lineage that evolved subsequent to the bifurcation of the chimpanzee lineage.

australopith: a non-taxonomic term used informally to refer to hominins that do not belong to the genus *Homo*.

The taxon comprised of *Homo* and *Pan* is not formally named here. Rather, it is simply referred to as an aggregate of the genus names (*Homo-Pan*) and contrasted with the genus *Gorilla*.

Genus names for extant taxa are abbreviated in some of the tables within this text. In most cases, the first four letters of the genus are used as the designation; *Procolobus*, however, is abbreviated as “Pcol.” *Homo* and *Pan* are never abbreviated. Genus names for fossil taxa are also abbreviated in some tables. This was usually accomplished by dropping “pithecus” from the end of the name. *Paranthropus*, however, is abbreviated as “Paranth.”

OVERVIEW OF THE TEXT

Beyond the three analytical sections, this text contains several chapters which provide a framework for the overall project. Chapter 2 gives a brief review of the history of hominoid phylogenetic research, focusing on the taxa analyzed here. As two analytical units are concerned with specific craniofacial regions, this chapter also reviews the use of supraorbital and palatal morphology in phylogeny reconstruction. Chapter 3 describes the sample upon which these analyses were based. For extant specimens, this includes sample size information by taxon (genus, species, subspecies) and sex, as well as locality data. Discussion of fossil specimens includes information on provenance, the institutions in which they are kept, and brief descriptions of their preservation. Chapter 4 reviews methods used for data collection and processing; this includes discussions of landmark descriptions, data collection equipment, multi-view data collection, measurement error.

and reconstruction of missing bilateral landmark data. Chapter 5 outlines the morphometric and statistical methods used throughout the project. It also includes analyses of the role that allometry plays in this dataset and a rationale for applying—or not applying—a size adjustment. Chapters 6-8 present analyses of the whole cranial, supraorbital, and palatal datasets, respectively. Finally, Chapter 9 brings together all results, summarizing the information learned through pursuit of this project.

CHAPTER 2: OVERVIEW OF HOMINOID PHYLOGENETIC STUDIES

Relationships among the extant apes have been of great interest since Linnaeus classified humans among them in his 1758 taxonomy. Traditionally, living hominoids were organized gradistically into a primitive hylobatid grade, more advanced great apes, and a highly evolved human grade (e.g., Simpson, 1945, 1953). Towards the latter half of the twentieth century, however, opinions among researchers began to change, due in large part to advances in molecular systematics and cladistic methodology (see Pilbeam, 1997). Currently, consensus opinion holds that the Hylobatidae is the sister taxon to great apes and humans, *Pongo* is the sister taxon to African apes and humans, and *Gorilla* is the sister taxon to a *Homo-Pan* clade (e.g., Goodman, 1963; Groves, 1986; Pilbeam, 1996; Begun *et al.*, 1997; but see Schwartz, 1984)—with some disagreement about hominine relationships (e.g., Martin, 1985; Andrews, 1987, 1992; Dean & Delson, 1992; Andrews & Delson, 2000; Köhler *et al.*, 2001).

While the phylogeny of extant hominoids is largely agreed upon, placement of the diverse fossil taxa has been the cause of considerable debate. The earliest descriptions of fossil apes were mostly of isolated teeth and mandibles (e.g., Lartet, 1856; Falconer, 1868; Lydekker, 1879; Pilgrim, 1915; Gregory *et al.*, 1938). The 1948 skull of *Proconsul* from Rusinga was the first relatively complete craniodental fossil of a non-human (putative) hominoid (Le Gros Clark & Leakey, 1951). In 1965, Simons and Pilbeam published the first “modern” comprehensive revision of the hominoid fossil material. With relatively few fossil taxa known at the time, all were thought to be fairly closely related and placed within the genus *Dryopithecus*. As the fossil record became better known, however, further taxonomic and phylogenetic revisions were published (e.g.,

Greenfield, 1979, 1980; Pilbeam 1979; Kay & Simons, 1983; Kelley & Pilbeam, 1986; Andrews & Martin, 1987; Begun *et al.*, 1997) and hominoid relationships grew more complicated. This chapter gives a brief review of historical and contemporary opinions regarding the taxonomy and phylogeny of the fossil hominoids and some non-cercopithecoid catarrhines analyzed in this study. Following that is an overview of the use of supraorbital and palatal morphologies in constructing hominoid phylogeny hypotheses.

EARLY MIOCENE AFRICAN TAXA

The fossil record from the latest Oligocene and Early Miocene of East Africa is replete with a broad diversity of catarrhines. There are at least 13 non-cercopithecoid catarrhine genera named from localities in Kenya and Uganda dating to this interval. As such, these fossils are a potentially rich source of information about the origin of the Hominoidea from a lineage of basal catarrhines (see Harrison, 2002 and references therein). The array of Early Miocene taxa from East Africa comprises a diverse range of sizes (e.g., Sanders & Bodenbender, 1994; Rafferty *et al.*, 1995), diets (e.g., Kay & Ungar, 1997), postures (e.g., Gebo *et al.*, 1997), and craniofacial morphologies (e.g., Ward & Kimbel, 1983; Leakey & Leakey, 1986a,b). Opinions on the phylogenetic relationships of these taxa vary (compare Walker & Teaford, 1989; Andrews, 1992; Rae, 1997; Harrison, 2002), yet most authors agree that at least some specimens belong to the hominoid superfamily, while others are basal catarrhines (Harrison, 2002).

Proconsul

First described by Hopwood (1933), the *Proconsul* hypodigm has grown substantially so that nearly every bony element is now represented (Walker, 1997). Most authors recognize four distinct *Proconsul* species (*P. africanus*, *P. heseloni*, *P. nyanzae*, and *P. major*), though there has been some disagreement over the number of species represented at the Kisingiri sites (compare Kelley, 1986; Ruff *et al.*, 1989; see Teaford *et al.*, 1993, for a review). Senut *et al.* (2000) have transferred material originally referred to *P. major* to the new genus *Ugandapithecus*, but the generic distinction of these specimens is not widely accepted. Hopwood (1933) originally hypothesized that *Proconsul* was ancestral to the chimpanzee; Pilbeam (1969) later argued that *P. major* was ancestral to the gorilla, while *P. africanus* was probably ancestral to *Pan troglodytes*. The discovery of additional specimens of this and other taxa, however, cast doubt on such direct ancestor-descendant relationships (Pilbeam, 1997; Walker, 1997; Harrison, 2002). Currently, most authors subscribe to one of three phylogenetic hypotheses concerning *Proconsul*.

The most popular view among researchers posits that *Proconsul* is the sister taxon to all living apes (e.g. Rose, 1983, 1992, 1997; Andrews, 1985, 1992; Martin, 1986; Andrews & Martin, 1987; Begun *et al.*, 1997; Rae, 1999). In defense of this hypothesis, authors cite several hominoid postcranial synapomorphies, including: increased mobility of the shoulder and ulno-carpal joints, enlarged humeral trochlear keels, increased stability of the radius in pronation and supination, complete opposability of the hallux, six lumbar vertebrae, narrow sacrum, a derived carpo-metacarpus, and lack of a tail (Andrews, 1992; Rose, 1992, 1997; Ward, 1997; but see Harrison, 1987, 1993). In

addition to these, Andrews (1985, 1992) listed several craniodental apomorphies shared by *Proconsul* and extant apes: increased encephalization, frontal bone wide posteriorly narrowing anteriorly, a low-crowned P₃, reduced cusp heteromorphy on upper premolars, and a well-developed maxillary jugum. More recently, Rae (1999) grouped *Proconsul* among hominoids based on ape-like premaxillary-maxillary suture morphology, non-projecting nasal bones, a wide anterior palate, and a tall nasoalveolar clivus. Despite these characteristics, most authors agree that the overall design of *Proconsul* is fairly conservative (Harrison, 2002).

An alternative view given by Walker (1997) and others (e.g., Walker & Teaford, 1989; Rae, 1993, 1997) proposes that *Proconsul* is the sister-taxon to the Hominidae. Traits used to support this relationship include: brachial index, fibular and hallucial metatarsal morphology, scapular morphology, a postero-medially facing humeral head, presence of a sinus in the frontal bone, and a lack of ischial callosities (Napier & Davis, 1959; Walker, 1997). The acceptance of these postcranial features as *hominid* synapomorphies, however, requires that additional features shared by all extant apes be regarded as parallelisms (see Larson, 1998). This seems unlikely given the markedly conservative nature of the *Proconsul* postcranium (e.g., Harrison, 1982, 1987; Rose, 1993, 1997; Ward, 1997). Frontal sinuses, on the other hand, are found among extant catarrhines only in the African apes (Cave & Haines, 1940; Walker, 1997; Márquez *et al.*, 1999); *Pongo* can also exhibit frontal sinuses, but derived from the maxillary sinus rather than ethmoidal air cells (Márquez *et al.*, 1999). As such, the presence of a sinus in the frontal bone of *Proconsul* (Le Gros Clark & Leakey, 1951) could argue for its hominid affinities (Walker, 1997). A similar distribution has also been demonstrated for ischial

callosities. Ubiquitous among cercopithecoids, callosities are completely absent in African apes; hylobatids develop them fairly late (relative to cercopithecoids), but consistently during ontogeny, while they appear in *Pongo* even later and only variably (Pocock, 1925; Rose, 1974). If ischial callosities were present in the sister taxon to crown catarrhines (Delson & Andrews, 1975), then their absence in *Proconsul* could be a synapomorphy linking this genus with the great apes; note that this evidence also supports the hypothesis that *Proconsul* is a stem catarrhine retaining the primitive anthropoid condition. Neither position supports the hypothesis that *Proconsul* is a stem hominoid, which would require independent acquisition of ischial callosities in cercopithecoids and hylobatids.

Harrison (1982, 1987, 1993, 2002) has been the main proponent of a third phylogenetic placement for this genus. He and others (Harrison & Sanders, 1999) have argued that *Proconsul* lacks both cranial and postcranial features shared among crown catarrhines. Based on its many conservative features (Harrison 1982, 1987, 1993; Rose, 1997; Harrison & Rook, 1997; Walker, 1997; C. Ward, 1997), then, it can only be regarded as a stem catarrhine (Harrison, 2002).

Rangwapithecus

The specimen KNM-SO 700 was discovered at Songhor by L.S.B. Leakey and originally attributed to the genus *Proconsul* (Andrews, 1970); Andrews (1974) later made this specimen the holotype for *Rangwapithecus gordonii*. Originally recognized as a subgenus of *Dryopithecus* (Andrews, 1974) or *Proconsul* (Andrews, 1978), Pilbeam *et al.* (1977) elevated *Rangwapithecus* to generic status. Also included in this genus were remains of a smaller primate *R. vancouveringi* (Andrews, 1974); Harrison (1986).

however, transferred this species to the genus *Nyanzapithecus* and emended its spelling to reflect the two researchers for which it was named (*N. vancouveringorum*).

Rangwapithecus is known largely from mandibular and maxillary specimens, isolated teeth, and several referred postcrania.

Hypotheses about the phylogenetic relationships of this taxon follow those proposed for *Proconsul*, as most authors regard the two as belonging to the same lineage. Thus, *Rangwapithecus* is seen as belonging either to a radiation of stem catarrhines (e.g., Harrison, 1987, 1993, 2002), hominoids (e.g., Andrews, 1978), or hominids (Delson & Andrews, 1975; Rae 1993, 1997). Postcranially, *Rangwapithecus* and *Proconsul* are nearly identical, sharing a primitive catarrhine *Bauplan* (C. Ward, 1997). The palatal morphology of the most complete cranial specimen (SO 700) is also regarded as similar to that of *Proconsul* (e.g., Ward & Kimbel, 1983; Kelley & Pilbeam, 1986). Several authors (Ward & Kimbel, 1983; Ward & Pilbeam, 1983; Kelley & Pilbeam, 1986; Benefit & McCrossin, 1995), however, have remarked on similarities between SO 700 and extant hominids—particularly *Gorilla*—in some palatal features.

Morotopithecus

Early Miocene fossils were also discovered in Uganda, beginning with the fieldwork of Bishop and colleagues. A nearly complete palate, several other facial fragments, and some associated postcrania were discovered at the site of Moroto, Uganda and attributed to the largest species of *Proconsul*, *P. major* (Allbrook & Bishop, 1963; Bishop, 1964; Pilbeam, 1969). Although the craniofacial elements were considered to be very conservative (Allbrook & Bishop, 1963; Pilbeam, 1969; Andrews, 1978; Leakey *et al.*, 1988a; Begun, 1994), the lumbar vertebrae from Moroto have long been regarded as

reflecting a more orthograde posture, like those of extant hominoids (Walker & Rose, 1968; C. Ward, 1993, 1997; Sanders & Bodenbender, 1994; Rose, 1997; MacLatchy *et al.*, 2000). The discovery of additional postcranial remains led Gebo and colleagues (1997) to remove the large-bodied Moroto catarrhine from *Proconsul* (or *Afropithecus*, to which some had referred it—see below) and place it in the new genus *Morotopithecus*. Derived features of the vertebrae, distal femur, and scapular glenoid fossa have led some researchers to place *Morotopithecus* as the sister taxon to crown hominoids (MacLatchy *et al.*, 2000; Harrison 2002) or even hominids (see Sanders & Bodenbender, 1994; Gebo *et al.*, 1997); the proximal femur, on the other hand, retains many aspects of the inferred primitive catarrhine morphotype (MacLatchy *et al.*, 2000).

Afropithecus

The discovery of a fairly complete cranial specimen of a large-bodied primate from Kalodirr, Kenya added another genus to the cadre of Early Miocene East African catarrhines. In addition to this well-preserved cranium, a number of cranial, dental, mandibular, and postcranial elements have also been included in the *Afropithecus* hypodigm (Leakey & Leakey, 1986a; Anyonge, 1991). *Afropithecus* was initially regarded (Leakey & Leakey, 1986a) as autapomorphic, not clearly associated with any specimens known at the time. Andrews & Martin (1987) suggested that the maxillary fragment and associated teeth from Ad Dabtiyah, Saudi Arabia might belong to this genus; they and other researchers (e.g., Leakey *et al.*, 1988b; Andrews, 1992) have also likened the larger Moroto primate to *Afropithecus*. Features of the *Afropithecus* postcranium indicate a conservative, pronograde posture resembling that of *Proconsul* (e.g., Rose, 1997; Ward, 1997). Yet, Leakey & Walker (1997) have reported the presence

of a narrow, inclined incisive canal—a feature associated with extant hominids. Evidence of this latter feature has not been formally published, however, and cannot be assessed visually on the specimen as the nasal cavity is filled with matrix.

Those who view *Afropithecus* as belonging to the lineage of proconsulids regard it phylogenetically as a stem hominoid (e.g., Leakey *et al.*, 1988b; Rae, 1993, 1997; Leakey & Walker, 1997) or catarrhine (e.g., Harrison, 2002). Similarities in the craniofacial architecture of *Afropithecus* and *Propithecus* have led some (Leakey *et al.*, 1991; Benefit & McCrossin, 1995) to speculate that these features are representative of the primitive catarrhine morphotype, without disavowing the hominoid status of this genus. Finally, many authors have linked *Afropithecus* to Middle Miocene taxa from both Africa and Eurasia (Andrews, 1992; Ciochon & Etler, 1994; Rae, 1999; S. Ward *et al.*, 1999; Singleton, 2000; Ward & Duren, 2002).

Turkanapithecus

A second fairly complete cranium was announced simultaneously with *Afropithecus* and placed in the new genus *Turkanapithecus* (Leakey & Leakey, 1986b). Subsequent to these initial descriptions, the smaller catarrhine from Kalodirr has received far less attention than its counterpart (see Rae, 1993). Known primarily from a single, well-preserved cranium (KNM-WK 16950), several postcranial elements have also been attributed to *Turkanapithecus* (Leakey *et al.*, 1988a; Rose, 1993, 1994, 1997; C. Ward, 1997). As with most of the Early Miocene forms from East Africa, *Turkanapithecus* is thought to be a primitive hominid (Rae, 1993, 1997), basal hominoid (Leakey *et al.*, 1988b, Rose, 1997; Ward, 1997; Rae, 1999) or stem catarrhine (Harrison, 1993, 2002).

MIDDLE AND LATE MIOCENE EURASIAN TAXA

The Middle Miocene of Africa is poorly known relative to the Early Miocene fossil record, and none of the specimens from this interval was complete enough to include in this project. The discovery of significant new fossils (e.g., Conroy *et al.*, 1992; Ward *et al.*, 1999; Ishida *et al.*, 1999), however, gives hope that suitable material may be forthcoming. What is known of these Middle Miocene specimens is thought by many authors (e.g., Leakey, 1962; Pickford, 1985; Andrews, 1992; Benefit & McCrossin, 1995; McCrossin & Benefit, 1997; Ward *et al.*, 1999; Ward & Duren, 2002) to represent a more advanced grade of hominoid than the “proconsulids,” although both groups share several plesiomorphic features of the postcranium (e.g., Begun, 1992; Ward *et al.*, 1999; Ward & Duren, 2002). *Kenyapithecus*, the longest-known Middle Miocene hominoid from Africa, has been regarded by many researchers (e.g., Greenfield, 1980; Kelley & Pilbeam, 1986; Martin, 1986; Andrews & Martin, 1987; Andrews, 1992; McCrossin & Benefit, 1994; Moyà Solà & Köhler, 1995; Ward & Duren, 2002; but see Benefit & McCrossin, 1995) as a member of the Hominidae. Of the more recently discovered genera, Ward & Duren (2002) have suggested that both *Equatorius* and *Nacholapithecus* may represent an extension of the *Afropithecus* lineage; several authors (Andrews, 1992; Ciochon & Etler, 1994; Singleton, 2000) have also posed a similar hypothesis for *Otavipithecus* (but see Pickford *et al.*, 1997), albeit more tentatively. Note, however, that a close relationship between these Middle Miocene taxa and *Afropithecus* does not necessarily exclude them from the Proconsulidae (cf. Harrison, 2002).

Many researchers (e.g., Andrews & Tobien, 1977; Kelley & Pilbeam, 1986; Andrews, 1992; Andrews *et al.*, 1996; Ward *et al.*, 1999; Ward & Duren, 2002) have

favorably compared *Kenyapithecus* dental remains with some or all of the specimens from the Middle Miocene sites of Paşalar and Çandır in Turkey, Neudorf Sandberg in the Czech Republic, and Klein Hadersdorf, Austria; Begun (2000, 2002), argued that material attributed to *Equatorius africanus* was in fact congeneric with *Griphopithecus*—the latter genus name having priority. This affinity appears to be the best-known connection between African hominoids and putative hominoids and the Middle Miocene hominoids of Eurasia.

Dryopithecus

Specimens attributed to *Dryopithecus* (Lartet, 1856) represent some of the first fossils reliably placed in the Hominoidea. Through the ensuing development of paleoprimatology, fossil materials from East Africa, western Europe, eastern Europe, Turkey, China, and the Indo-Pakistan Siwaliks have all been attributed, at one time or another, to this genus (e.g. Simons & Pilbeam, 1965; Andrews, 1978; Szalay & Delson, 1979; Xue & Delson, 1989; see Begun, 2002; Kelley, 2002). Many of the non-European specimens have since been transferred out of this genus, though material from the Gansu Province, China is still referred here. While the holotype of *Dryopithecus* came from St. Gaudens, France, this genus is best known anatomically from the Spanish site of Can Llobateres and the Hungarian site of Rudabánya (Andrews, 1992; Moyà Solà & Köhler, 1993, 1995; Andrews *et al.*, 1996; Begun & Kordos, 1997). Excavations at both sites have yielded many cranial and postcranial fossils, including three partial crania and at least one partial skeleton (Moyà Solà & Köhler, 1993, 1995; Kordos & Begun, 2001; see also Kordos & Begun, 1999).

As summarized in Chapter 1, there are several competing hypotheses about the phylogenetic relationships of *Dryopithecus*. Begun (e.g., 1994, 2002) and colleagues (Begun & Kordos, 1997; Begun *et al.*, 1997; Kordos & Begun, 2001) argue that *Dryopithecus* is the sister taxon to the African apes, based on a suite of shared, derived characters (see Begun, 1994: Table 4). Others (e.g. Andrews & Martin, 1987; Andrews, 1992; Andrews *et al.*, 1996; Rose, 1997; C. Ward, 1997) have argued that while *Dryopithecus* shares apomorphic features with extant hominids, it does not clearly display hominine morphology. Alternatively, Moyà Solà & Köhler (1993, 1995) and Köhler *et al.* (2001) include many of the Middle and Late Miocene Eurasian hominoids, including *Dryopithecus*, in the pongine lineage. Finally, Benefit & McCrossin (1995; McCrossin & Benefit, 1997) have suggested that this genus is merely an extension of a more primitive radiation of hominoids, only broadly ancestral to extant apes.

Sivapithecus

Fossil specimens from the Siwalik localities of India and Pakistan have been discovered and described now for nearly 200 years; during this time, specimens have undergone a complex series of taxonomic naming, renaming, and consolidating (see Kelley, 2002 for an excellent review of this history). Though fossil hominoids are rare in this fauna, a substantial collection of specimens attributed to *Sivapithecus* has been accumulated (e.g., Pilbeam *et al.*, 1980). Known primarily from cranio-dental remains, several provocative postcranial specimens are also attributed to this genus. Kelley (2002) recognizes three species of *Sivapithecus* (*S. indicus*, *S. sivalensis*, and *S. parvada*) all deriving from the Siwaliks; specimens from other sites that have been referred to

Sivapithecus (see Szalay & Delson, 1979) have mostly been transferred to other taxa (e.g., Alpagut *et al.*, 1996; see Andrews *et al.*, 1996; Kelley, 2002).

A variety of opinions about the affinities of this genus have been argued through the history of Siwaliks research. The discovery of a fairly complete palate and upper face of *S. indicus* (Pilbeam, 1982), however, convinced many that this genus belonged to the orangutan lineage. The subsequent discovery of humeri attributed to *Sivapithecus* cast doubt on this conclusion (Pilbeam *et al.*, 1990; Pilbeam, 1997; Ward, 1997; Pilbeam & Young, 2001). On one hand, *Sivapithecus* and *Pongo* share a suite of craniodental features (e.g. Andrews & Cronin, 1982; Ward & Kimbel, 1983; Ward & Brown, 1986; Andrews & Martin, 1987; Andrews, 1992; Begun, 1994; Moyà Solà & Köhler, 1993, 1995; Begun *et al.*, 1997), some of which are not found in any other primates; the terrestrially adapted *Sivapithecus* humerus, however, lacks many of the presumed synapomorphies of the arboreal, orthograde extant hominids (Pilbeam, 1996, 1997; Pilbeam & Young, 2001; Kelley, 2002; but see Richmond & Whelan, 2001). As such, the overall morphology of *Sivapithecus* could represent a more primitive hominoid condition (Corrucini & McHenry, 1980; Pilbeam *et al.*, 1990; Pilbeam & Young, 2001), with its pongine affinities independently derived (Pilbeam, 1997). Indeed, some authors (e.g., Leakey *et al.*, 1991; Benefit & McCrossin, 1993, 1995) have concluded that similarities in the middle and upper facial morphology of *Propliopithecus*, *Afropithecus*, *Victoriapithecus*, *Sivapithecus*, and *Pongo* suggest that this suite of features was part of the ancestral catarrhine morphotype. As such, they would be primitive retentions in *Sivapithecus*. Nevertheless, most workers today probably accept the pongine affinities of this taxon.

Graecopithecus

The type specimen of *Graecopithecus* is a badly preserved mandible from the Late Miocene site of Pyrgos, southern Greece. Although Freyberg originally referred to it in a faunal list as the cercopithecoid *Mesopithecus* (see Begun, 2002), von Koenigswald (1972) placed it in a new hominoid genus *Graecopithecus*. Subsequently discovered specimens from northern Greece (e.g., Bonis *et al.*, 1975, 1990; Bonis & Melentis, 1977; Koufos *et al.*, 1991; Bonis & Koufos, 1993; Koufos, 1993, 1995) were better preserved and attributed to *Ouranopithecus macedoniensis* (Bonis & Melentis, 1977); yet, mandibular remains of *Ouranopithecus* are not significantly distinct from the type mandible of *G. freybergi* (owing, perhaps, to the poor preservation of the latter). Therefore, the genus name *Graecopithecus* is retained throughout this work.

Debates over the phylogenetic status of *Graecopithecus* largely mirror those surrounding *Dryopithecus*. Initially, this genus was considered an ally to *Sivapithecus* and, by extension, a pongine (e.g., Andrews & Cronin, 1982; Kay & Simons, 1983; Andrews, 1985). Fewer researchers (Moya Solà & Köhler, 1993, 1995; Köhler *et al.*, 2001) still support this view. The consensus opinion holds that *Graecopithecus* is a stem hominine, sharing several features with extant African apes and humans (Andrews, 1992; Begun, 1994, 2002; Benefit & McCrossin, 1995; Andrews *et al.*, 1996; Begun & Kordos, 1997; Begun *et al.*, 1997). Dean & Delson (1992) have suggested that *Graecopithecus* shares some features specifically with extant gorillas, particularly in the supraorbital region. Alternatively, Bonis & Koufos (e.g., 1993, 1994, 1997, 2001) argue that it belongs to the human lineage, based largely on dental evidence and glabellar morphology shared with *Australopithecus* spp. (see Bonis & Koufos, 2001: 264).

PLIO-PLEISTOCENE HOMININS

Connections between any Miocene hominoid genus and those of the living apes are tenuous at best. The pongine affinities of *Sivapithecus* represent the best ancestor-descendant hypothesis, but this is by no means uncontested. Fossil hylobatids and pongines are known from Pleistocene sites in Asia (see, e.g., Szalay & Delson, 1979), but these specimens have either been or probably should be referred to the extant genera (see Kelley, 2002). Among extant hominines, the fossil record of gorillas and chimpanzees is non-existent or, at best, dubious (Cote, 2003). Only the human lineage has a rich diversity of fossil forbears.

Still, the link between Miocene apes and Pliocene hominins is not clear. The hypothesis that the common ancestor of extant hominines arose in Europe and then migrated to Africa (e.g., Begun *et al.*, 1997; Sterward & Disotell, 1998; Begun, 2002) has gained support in the last decade (but see Pilbeam & Young, 2001; Pilbeam, 2002). Several authors have described the African ape affinities of *Graecopithecus* as a basal hominine, primitive gorilla, or stem hominin. The fossil record in Africa between 14-7 Ma is poorly known, however, yielding only fragmentary hominoid remains (e.g., Hill & Ward, 1988). This lack makes it difficult to assess the validity of a possible African hominine ancestor. Recent discoveries of the fossil hominin *Ardipithecus ramidus* (Haile-Selassie, 2001) and putative hominins *Orrorin tugenensis* (Senut *et al.*, 2001) and *Sahelanthropus tchadensis* (Brunet *et al.*, 2002) from the Late Miocene of Africa may help to bridge the gap between extant hominines and Miocene apes.

Australopithecus

The discovery and publication of a juvenile hominin skull from Taung, South Africa initiated a slow shift towards Africa in the search for human origins. Though largely unaccepted as such at the time, *Australopithecus africanus* (Dart, 1925) represented a fossil human substantially more primitive than those already known. The eventual debunking of Piltdown Man confirmed for most researchers the place of *Australopithecus* in the human lineage (White, 2002). Since that time, dozens of new sites and hundreds of new fossils have been discovered. In addition to the South African species *A. africanus*, most workers also recognize the East African species *A. afarensis* (Johanson *et al.*, 1978) and the more primitive *A. anamensis* (Leakey *et al.*, 1995). Fragmentary remains from the Koro Toro region of Chad (Brunet *et al.*, 1995) and from Bouri, Ethiopia (Asfaw, 1999) have each been assigned to new species (*A. bahrelghazali* and *A. garhi*, respectively); widespread acceptance of these designations, however, is pending additional material and critical comparative analyses. Specimens of the robust lineage of australopiths are not included in this genus (see below). In all, *Australopithecus* is well represented by a multitude of cranial, mandibular, and postcranial elements. The eventual excavation and preparation of the nearly complete, articulated skeleton from Sterkfontein (Clarke, 1998) will certainly add an exclamation point to this.

Most researchers regard *Australopithecus* as broadly ancestral to the genus *Homo* (White, 2002). Within this genus, however, opinions vary as to which species is closest to the more modern hominins. *A. anamensis* is likely the most primitive *Australopithecus* species (Leakey *et al.*, 1995), exhibiting several features that are intermediate in

morphology between the stem hominin *Ardipithecus* and later *A. afarensis* (Leakey *et al.*, 1995, 1998; C. Ward *et al.*, 1999; Wood & Richmond, 2000). *A. afarensis*, the best known species of early hominin, may have been ancestral to some or all of the later hominin species (White, 2002), yet it does not bear a special affinity to early members of the genus *Homo* (e.g., White *et al.*, 1981). *A. africanus* has long been regarded as a more advanced grade of *Australopithecus* and perhaps ancestral to *Homo* (Campbell, 1963; Le Gros Clark, 1964; Robinson, 1972; Olson, 1985; Tobias, 1991); this opinion is rejected, however, by those who feel that *A. africanus* is derived in the direction of *Paranthropus* (e.g., Rak, 1983). Finally, Asfaw *et al.* (1999) put forth the newly named *A. garhi* as the immediate precursor to the genus *Homo*. Evaluation of this hypothesis awaits further analysis of these fragmentary remains.

Paranthropus

The first specimens of a “robust” lineage of humans from South Africa were placed into the taxon *Paranthropus robustus* by Broom (1938). In 1959, L.S.B. Leakey announced the discovery of *P. [“Zinjanthropus”] boisei*, a robust australopith from Olduvai Gorge, Tanzania. The highly derived craniodental morphology of *Paranthropus* hindered its comparison with the more primitive *Australopithecus* species. Yet, some authors recognized distinctly robust features in *A. africanus* (e.g., Johanson & White, 1979; White *et al.*, 1981; Rak, 1983; Tobias, 1985). The discovery of a more primitive cranium of *Paranthropus* (Walker *et al.*, 1986), however, demonstrated a unique combination of features seen in *Paranthropus* and *A. afarensis* (Kimbel *et al.*, 1988). Currently, there is a broad consensus over the number of species within *Paranthropus*: *P. robustus*, *P. aethiopicus*, and *P. boisei*. Grine (1993) provided a concise review of the

phylogenetic hypotheses proposed for *Paranthropus* and other early hominins. Most of these recognize the holophyly of *Paranthropus* either as geographically diverse subspecies (e.g., Tobias 1980, 1988) or as a separate, derived clade of species (e.g., Robinson, 1972; Tobias 1980, 1988; White *et al.*, 1981; Grine, 1988; Kimbel *et al.*, 1988). Skelton *et al.* (1986) also recognized the holophyly of *Paranthropus*, but placed it as the sister taxon to *Homo*. In contrast Walker *et al.* (1986) argued that *Paranthropus* is polyphyletic, with separate eastern and southern African lineages derived independently. McCollum (1999) has resurrected this notion by suggesting that the suite of synapomorphies uniting this genus might derive morphogenetically from a single adaptation in dental size and proportions (p. 304).

African early *Homo*

By the mid-twentieth century, a number of fossil human specimens had been discovered throughout Eurasia. The division between early human fossils (*Australopithecus* and *Paranthropus*) and these later specimens of *Homo* was demarcated by a threshold of cranial capacity. This “cerebral Rubicon” was variously placed between 700-800 cm³ (see Leakey *et al.*, 1964); specimens with smaller brains were not considered to be in the modern human genus. This changed when Leakey and colleagues (1964) announced a new species of smaller-brained *Homo* (but see Holloway, 1980) from Olduvai Gorge: *H. habilis*. Since then, a multitude of cranial and postcranial remains attributed to both *H. habilis* and *H. erectus* have been discovered in East Africa. Groves (1989) and Wood (1992) argued that the polymorphic *H. habilis* should be split into two species, with KNM-ER 1470 typifying the new *H. rudolfensis*. This taxonomy reflects a consensus opinion (Dunsworth & Walker, 2002) and is used here. Note, however, that a

new find by Blumenschine *et al.*, (2003) may prove ER 1470 to be conspecific with the type specimen of *H. habilis*; this would make *H. rudolfensis* a junior synonym of *H. habilis*, although it does not necessarily disprove the existence of two species within the *H. habilis* (*sensu lato*) hypodigm (see Wood, 1992). This new fossil would also seem to cast doubt on the claim of Leakey *et al.* (2001) that ER 1470 is generically distinct from *Homo*, belonging in the newly named genus *Kenyanthropus*. The species *H. ergaster* (Groves & Mazak, 1975) is also regarded here as a junior synonym of *H. erectus*.

The phylogenetic relationships of early *Homo* are not easily determined. Lieberman *et al.* (1996) demonstrated that ER 1470 has facial affinities with *Australopithecus*, but an expanded brain case. This contrasts with an ER 1813 group that has a smaller brain, but a face more like later *Homo*. This mosaic of advanced features in both groups precludes a consensus on the origin of these species or their relationship with *H. erectus* (see Dunsworth & Walker, 2002). Most researchers concur, however, that *H. erectus* (or some subset thereof) was ancestral to *Homo sapiens*.

SUPRAORBITAL MORPHOLOGY IN PHYLOGENY RECONSTRUCTION

The above overview of hominoid and putative hominoid systematic relationships was based on analyses of a wide range of character complexes. As this project presents detailed examinations of supraorbital and palatal morphologies, a brief summary of previous studies of these regions is given here. Circumorbital morphology has always been an important area of research in primate evolution. The postorbital bar is common to all living primates and found in few other mammalian taxa—never consistently at the ordinal level. Similarly, a postorbital septum divides all living haplorhines from the

strepsirrhine primates. Because of this, both phylogenetic and functional analyses have focused on this region in discussing the origin and evolution of primate taxa. In phylogenetic analyses of the hominoid clade, more attention has been paid to the supraorbital region, as postorbital bars and septa are invariably present in all apes.

Relatively simple terminology is typically used to describe supraorbital morphology in extant hominoids: supraorbital ridges or rims in hylobatids, costae (i.e. ribs) in *Pongo* (and *Paranthropus*; see Clarke, 1977), a supraorbital torus for African apes, and superciliary arches in humans. Strict (or even similar) definitions of these terms, however, are not often observed (compare, e.g., Begun, 1994; Benefit & McCrossin, 1995). Moreover, variability observed in the supraorbital region reduces the explanatory power of any monolithic definition. Several authors (Santa Luca, 1980; Aiello & Dean, 1990; Dean, 1993) have used a system that divides human supraorbital morphology into a glabellar portion, superciliary arches (glabella to supraorbital notch), and supraorbital trigones (supraorbital notch to the fronto-malar suture). While useful in descriptive terms, this approach does not help to differentiate among the diversity of character states found among extant hominoids and their allies. Discussions of this region in fossil taxa are generally limited to using the above terminology—often with a qualifier (e.g. “poorly developed”)—as the character state for a taxon (e.g. Kay & Simons, 1983; Kelley & Pilbeam, 1986; Ward & Brown, 1986; Alpagut *et al.*, 1996; Begun *et al.*, 1997), or creating finely detailed descriptions of the anatomy (e.g. Begun, 1994). Due, in part, to the inherently qualitative nature of this system, however, disagreement still abounds.

Quantitative analyses of supraorbital morphology have been few, and typically use caliper data. Bilsborough & Wood (1988), for example, used three bilateral

measurements (transverse breadth, lateral thickness, transverse arc of superior toral border) and a midline measurement of medial thickness to characterize the brow. While this method does quantify some of the relevant morphology, it lacks the detailed resolution of descriptive approaches. Dean (1993) has shown that geometric morphometrics can be successfully applied to characterize this region in three dimensions for the human lineage. Similar studies have also adopted this approach with cercopithecines (Frost *et al.*, 1998; Marcus *et al.*, 1999), as well as preliminary analyses of hominoid brows (McNulty, 2001). These three-dimensional approaches remove much of the subjectivity inherent to qualitative description, yet still incorporate more of the detailed morphology than do traditional metrics.

PALATAL MORPHOLOGY IN PHYLOGENY RECONSTRUCTION

The persistence of palatal remains in the fossil record has made this anatomical feature important in comparative analyses. The shape of the dental arcade was used historically (e.g., Lewis, 1934; Gregory *et al.*, 1938; Simons & Pilbeam, 1965) to distinguish members of the human lineage from other hominoids. Harrison (1987) and others (Rae, 1993, 1997; Harrison & Rook, 1997) have cited palatal features among the few craniodental synapomorphies distinguishing hominoids from the inferred ancestor of crown catarrhines.

In the past twenty years, the phylogenetic import of the palate has largely focused on the subnasal region. Ward and colleagues (Ward & Kimbel, 1983; Ward & Pilbeam, 1983; Ward & Brown, 1986; Brown & Ward, 1988; McCollum *et al.*, 1993; McCollum & Ward, 1997; McCollum, 1999) have produced detailed descriptive and traditional

morphometric analyses of this morphology in hominoids. Early work recognized three distinct subnasal morphotypes based on examinations of both fossil and extant hominoid specimens: a Miocene African pattern, an Asian pattern, and a Pliocene-Recent African pattern. The Miocene African pattern is characterized by features such as a short premaxilla, an oval-shaped nasoalveolar clivus (in sagittal section), a medio-laterally expanded incisive fossa, and a broad incisive foramen. This morphology is shared by *Proconsul* and most (but see *Afropithecus* and *Rangwapithecus* above) of its Miocene catarrhine contemporaries (e.g., Ward & Kimbel, 1983; Rae, 1997). The hylobatids also share this pattern, while displaying some additional autapomorphic features (McCollum & Ward, 1997). As the Miocene African morphotype is generally similar to morphology found in cercopithecoids, it is presumed to resemble the ancestral condition for extant catarrhines (e.g. Ward & Kimbel, 1983).

The Asian pattern is shared definitively by *Sivapithecus* and *Pongo* (Ward & Pilbeam, 1983; Ward & Kimbel, 1983; Ward & Brown, 1986; Brown & Ward, 1988), and characterized by several unique features: a long, posteriorly arching premaxilla; a small recessed incisive fossa; extreme reduction in the caliber of the incisive canal; and little or no change in relief between the nasoalveolar clivus and the nasal floor. The third pattern, Pliocene-Recent African, is found in *Pan*, *Gorilla*, and early fossil humans (Ward & Kimbel, 1983). This morphology is characterized by a moderately long premaxilla that is ovoid in section (although truncated in male gorillas), a broad incisive fossa near the nasal aperture, a large incisive canal, and stepped relief between the nasoalveolar clivus and the floor of the nasal cavity. The autapomorphic modern human cranium is thought to have a modified Pliocene-Recent African pattern (Ward & Kimbel, 1983). Other fossil

hominoids have been assigned to these broad categories with somewhat less consensus (compare, e.g., Begun, 1994; Moyà Solà & Köhler, 1995).

McCollum & Ward (1997) presented traditional morphometric data on subnasal morphology from four distance measurements of subnasal elements. This work supported earlier descriptive analyses (e.g., Ward & Kimbel, 1983; McCollum *et al.*, 1993), finding 3 distinct morphotypes among extant hominoids. Not all fossil specimens conform to these groups, however. For example, Ward & Kimbel (1983) and others (e.g., Ward & Brown, 1986; Moyà Solà & Köhler, 1993, 1995) have argued that *Dryopithecus* shares (perhaps somewhat modified; Ward & Kimbel, 1983) a Miocene African subnasal morphology with *Proconsul*, *Hylobates*, and others. Alternatively, Begun (1992, 1994) has grouped *Dryopithecus* with the extant hominines based on these same features. Benefit & McCrossin (1995) offer a third alternative, arguing that morphology shared by some hylobatids and gorillas may be primitive for hominoids, making both of the previous comparisons meaningless.

These studies demonstrate how the complex morphology of this region, combined with the diversity of Miocene hominoids, can make it difficult to place fossil taxa into such broad descriptive categories. The aim of this work is to use geometric morphometric analyses to go beyond this typological approach in examining palatal affinities and to explore variation that corresponds to differences between extant crown clades.

CHAPTER 3: MATERIALS

This chapter outlines the extant and fossil samples used in this project. For extant taxa, this includes details of taxonomy, sample size, sex, age and the criteria used in choosing particular specimens. Fossil specimens are discussed with references to provenance, the institutions in which they are kept, and brief descriptions of their preservation.

EXTANT SPECIMENS

This study included a comparative sample of specimens from each of the five extant hominoid genera (*Gorilla*, *Homo*, *Hylobates*, *Pan*, and *Pongo*). Excepting *Hylobates*, specimens from each of the commonly recognized subspecies were sampled in order to characterize the diversity within each species and genus. The possibility of sampling every subspecies of hylobatid was rejected both because of time constraints and to avoid heavily biasing statistical models toward this genus. In addition to extant hominoids, several other anthropoid taxa were sampled, including two cercopithecines (*Papio hamadryas anubis* and *Cercopithecus mitis*), one colobine (*Procolobus badius*), and two platyrrhines (*Ateles geoffroyi* and *Cebus apella*). These were used to provide a context for comparing hominoid morphologies within a broader spectrum of anthropoid crania. Moreover, hypotheses concerning stem hominoids and putative hominoids cannot be adequately assessed without comparative samples of both Old World monkeys and New World anthropoids. All non-hominoid adult samples were comprised exclusively of a single subspecies.

The target sample size for each species of great ape was 50 adult specimens from one representative subspecies, plus an additional 20 specimens of any other subspecies sampled. This goal was met or exceeded in most cases except for *Gorilla gorilla graueri* and *Pan troglodytes schweinfurthii*. As the primary focus of this study was on generic-level analyses, hylobatid sampling was approached differently due to the large number of taxa (see below). Non-hominoid anthropoid taxa were sampled at 10 adult specimens for each species. For all extant genera, every effort was made to evenly represent male and female specimens. Hominid specimens whose sex was not clearly indicated on labels were judged to be male or female based on common sexually dimorphic features (canine size, cranial crests, robusticity). Hylobatid specimens of unknown sex were labeled as such and only used in pooled-sex analyses; three bonobos were also treated in this manner. Because the project was designed to circumvent difficulties with missing data (specifically, incomplete fossil specimens), some incomplete extant specimens were included in analyses for which they preserved the relevant morphology. Table 3-1 provides a summary of the total numbers of extant specimens used in this project.

Only adult specimens were included in this study, as judged by full occlusion of both M3s and canines. Several additional criteria were used to determine which specimens were sampled. Firstly, all zoo specimens and those with an obvious pathology were excluded. Secondly, specimens were chosen based on the preservation and discernibility of landmarks and morphology. To bolster sample sizes, some damaged crania were included for analyses in which only the undamaged region of the specimen was examined. Thirdly, specimens with recorded sex, weight, and locality information were given preference over others.

Table 3-1 Sample sizes divided by species, subspecies and sex for all extant taxa used in this study.

	Female	Male	Unknown	Total
<i>Gorilla</i> (n=119)				
<i>G. gorilla beringei</i>	10	15	--	25
<i>G. gorilla gorilla</i>	34	57	--	91
<i>G. gorilla graueri</i>	1	2	--	3
<i>Homo sapiens</i>	20	20	--	40
<i>Hylobates</i> (n=136)				
<i>H. agilis agilis</i>	10	14	--	24
<i>H. agilis albibarbis</i>	8	8	--	16
<i>H. agilis unko</i>	3	7	3	13
<i>H. muelleri abbotti</i>	17	14	5	36
<i>H. muelleri funereus</i>	7	10	--	17
<i>H. syndactylus syndactylus</i>	16	14	--	30
<i>Pan</i> (n=164)				
<i>P. troglodytes schweinfurthii</i>	3	10	--	13
<i>P. troglodytes troglodytes</i>	50	30	--	80
<i>P. troglodytes verus</i>	12	12	--	24
<i>P. paniscus</i>	24	20	3	47
<i>Pongo</i> (n=79)				
<i>P. pygmaeus abelii</i>	11	11	--	22
<i>P. pygmaeus pygmaeus</i>	31	26	--	57
<i>Ateles geoffroyi vellerosus</i>	5	5	--	10
<i>Cebus apella</i>	5	5	--	10
<i>Cercopithecus mitis stuhlmanni</i>	5	5	--	10
<i>Papio hamadryas anubis</i>	5	5	--	10
<i>Procolobus badius oustaleti</i>	5	5	--	10

Gorilla

Specimens of *Gorilla gorilla* were measured from samples at the American Museum of Natural History (New York, U.S.A.), Museum of Comparative Zoology (Cambridge, U.S.A.), Humboldt University Museum für Naturkunde (Berlin, Germany), Powell-Cotton Museum (Birchington, U.K.), and Smithsonian Institution—National

Museum of Natural History (Washington, D.C., USA). *G. g. gorilla* specimens comprise the majority of this sample and represent several populations from both Cameroon and the Republic of Congo. *G. g. beringei* specimens derive mostly from two populations in the Virunga and Alumbongo mountain ranges of the Democratic Republic of Congo. The scarcity of eastern lowland gorillas in museum collections resulted in the poor representation of *G. g. graueri* in this study. These all derive from a single population 80 km northwest of the Boko village in the Democratic Republic of Congo.

Hylobates

Hylobatid specimens were collected at the American Museum of Natural History, Museum of Comparative Zoology, and Humboldt University Museum für Naturkunde. Among living hominoids, only *Hylobates* is represented by a complicated hierarchy of subgeneric, specific, and subspecific taxonomic groups. Sampling of this genus, then, was a compromise between adequately representing its diversity without unduly biasing the hominoid sample toward hylobatids. Of the four subgenera of *Hylobates*, two were included in this project: *H. (Hylobates)* and *H. (Symphalangus)*. The lar group is represented by *H. agilis* and *H. muelleri*. Specimens of *H. a. agilis* make up the majority of the agile gibbon sample and are mainly from two populations at Macarah Doewa and Boekit Sanggoel, Sumatra. *H. a. unko* specimens derive from several different Sumatran populations. The agile gibbon from Borneo, *H. a. albibarbis*, was measured from the populations of Sampit Parit and Riam. The three subspecies of Mueller's gibbon are all found in Borneo. *H. m. abbotti* is the main representative of this species and was chiefly measured from populations at Perboewa and Kapuas. *H. m. funereus* was sampled from Badang and Peleben and makes up the rest of the sample. Siamangs (*H. syndactylus*)

were sampled primarily from populations in Sumatra near Moeara Doewa, Boekit Doeloe, and Loeboek Linggan.

The hylobatid samples included here represent diversity at subspecific, specific, and subgeneric levels without sampling each hylobatid taxon. In this manner, the total contribution of *Hylobates* to the hominoid sample is roughly equivalent to those of the other ape genera, while still representing much of the diversity in this genus.

Homo

Modern human specimens were collected from the Department of Anthropology at the American Museum of Natural History. The sample was taken from two populations chosen to represent some of the diversity in modern humans populations: Keszö-Hidegkuti (Hungary) and Calabar (Nigeria). The degree of modern human diversity, combined with a highly derived cranial morphology makes it unlikely that a complete sampling of modern human variability can inform analyses of other extant and fossil hominoids. Therefore, forty adult specimens (ten males and ten females from each population) were included in this study.

Pan

Specimens of *Pan troglodytes* were measured in the American Museum of Natural History, Museum of Comparative Zoology, Peabody Museum (Cambridge, U.S.A.), Powell-Cotton Museum, and Smithsonian Institution. *Pan paniscus* crania were measured primarily at the Musée royal de l'Afrique Centrale (Tervuren, Belgium), with several additional specimens measured at the American Museum of Natural History, Museum of Comparative Zoology, and Smithsonian Museum of Natural History. *P. t. troglodytes* makes up most of the common chimpanzee sample, with specimens

representing populations from Cameroon, the Republic of Congo, Ivory Coast, and Liberia. Most of the *P. t. verus* sample was taken from a single population near Monrovia, Liberia; additional specimens came from Durkoue, Ivory Coast. *P. t. schweinfurthii* specimens were from the Republic of Congo, Democratic Republic of Congo, and Uganda. The bonobo sample derives from several populations, all from the Democratic Republic of Congo. The 47 bonobo specimens make up roughly one quarter of the total sample of *Pan*.

Pongo

Orangutan specimens were measured at the American Museum of Natural History, Museum of Comparative Zoology, Humboldt University Museum für Naturkunde, and Smithsonian Institution. Taxonomically, this study treated the two orangutan populations as subspecies of *Pongo pygmaeus*. *P. p. pygmaeus* specimens make up the majority of the sample and mostly represent three Borneo river localities: Sakaia, Semandang, and Kendawangan. Specimens of *P. p. abelii* were taken from a single population in the Aru Bay area, Sumatra.

Non-hominoid Taxa

The majority of non-hominoid specimens were collected from the American Museum of Natural History. Some specimens of *Papio hamadryas anubis* were measured at the Humboldt University Museum für Naturkunde, and a few specimens of *Procolobus* and *Ateles* were collected from the Museum of Comparative Zoology. All five non-hominoid taxa have a sample size of five adult females and five adult males.

FOSSIL SPECIMENS

Miocene and Plio-Pleistocene hominoid and non-cercopithecoid catarrhine specimens are discussed below under their generic designations. In addition to these fossil taxa, the basal catarrhine *Propliopithecus zeuxis* was also included for comparison. An effort was made to measure original specimens although some high-resolution casts were included due to the unavailability of specimens or funds—these are indicated in the discussion below. Morphometric analysis of fossil specimens is easily confounded by morphology that is warped or missing. In landmark-based morphometrics, these are essentially the same problem, as altered morphology is typically left out of analysis. To increase the number of fossil specimens that were analyzed, missing or warped bilateral landmarks were reconstructed by reflecting their antimeres across the sagittal plane. This process is discussed in detail in Chapter 4.

Basal catarrhines

Propliopithecus

Data from three specimens of *Propliopithecus* [= *Aegyptopithecus*] *zeuxis* were collected from high-resolution casts: DPC 2803, DPC 3161, and CGM 42842 (Simons, 1987). All three preserve most of the facial morphology, with little or no neurocranial anatomy present. DPC 2803 is an old adult specimen preserving the entire face except the right zygoma and superior margin of the nasal aperture. It is not clear that the termination of the right frontal is a suture rather than a break and so the supraorbital line was reconstructed by mirroring the morphology from the left side. In the palate, I¹-P³ are missing from both sides; the alveoli are intact, however, so the corresponding inter-dental

landmarks were collected. DPC 3161 is a nearly adult specimen with M³s not quite in full occlusion. This specimen is missing most of the left premaxilla and the superior margin of the nasal aperture; the right premaxilla is well preserved, however, and was therefore used to reconstruct the missing points. I¹-C are missing from both sides. CGM 42842 is another old individual, missing much of the premaxillary morphology; this prevented collection of any landmarks anterior to the canines. Most of the nasal aperture margin is also broken. None of these three specimens is visibly warped.

Early Miocene putative hominoids

Afropithecus

The partial cranium of *Afropithecus turkanensis* (KNM-WK 16999; Leakey & Leakey, 1986a) from the locality of Kalodirr, Kenya was measured at the National Museums of Kenya (KNM) in Nairobi. This fossil consists almost entirely of a face, with little neurocranium preserved. The right half is in good condition, preserving most of the facial anatomy. The right zygomatic arch is broken near the zygomatico-temporal suture. The left half of this specimen is broken laterally, truncating the malar near its root and eliminating the lateral orbital margin. Orbital and nasal apertures are filled with matrix. The left palatine process of the maxilla is significantly warped, compressing it medially posterior to the canine. This warped morphology was treated as missing data and reconstructed during data processing.

Morotopithecus

Data for *Morotopithecus* were collected from a high-resolution cast of UMP 62-11 (Bishop & White, 1962). This is a fairly complete palatal specimen preserving most of the dental, alveolar, and nasal floor morphology. The medial aspect of the palate is

broken posterior from mid-M³. Both tooth rows are complete with the exception of a missing right I¹. Despite minimal preservation of morphology superior to the palate, the malar root origin is discernible on the left side.

Proconsul

A single specimen of *Proconsul heseloni* (RU 16000) was included in this project. Data were collected on the original specimen at the National Museums of Kenya. This fossil is a nearly complete palate attached to a substantial portion of the left zygoma (Teaford *et al.*, 1988). Although the anterior dentition is missing, the alveoli and subnasal clivus morphology are intact on the right side; the left anterior inter-dental landmarks have been eroded away and were therefore reconstructed from the right. Posterior on the palate, the right horizontal plate of the palatine bone is broken. There is some disagreement over the species designation of this fossil (see, e.g., Walker, 1997), but this does not impact the generic-level analyses presented here.

Rangwapithecus

The type specimen of *Rangwapithecus gordonii* (SO 700; Andrews, 1974) was measured from the original specimen at the National Museum of Kenya. This is a nearly complete palate preserving much of the superior maxillary morphology, but truncated below the orbital rims. The palate itself is well preserved and appears to be undistorted. It is missing only the anterior dentition and pieces of the post-M³ alveolar region. The left anterior alveoli have been eroded and were not used here. Posterior incisive canal landmarks are not discernible in the nasal cavity; the malar root origin, however, is preserved on the right side of the specimen.

Turkanapithecus

The only known cranial specimen of *Turkanapithecus kalakolensis* (WK 16950) was examined from original material at the National Museums of Kenya. This specimen is a partial cranium retaining much of the overall facial morphology and quite a bit of the frontal bone (Leakey & Leakey, 1986b). The right face is fairly well preserved with most of the orbital rim intact, although somewhat warped inferior to frontomale orbitale. The right zygomatic is preserved intact along with most of the glenoid fossa. The left side is somewhat less well preserved, with gaps and distortion in the orbital region. This morphology was reconstructed from the right side. The inferior premaxilla is completely missing, as is much of the nasal aperture margin.

Late Miocene hominoids

Dryopithecus

Dryopithecus brancoi is represented by three specimens from Rudabánya, Hungary. Data from RUD 77 (Kordos, 1987) and RUD 200 (Kordos & Begun, 2001) were collected on original specimens at the Geological Institute of Hungary in Budapest. RUD 77 is a small cranium preserving parts of the neurocranium and upper face (Kordos, 1987). While much of the right neurocranium is preserved, most of the left neurocranium and the entire occipital region are missing. The right orbital rim extends as far as the fronto-malar suture. RUD 200 is a small female cranium with recently erupted M3s (Kordos & Begun, 2001). The right superior neurocranium is preserved from the supraorbital region back to inion. Some of the left neurocranium is preserved anteriorly. The connection between the neurocranium and the right zygomatic is only along the orbital ridge, but is undistorted and fits tightly together. The malar itself is truncated just

posterior to jugale. The supraorbital region is preserved on the right side and then laterally to the midline of the left orbit. The palate connects to the malar region via a thin, but well-preserved zygomatic root. The palate ends just posterior to M^2 , although both M^3 's were recovered. There is no evidence for the palatine-maxillary suture.

Data for *Dryopithecus laietanus* were collected from a high-resolution cast of a single fossil specimen (IPMC 18000-1) from Can Llobateres, Spain (Moyà Solà & Köhler, 1993). This fossil preserves the left supraorbital morphology from the midline to the left fronto-malar suture (Begun, 1994). Both nasion and glabella are discernible. The right morphology was reconstructed from this specimen.

Graecopithecus

Two specimens of *Graecopithecus freybergi* (XIR 1 and RPI 128) measured from high-resolution casts. XIR 1 is a relatively complete facial specimen from the site of Xirochori, Greece (Bonis & Koufos, 1993). Nearly all of the right facial morphology is preserved—including dentition—except the right M^3 . The left side is broken just lateral to glabella and just superior to the malar root. Despite the excellent preservation of this specimen, warping of the upper face relative to the lower (Köhler *et al.*, 2001) prevented its use here in analyses of the whole cranium; rather, both supraorbital and palatal morphologies were analyzed separately. RPI 128 is a fairly well preserved palatal specimen from Ravin de la Pluie (Greece) with much of the maxilla and premaxilla preserved nearly to the level of rhinion. While all of the teeth remain intact, it is clear that the right tooth row has been warped laterally behind the canine. Therefore, these landmarks were reconstructed from the left side.

Sivapithecus

Sivapithecus is represented in this project by measurements collected from the original specimen of GSP 15000 from Pakistan (Pilbeam, 1982). This specimen consists of two main pieces: a left periorbital fragment and a palate. The periorbital piece preserves a nearly complete left orbital rim with the infero-medial corner broken into a separate piece. The interorbital region is preserved to the midline, as are most of the left malar and the midface. The palate is nearly complete, retaining complete dentition and alveoli, pterygoid morphology, as well as the nasal floor and much of the aperture. Data were collected from this specimen courtesy of Dr. Jay Kelley (University of Illinois, College of Dentistry) while the specimen was in his care.

Plio-Pleistocene hominins

Australopithecus

A high-resolution cast of Sts 5 (Broom, 1947) from Sterkfontein, South Africa was included in this project to represent the genus *Australopithecus*. This specimen is a nearly complete cranium preserving most of the landmarks used in this analysis. Unfortunately, much of the alveolar region is eroded and so inter-dental landmarks were not collected.

Homo

Specimens of early *Homo* were also included from the species *H. habilis* (KNM-ER 1813), *H. rudolfensis* (KNM-ER 1470, 3732), and *H. erectus* (KNM-ER 3733, 3883). Data were measured from each of these on original specimens housed in the National Museums of Kenya. ER 1813 is a fairly complete cranium with damage to the superior nasal aperture, cranial base, and left zygomatic region (Leakey, 1974). *H. rudolfensis* is

best known from the Koobi Fora cranium ER 1470 (Leakey, 1973). While much of the original structure is intact, substantial erosion of the morphology has obscured or altered many of the landmarks used here. ER 3732 is a partial cranium of *H. rudolfensis* (Wood, 1991) preserving the left brow ridge, part of the left orbital rim, and substantial neurocranium (Leakey, 1976). ER 3733 and 3883 are both fairly complete neurocranial specimens with some attached facial morphology. The former is missing subnasal and palate features (Leakey, 1976). ER 3883 is less intact, retaining a brow ridge and much of the upper right face. Of these specimens, only ER 1813 and ER 3733 were complete enough to include in the cranial analyses; all five were analyzed in the supraorbital unit.

Paranthropus

The genus *Paranthropus* was represented by one specimen of *P. aethiopicus* (KNM-WT 17000) and three fossils attributed to *P. boisei* (KNM-ER 406, 732, 13750). All original specimens were studied in the National Museums of Kenya. WT 17000 is a fairly complete cranium, with substantially missing portions in the anterior neurocranial, orbital, and zygomatic regions (Walker *et al.*, 1986). Careful examination of the preserved morphology suggests that its current state is indicative of the original morphology—with little visible warping.

ER 406 is a nearly complete cranium with moderate erosion on its inferior surfaces (Leakey, 1970). Many of the palatal landmarks were obscured or missing. Similarly, the left orbital border is too eroded to be reliable. Most of the other landmarks, however, were collected. ER 732 is putatively a female cranium missing most of the left neurocranium, orbit, nasal aperture, and palate (Leakey, 1971). The morphology that is

preserved, however, seems undistorted. ER 13750 consists only of the upper neurocranium, complete brow ridge, and some of the right malar region.

CHAPTER 4: LANDMARKS, DATA COLLECTION AND PROCESSING

This chapter outlines the processes through which geometric morphometric data were collected and prepared for analysis. The discussion includes definitions of the landmarks used in this project, followed by a brief overview of the hardware, software, and set-up of the data collection system. Also discussed here is the procedure used for fitting together data that were collected from different views on the same specimen. Descriptive statistics from a series of replicate data collected from a single specimen are given along with discussion of the measurement precision associated with data collection. The chapter ends with a description of the process used to reconstruct missing data from bilateral landmarks.

LANDMARKS

While traditional morphometrics are concerned with linear measurements and angles, geometric morphometric analyses examine shape through point coordinate data: landmarks (Marcus, 1990). A landmark in this case can be defined as a point on a specimen that is identifiable by some criteria and presumed to correspond to homologues across specimens in the dataset (Slice *et al.*, 1996). The landmarks used in this project are listed and defined in Table 4-1; the abbreviations given for the landmarks are used throughout this text. Figures 4-1, 4-2, and 4-3 illustrate the positions of each landmark on the hominoid cranium. Statistical analyses in this project were performed on coordinate data from landmarks configurations, or subsets thereof; in examining three-dimensional morphology, this yields a total number of variables equal to three times the number of landmarks used in analysis.

Table 4-1 Landmark definitions used in this project. Abbreviations (Abbr.) for the landmarks are used in the text and figures throughout this work. All definitions refer to a Frankfurt horizontal orientation. See text for further discussion.

Landmark	Abbr.	View	Type	Definition
Midline landmarks:				
Opisthocranium	OPC	dorsal	II	most posterior midline point on the cranium
Bregma	BRE	dorsal	I	junction of coronal and sagittal sutures
Post-toral sulcus	PTS	dorsal	II	bottom of the post-glabellar concavity in midline
Glabella	GLA	dorsal	II	most anterior midline point on the frontal bone
Nasion	NAS	dorsal	I	junction of naso-frontal and inter-nasal sutures
Rhinion	RHI	dorsal	I	most inferior point of inter-nasal suture
Posterior clivus	CLI	dorsal	II	most posterior midline point on the subnasal clivus
Anterior attachment of nasal septum	ANS	dorsal	I	most anterior insertion of cartilaginous nasal septum
Alveolare	ALV	dorsal	II	most inferior midline point on the maxilla
Opisthion	OPI	ventral	II	midline posterior margin of the foramen magnum
Basion	BAS	ventral	II	midline anterior margin of the foramen magnum
Hormion	HOR	ventral	I	most posterior midline point on the vomer
Staphylion	STA	ventral	II	most posterior midline point on the hard palate
Midline anterior palatine	MAP	ventral	I	junction of palato-maxillary and inter-palatine sutures
Incisvion	INC	ventral	I	most posterior point of (oral) incisive foramen
Bilateral landmarks:				
Porion	POR	dorsal	II	most superior point on the margin of the external auditory meatus
Superior zygomatico-temporal suture	SZT	dorsal	II	most superior point on the zygomatico-temporal suture of the zygomatic arch
Jugale	JUG	dorsal	II	deepest point in the notch between temporal and frontal processes of the zygomatic bone
Frontomolare temporale	FMT	dorsal	I	junction of fronto-zygomatic suture & temporal line
Frontomolare orbitale	FMO	dorsal	I	junction of fronto-zygomatic suture & orbital rim
Mid-orbit torus inferior	MTI	dorsal	II	midline point on the superior margin of the orbit
Mid-orbit torus superior	MTS	dorsal	II	most superior point on the supraorbital "torus" projected directly above MTI
Dacryon	DAC	dorsal	I	junction of lacrimal, frontal, and maxilla
Orbitale	ORB	dorsal	II	most inferior point on the inferior orbital margin
Apex of orbital cone	AOC	dorsal	I	most posterior point in the orbital cone; collected at the superior margin of the superior orbital fissure
Zygoorbitale	ZYO	dorsal	I	junction of zygo-maxillary suture and the orbital rim
Malar foramen	MLF	dorsal	I	superior margin of the largest malar foramen
Infraorbital foramen	IOF	dorsal	I	superior margin of the largest infraorbital foramen
Zygomaxillare	ZYM	dorsal	I	most inferior point on the zygo-maxillary suture
Malar root origin	MRO	dorsal	II	root of the zygomatic process; antero-inferior margin
Alare	ALA	dorsal	II	most lateral point on the margin of the nasal aperture
Posterior incisive canal	PIC	dorsal	I	most posterior point of the (nasal) incisive canal
I ¹ -I ² contact	I12	dorsal	II	most inferior point on the maxilla between I ¹ and I ²
Inferior premaxillo-maxillary suture	IPM	dorsal	I	most inferior point on premaxillo-maxillary suture
Posterior glenoid tip	PGT	ventral	II	inferior tip of the posterior glenoid process
Lingual canine margin	LCM	ventral	II	most lingual point on the canine alveolar margin
Canine-premolar contact	CPC	ventral	II	C/P contact projected laterally to the alveolar margin
Premolar-molar contact	PMC	ventral	II	P/M contact projected laterally to the alveolar margin
Distal molar	DM3	ventral	II	most distal molar point on M3 projected laterally to the alveolar margin
Inferior zygomatico-temporal suture	IZT	ventral	II	most superior point on the zygomatico-temporal suture of the zygomatic arch

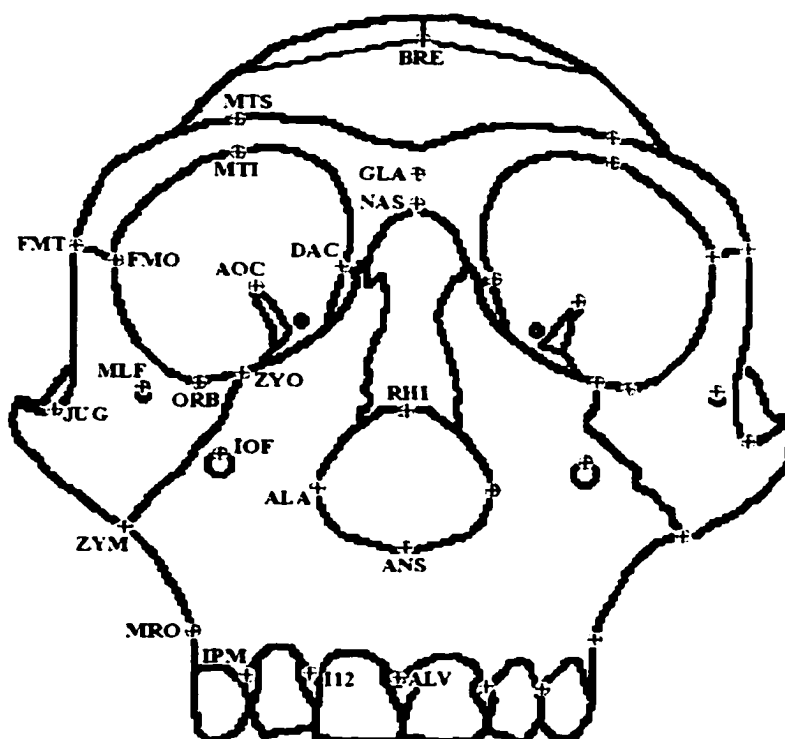


Figure 4-1 Frontal illustration of some landmarks used in this project; only right side (anatomically) and midline landmarks are labeled. See Figures 4-2 and 4-3 for additional landmark illustrations. Landmark abbreviations are given in Table 4-1.

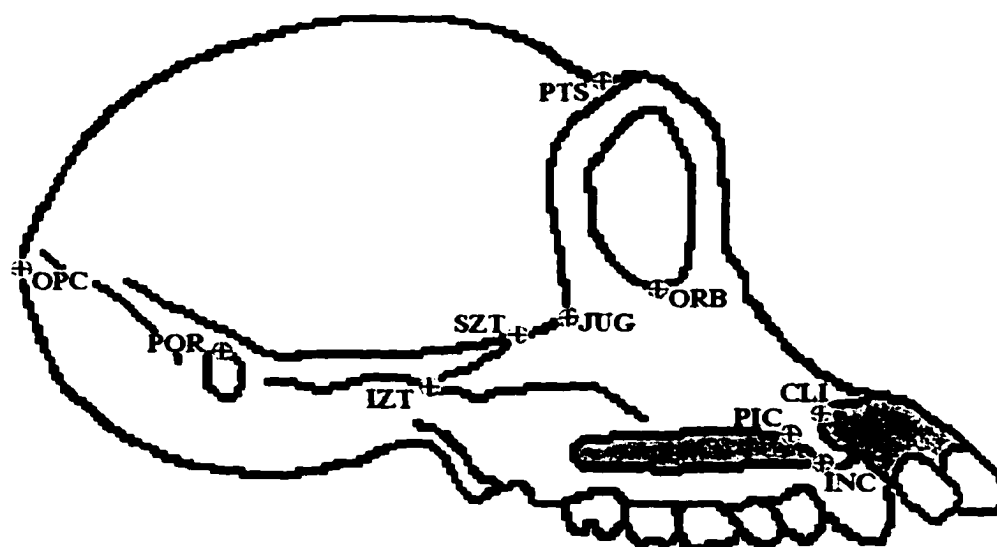


Figure 4-2 Lateral illustration of some landmarks used in this project; subnasal and palatal morphology is depicted as hemi-sectioned. See Figures 4-1 and 4-3 for additional landmark illustrations. Landmark abbreviations are given in Table 4-1.

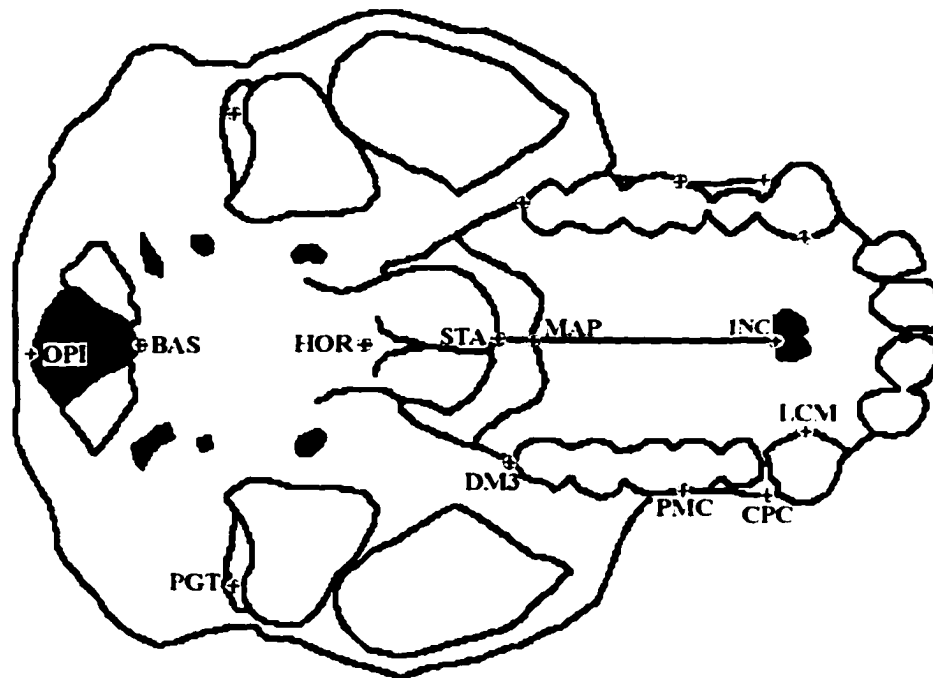


Figure 4-3 Basal illustration of some landmarks used in this project; only left side (anatomically) and midline landmarks are labeled. See Figures 4-1 and 4-2 for additional landmark illustrations. Landmark abbreviations are given in Table 4-1.

Three classes of landmarks are recognized in geometric morphometric studies (Bookstein, 1990; Slice *et al.*, 1996; Valeri *et al.*, 1998). Type I landmarks are points associated with sutural intersections, junctions of disparate tissue types, or foramina. These are generally considered to have the strongest support as homologous points across a dataset. Type II landmarks are defined geometrically as minima or maxima with regard to a particular structure; the homology of such points is regarded to be less well supported than Type I landmarks. The majority of landmarks used in this study are either of Type I or II (see Table 4-1), most representing standard osteometric points. Type III landmarks are those defined only in reference to another landmark and, as such, have at

least one deficient coordinate (Slice *et al.*, 1996). Some Type III landmarks, or semi-landmarks, were used in analyses of supraorbital morphology. These are discussed below.

SEMI-LANDMARKS

One of the real advantages of landmark-based morphometric analyses is that they can approach the level of morphological detail attainable through descriptive analysis, while incorporating more rigorous statistical methods of traditional morphometrics. Yet, many features that are ubiquitously described in studies of fossil hominoids—and, indeed, studies of any morphology—do not meet the criteria established for Type I and Type II landmarks. In order to include such features in geometric morphometric analyses, some authors have collected Type III landmarks, or semi-landmarks, for analysis (e.g., Dean, 1993; Harvati, 2001; McNulty, 2001; Gunz *et al.*, 2002; Mitteroecker, *et al.*, 2003; Weber *et al.*, 2003). In this project, semi-landmarks were collected along the ridge curve of the supraorbital region. Dean (1993) defined a ridge curve as “a three-dimensional curving line on the surface of a biological structure” (p. xiii). Supraorbital morphology was digitized as a series of minimally-spaced data points along the ridge curve, bounded on either end by type I landmarks (right **FMT**, left **FMT**). Unlike Type I and II landmarks, these semi-landmarks were treated somewhat differently during data processing. First, ridge curve “lines” were resampled in order to create equal numbers of equally spaced corresponding points on all specimens. Second, semi-landmarks were not included in computations of Procrustes fitting technique (see Chapter 5), due to their reduced degrees of freedom. The use of semi-landmarks in this project, however, allowed

for a more detailed quantification and analysis of the complex morphology of the supraorbital region.

DATA COLLECTION

Three-dimensional coordinate data were collected from all specimens using a Microscribe 3DX mechanical digitizer (Immersion Corp.) connected to a Compaq Presario 1800T laptop computer. The Microscribe is a three-segmented "arm" attached to a base and with a stylus at the tip; the fine tip was used exclusively in this study. Based on the orientation of each arm segment and its total length, the Microscribe calculates the 3D coordinates of the stylus tip. A foot-pedal was used to initiate calculation, and data were written to a computer through the serial port. *Inscribe32* for Windows was used to interpret the serial input. This program, designed to coordinate with multiple software packages, translated three-dimensional coordinate data from the Microscribe to a Microsoft Excel spreadsheet. A coordinate system was constructed by defining a digitizing plane, an origin, and points in the X- and Y-axes (within the digitizing plane); the Z-axis corresponded to the dimension orthogonal to the digitizing plane. Coordinate data were recorded in centimeters, to four places after the decimal.

Each specimen was mounted on the digitizing platform with two clay supports: one cradling the neurocranium, one securing the rostrum. Care was taken to orient specimens in the Frankfurt horizontal plane for the collection of dorsal landmarks; specimens were turned over to collect ventral points and oriented approximately in *norma basalis*. Most specimens were firmly but gently pressed into the clay foundations until they were locked into a single position; the more fragile fossil specimens, however, were

not pressed into clay, but secured by additional clay supports. All specimens were measured with the snout directed toward the collector.

PROCEDURE FOR COLLECTING DATA IN MULTIPLE VIEWS

Because specimens must be rigidly secured in order to maintain the integrity of measurements, restraining supports inevitably obscure some aspects of the morphology. In this study, the majority of landmarks were collected in dorsal view (see Table 4-1) with the base of the cranium secured to the digitizing platform. To digitize morphology on the ventral side, specimens were turned over and re-secured to the foundation. This, however, resulted in separate configurations for dorsal and ventral landmarks.

In order to combine these into one configuration, four orientation points (OPs) were established on each specimen prior to data collection. These were marked by small “dots” of clay adhering to different aspects of the cranium; coordinates of OPs were collected in both dorsal and ventral views. Following data collection, the two views were fit into a single coordinate system by a rigid rotation of the ventral landmarks according to a least squares fit of ventral OPs onto dorsal OPs (Frost *et al.*, in press); dorso-ventral fitting was computed in *Matlab 5.0* and applied to all specimens using a Perl script. This process resulted in one configuration for each specimen, with dorsal and ventral landmarks restored to their original geometric relationships (see Frost *et al.*, in press).

PRECISION AND MEASUREMENT ERROR

All of the data in this project were collected by the author. To assess error in the observer and collection system, ten replicate landmark configurations were collected

from an adult female gorilla. Distances were calculated from each replicate landmark to the consensus landmark, in order to compute the mean deviation. Table 4-2 lists the mean, minimum, and maximum deviations of each landmark from the consensus. In order to estimate mean percent error, landmark mean deviations were divided by the distance between the consensus landmark and the centroid (Singleton, 2002); these results are also shown in Table 4-2. Across all landmarks, the grand mean error in deviations was 0.03 cm; the grand mean percentage error was 0.68%. Both of these terms are considered to be negligible. It should be pointed out, however, that *Gorilla* is the largest of the anthropoids used in this study; similar error magnitudes in the smaller taxa would therefore yield higher percentage errors. To estimate these, centroid sizes of the smallest specimens from each genus were divided by the mean centroid size (57.52 cm) of the gorilla used in this precision study. Then, the grand mean percent error was divided by each of these ratios in order to scale the error term for each genus. Resulting estimates are given in Table 4-3. Note, that by using the smallest individual from each genus, the mean percent error estimate is maximized. Even so, the smallest specimen overall (from *Cebus*) yielded a percent error estimate of only 1.7%.

Table 4-2 Observer error calculated from 10 replicate configurations of a female gorilla cranium. Mean, minimum, and maximum distances for each landmark to the consensus landmark are shown. Mean percentage error was calculated as the mean landmark error divided by the mean distance between landmark and centroid, multiplied by 100. See Table 4-1 for the key to landmark abbreviations.

Landmark	Mean(cm)	Min.(cm)	Max.(cm)	Mean Percent Error (%)
Midline landmarks:				
OPC	0.01	0.01	0.01	0.07
BRE	0.03	0.02	0.05	0.26
PTS	0.02	0.01	0.03	0.38
GLA	0.05	0.01	0.19	1.24
NAS	0.05	0.02	0.21	1.08
RHI	0.02	0.01	0.05	0.66
CLI	0.04	0.02	0.08	0.98
ANS	0.03	0.01	0.07	0.55
ALV	0.03	0.01	0.05	0.32
OPI	0.02	0.01	0.05	0.18
BAS	0.02	0.01	0.04	0.26
HOR	0.02	0.01	0.04	0.31
STA	0.02	0.01	0.03	0.56
MAP	0.02	0.01	0.03	1.28
INC	0.02	0.01	0.03	0.38
Right bilateral landmarks:				
POR	0.04	0.02	0.10	0.42
SZT	0.03	0.01	0.09	0.45
JUG	0.02	0.01	0.05	0.43
FMT	0.02	0.01	0.05	0.34
FMO	0.02	0.01	0.03	0.39
MTI	0.02	0.01	0.05	0.46
MTS	0.04	0.01	0.17	0.55
DAC	0.04	0.01	0.21	1.32
ORB	0.05	0.01	0.21	1.74
AOC	0.05	0.01	0.08	0.88
ZYO	0.01	0.01	0.02	0.46
MLF	0.01	0.01	0.02	0.25
IOF	0.02	0.01	0.03	0.47
ZYM	0.04	0.01	0.07	0.72
MRO	0.05	0.01	0.03	1.08
ALA	0.04	0.01	0.08	1.02
PIC	0.03	0.01	0.06	0.64
II2	0.04	0.02	0.10	0.56
IPM	0.03	0.01	0.07	0.43
PGT	0.01	0.01	0.03	0.16
LCM	0.02	0.01	0.08	0.31
CPC	0.03	0.01	0.05	0.44
PMC	0.03	0.02	0.06	0.54
DM3	0.04	0.01	0.11	0.80
IZT	0.02	0.01	0.04	0.27

Table 4-2 (cont.)

Landmark	Mean(cm)	Min.(cm)	Max.(cm)	Mean Percent Error (%)
Left bilateral landmarks:				
POR	0.05	0.01	0.12	0.53
SZT	0.01	0.01	0.02	0.20
JUG	0.06	0.02	0.14	0.92
FMT	0.02	0.01	0.05	1.00
FMO	0.03	0.01	0.05	0.49
MTI	0.07	0.03	0.10	1.14
MTS	0.08	0.02	0.19	1.28
DAC	0.02	0.01	0.03	0.49
ORB	0.05	0.02	0.09	1.39
AOC	0.08	0.01	0.23	1.47
ZYO	0.03	0.02	0.13	1.10
MLF	0.02	0.01	0.03	0.28
IOF	0.03	0.02	0.05	0.87
ZYM	0.06	0.03	0.09	1.20
MRO	0.06	0.03	0.12	2.05
ALA	0.05	0.01	0.13	1.34
PIC	0.01	0.01	0.03	0.38
II2	0.04	0.01	0.08	0.46
IPM	0.04	0.01	0.10	0.60
PGT	0.02	0.01	0.04	0.22
LCM	0.01	0.01	0.02	0.23
CPC	0.04	0.01	0.09	0.63
PMC	0.03	0.02	0.06	0.62
DM3	0.06	0.02	0.09	1.54
IZT	0.03	0.02	0.08	0.40
Grand Mean	0.03			0.68

Table 4-3 Mean percent error estimates for each genus. For each genus is listed the centroid size of the smallest specimen, the ratio of that to the mean centroid size of the cranium measured in the precision study (57.52 cm), and the mean percent error estimate. Size ratios were used to scale the grand mean percent error (0.68%) in order to estimate mean percent error for each genus. As percent error in this study is a function of centroid size, these estimates are maximum error values.

Genus	Centroid Size(cm)	Size ratio	Mean Percent Error Estimate (%)
<i>Ateles</i>	26.23	0.46	1.48
<i>Cebus</i>	22.91	0.40	1.70
<i>Cercopithecus</i>	24.05	0.42	1.62
<i>Gorilla</i>	56.78	0.98	0.69
<i>Homo</i>	47.59	0.82	0.83
<i>Hylobates</i>	25.14	0.43	1.58
<i>Pan</i>	41.35	0.72	0.94
<i>Papio</i>	41.42	0.72	0.94
<i>Pongo</i>	47.31	0.82	0.83
<i>Procolobus</i>	27.51	0.48	1.42

MISSING DATA AND LANDMARK RECONSTRUCTION

One of the most confounding problems in morphometric analyses is that of missing data. While visualization tools have been designed to accommodate this inevitable problem, it is nevertheless difficult to compute the statistical properties of a specimen when some of its measurements are missing. As a partial solution, this project made restricted use of bilateral data interpolation: missing bilateral landmarks were reconstructed by reflecting their antimeres across the sagittal plane. This technique was also used to reconstruct obviously warped morphology in fossil specimens (see Chapter 3). Mirroring landmarks across the sagittal plane requires the implicit assumption that bilateral asymmetry is negligible or uninformative. While neither of these is necessarily true, for this project it is only necessary that variation due to bilateral asymmetry be negligible *relative to variation among genera*. Midline landmarks were not reconstructed for this project.

In extant specimens, missing bilateral landmarks were reconstructed by creating a mirrored version of each specimen, superimposing (via GPA; see Chapter 5) both specimens and mirrors, then substituting the mirrored data for any missing data. This was only done for landmarks; the supraorbital ridge curve was not reconstructed in extant specimens. A similar method, with minor modifications, was used to reconstruct missing landmarks in fossils. In specimens with a substantial number of missing landmarks, a GPA (based largely on missing data) can skew the alignments of the original and that of its mirror (personal observation). Therefore, fossil specimens were aligned using only midline landmarks, with the rest of the configuration carried along through the transformation matrix. This ensured that both mirrored and original specimens were

properly aligned across the sagittal plane. Mirrored landmarks, then, were substituted for those missing from the original configuration. The supraorbital ridge curve was reconstructed in fossil specimens (e.g., GSP 15000) to enable their inclusion in analyses.

CHAPTER 5: MORPHOMETRIC AND STATISTICAL METHODS

This chapter describes the different methods used in morphometric and statistical analyses throughout this project. The beginning section provides a description of the Procrustean superimposition technique employed to standardize the orientation and geometric size of all specimens. Following that, the issues of size and scaling are discussed, including a description and justification for the size adjustment used in cranial analyses. The chapter concludes with an outline of the multivariate statistical approaches used here. Initial analyses of principal components, canonical variates, and Mahalanobis D^2 are standard techniques used in biometrics to explore variance among specimens and groups. Phylogenetic node discrimination is then introduced as a method to examine morphological differences between crown clades. Based on an assumed phylogeny, this approach uses a series of discriminant analyses to test the degree of overlap and visualize shape differences between extant clades. It is also used to assess the affinities of fossil specimens according to the features that distinguish between crown taxa.

GEOMETRIC MORPHOMETRIC METHODS

The data used for all analyses in this work derive from the coordinates of three-dimensional cranial landmarks and semi-landmarks (see Chapter 4). Embedded in these raw landmark configurations are differences due to the size, location, and orientation, as well as shape, of the specimens. Therefore, landmark configurations were superimposed in *tpsSmall* (Rohlf, 1998) using a generalized Procrustes analysis (GPA). This is an iterative procedure which translates specimens to a common centroid, isometrically scales them to a unit centroid size, and rotates them using a least squares criterion across

all landmarks and specimens (e.g., Rohlf & Marcus, 1993; Slice *et al.*, 1996; Dryden & Mardia, 1998). This process eliminates differences among specimens due to size, location, and rotation, so that remaining variability is due primarily to shape (Slice *et al.*, 1996). Here, the centroid is the point defined by the mean value of each dimension (e.g., x, y, z) for all coordinates in a landmark configuration: the “center of gravity.” Centroid size is the square root of the sum of the squared distances from each landmark to the centroid; this is the preferred size measure for use in geometric morphometrics as it is approximately uncorrelated with shape variables when data are distributed in uniformly (spherical) small variances about each mean landmark (Slice *et al.*, 1996). The consensus configuration is computed as the mean of each landmark across all specimens: the “average” of the specimens. Separate superimpositions were undertaken for the whole cranium, the supraorbital region, and the palate. For the supraorbital configurations, the GPA was computed on landmarks only; semi-landmarks (see Chapter 4) were then superimposed according to that transformation matrix.

Superimposed landmark configurations lie in a hemispherical variant of Kendall’s (1984) shape space (Slice, 2001)—a non-Euclidean space that is inappropriate for statistical analyses utilizing linear models. For this reason, superimposed coordinate data were projected into a Euclidean space, tangent to the shape space at the consensus configuration (Dryden & Mardia, 1998). The congruence between specimens in shape space and tangent space was tested in *tpsSmall* (Rohlf, 1998) by comparing Procrustes distances between specimens in shape space with the equivalent Euclidean distances in tangent space. Procrustes distance is defined as an approximation of the square root of the sum of squared differences between the landmark positions of two superimposed

specimens at centroid size (Slice *et al.*, 1996; see Bookstein, 1996). In all three cases, the correlations were very strong (cranial: correlation = 0.9999, root MS error = 0.0001; supraorbital: correlation = 0.9999, root MS error = 0.00001; palatal: correlation = 0.9999, root MS error = 0.0001). Therefore, coordinates of superimposed specimens projected into tangent space formed the dataset on which all statistical analyses were performed; analyses of coordinate data in shape space were not performed in this project.

SIZE, SCALING, AND SIZE-ADJUSTED DATA

The interaction between an organism's shape and its size has been the occasional subject of biological discourse for well over a century (e.g. Spencer, 1864; Thompson, 1917; Huxley, 1932). More recently, the topics of body size and scaling have received greater attention as researchers (e.g. Cock, 1966; Gould, 1971; Schmidt-Nielsen, 1984; Jungers, 1985; Damuth & MacFadden, 1990; Jungers *et al.*, 1995; McMahon, 1999) began to explore the effects of size on all aspects of biology (Swartz & Biewener, 1992). "Size", in a biometric sense, can be decomposed into two related concepts: geometric size and scaling. The former term refers essentially to the common definition of size—some measure of an object's spatial dimensions (McMahon, 1999). Scaling, on the other hand, is the *relationship* between geometric size and shape. An object that changes shape in correlation with a change in size scales allometrically; when a change in size yields no corresponding change in shape, the object scales isometrically (Jungers *et al.*, 1995).

Definitions

There is some confusion over this terminology in the literature, deriving largely from disjunct usage of the related words "scale" and "scaling." Schmidt-Nielsen (1984)

defines scaling as “the structural and functional consequences of changes in size or scale among otherwise similar organisms” (p. 7). This definition has hints of circularity (expressing scaling in terms of scale) and blurs the distinction between geometric size and patterns of size-correlated shape change. Similarly, McMahon (1999) uses geometric size, size, and scale interchangeably, but reserves *scaling* for discussions of allometry and isometry; these usages are fairly standard in the physical anthropology literature. In geometric morphometrics, however, “scale” is frequently used as a verb with regard to standardizing centroid sizes in a generalized Procrustes analysis. To further complicate this issue, isometry has a different meaning among mathematicians, referring to transformations that preserve the original measure (not just the shape) of the object. By this definition, only translation, rotation, and mirroring are mathematically isometric (Slice *et al.*, 1996); change in centroid size is, strictly speaking, isogonic: preserving angular relationships among landmarks.

Wary of draining all richness from the concept (see Mosimann & Malley, 1979), this work nevertheless restricts “size” to notions of geometric size: in any analytical context, this was measured as centroid size. “Scale” and all derivatives thereof (e.g., scaled, scaling) strictly reference the patterns of size-correlated shape change: allometry and isometry, in their biological senses. While these latter terms do not accord with their mathematical definition, they adhere to their common usages among biologists (e.g. Jungers, 1985 and papers therein). Hence, the change in centroid size effected through a GPA is an isometric scaling of each object to a unit centroid size.

Allometry and size corrections

This project is primarily concerned with differences in shape that are independent of scaling effects. An isometric size adjustment is inherent to any study using GPA, as centroid sizes across all specimens are equalized. Centroid size is mathematically related to Mosimann shape variables (Mosimann & Malley, 1979; Reyment, 1991), making this adjustment a multivariate extension of bivariate shape ratios (Singleton, 2002). While the GPA eliminates differences in centroid size among all specimens, allometric effects—typically associated with structural and functional constraints (Schmidt-Nielsen, 1984)—may still remain. Indeed, differences in shape among Procrustes aligned specimens result from the interaction of allometric, phylogenetic, functional, and other diverse factors.

To determine whether size was still a significant factor contributing to variability in this sample after Procrustes superimposition, a PCA was performed for each of the analytical units (cranial, supraorbital, palatal) and resulting eigenvectors were regressed against the log of centroid size. This revealed the extent to which the size variable explains the distribution of specimens on each PC axis. Principal components (rather than individual coordinates) were chosen for this analysis because they are ordinated by decreasing amounts of explained variance (e.g., Neff & Marcus, 1980; Reyment, 1991; see below). This allows one to assess the impact of size correlations on subsequent analyses: correlations in initial components indicate that size accounts for a large proportion of the sample variance; correlations with later axes explain negligible amounts of variation. Table 5-1 lists the results of both PCA and regression analyses for the first ten PCs from each analytical unit; significant size correlations were not found on higher ranked components. In each of the three analytical units, several PC axes were found to

be highly correlated with size. This indicates that a substantial portion of the sample variance among Procrustes-aligned specimens may result from the effects of allometry.

Table 5-1 Summary of PCA and regression results for the first ten principal component axes, computed separately for (a) the entire set of cranial landmarks, (b) supraorbital landmarks and semi-landmarks, and (c) palatal landmarks. PCA results give statistics for the latent roots of the sample variance (eigenvalues), the proportion of variance explained by each component, and the cumulative proportion of the variance summarized by each PC and those preceding it. Coefficients of determination (R^2) and probability (Pr) values are shown for regressions.

	PRINCIPAL COMPONENTS ANALYSIS			REGRESSION ANALYSIS	
	Eigenvalue	Proportion	Cumulative	R^2	Pr > F
a. Cranial					
PC 1	0.00894082	0.4440	0.4440	0.6980	<0.0001
PC 2	0.00386649	0.1920	0.6360	0.0795	<0.0001
PC 3	0.00126139	0.0626	0.6987	0.0122	0.0105
PC 4	0.00080921	0.0402	0.7389	0.0991	<0.0001
PC 5	0.00067342	0.0334	0.7723	0.0406	<0.0001
PC 6	0.00045820	0.0228	0.7951	0.0030	0.2057
PC 7	0.00029300	0.0146	0.8096	0.0008	0.5054
PC 8	0.00025727	0.0128	0.8224	0.0094	0.0247
PC 9	0.00024621	0.0122	0.8346	0.0015	0.3709
PC 10	0.00022144	0.0110	0.8456	0.0018	0.3321
b. Supraorbital					
PC 1	0.01016723	0.3951	0.3951	0.3314	<0.0001
PC 2	0.00408855	0.1589	0.5540	0.1540	<0.0001
PC 3	0.00214938	0.0835	0.6375	0.0466	<0.0001
PC 4	0.00164794	0.0640	0.7016	0.0098	0.0151
PC 5	0.00159114	0.0618	0.7634	0.0465	<0.0001
PC 6	0.00115384	0.0448	0.8082	0.0024	0.2260
PC 7	0.00060782	0.0236	0.8318	0.0002	0.7126
PC 8	0.00055621	0.0216	0.8535	0.0017	0.3074
PC 9	0.00045563	0.0177	0.8712	0.0438	<0.0001
PC 10	0.00037046	0.0144	0.8856	0.0006	0.5371
c. Palatal					
PC 1	0.01245742	0.4902	0.4902	0.4929	<0.0001
PC 2	0.00386700	0.1522	0.6423	0.1866	<0.0001
PC 3	0.00158999	0.0626	0.7049	0.0823	<0.0001
PC 4	0.00113715	0.0447	0.7496	0.0410	<0.0001
PC 5	0.00104652	0.0412	0.7908	0.0003	0.6586
PC 6	0.00063767	0.0251	0.8159	0.0000	0.9694
PC 7	0.00060673	0.0239	0.8398	0.0000	0.8892
PC 8	0.00046686	0.0184	0.8581	0.0009	0.4760
PC 9	0.00037344	0.0147	0.8728	0.0006	0.5430
PC 10	0.00028439	0.0112	0.8840	0.0007	0.5113

In a study such as this, it may be desirable to identify and adjust for allometric effects in order to examine the differences between individual variation within and phylogenetic variation among taxa (Harvey & Pagel, 1991). This view, however, suggests a false dichotomy between allometric and phylogenetic differences. Examining the affinities and relatedness of biological organisms, one must be concerned that the physical requirements of being large or small will cause homoplastic similarities within size classes to obscure homologous similarities among size classes. This can be particularly problematic when studying the Hominoidea (Creel, 1986), which comprises a wide distribution of body sizes. On the other hand, allometric differences may have a strong phylogenetic component to them: the evolution of a lineage is intimately tied to size differences within that lineage (Simpson, 1953). Thus, the sequestering of size-correlated shape change from a dataset can have the adverse effect of eliminating important phylogenetic information.

Any size adjustment applied to metric data removes variance from the sample; in most cases, however, one cannot control the nature of the sequestered variability, beyond its basic correlation with size. Implementation of an adjustment, therefore, betokens a compromise between eliminating potentially confounding homoplastic effects and losing valuable phylogenetic information. This conflict is clearly manifest among extant apes, where the principal distinction in body size (lesser apes vs. great apes) is superimposed over a primary division in taxonomy and phylogeny (Hylobatidae vs. Hominidae). Thus, *any* shape differences between the hylobatid and hominid families will be correlated with size, regardless of whether the difference is allometric, phylogenetic, or both. Put another way, one expects a gibbon and a gorilla to differ because the requirements of being small

and large are different, and because they have different evolutionary histories. The difference in body size, however, means that *both* morphogenetic factors will be correlated with size. Thus, it may not always be possible to decouple allometric effects from those due to phylogeny. An analogous problem is also manifest in variation due to sexual dimorphism, as male and female anthropoids tend to have distinct differences in body size (e.g., Plavcan, 2001).

Having demonstrated that significant size correlations are present in Procrustes-aligned data (see Table 5-1), an assessment had to be made as to the usefulness of applying a size adjustment. As a benchmark for this project, it was decided that a size adjustment should be applied only if significant size correlations could be demonstrated beyond those explained by differences in taxonomy (genus) or sex. If variances associated with generic and sex differences could account for all size correlations, then the consequences of losing phylogenetic information were judged to outweigh any benefits of a size adjustment, and *no* size adjustment was applied. Alternatively, if size were shown to be a persistent factor beyond these variances, then a size adjustment was determined to be appropriate. This approach does not obviate the tradeoff involved with applying a size adjustment. It does, however, provide a reasonable standard for assessing the relative merits of an adjustment, based on observable, sample-specific criteria.

The following procedure was adopted in order to determine the contribution of size, apart from taxonomic and sex effects, to the sample variance. For each genus, a binary class variable was created such that specimens belonging to that genus were coded as **1**, while specimens belonging to other genera were coded as **0**; a binary class variable was also created for sex (male = **0**, female = **1**; specimens of unknown sex were not

used). Coordinate data were then regressed against this series of class variables in order to compute residuals. For each class variable, the regression eliminates variance due to membership or non-membership in the class (see Bookstein, 1996; Frost *et al.*, in press). Thus, the residuals are free of variation due to differences among genera or between sexes; any correlations with size among these residuals, therefore, indicate that global aspects of allometry contribute to the sample variance beyond such differences. To test this, residuals were analyzed by PCA, and resulting components were regressed against centroid size. Having removed genus and sex effects, any persistent size correlation would indicate that a size adjustment is warranted; lack of correlations at this stage suggests that allometric effects cannot be decoupled from taxonomic (and presumably phylogenetic) and sex differences, recommending no adjustment. Results from tests of each analytical units are discussed below.

Cranial morphology

In an initial PCA of all cranial landmarks, six principal component axes (PC 1-5, 8) were significantly correlated with size (see Table 5-1). After generic and sex effects were removed, a PCA of residuals (Table 5-2) still found PC 1 correlated ($p = 0.0002$) with centroid size. This suggests that allometry in the cranium contributes significantly to the variation among specimens beyond those features associated with taxonomic and sex differences. Therefore, it was deemed necessary to adjust for the allometric component of shape before comparing cranial data across size and taxonomic groups.

A common biometric approach for partitioning size-correlated shape variation is to regress variables against a size measure and use the residuals in statistical analyses (see Albrecht *et al.*, 1993). This process removes common allometric shape components from

the entire sample. In Procrustes-based studies, centroid size is the appropriate measure to use when implementing a size adjustment. It is preferable to using body weight for two reasons. First, weight itself scales allometrically with size, as the requirements for being heavy (as opposed to being large) are different from those of being light (e.g., Thompson, 1917; Huxley, 1932; Simpson, 1953; Bromage *et al.*, 1997). Thus, body weight is not a measure of size, but a measure of the interaction between gravity and size (see McMahon, 1999 for a complete discussion). And, while appropriate for many studies, body weight may be less suitable for analyses of the non-weight bearing cranial anatomy. Nevertheless, McMahon (1999) demonstrated that centroid size closely approximates ($R^2 = 0.9997$, $p < 0.0001$) the dry cranial weight of a broad sample of anthropoids. The second reason that centroid size is a preferable size measure is that body mass is often not known for many specimens. Thus, centroid size was used as a criterion of subtraction to produce residual data that were uncorrelated with size (Gould, 1975).

Table 5-2 Summary of PCA and Regression results for PCs 1-10 computed from residuals of the entire set of cranial landmarks after regression against binary taxon and sex variables. PCA results give statistics for the latent roots of the sample variance (eigenvalues), the proportion of variance explained by each component, and the cumulative proportion of the variance summarized by each PC and those preceding it. Value of the F-statistic and probability (Pr) values are shown for regressions.

	PRINCIPAL COMPONENTS ANALYSIS			REGRESSION ANALYSIS	
	Eigenvalue	Proportion	Cumulative	F Value	Pr > F
PC 1	0.00079124	0.1460	0.1460	14.57	0.0002
PC 2	0.00069952	0.1290	0.2750	2.79	0.0957
PC 3	0.00029892	0.0551	0.3301	0.15	0.7004
PC 4	0.00021748	0.0401	0.3703	0.63	0.4293
PC 5	0.00018519	0.0342	0.4044	0.29	0.5906
PC 6	0.00017839	0.0329	0.4373	0.19	0.6630
PC 7	0.00016893	0.0312	0.4685	0.03	0.8693
PC 8	0.00014730	0.0272	0.4957	0.19	0.6597
PC 9	0.00013155	0.0243	0.5199	0.17	0.6835
PC 10	0.00011733	0.0216	0.5416	0.11	0.7442

This method of size adjustment, however, is based on the assumption that patterns of covariation between size and shape are homogeneous across all groups. To test this assumption, specimen scores from the initial PCA of the aligned specimens were plotted against the log of centroid size, and parametric t-tests were performed on the estimated slope differences for each pair of genera. PC 1 was chosen because its correlation with centroid size is highly significant ($p < 0.0001$) and it is the only axis with a specimen distribution explained largely by centroid size ($R^2 = 0.6980$); other axes with significant size correlations have very low R^2 values. Results of the pairwise t-tests (Table 5-3) adjusted by a Bonferroni correction (see, e.g., Sokal & Rohlf, 1995) indicate that there are no significant differences in slope between pairs of genera. This suggests that patterns of size-correlated shape change among genera are not significantly different. As such, a size adjustment using centroid size as a criterion of subtraction is appropriate for these data. Analyses on the whole set of cranial landmarks (Chapter 6) were therefore based on residuals from aligned coordinates regressed against centroid size. These data are referred to hereafter as size-adjusted coordinates.

Table 5-3 Results of parametric t-tests for comparisons of slope estimates of PC 1 * log(centroid size) for every pair of genera. Values shown are Bonferroni-adjusted p-values. None of the pairwise slope differences are significant.

Genus	Atel	Cebu	Cerc	Gori	Homo	Hylo	Pan	Papi	Pcol	Pong
Atel		1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
Cebu	1.0000		0.345	1.0000	1.0000	1.0000	1.0000	0.2576	0.7452	0.7268
Cerc	1.0000	0.345		0.2254	0.7176	0.3036	1.0000	1.0000	1.0000	1.0000
Gori	1.0000	1.0000	0.2254		1.0000	1.0000	1.0000	0.0692	1.0000	1.0000
Homo	1.0000	1.0000	0.7176	1.0000		1.0000	1.0000	0.5106	1.0000	1.0000
Hylo	1.0000	1.0000	0.3036	1.0000	1.0000		1.0000	0.0874	1.0000	0.3036
Pan	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000		1.0000	1.0000	1.0000
Papi	1.0000	0.2576	1.0000	0.0692	0.5106	0.0874	1.0000		1.0000	1.0000
Pcol	1.0000	0.7452	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000		1.0000
Pong	1.0000	0.7268	1.0000	1.0000	1.0000	0.3036	1.0000	1.0000	1.0000	

Supraorbital morphology

Six PC axes (1-5, 9) from the initial PCA of supraorbital data were significantly correlated with centroid size. Therefore, aligned coordinate data were regressed against the binary genus and sex variables in order to remove shape variations due to taxonomy and sexual dimorphism. A PCA was then performed on the residuals, and resulting eigenvectors were regressed against centroid size; Table 5-4 lists both PCA and regression results. In this case, there were no significant size correlations found. Such a result recommends against the application of a size adjustment. This is not to say that allometry plays no role in the variation among anthropoid supraorbital morphologies. Rather, this analysis demonstrates that any allometric effects are intimately tied to differences among taxa or between sexes; any size adjustment could remove potentially informative phylogenetic information. Therefore, supraorbital data were analyzed using raw, Procrustes-aligned coordinate data.

Table 5-4 Summary of PCA and Regression results for PCs 1-10 computed from residuals of the supraorbital coordinate data after regression against binary taxon and sex variables. PCA results give statistics for the latent roots of the sample variance (eigenvalues), the proportion of variance explained by each component, and the cumulative proportion of the variance summarized by each PC and those preceding it. Coefficients of determination (R^2) and probability (Pr) values are shown for regressions.

	PRINCIPAL COMPONENTS ANALYSIS			REGRESSION ANALYSIS	
	Eigenvalue	Proportion	Cumulative	R^2	Pr > F
PC 1	0.00259982	0.2181	0.2181	0.0046	0.0941
PC 2	0.00166727	0.1399	0.3580	0.0007	0.5231
PC 3	0.00120710	0.1013	0.4593	0.0055	0.0680
PC 4	0.00086495	0.0726	0.5318	0.0014	0.3590
PC 5	0.00076125	0.0639	0.5957	0.0000	0.8624
PC 6	0.00058745	0.0493	0.6450	0.0000	0.9892
PC 7	0.00056630	0.0475	0.6925	0.0000	0.8177
PC 8	0.00039747	0.0333	0.7258	0.0000	0.9679
PC 9	0.00036470	0.0306	0.7564	0.0023	0.2415
PC 10	0.00030702	0.0258	0.7822	0.0004	0.6452

Palatal morphology

The first four eigenvectors from the initial PCA of palatal landmarks were significantly correlated with centroid size. Generic and sex effects were then regressed from the data as described above. PC axes computed from the residuals were regressed against centroid size, with results listed in Table 5-5. As with the supraorbital morphology, none of the PC axes was found to correlate significantly with centroid size. While allometry may well play a role in producing variation in the palatal morphology of anthropoids, it is not discernible in these data from shape differences due to taxonomy (and presumably phylogeny) or sexual dimorphism. Therefore, no size adjustment was applied to palatal data, and aligned coordinates were used in all statistical analyses.

Table 5-5 Summary of PCA and Regression results for PCs 1-10 computed from residuals of the palatal coordinate data after regression against binary taxon and sex variables. PCA results give statistics for the latent roots of the sample variance (eigenvalues), the proportion of variance explained by each component, and the cumulative proportion of the variance summarized by each PC and those preceding it. Coefficients of determination (R^2) and probability (Pr) values are shown for regressions.

	PRINCIPAL COMPONENTS ANALYSIS			REGRESSION ANALYSIS	
	Eigenvalue	Proportion	Cumulative	R^2	Pr > F
PC 1	0.00159795	0.2001	0.2001	0.0061	0.0521
PC 2	0.00073233	0.0917	0.2918	0.0044	0.0609
PC 3	0.00070354	0.0881	0.3799	0.0007	0.5275
PC 4	0.00055377	0.0693	0.4492	0.0017	0.3181
PC 5	0.00044391	0.0556	0.5048	0.0000	0.9438
PC 6	0.00040449	0.0507	0.5555	0.0061	0.0592
PC 7	0.00035464	0.0444	0.5999	0.0002	0.7184
PC 8	0.00031198	0.0391	0.6390	0.0002	0.7663
PC 9	0.00024607	0.0308	0.6698	0.0009	0.4773
PC 10	0.00020760	0.0260	0.6958	0.0001	0.8037

STATISTICAL METHODS

The same battery of statistical analyses was used to examine all three morphological units (cranial, supraorbital, and palatal). All statistics were computed in *SAS* (SAS Institute, Inc., 1999); statistical plots were generated from the *SAS* output in *STATISTICA* (StatSoft, Inc., 1998) to allow more graphical flexibility.

Principal components analysis

The first step in analyzing each morphological unit was to perform a principal components analysis (PCA) on the covariance matrix of the aligned coordinate data. In geometric terms, a PCA rigidly rotates multivariate data in order to establish ordinated axes that summarize successively smaller amounts of the total variance among specimens (e.g., Neff & Marcus, 1980; Reyment, 1991). As such, PCA allows a large proportion of the variance to be examined in relatively few dimensions. Resulting components are linear combinations of the original variables and statistically orthogonal to each other. In each of the three analytical units, PCA was used to explore patterns of variation among specimens. For each PC axis, a one-way analysis of variance (ANOVA) was computed in order to test for differences among genera. When significance was found, pairwise parametric t-tests were performed to determine between which genera such differences occurred; a Bonferroni adjustment was applied to all probabilities computed in multiple comparison tests (e.g., t-tests). Fossil specimens were included in PCA, but were excluded from ANOVA and t-test computations.

Beyond statistical analysis of principal components, the shape differences summarized in each axis were explored by warping the consensus landmark configuration by each eigenvector. To do this, aligned coordinate data were regressed

against each PC: the vector of regression coefficients, representing the eigenvector loadings, was then added to (and subtracted from) the consensus coordinates to illustrate shape deformation. Graphical output was created in *GRF-ND* (Slice, 1999). Shape differences were visualized as superimposed configurations representing the positive and negative loadings of each eigenvector. Links between landmarks were added to aid in visualization of the morphology: these do not necessarily represent any structural or functional relationship between any two landmarks. It should be reiterated that these visualizations are based on the application of shape vectors to the consensus landmark configuration. Therefore, superimposed shapes represent deformations of the consensus, not actual or even “average” specimens. Take, for example, an eigenvector separating *Homo* (positive loadings) from the other taxa (negative loadings). The visualization of the positive loadings would not resemble a modern human, *per se*. Rather, it would show the consensus configuration warped according to some of the differences between *Homo* and the other specimens, as summarized by that eigenvector.

An additional use of PCA is to reduce the dimensionality of a dataset. A GPA of landmark configurations eliminates the portions of sample variance accounted for by differences in translation, scaling, rotation, and projection into tangent space. (e.g., Dryden & Mardia, 1998; Rohlf, 1999). Thus, a PCA of three-dimensional Procrustes aligned coordinates results in seven eigenvectors with zero variance. These PCs were dropped from all subsequent analyses.

Canonical variates analysis

Following PCA, canonical variates analysis (CVA) was performed on the non-zero principal components in each analytical unit. Geometrically, a CVA transforms the

multivariate space in order to minimize within-groups variability, and then performs a PCA on group centroids (Neff & Marcus, 1980). This results in canonical variates that summarize variability among sample groups, with minimal variation within them. These axes are not orthogonal to each other relative to the original variables—though they are orthogonal to other CV axes within the transformed canonical space (Neff & Marcus, 1980; Reyment, 1991). CVA, unlike PCA, requires reliably known group information in order to compute within-group variances; therefore, fossil taxa were by necessity excluded from these analyses. CVA was used to examine differences that distinguish among extant genera. As done in PCA, one-way ANOVAs were run on CV scores in order to test for differences among genera; t-tests with a Bonferroni correction were implemented to show where such differences occurred. Shape differences for each canonical variate were visualized using the method described above for PCA.

Cross-validations were also computed for every CVA in order to assess the robusticity of the CVs in separating groups. This involved removing each specimen, one at a time, recalculating the canonical variates, and then assigning the excluded specimen to a group. Thus, cross-validation results show, for each group, the number of its constituents that were assigned correctly, the number assigned incorrectly, and the groups in which these latter were misplaced. This “jackknife” style approach produces a much better estimate of the robusticity of the discriminant function than does a simple re-substitution (where test specimens were part of the original computation of the variates) (Neff & Marcus, 1980).

Mahalanobis distance

In addition to exploring differences among groups in reduced dimensions, CVA was also used to generate a distance metric for each pair of genera. Mahalanobis distance represents the distance in canonical variates space between the true population centroids from which samples were derived (Neff & Marcus, 1980; Reyment, 1991).

Mahalanobis D^2 is a statistical estimate of this distance squared. It is a useful measure in that it takes into consideration the variance and covariance within groups, and it is easily computed from a CVA. D^2 is also the basis for the multivariate extension of pairwise t-tests, Hotelling's T^2 , and follows an F distribution (Reyment, 1991). Thus, it was used to evaluate the probability that two population centroids are statistically different.

Mahalanobis D^2 is a biased estimator, however, tending to overestimate the true squared distance. Therefore, a correction (Rao, 1952; Marcus, 1969; see Sarmiento & Marcus, 2000) was applied to produce unbiased D^2 values.

An unbiased Mahalanobis D^2 matrix was computed for each CVA performed in this project. D^2 statistics were then used in Hotelling's T^2 to test the null hypothesis that pairs of genus means share a common centroid (Reyment, 1991). Mahalanobis D^2 values represent distances in a canonical space scaled according to the sample used. As such, differences in group sample sizes can affect the scaling of canonical axes (Neff & Marcus, 1980). To assess the impact of the unequal sample sizes used in this study, a randomization procedure was employed. For this, specimens were chosen at random from each group of the class variable, up to the maximum number of the smallest group (for genus-level analyses, $n = 10$). Based on these equal-sample groups, unbiased Mahalanobis D^2 values were computed and recorded. This process was performed 10,000

times and mean D^2 values were calculated. In some analyses, the difference between whole-sample values and equal-sample means was negligible; others were impacted significantly by unequal sample sizes. Values from both whole-sample and equal-sample analyses are provided throughout the text.

In every case during these analyses, Hotelling's T^2 results indicated highly significant differences ($p < 0.0001$) between all pairs of genera. This is not surprising, perhaps, for a generic-level analysis in which among-group differences are maximized. However, in this case where *every* group difference is significant, relationships among groups can only be interpreted by relative distances; simply reporting that all groups are different does not further our understanding of the relationships among them. One method for studying these relative distances is simply to peruse the matrix of calculated D^2 values. To aid in interpretation, minimum spanning trees (MSTs) were created from D^2 values using Kruskal's (1956) algorithm; each MST represents the shortest tree that links together all groups in the sample. Essentially, this means that nearest-neighbors are all joined together; disjoint trees are then connected through the closest link between any of their constituents. MSTs are frequently projected onto canonical space as indicators of how well reduced dimensional displays represent the true canonical distance. In this analysis, however, MSTs were drawn by hand only to visualize nearest-neighbor relationships; distances between connected genera are drawn to scale; distances between unlinked points *are not to scale*.

Mahalanobis D^2 values were also interpreted hierarchically using UPGMA cluster analysis. Clustering was performed and graphed in *SAS*. The unweighted pair-group method using arithmetic averages (UPGMA) was chosen as it performs well with

naturally “clumped” groups or elongated cluster chains (Sneath & Sokal, 1973). Like any clustering technique, this method initially treats each taxon as a cluster. The two closest groups (according to the metric used) are joined together into a new cluster and the total number of clusters decreases by one. This proceeds systematically until the final two clusters are joined. Different clustering methods vary by the rules used to join clusters. UPGMA computes the distance between two clusters as the average distance between all pairs of objects (i.e., taxa) in the clusters (Sneath & Sokal, 1973). Because of the possibility of skewed results due to unequal sample sizes, clustering was performed on both whole-sample and equal-sample distances. Unlike MSTs, clustering takes into account all of the D^2 values when joining groups together; thus, the position of each taxon in a cluster is influenced by the pairwise distances between all other taxa. The amalgamation criterion, however, can obscure the true distances between specific taxon pairs. Therefore, MSTs and UPGMA phenograms, as well as the distance matrix itself, are discussed in conjunction in order to evaluate group differences.

Phylogenetic node discrimination

Shape differences between crown clades

The analyses described above are purely phenetic and therefore based on few or no *phylogenetic* assumptions—CVA and Mahalanobis D^2 calculations require only the basic taxonomic assumption that extant specimens can reliably be classified into distinct genera. As such, these techniques are useful in exploring variations among specimens or genera that are manifest within the data themselves. It is well documented (e.g., Harvey & Pagel, 1991), however, that the distributions of multiple morphological features among extant taxa will not all support the true phylogeny of the group—one should not expect

every character tree to be isomorphic with the true phylogeny. It is for this reason that methods of parsimony and maximum-likelihood were developed (Harvey & Pagel, 1991). Among hominoids, however, most morphological analyses (e.g., Schultz, 1968; Tuttle, 1975; Kluge, 1983; Schwartz, 1984; Andrews & Martin, 1987; Hartman, 1988; Uchida, 1998; Collard & Wood, 2000, 2001; see Creel, 1986) have failed to recreate what many now regard to be the consensus phylogeny (Figure 5-1; Goodman, 1963; Groves, 1986; Begun, 1994; Ruvolo, 1994, 1997; Begun *et al.*, 1997; Collard & Wood, 2000, 2001; Pilbeam & Young, 2001). Cranial morphology in particular has been criticized (Hartman, 1988; Collard & Wood, 2000, 2001; Pilbeam & Young, 2001) as not useful in reconstructing hominoid phylogeny. This supposition is based primarily on the failure of parsimony-based analyses to correctly replicate phylogenies derived from molecular data. A solution posed by some of these authors (Collard & Wood, 2000) was the development of morphological analyses that are more sensitive to phylogenetic signal. Implicit to this prescription is the ability to identify features that support—at least partially—a consensus phylogeny. Setting aside criticisms of their analysis (e.g., Alba *et al.*, 2001; see McNulty, 2002), most researchers can agree that this is a laudable goal.

Toward that end, discriminant analyses (DAs) were used here to examine differences in the morphologies defined by the extant crown clades at each node in the consensus phylogeny (see Figure 5-1). Mathematically, discriminant analysis is closely related to canonical variates analysis, the two differing mainly in their goals. In fact, in the two-group DA used here, the computed discriminant function is identical to the only canonical variate axis (Neff & Marcus, 1980; Reyment, 1991). Thus, canonical DA uses a multivariate space scaled so as to minimize within-groups and maximize among-groups

variation. Put another way, features that are variable within the class groups figure only marginally in the discriminant function; features that are shared within groups, but different between them, load strongly on the resulting axis.

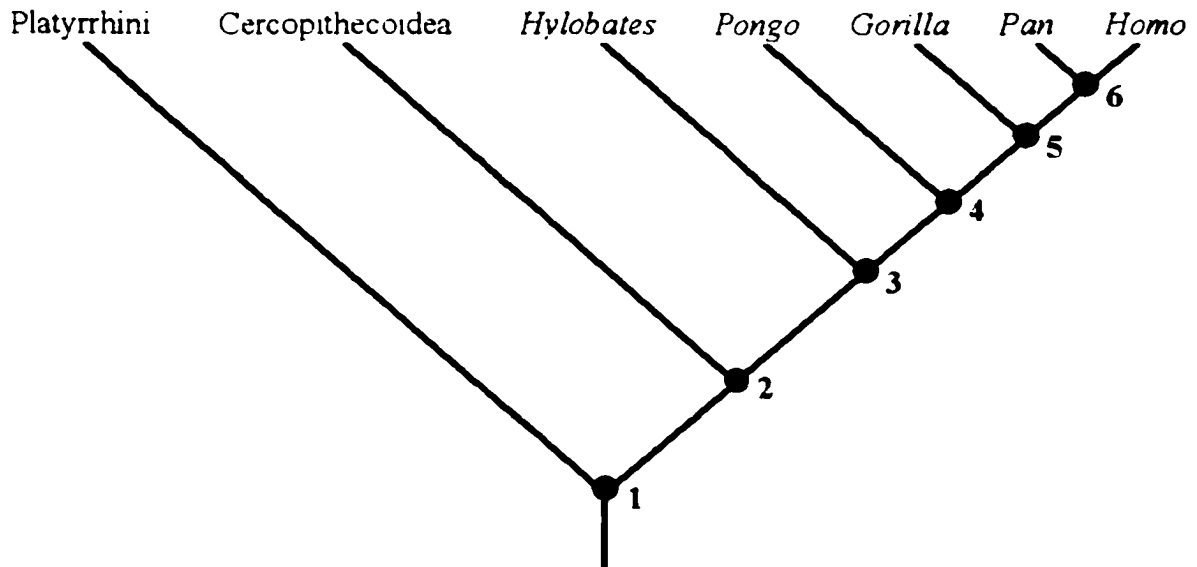


Figure 5-1 Consensus phylogeny of the relationships among extant apes and the main anthropoid clades. Nodes are referred to by number in the text.

The data collected for this project are ideal for distilling those features common to one phylogenetic branch, but distinct from the other. Assuming the relationships shown in the consensus phylogeny, the morphology defining each branch was modeled as a series of successive, two-group discriminant analyses: platyrrhine vs. catarrhine, cercopithecoid vs. hominoid, hylobatid vs. hominid, etc. Each discriminant axis thereby summarizes the differences between branches in those features that are minimally variable in either branch. Among extant taxa, the goals of phylogenetic node discrimination are twofold: 1) test the amount of overlap between the morphologies of

crown clades, and 2) determine the shape differences that distinguish these clades. The first goal was accomplished through cross-validation of the discriminant function. This provides a conservative estimate of the overlap between groups (Neff & Marcus, 1980), i.e., the ability of the discriminant function to separate them. The second goal was realized by deforming the consensus configuration by the CV regression coefficients (as described above for PCA). This provided a visualization of the shape differences summarized by the discriminant function. Thus, phylogenetic node discrimination was used to demonstrate the morphological regions and features that were most affected by the assumed cladistic event, and to evaluate the significance of those differences.

Accordingly, all extant specimens were appropriately assigned to one of the three branches (two derived, one primitive) for each node in Figure 5-1. Specimens were chosen from each of the derived clades, and a two-group DA was performed on their non-zero principal component scores. Equal sample sizes were used based on the smaller of the maximum number of specimens for either group. All samples contained equal numbers of males and females, and those comprising multiple genera were represented by equal numbers of each. Within these parameters, specimens were randomly chosen. Because of potential sampling error, analyses were run several times on different samples and once on the sample of all pertinent specimens. No differences in shape interpretation were detectable in any of these replicates.

Obviously, this analysis is based on two substantial phylogenetic assumptions—the foremost being the phylogeny of extant anthropoid taxa. A further assumption, however, is that some record of the cladogenetic event has been preserved within the morphology of the extant clade members. Such an assumption is difficult, if not

impossible, to test. Yet, it is a common assumption that underlies any cladistic—or even evolutionary—study. It should be noted here that, ultimately, this is still a phenetic procedure. All of the analyses in this project represent different ways to measure and describe similarity. Yet, unlike the principal components and canonical variates analyses described above, these phylogenetic node discriminations were directed by a consensus phylogeny, itself arrived at through cladistic analysis by many authors. Thus, rather than looking for similarities emergent from the data, this approach specifically seeks differences among well-established clades. As such, this project was able to test for morphological differences between crown clades and illustrate those regions that best differentiate between them.

Phylogenetic node discriminations of fossil specimens

The goal of discriminant analysis proper is usually assignment of unknown specimens to known groups (Neff & Marcus, 1980). Having already used similar methods to determine and test shape differences between crown clades, the final analysis in each analytical unit was designed to assign fossil specimens according to these discriminant functions. First, however, fossils were tested for their affinities to extant genera. To do this, a DA was computed for all extant specimens, with genus as the class variable. Based on this DA, each fossil specimen was assigned to a modern genus using discriminant functions derived from all extant genera. This initial discrimination was computed for the whole sample of extant specimens, resulting in a single classification for every fossil. To assess the bias of unequal sample sizes, however, 1000 randomized equal-sample replicate DAs were also performed in a manner similar to that described above (see Mahalanobis distance); since large numbers of randomized samples were run,

specimens were chosen randomly from each group—without regard for balanced sex and taxon ratios. Thus, each fossil specimen was given a whole-sample assignment, as well as a distribution of assignments from the 1000 replicates. These provided a measure of the affinities among fossils and extant genera.

After this, discriminant analyses were calculated for each node in the consensus phylogeny in order to assign fossil specimens. Thus, each fossil was assigned to one of two crown clades based on the morphology that distinguishes them. Again, classifications from both whole-sample and 1000 equal-sample randomized DAs were computed at each node. For all of these discriminant analyses, tallied statistics included the percentage of extant specimens correctly reclassified in cross-validation and the assignment of each fossil specimen. In most cases, the whole-sample fossil assignment agreed with the majority of equal-sample replicate assignments; discrepancies are discussed in the text.

A fundamental assumption made here is that the fossil specimens actually belong to one of the test groups; discriminant analysis will assign specimens without regard to the validity of this assumption. For generic discrimination, this assumption is taken to be *false*. None of the fossils here is likely to belong within an extant anthropoid genus. The discriminant analysis is useful nevertheless to examine the morphological affinities of the fossil specimens. Of more concern regarding this assumption are the node analyses. In trying to infer phylogenetic information from these tests, it is important to assess whether or not the discriminant assignments are spurious.

This project adopted a two-tiered approach for testing this assumption. First, the randomization provides an estimate of the robusticity of the assignment. A specimen that is nearly equidistant from both group centroids will tend to have an even distribution of

assignments, as randomized sampling causes it to fall on one or the other side of the function midpoint. In this circumstance, the specimen clearly does not belong in either of the groups. A χ^2 test for equal proportions was used to determine whether there were significant differences within assignment distributions. Note that equidistance from group centroids does not imply minimal distance from them. A specimen with an even assignment distribution need not lie on the midpoint of the discriminant function. Rather, it could be placed anywhere on or near the hyperplane that orthogonally bisects the discriminant function. Thus, one should be extremely cautious in interpreting an equal distribution as an evolving lineage, midway between morphologies; such a claim must be well supported with evidence from genus-level discriminations.

Thus, analysis of the distribution proportions is useful in determining if specimens are equally dissimilar to both test groups, and therefore spuriously assigned. It will give a false determination, however, in cases where specimens are systematically more similar to a group in which they do not belong. This circumstance might arise if one of the test groups were highly autapomorphic. Imagine, for example, trying to classify a *Lemur* cranium based on a discrimination between *Gorilla* and modern *Homo*. Clearly the lemur belongs to neither group. Yet, because the cranium of *Homo* is so unique, the lemur specimen might consistently place among the gorillas. Looking only at the distribution of assignments would lead one to the incorrect conclusion that the lemur had strong affinities with *Gorilla* crania. Therefore, a second level of analysis was added in order to test the assumption of non-spurious assignment. In addition to the 2-group whole-sample and equal-sample tests, 3-group DAs were also performed at each node (except node 1). The third group was made up of those taxa external to the node being tested. Therefore,

each specimen was first tested for its affinities to the two extant clades. It was then given the option of assignment in a group composed of all other extant taxa in the sample. This third group is labeled “primitive” for convenience only, not to imbue it with any evolutionary significance. Like the 2-group analyses, 3-group tests were also done both on the whole-group and for 1000 equal-sample randomized replicates.

There is a clear hierarchy here for testing the assumption that fossils are not spuriously assigned. If the distributions are even in the 2-group test, then the specimen clearly does not belong in either group; the 3-group test in this case becomes irrelevant. If assignments are unequally distributed, however, one still must determine whether this implies a real similarity to one test group, or a strong dissimilarity to the other. Then the 3-group analysis becomes important, as it provides an additional option for classification. This will be especially useful in recognizing when fossils belong on lower branches of the phylogenetic tree. While the approach adopted here is not foolproof, used together the 2- and 3-group phylogenetic node discriminations, in conjunction with genus-level DAs, provide a useful tool for testing the affinities of fossils based on shape differences between crown clades.

CHAPTER 6: MORPHOMETRIC ANALYSIS OF CRANIAL MORPHOLOGY

This chapter details the morphometric and statistical analyses that were performed on the entire set of cranial landmarks. The first sections explore variability across all specimens and differences among taxa by way of principal components and canonical variates analyses. Mahalanobis distances generated from the latter are discussed and clustering techniques are employed to discern hierarchical relationships among extant genera. In later sections, discriminant analyses are used to reveal the patterns of shape change that define specific branches in a consensus phylogeny of extant anthropoids. Those fossil specimens preserving substantial facial morphology are then tested at each node on this tree in order to determine their closest affinities.

LANDMARK CONFIGURATIONS

Landmarks used in this chapter are listed in Table 6-1 along with the abbreviations used in this text (see Table 4-1 for landmark definitions). Figures 6-1 and 6-2 depict the consensus configuration of all specimens in lateral and frontal views, respectively. All subsequent figures used to illustrate shape differences show these same two perspectives. Thus, the labels here serve as a reference for later figures in this chapter. Unlike Figures 6-1 and 6-2, however, visualizing shape differences requires the superimposition of *two* landmark configurations—representing deformations of the consensus by contrasting shape vectors (see chapter 5). The resulting figure can be difficult to interpret visually due to the density of landmarks.

Table 6-1 Landmarks used in analyses of the entire cranium. See Chapter 4 for definitions and discussion.

Landmark	Abbreviation
Midline:	
Opisthocranium	OPC
Bregma	BRE
Post-toral sulcus	PTS
Glabella	GLA
Nasion	NAS
Rhinion	RHI
Posterior clivus	CLI
Anterior nasal spine	ANS
Alveolare	ALV
Opisthion	OPI
Basion	BAS
Hormion	HOR
Staphylion	STA
Midline anterior palatine	MAP
Incisivion	INC
Bilateral:	
Porion	POR
Superior zygomatico-temporal suture	SZT
Jugale	JUG
Frontomolare temporale	FMT
Frontomolare orbitale	FMO
Mid-orbit torus inferior	MTI
Mid-orbit torus superior	MTS
Dacryon	DAC
Orbitale	ORB
Apex of orbital cone	AOC
Zygoorbitale	ZYO
Malar foramen	MLF
Infraorbital foramen	IOF
Zygomaxillare	ZYM
Malar root origin	MRO
Alare	ALA
Posterior incisive canal	PIC
I ¹ -I ² contact	I12
Inferior premaxillo-maxillary suture	IPM
Postglenoid tip	PGT
Lingual canine margin	LCM
Canine-premolar contact	CPC
Premolar-molar contact	PMC
Distal molar	DM3
Inferior zygomatico- temporal suture	IZT

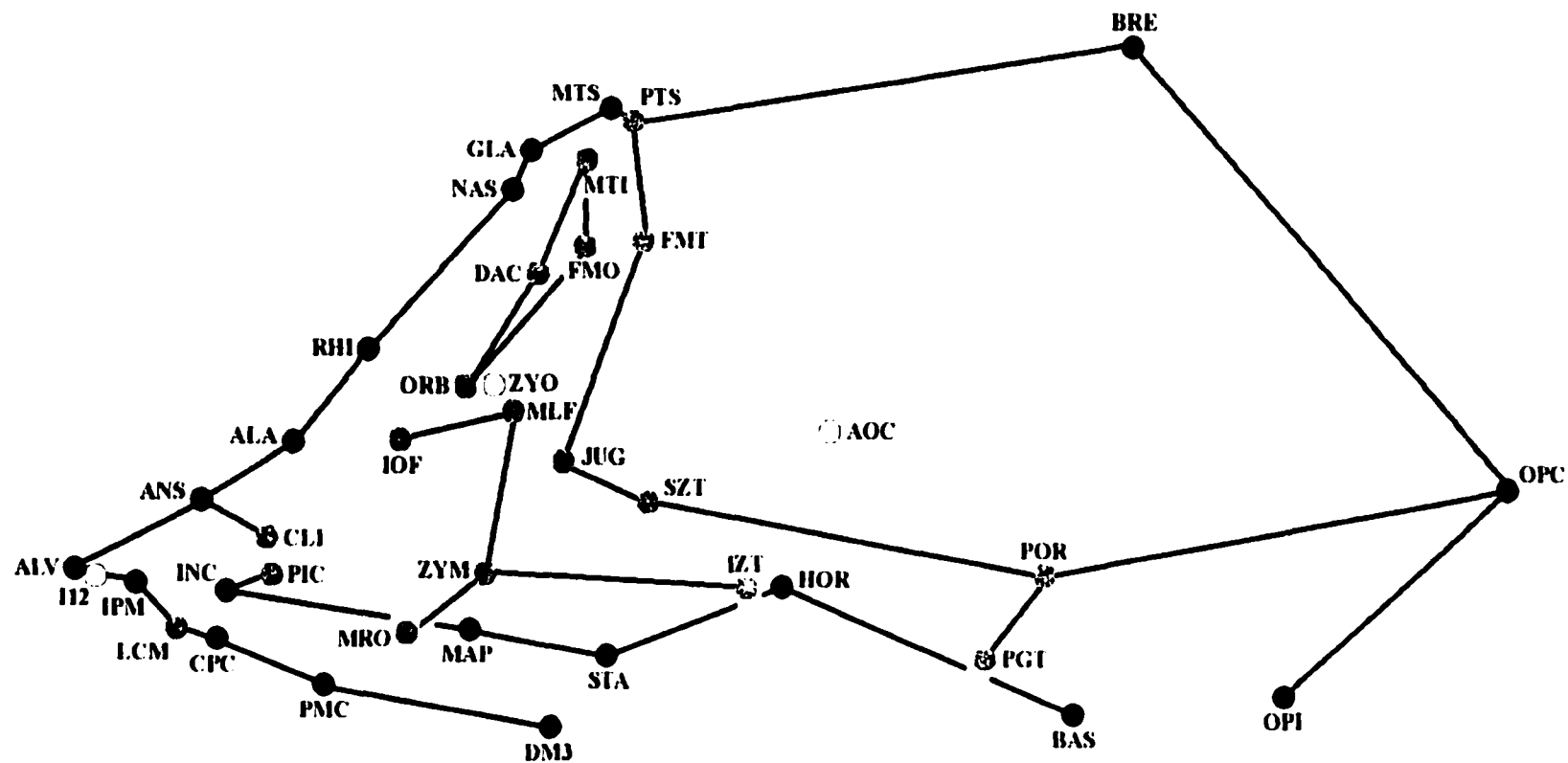


Figure 6-1 Lateral view of the consensus configuration with landmark abbreviations (see Table 6-1 for landmark names). Primary landmarks are denoted by black dots; these are used to visualize cranial shape, regardless of their loading scores, in all profile figures. Landmarks with solid gray dots are secondary: only included in figures when they load heavily on that multivariate axis. Open gray dots indicate landmarks that are not used in lateral views in this chapter. Lines connecting landmarks are strictly to aid in visualizing shape differences. See text for further discussion.

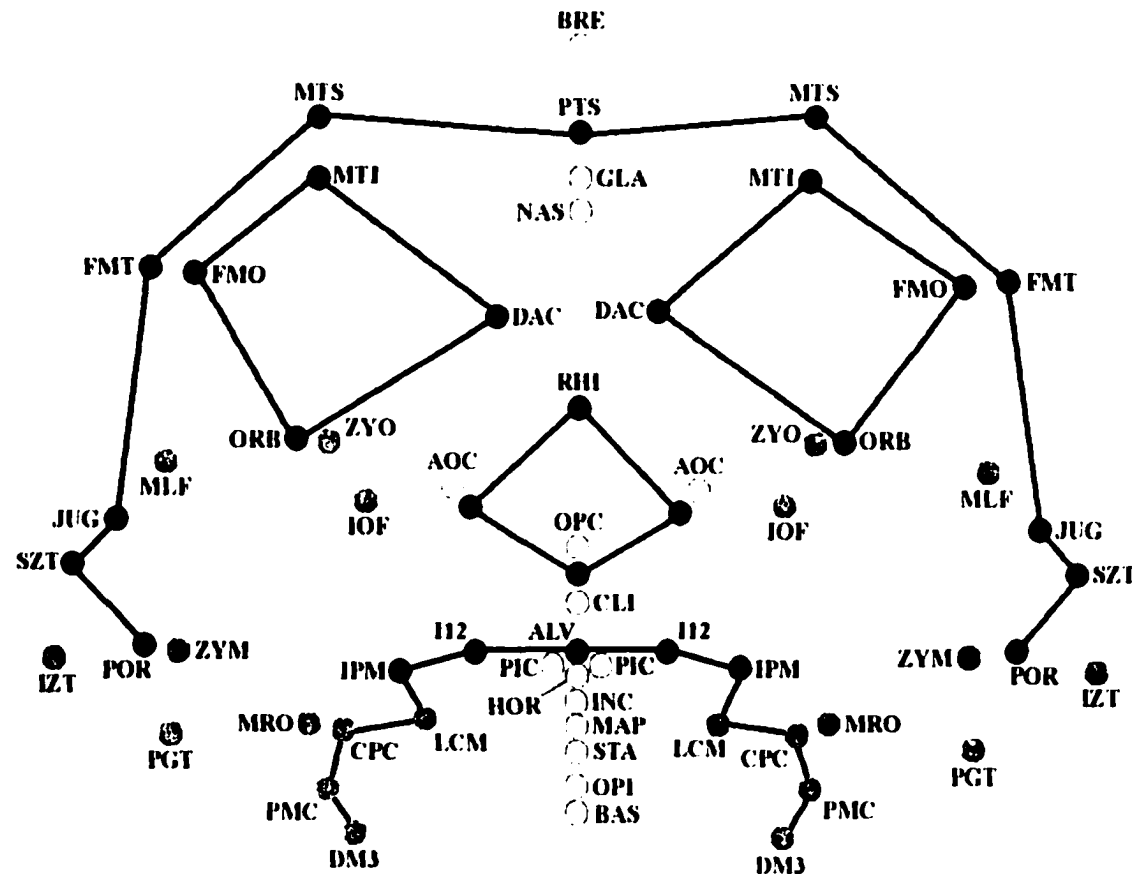


Figure 6-2 Frontal view of the consensus configuration with landmark abbreviations (see Table 6-1 for landmark names). Primary landmarks—denoted by black dots—are used to illustrate cranial shape, regardless of their loading scores, in all frontal view figures. Secondary landmarks are shown with solid gray dots; these are only included in figures when they load heavily on that multivariate axis. Open gray dots indicate landmarks that are not used in frontal views in this chapter. Note that most of these are midline: the constraints of bilateral symmetry enable their shape differences to be summarized in lateral view. Lines connecting landmarks are strictly to aid in visualizing shape differences. See text for further discussion.

Therefore, two approaches were adopted in order to clarify figures yet still convey the essential information. First, landmarks were divided into primary and secondary groups (see Figures 6-1, 6-2). Primary landmarks are those necessary to give shape to the figures—providing a context in which shape differences can be interpreted. These landmarks were included in all shape-figures in this chapter and are generally not labeled. Secondary landmarks were only included in depictions of eigenvectors on which they loaded strongly; these were labeled more often for clarity. Note that primary landmarks for the lateral perspective may not be primary for the frontal perspective, and *vice versa*. The second approach adopted was to provide magnified insets for lateral views of the subnasal and orbital regions. Both of these areas have a high density of landmarks in lateral perspective and can be more easily visualized in separate, expanded diagrams. As with secondary landmarks, these insets were only used when the relevant morphology was determined to substantially contribute to the multivariate axis.

SAMPLE TAXA

Ten extant anthropoid genera (see Chapter 3) were sampled for this project to analyze and interpret the morphological differences among hominoid primates. Preliminary phenetic analyses found that multiple, high-order principal component and canonical variate axes were dominated by the autapomorphic morphologies of *Homo* and *Papio* (see, e.g., Figure 6-3). The panoramic perspective necessary to encompass their cranial differences resulted in poor resolution of differences among other taxa. Moreover, Mahalanobis distance clustering showed them to be successive phenetic “outgroups” to the rest of the genera—similar neither to each other, nor to any other genus. As

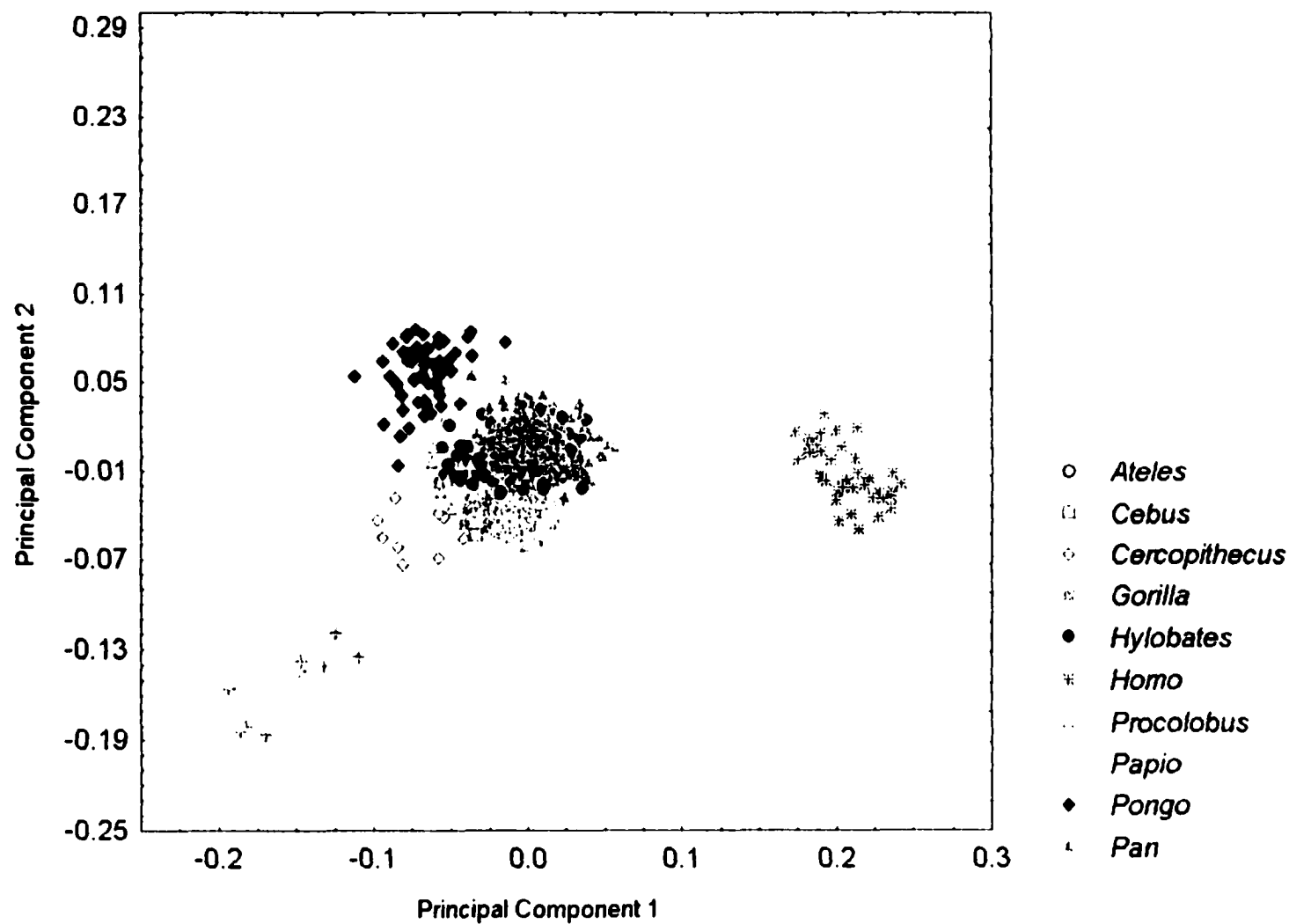


Figure 6-3 Plot of scores for PC 1 and PC 2 from a PCA of all ten extant genera. This provides a graphical representation of the overwhelming effect that highly autapomorphic specimens can have on multivariate ordinations. For this reason, *Homo* and *Papio* were excluded from some analyses.

obfuscating factors, *Homo* and *Papio* were excluded from the initial exploratory analyses (PCA, CVA, UPGMA; see Singleton, 2002); both were included, however, in later phylogenetic node discriminations as important members of their respective clades.

PRINCIPAL COMPONENTS ANALYSIS

In order to explore shape variation across all specimens, a principal components analysis was performed on the covariance matrix of size-adjusted (see Chapter 5) coordinate data for all 65 landmarks. One-way analyses of variance (ANOVAs) on PC scores were used to test for statistical differences among genera for each axis. Results of the PCA and ANOVAs are shown in Table 6-2 for the first 15 PCs; subsequent axes—comprising less than 1% each of the total group variability—were examined but are not listed here. ANOVA results indicate highly significant differences among genera on each eigenvector. Therefore, pairwise t-tests with a Bonferroni adjustment were performed on the least squares adjusted means for each genus (see Table 6-3). The first four principal component axes are discussed in detail below.

Principal component 1

The first principal component represents nearly 29% of the total variability among the sample. T-test results are displayed in Table 6-3; a graph of specimen scores for PC1 and PC2 is shown in Figure 6-4. As indicated in both the table and graph, the greatest axis of variation clearly separates *Gorilla* and *Hylobates* from the other taxa. Although there is some overlap near the midline, this distinction is quite pronounced. T-test results also show *Pan* to be statistically distinct from all others but *Pongo* and *Cercopithecus*. This difference is somewhat less meaningful, however, as the range of chimpanzee scores

on PC1 encompasses nearly all of the non-hylobatid and non-gorilla specimens. In addition to taxonomic differences, sexes of both *Gorilla* and *Pongo* are highly significantly different ($p < 0.0001$) centroids, with females scoring more positively (see Figure 6-4); significant intrageneric sorting was not found among any other taxa.

Table 6-2 Summary of PCA and ANOVA results for the first fifteen principal component axes. PCA results give statistics for the latent roots of the sample variance (eigenvalues), the proportion of variance explained by each component, and the cumulative proportion of the variance summarized by each PC and those preceding it. One-way ANOVAs were performed on each component to test for significant differences among genera; F-values and probabilities are given for tests of the null-hypothesis that all genera share a common mean.

	PRINCIPAL COMPONENTS ANALYSIS			ANALYSIS OF VARIANCE	
	Eigenvalue	Proportion	Cumulative	F Value	Pr > F
PC 1	0.00280157	0.2862	0.2862	252.60	<0.0001
PC 2	0.00142191	0.1453	0.4315	224.82	<0.0001
PC 3	0.00078273	0.0800	0.5115	83.12	<0.0001
PC 4	0.00046825	0.0478	0.5593	84.52	<0.0001
PC 5	0.00030407	0.0311	0.5904	15.48	<0.0001
PC 6	0.00027842	0.0284	0.6189	37.86	<0.0001
PC 7	0.00023702	0.0242	0.6431	18.44	<0.0001
PC 8	0.00023430	0.0239	0.6670	36.32	<0.0001
PC 9	0.00020410	0.0209	0.6879	8.48	<0.0001
PC 10	0.00017415	0.0178	0.7057	3.97	0.0003
PC 11	0.00016061	0.0164	0.7221	10.65	<0.0001
PC 12	0.00014758	0.0151	0.7372	3.95	0.0003
PC 13	0.00011743	0.0120	0.7492	6.78	<0.0001
PC 14	0.00010489	0.0107	0.7599	5.88	<0.0001
PC 15	0.00010189	0.0104	0.7703	6.96	<0.0001

Table 6-3 Results of pairwise t-tests between genera for PCs 1-4. Bonferroni adjusted p-values are given in the lower triangle. * indicates significance at $\alpha=0.05$

P C 1	Genus	Atel	Cebu	Cerc	Gori	Hylo	Pan	Pcol	Pong
	Atel			*	*	*	*		*
	Cebu	1.0000			*	*	*		
	Cerc	0.0467	1.0000		*	*			
	Gori	<0.0001	<0.0001	<0.0001			*	*	*
	Hylo	<0.0001	<0.0001	<0.0001	1.0000		*	*	*
	Pan	<0.0001	0.0053	1.0000	<0.0001	<0.0001		*	
	Pcol	1.0000	1.0000	1.0000	<0.0001	<0.0001	0.0344		
	Pong	0.0012	0.4195	1.0000	<0.0001	<0.0001	0.3636	1.0000	
P C 2	Genus	Atel	Cebu	Cerc	Gori	Hylo	Pan	Pcol	Pong
	Atel				*	*	*		*
	Cebu	1.0000			*		*		*
	Cerc	1.0000	0.0948		*	*	*		*
	Gori	<0.0001	0.0006	<0.0001		*		*	*
	Hylo	0.0374	1.0000	<0.0001	<0.0001		*	*	*
	Pan	<0.0001	<0.0001	<0.0001	0.1239	<0.0001		*	*
	Pcol	1.0000	0.5305	1.0000	<0.0001	<0.0001	*		*
	Pong	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	
P C 3	Genus	Atel	Cebu	Cerc	Gori	Hylo	Pan	Pcol	Pong
	Atel				*	*	*		*
	Cebu	0.9077			*	*	*	*	*
	Cerc	1.0000	1.0000		*	*	*	*	*
	Gori	<0.0001	<0.0001	<0.0001		*	*		*
	Hylo	<0.0001	<0.0001	<0.0001	<0.0001			*	
	Pan	<0.0001	<0.0001	<0.0001	<0.0001	0.6507		*	
	Pcol	0.0721	<0.0001	0.0032	1.0000	<0.0001	<0.0001		*
	Pong	<0.0001	<0.0001	<0.0001	<0.0001	1.0000	1.0000	<0.0001	
P C 4	Genus	Atel	Cebu	Cerc	Gori	Hylo	Pan	Pcol	Pong
	Atel		*	*	*	*	*	*	
	Cebu	<0.0001		*	*	*	*	*	*
	Cerc	<0.0001	<0.0001		*	*	*	*	*
	Gori	0.0097	<0.0001	<0.0001				*	*
	Hylo	0.0170	<0.0001	<0.0001	1.0000			*	*
	Pan	0.0004	<0.0001	<0.0001	1.0000	0.1135		*	*
	Pcol	<0.0001	<0.0001	0.0001	<0.0001	<0.0001	<0.0001		*
	Pong	1.0000	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	

Shape change in the neurocranium (Figure 6-5) shows a somewhat flatter vault toward the negative pole, accompanied by a superior shift in the occipital morphology. There is also a substantial change in facial morphology, with a relatively shorter, more generally protruding face in *Gorilla* and *Hylobates*. *Pan* has a taller, flatter face, protruding more in the subnasal region. *Pongo* and the non-hominoid taxa range between these two extremes. Perhaps most interesting are differences in subnasal morphology (see Figure 6-5c). Positively scoring specimens have greatly expanded the subnasal clivus height and anterior palate thickness. Indeed, close inspection of these landmarks shows this representing antero-inferior expansion of the premaxilla and dental arcade. These results suggest a closer affinity between hylobatid and gorilla subnasal anatomy than suggested by some authors (Ward & Kimbel, 1983; Ward & Brown, 1986; Brown & Ward, 1988). Benefit & McCrossin (1995) noted some similarities among individual siamang and gorilla specimens, though McCollum & Ward (1997) argued that these are superficial and independently derived. Nevertheless, affinities between subnasal morphologies of *Pan* and *Pongo* (McCollum & Ward, 1997; see Chapter 8) might indicate that *Gorilla* is more similar to the ancestral hominid morphology. Results here tend to support this supposition; Chapter 8 fully addresses this issue in a more appropriate context.

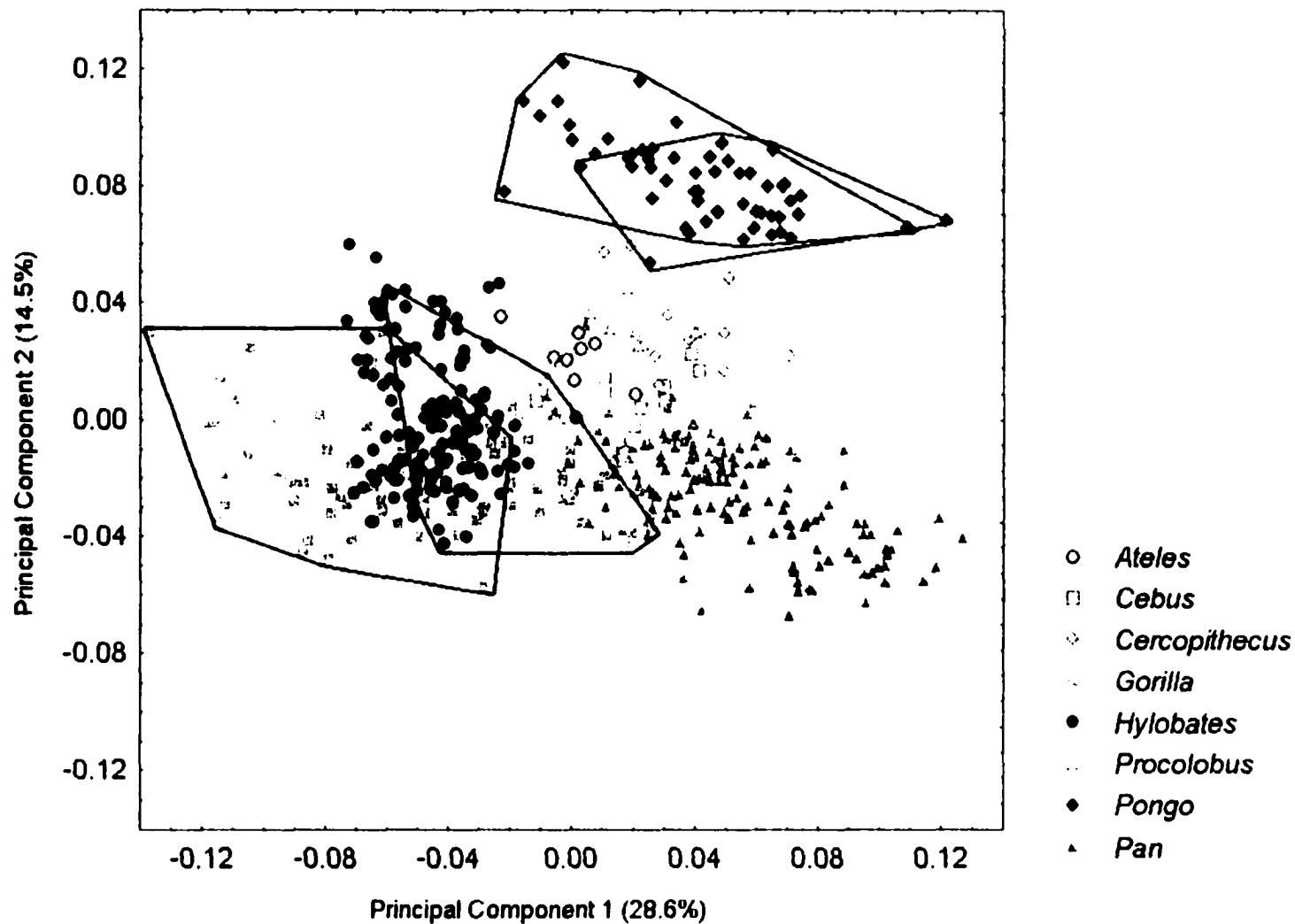


Figure 6-4 Plot of principal component scores for PC 1 and PC 2. PC 1 separates *Gorilla* and *Hylobates* from the other anthropoids. Males (negative) and females (positive) of *Gorilla* and *Pongo* also sort along this axis, as illustrated by the convex hulls. PC 2 separates *Pongo* from all other taxa and separates hylobatids into two distinct clusters, with siamangs scoring more positively.

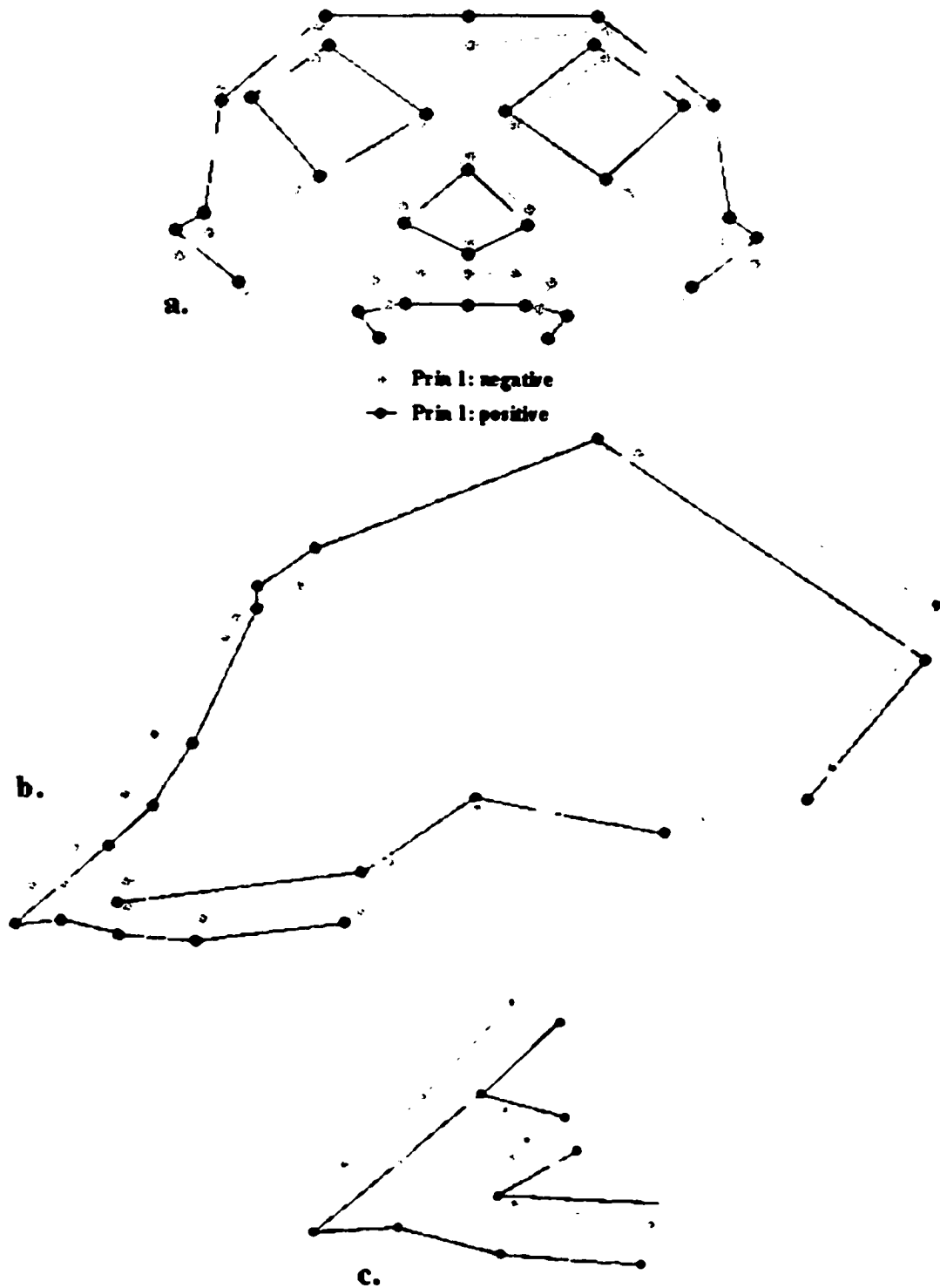


Figure 6-5 Shape change along PC 1. Black lines represent the positive loadings, gray lines show the negative loadings. (a) frontal view; (b) lateral view; (c) magnification of the subnasal region (lateral view). See Figures 6-1 and 6-2 for landmark references.

Principal component 2

PC2 represents nearly 15% of the total variability among specimens. ANOVA results indicate that mean scores for genera are again highly significantly different, with pairwise comparisons given in Table 6-3. As Figure 6-4 illustrates, the greatest distinction among taxa on this eigenvector separates *Pongo* from the other genera. In some sense, then, this PC largely represents differences between the orangutan and the other apes. In addition, however, PC 2 clearly separates the hylobatids into two clusters—with siamangs offset in the direction of *Pongo*. Excepting *H. syndactylus*, three groups actually fall out on PC 2: *Pongo*, non-hominoids, and *Gorilla-Pan-Hylobates*. Although PC 2 appears to sort male and female orangutans (Figure 6-4), there were no significant intrageneric effects on this axis.

Shape differences correlated with PC 2 are illustrated in Figure 6-6. The positive pole, represented by *Pongo*, is characterized by relative decreases in brain case length and height with less flexion in the cranial base and a flattened glabellar region. Also, **PGT** sits well inferior and somewhat medial in *Pongo* compared to the other apes. The heaviest PC loadings are in the medial landmarks of the upper face. In profile, positive-scoring specimens slope gradually back above rhinion, largely uninterrupted until the post-toral sulcus; **MTS** is situated almost exactly on **PTS** in the positive profile and is thus obscured (Figure 6-6). More negative specimens have a sharper ascent from rhinion, growing steeper at nasion. In this case, **MTS** is situated both superior and anterior to **PTS**. While it is not surprising to find this latter morphology attributed to *Gorilla* and *Pan*, the inclusion of gibbons here is less intuitive. The anterior expansion of the medial upper face in most apes is not limited to the midline: **MTI**, **MTS**, **ORB**, and especially

DAC all exhibit antero-superior displacement on the negative pole of PC2; at the positive end, these points are nearly coplanar. Coincident with this is a relative widening of the upper face: toward the negative pole, orbital and peri-orbital landmarks shift away from the midline and generally superiorly. Conversely, *Pongo* tends toward a narrower upper face. In the lower face, positively loaded specimens show a marked anterior (and slightly superior) expansion in the premaxillary landmarks. Unlike in PC 1, however, this expansion does not correspond to a dramatic change in the relative positions of the subnasal features; it is more of a deflection of the morphology in a different direction. Also in the lower face, **ZYM** is highly variable along PC 2, extending infero-laterally as scores get bigger. In *Pongo*, this represents a much taller zygoma; there is no significant corresponding change, however, in the position of the malar root.

Principal component 3

PC 3 makes up 8% of the total sample variability; ANOVA results on genus means were highly significant. It is clear from both t-test comparisons (see Table 6-3) and the plot of PC scores (Figure 6-7) that the main distinction along this axis is between hominoids and non-hominoids. Mean scores for both platyrrhine genera and for *Cercopithecus* are highly significantly different from those of all the ape genera; *Procolobus* overlaps the range of *Gorilla* but is significantly different from the other hominoids. Differences between sexes or among infrageneric taxa are not manifest on this axis. There is a slight tendency for *G. g. gorilla* and *G. g. beringei* to sort along PC 3, but their means are not significantly different; excluding *G. g. gorilla* (the more negative scores among *Gorilla*) and re-computing means does not alter the results of the generic t-tests.

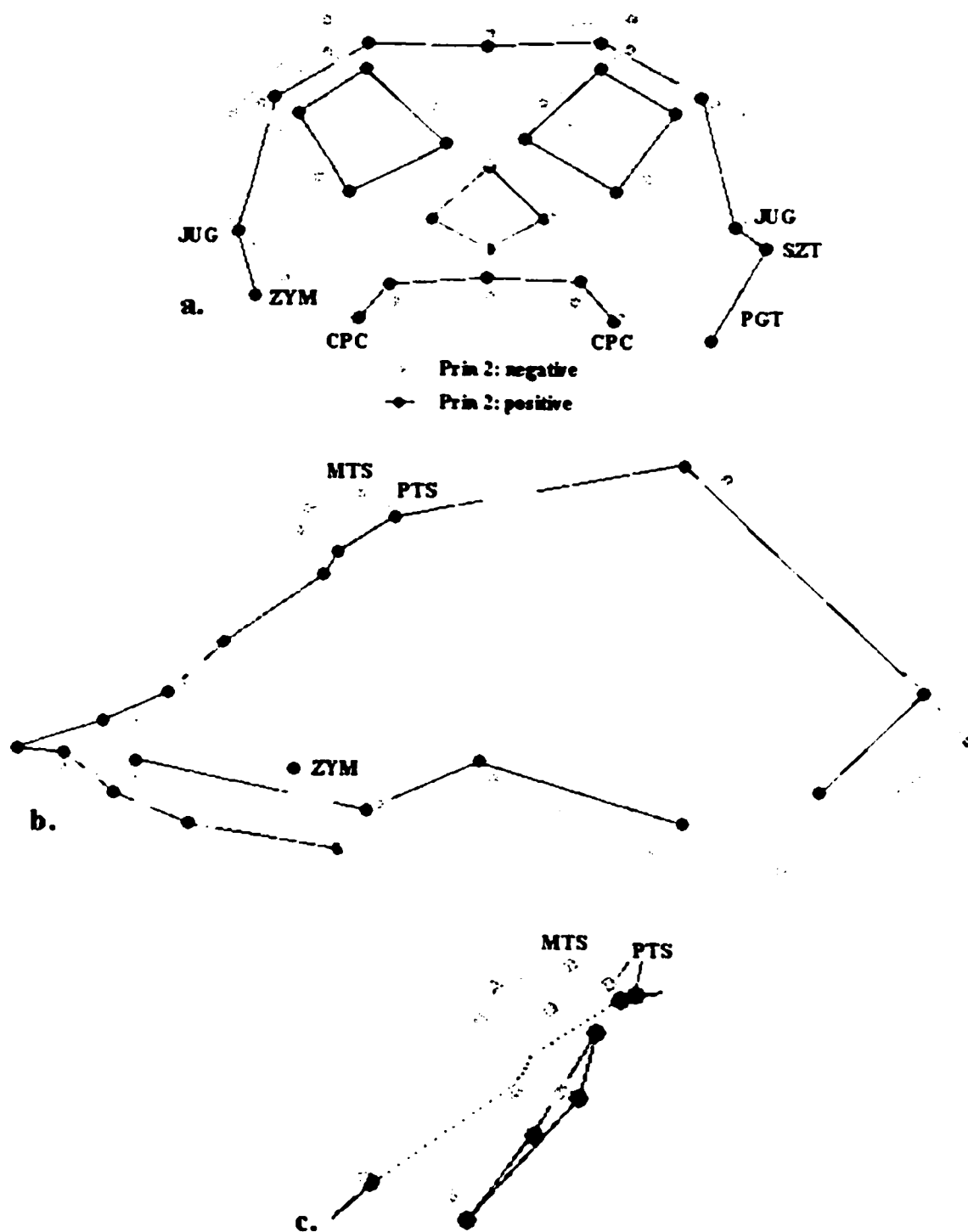


Figure 6-6 Shape change along PC 2. Black lines represent the positive loadings, gray lines show the negative loadings. (a) frontal view: right and left sides display different landmarks in order to depict shape changes in both anterior and posterior morphology; (b) lateral view; (c) magnification of the orbital region (lateral view). See Figures 6-1 and 6-2 for additional landmark references.

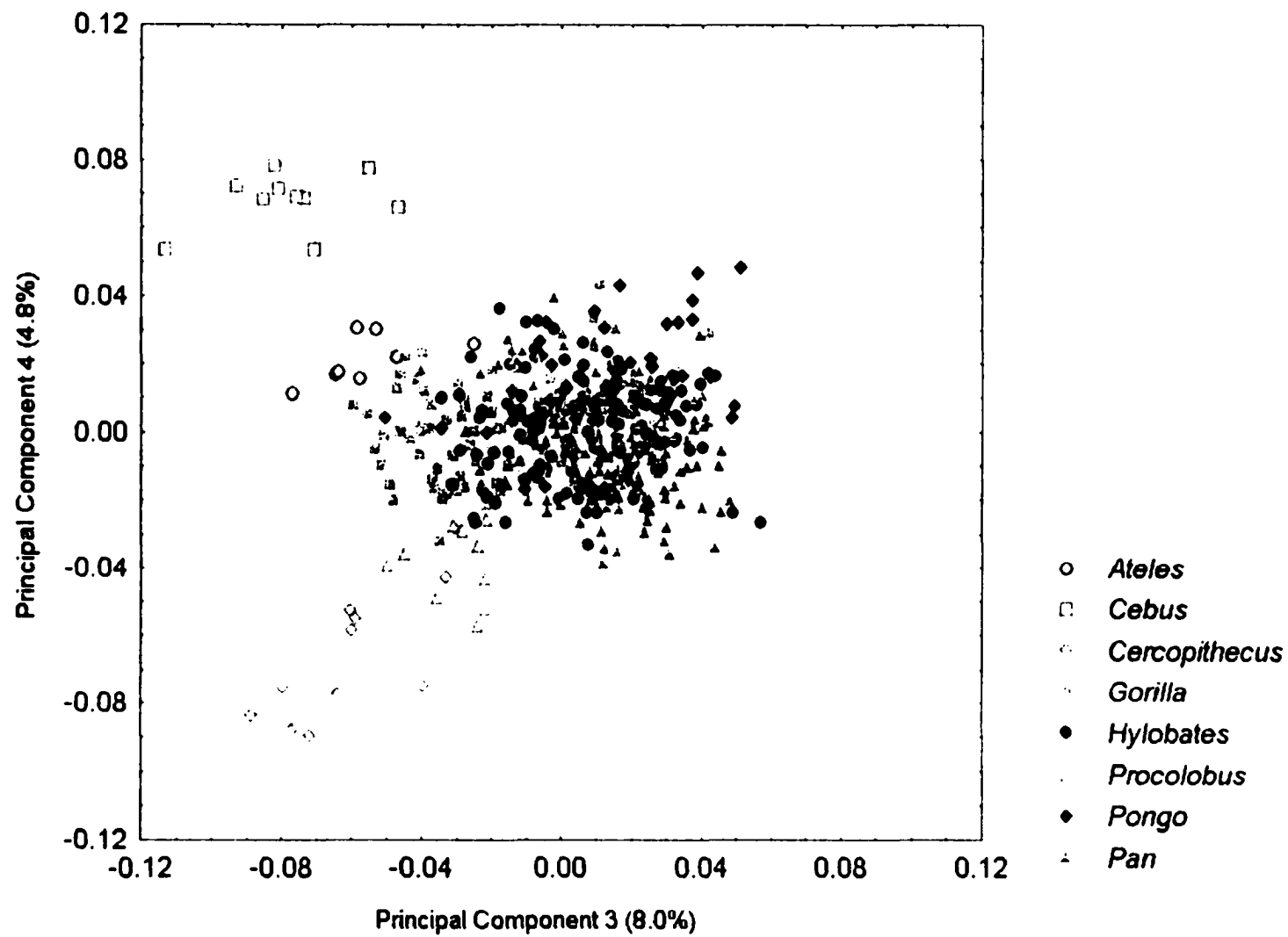


Figure 6-7 Plot of principal component scores for PC 3 and PC 4. PC 3 largely separates hominoid from non-hominoid specimens. PC 4 sorts platyrrhine and cercopithecoid specimens, with hominoids clustering around the center.

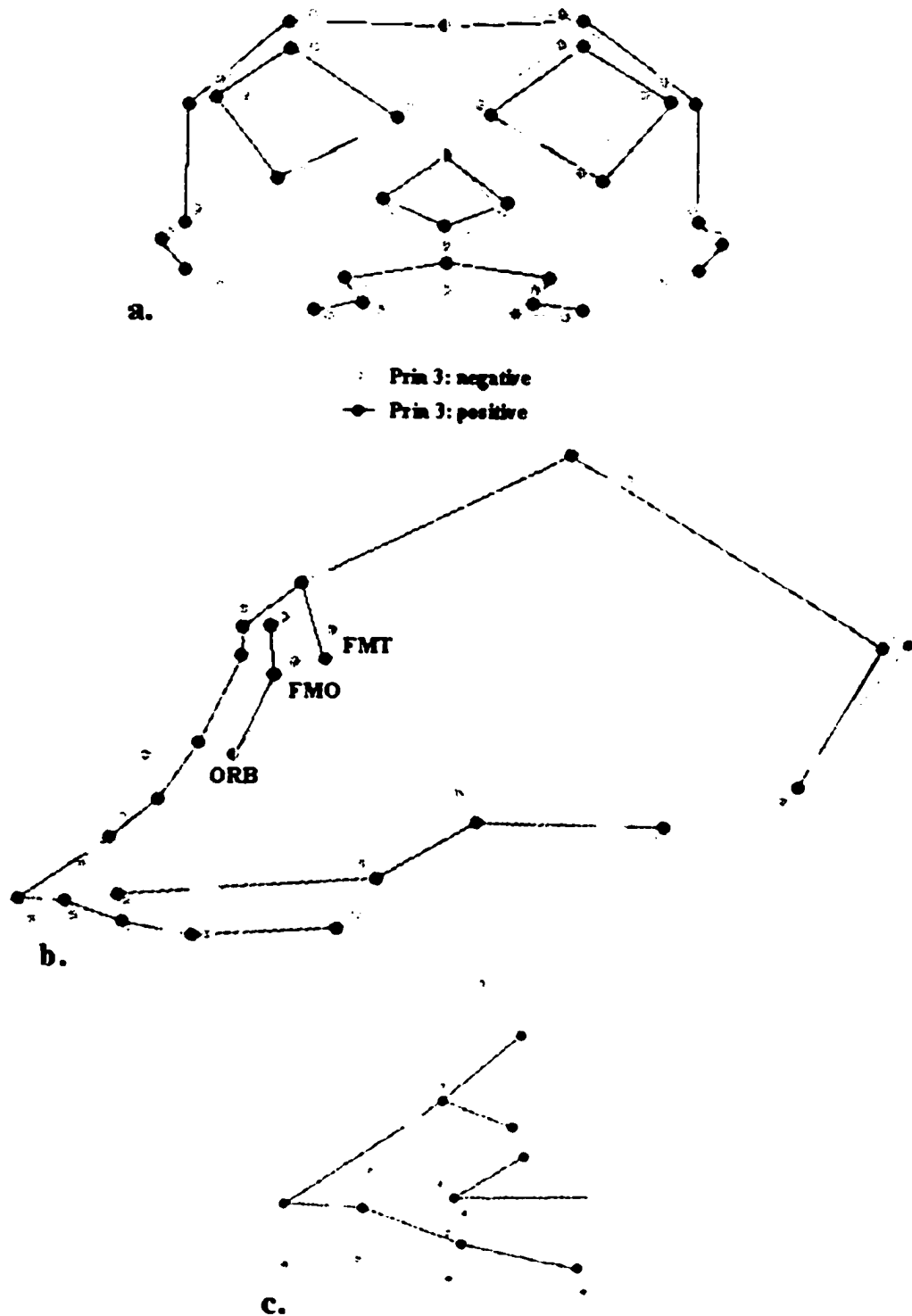


Figure 6-8 Shape change along PC 3. Black lines represent the positive loadings, gray lines show the negative loadings. (a) frontal view; (b) lateral view; (c) magnification of the subnasal region (lateral view). See Figures 6-1 and 6-2 for additional landmark references.

Shape change on PC 3 is illustrated in Figure 6-8. In the neurocranium, positive scores are characterized by a taller braincase as the distance between bregma and hormonion expands. The negative pole has a relatively shorter braincase, but substantially more flexion about hormonion. In the upper and mid face, non-hominoid specimens exhibit marked anterior expansion of the midline landmarks, but postero-medial displacement of lateral landmarks. Apes display the opposite trends, tending to be broader and flatter across the upper face. There is a slight overall shortening of the ape face relative to the non-hominoids. More interesting, however, are the relative distances between landmarks along the midline. The distance between nasion and rhinion in non-hominoids is greatly expanded, indicating substantially longer nasal bones. In the lower face, the subnasal clivus is much longer in the apes, with a substantially thicker palate and marked posterior displacement of PIC.

Principal component 4

PC 4 represents about 5% of the variation among specimens. Differences among genus means (Tables 6-3) on this axis tend to sort platyrrhines positively from cercopithecoids negatively, with hominoids clustering around zero (see Figure 6-7). T-test comparisons found significant differences between each non-hominoid genus and all other genera, with the exception of *Ateles*; this genus is distinct from all of the hominoids except *Pongo*. There are no statistical differences among *Gorilla*, *Pan*, and *Hylobates* along this axis. The mean of *Pongo* is distinct from every genus except *Ateles*, though its range overlaps those of other apes. Additional taxonomic or sex effects are not evident on PC 4.

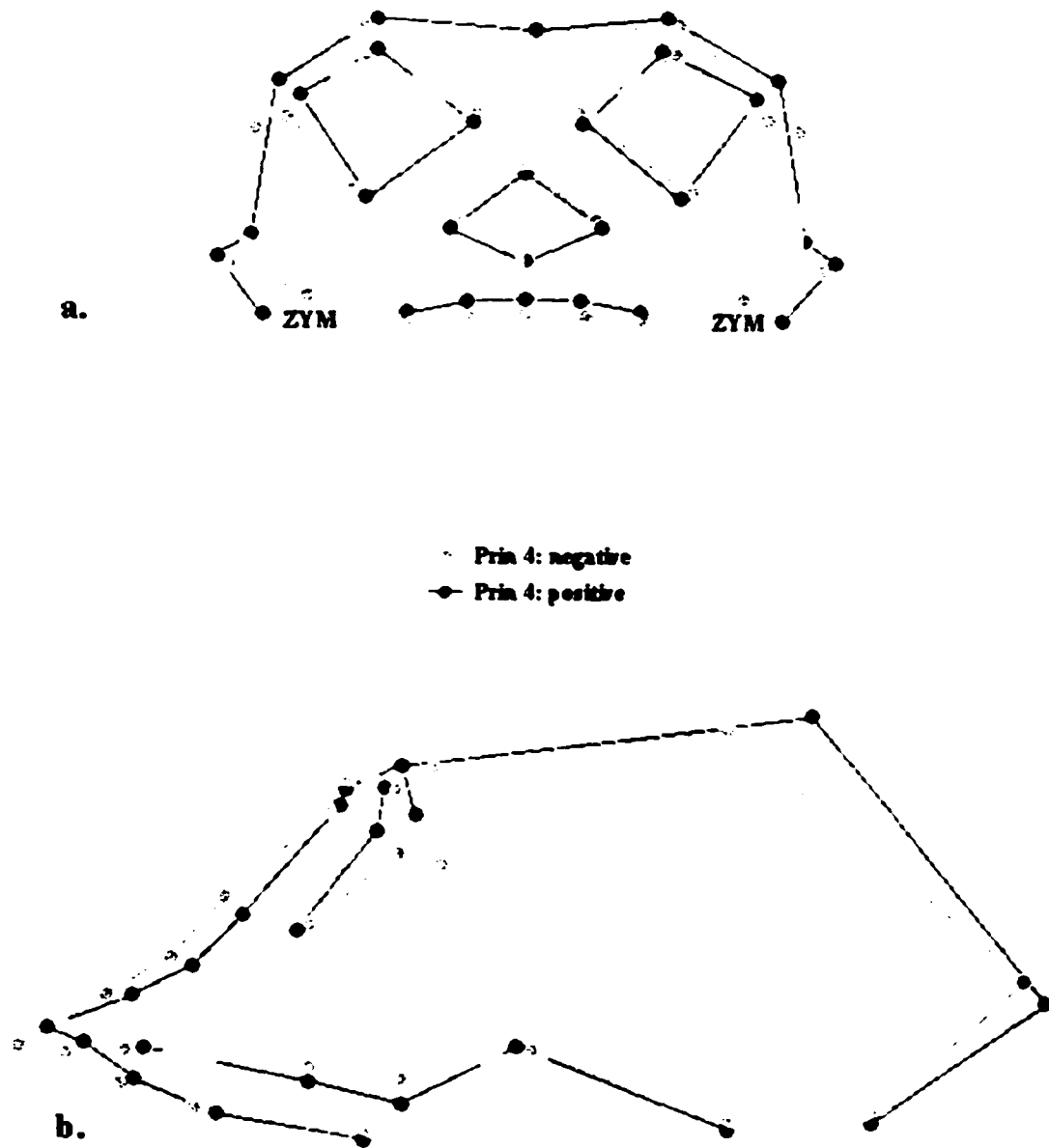


Figure 6-9 Shape change along PC 4. Black lines represent the positive loadings, gray lines show the negative loadings. (a) frontal view; (b) lateral view. See Figures 6-1 and 6-2 for additional landmark references.

Shape changes along the fourth PC axis (Figure 6-9) can generally be regarded as representing differences between the cercopithecoids and platyrrhines sampled here. Along the continuum between these poles, hominoid morphology clusters near the middle. The negative (cercopithecoid) extreme is characterized by antero-posterior shortening of the neurocranium; the orbital pillar is placed posteriorly on the cranium, with a substantial inferior migration of the fronto-malar suture. In the lower face, the zygo-maxillary suture is shorter, truncating the relative height of the cheekbone. And, the posterior palate midline slopes superiorly, reducing the offset between cranial base and palate. In contrast, the positive pole is represented by a longer, and somewhat taller neurocranium, a reduced angle in the upper face, a tall zygomatic root, and a more superiorly oriented palate midline. Nasal and subnasal landmarks loaded less strongly on this eigenvector, although it is clear that these regions do vary somewhat. The cercopithecoid morphology displays anterior expansion around the nasal aperture and antero-inferior expansion subnasally. This gives them a more prognathic and klinorhynch appearance compared to the platyrrhines.

CANONICAL VARIATES ANALYSIS

Canonical variates analysis was performed on all of the non-zero principal components (see Chapter 5) in order to explore shape differences among the extant genera. ANOVAs conducted on CV scores found highly significant differences among groups for each eigenvector. Both CVA and ANOVA results are listed in Table 6-4. A cross-validation was computed to assign each specimen to a genus based on discriminant functions computed from all other specimens. Results of this (Table 6-5) indicate that

these data are fairly robust for discriminating among these taxa: the few incorrect assignments were between *Gorilla* and *Hylobates*. Pairwise t-tests with a Bonferroni adjustment were also computed (see Table 6-6), and found significant differences between most pairs. This is not unexpected given the nature of canonical variates analysis. More useful are the clusters of genera within canonical axes, allowing for better interpretation of shape differences. The first four CV axes are discussed here; variates 5-7 represent little variability and are mainly concerned with distinguishing among the non-hominoid taxa.

Table 6-4 Summary of CVA and ANOVA results for all seven canonical variates. CVA results give statistics for the latent roots of the among-groups variance (eigenvalues), the proportion of variance explained by each variate, and the cumulative proportion of the variance summarized by that CV and those preceding it. One-way ANOVAs were performed on each axis to test for significant differences among genera; F-values and probabilities are given for tests of the null-hypothesis that all genera share a common mean.

	CANONICAL VARIATES ANALYSIS			ANALYSIS OF VARIANCE	
	Eigenvalue	Proportion	Cumulative	F Value	Pr > F
CV 1	49.7182	0.4105	0.4105	3392.01	<0.0001
CV 2	32.1391	0.2653	0.6758	2137.44	<0.0001
CV 3	18.0515	0.1490	0.8249	1179.13	<0.0001
CV 4	12.4575	0.1029	0.9277	826.56	<0.0001
CV 5	5.7592	0.0475	0.9753	374.11	<0.0001
CV 6	2.9116	0.0240	0.9993	209.35	<0.0001
CV 7	0.0844	0.0007	1.0000	14.06	<0.0001

Table 6-5 Cross-validation results from CVA of extant specimens. Each cell gives the number (n) and percent (%) of individuals from the genus on the left assigned to the genus across the top.

Genus		Atel	Cebu	Cerc	Gori	Hylo	Pan	Pcol	Pong
Atel	n	8							
	%	100.00							
Cebu	n		10						
	%		100.00						
Cerc	n			10					
	%			100.00					
Gori	n				88	4			
	%				95.65	4.35			
Hylo	n				3	142			
	%				2.07	97.93			
Pan	n						159		
	%						100.00		
Pcol	n							10	
	%							100.00	
Pong	n								56
	%								100.00

Canonical variate 1

CV 1 summarizes 41% of the among-groups variation in this sample. Figure 6-10 plots the scores for each specimen on the first two axes. While t-tests (see Table 6-6) were significant for every genus pair except *Pan-Cercopithecus*, this axis largely represents the difference between *Pongo*, with high positive scores, and the other taxa. CV scores for specimens of both platyrrhine genera are positive, tending toward *Pongo*, while *Gorilla* values cluster at the negative pole; *Pan* specimens cluster around zero and the remaining taxa scored negatively.

Table 6-6 Results of pairwise t-tests between genera for CVs 1-6. Bonferroni adjusted p-values are given in the lower triangle. * indicates significance at $\alpha=0.05$.

C V 1	Genus	Atel	Cebu	Cerc	Gori	Hylo	Pan	Pcol	Pong
	Atel		*	*	*	*	*	*	*
	Cebu	<0.0001		*	*	*	*	*	*
	Cerc	<0.0001	<0.0001		*	*		*	*
	Gori	<0.0001	<0.0001	<0.0001		*	*	*	*
	Hylo	<0.0001	<0.0001	<0.0001	<0.0001		*	*	*
	Pan	<0.0001	<0.0001	1.0000	<0.0001	<0.0001		*	*
	Pcol	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001		*
	Pong	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	
	C V 2	Genus	Atel	Cebu	Cerc	Gori	Hylo	Pan	Pcol
Atel			*	*	*		*		
Cebu		0.0011		*		*	*	*	*
Cerc		0.0011	<0.0001		*	*	*		*
Gori		0.0224	0.8560	<0.0001		*	*	*	*
Hylo		0.3170	<0.0001	0.0427	<0.0001		*		*
Pan		<0.0001	<0.0001	<0.0001	<0.0001	<0.0001		*	*
Pcol		0.8931	<0.0001	0.8892	<0.0001	1.0000	<0.0001		
Pong		1.0000	<0.0001	<0.0001	<0.0001	0.0005	<0.0001	0.6624	
C V 3	Genus	Atel	Cebu	Cerc	Gori	Hylo	Pan	Pcol	Pong
	Atel		*	*	*	*	*		*
	Cebu	<0.0001		*	*	*	*	*	*
	Cerc	<0.0001	<0.0001		*	*	*	*	*
	Gori	<0.0001	<0.0001	<0.0001		*		*	*
	Hylo	<0.0001	<0.0001	<0.0001	<0.0001		*	*	*
	Pan	<0.0001	<0.0001	<0.0001	0.4053	<0.0001		*	*
	Pcol	0.8722	<0.0001	0.0276	<0.0001	<0.0001	<0.0001		*
	Pong	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	
C V 4	Genus	Atel	Cebu	Cerc	Gori	Hylo	Pan	Pcol	Pong
	Atel		*	*	*	*	*	*	*
	Cebu	<0.0001		*	*	*	*	*	*
	Cerc	<0.0001	<0.0001		*	*	*	*	*
	Gori	<0.0001	<0.0001	<0.0001				*	*
	Hylo	<0.0001	<0.0001	<0.0001	1.0000			*	*
	Pan	<0.0001	<0.0001	<0.0001	1.0000	1.0000		*	*
	Pcol	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001		*
	Pong	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	

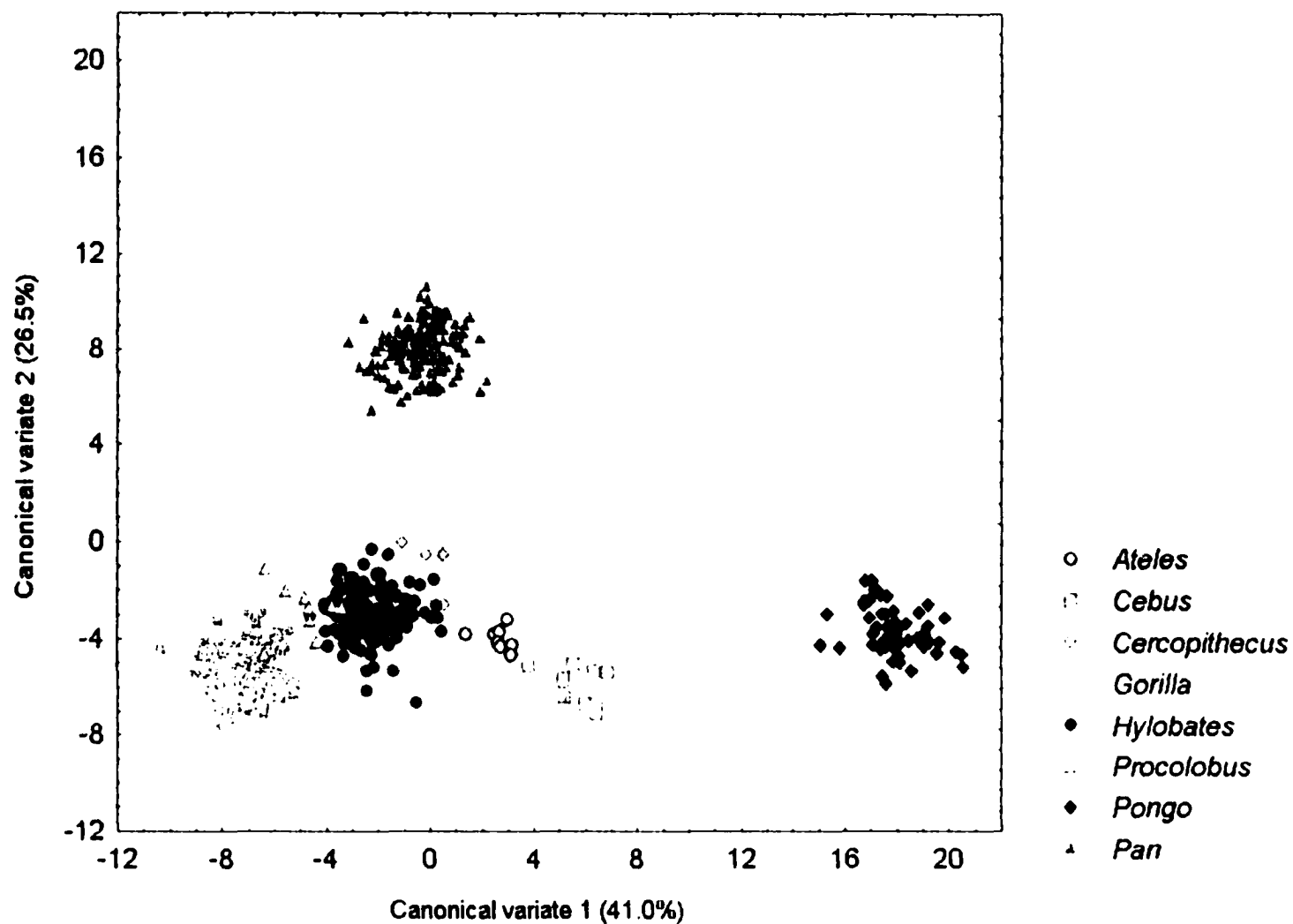


Figure 6-10 Plot of canonical variate scores for CV 1 and CV 2. CV 1 mostly separates *Pongo* from all other specimens; both platyrrhine taxa sort positively toward *Pongo*, while *Gorilla* is the most negative cluster. CV 2 distinguishes *Pan* from the other anthropoid taxa.

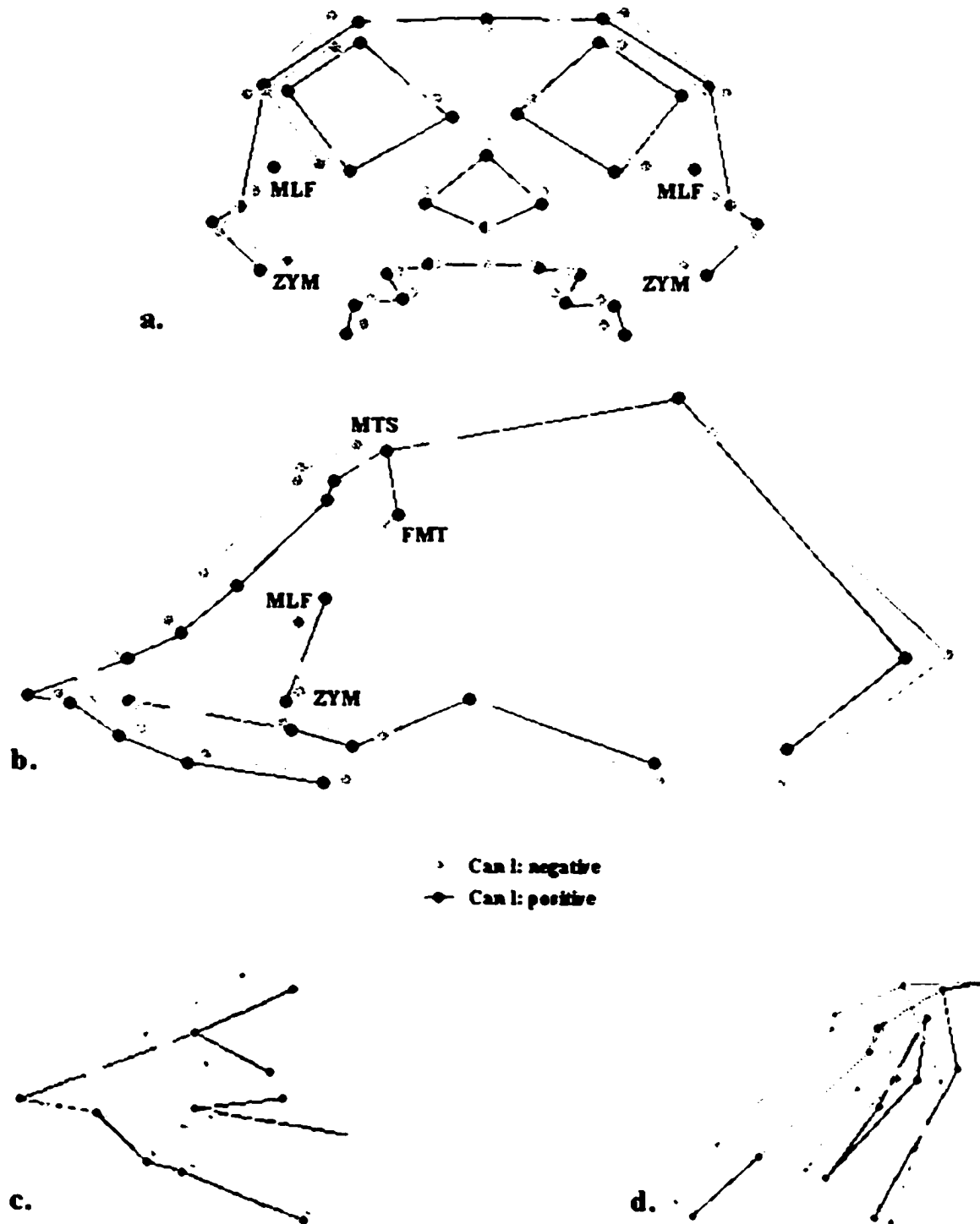


Figure 6-11 Shape change along CV 1. Black lines represent the positive loadings, gray lines show the negative loadings. (a) frontal view; (b) lateral view; (c) magnification of the subnasal region (lateral view); (d) magnification of the orbital region (lateral view). See Figures 6-1 and 6-2 for additional landmark references.

Shape change along this axis is illustrated in Figure 6-11. At the positive extreme (i.e., *Pongo*), there is a relative antero-posterior shortening, but also an upward shift of the entire neurocranium. This is coincident with a strong posterior and medial shift in the upper and middle facial landmarks. The posterior retraction is most evident along the midline (see Figure 6-11d), resulting in a flattening across the orbits. In contrast, the lower facial morphology at the positive pole is expanded anteriorly and laterally, with some inferior displacement in postcanine morphology. Antero-posterior expansion of the subnasal clivus combined with a thickening of the hard palate contributes to the proximity of **CLI** and **PIC** (see Figure 6-11c). It is interesting to note that the anterior palate at the positive pole is not displaced superiorly compared to the negative extreme. Rather, it is the posterior morphology that is deflected inferiorly. This is especially evident between *hormion* and *staphylion*.

Canonical variate 2

The second canonical variate comprises nearly 27% of the total between-group shape variation (see Table 6-4). As with CV 1, this axis is largely concerned with differentiating one genus from the others (See Figure 6-10). In this case, *Pan* specimens scored well above zero, while all other genera were negative. Other significant differences between genus means are reported in Table 6-6, but these are slight relative to the distinction of *Pan*.

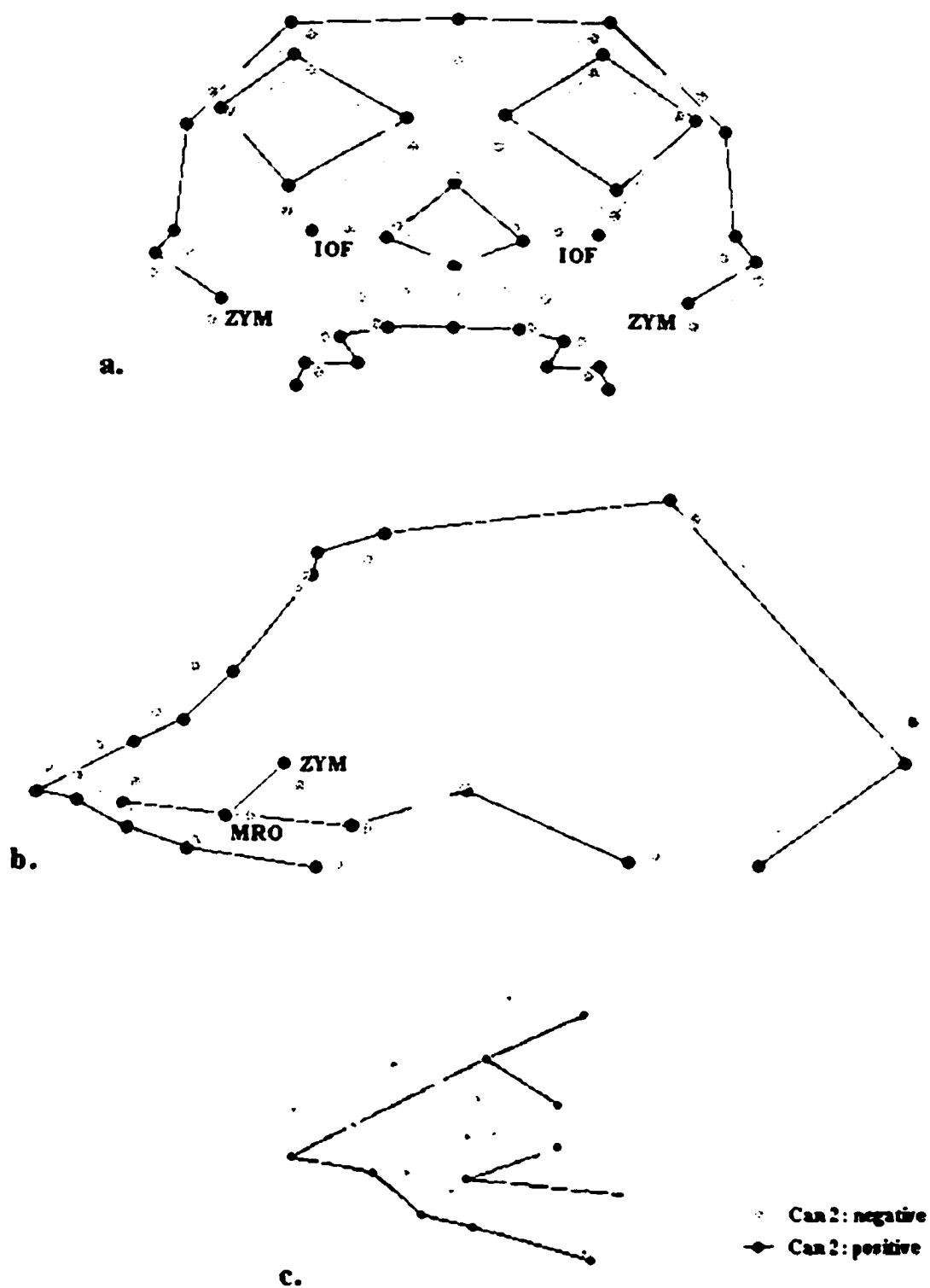


Figure 6-12 Shape change along CV 2. Black lines represent the positive loadings, gray lines show the negative loadings. (a) frontal view; (b) lateral view; (c) magnification of the subnasal region (lateral view). See Figures 6-1 and 6-2 for additional landmark references.

Shape change along CV 2 is illustrated in Figure 6-12. At the positive pole of this axis the neurocranium expands in height, resulting in a more globular appearance and a relatively larger braincase. This is especially evident from the inferior displacement of occipital landmarks. The face is also substantially taller in *Pan* relative to the other taxa. This is achieved in part through superior displacement of upper facial landmarks—particularly near the midline. A slight widening of the bi-orbital breadth is also evident, but less significant. Widening is more evident in the *Pan* midface, with a relatively broader nasal aperture and lateral displacement of the infraorbital foramina and orbital pillars. The most significant change in the midface is a posterior retraction of landmarks, thereby reducing midfacial protrusion. Landmarks from the lower face of *Pan* are generally displaced both inferiorly and laterally. An exception to this is the marked superior displacement of zygomaxillare. Thus, the relative expansion of facial height in *Pan* does not extend to the zygomatic bone, which is proportionately shorter. The subnasal region at the positive extreme shows a greatly expanded subnasal clivus and substantial thickening of the anterior hard palate (Figure 6-12c), but without the concomitant approximation of **CLI** and **PIC** seen in CV 1 for *Pongo*.

Canonical variate 3

CV 3 represents about 15% of the among-groups variability. The plot of canonical variates scores (Figure 6-13) clearly illustrates a distinction between hominoid and non-hominoid genera along this axis. Even within the cluster of apes all pairs of genus means are significantly different (see Table 6-6), excepting the means of *Gorilla* and *Pan*; non-hominoid means are all significantly different from each other.

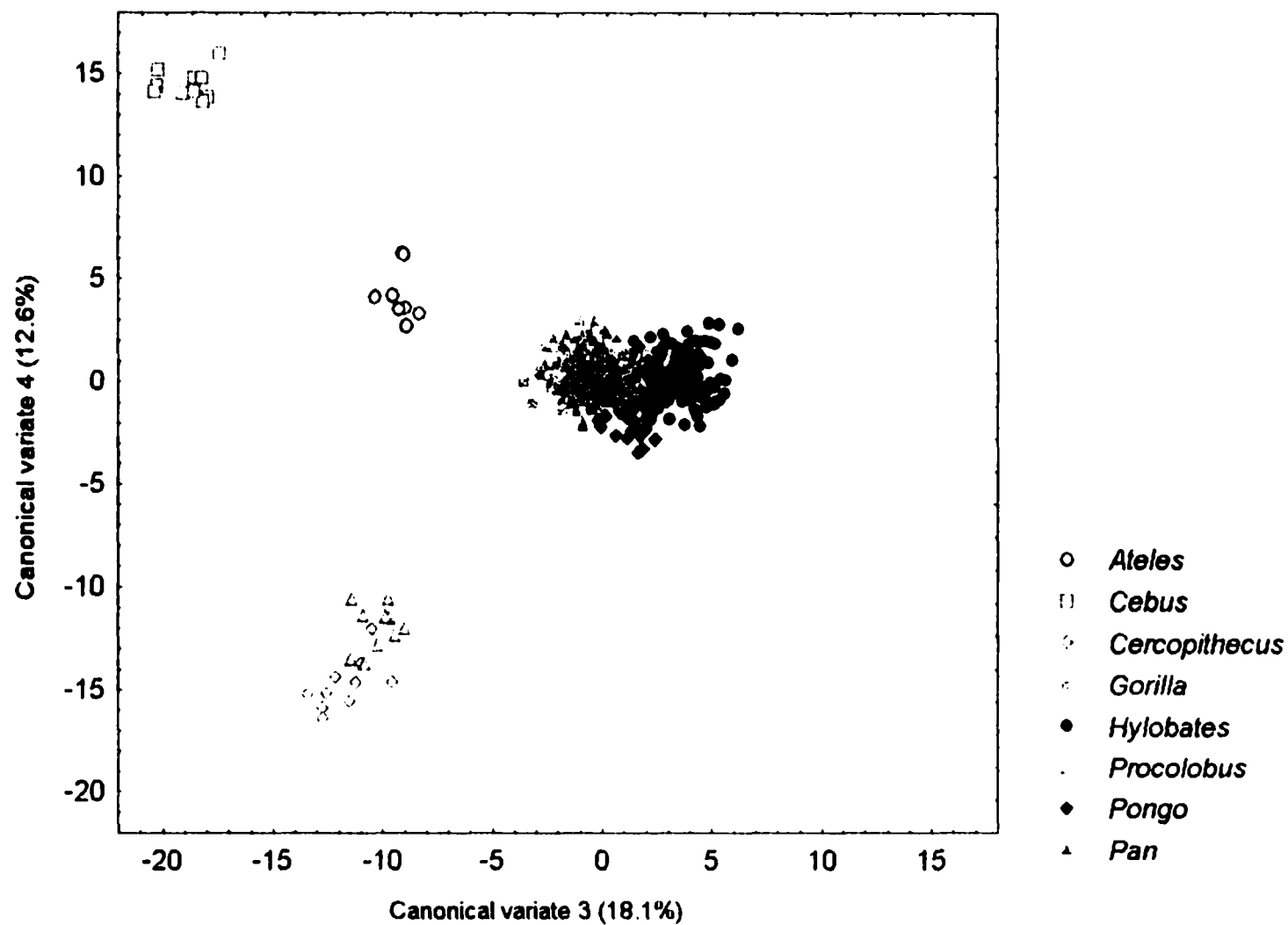
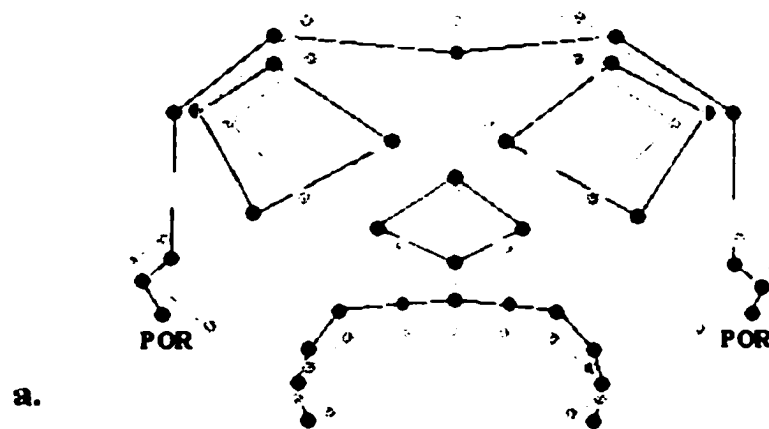


Figure 6-13 Plot of canonical variate scores for CV 3 and CV 4. CV 3 clearly discriminates between hominoid and non-hominoid specimens. CV 4 distinguishes cercopithecoids from platyrrhines, with hominoids clustering in the center. Note that the mean of *Ateles* is statistically different from all of the hominoid genera.



○ Can 3: negative
 ● Can 3: positive

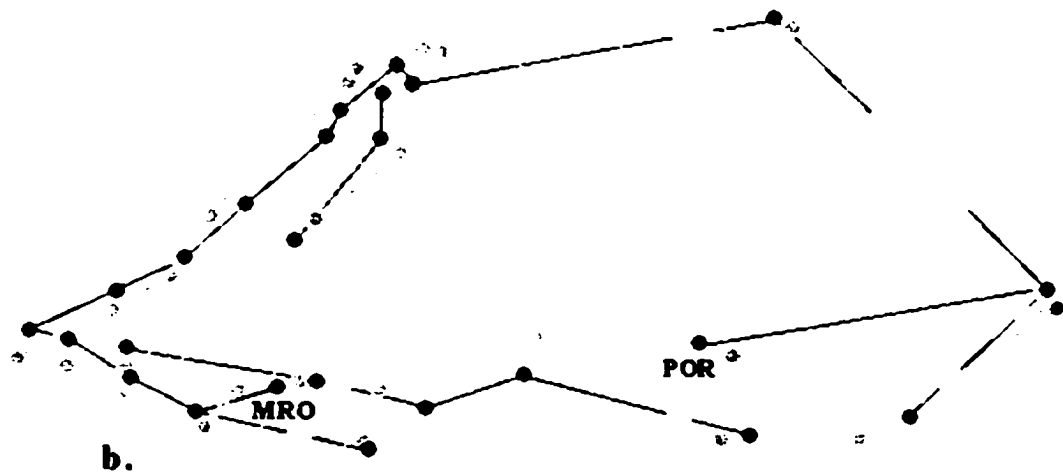


Figure 6-14 Shape change along CV 3. Black lines represent the positive loadings, gray lines show the negative loadings. (a) frontal view; (b) lateral view. See Figures 6-1 and 6-2 for additional landmark references.

Figure 6-14 illustrates the shape changes that correspond to the third canonical axis. The majority of change in the neurocranium occurs in the inferior morphology. Among the positive scores, the foramen magnum is shifted slightly posteriorly, while porion moves both anteriorly and strongly laterally. Hormion shows a strong inferior shift bringing the external occipital clivus nearly parallel to the palate midline. Based on the landmarks in this study, enlargement of the braincase in apes seems to occur through lateral and inferior expansion, as illustrated at porion and hormion respectively. Most of the facial differences along CV 3 occur in the upper and middle morphology. Generally, the apes have broader upper faces, narrowing toward jugale. This is correlated with an antero-lateral shift of the orbits, relative to the other anthropoids. While the hominoid orbits (especially the lateral aspect) shift anteriorly, the midline morphology regresses posteriorly yielding a flatter upper face. **PTS** in hominoids greatly shifts inferiorly relative to the height of **MTS** and there is a substantial shortening in the relative length of the nasal bones. The nasal aperture in the positive extreme is broader and placed relatively more superiorly on the face. In the lower face at the positive pole, premaxillary morphology is shifted superiorly. The zygomatic root is posteriorly placed, aligning it with the orbital plane; toward the non-hominoid extreme, the root is near the premolar-molar contact. Perhaps the greatest change occurs in the posterior palate, where the horizontal plate of the palatine in hominoids is greatly expanded. Combined with the inferior shift in hormion, this results in a marked morphological difference along the cranial base.

Canonical variate 4

The fourth canonical axis represents 10% of the total variability among these groups (see Table 6-4). Figure 6-13 plots the scores of CV 4 showing a differentiation of platyrrhines toward the positive pole, cercopithecoids at the negative, and hominoids clustering around zero. Although the range of scores for *Ateles* overlaps with the most positive hominoid scores, its mean is significantly different from all other genera (see Table 6-6). Within the hominoids, the means of *Gorilla*, *Hylobates*, and *Pan* do not differ significantly along this; *Pongo* is slightly more negative and is different from all taxa.

Figure 6-15 illustrates the shapes represented at each extreme of the fourth canonical axis. At the positive (i.e., platyrrhine) extreme, the neurocranium is somewhat longer and flatter with bregma falling far back on the cranium; it is also broader inferiorly with poria shifted antero-laterally. Shape change in the upper face is dominated by posterior retraction of the lateral morphology among cercopithecoids. Correlated with an infero-lateral shift in the orbital pillar, the cercopithecoid upper face is shortened, broad, and angled across the front. This angling trend is reversed in the midface: platyrrhines show an expansion of the antero-posterior distance between infraorbital foramen and zygomaxillare, while in the cercopithecoids these landmarks are more proximate. The lower face at the negative extreme is expanded antero-inferiorly, giving cercopithecoids a higher overall degree of facial protrusion.

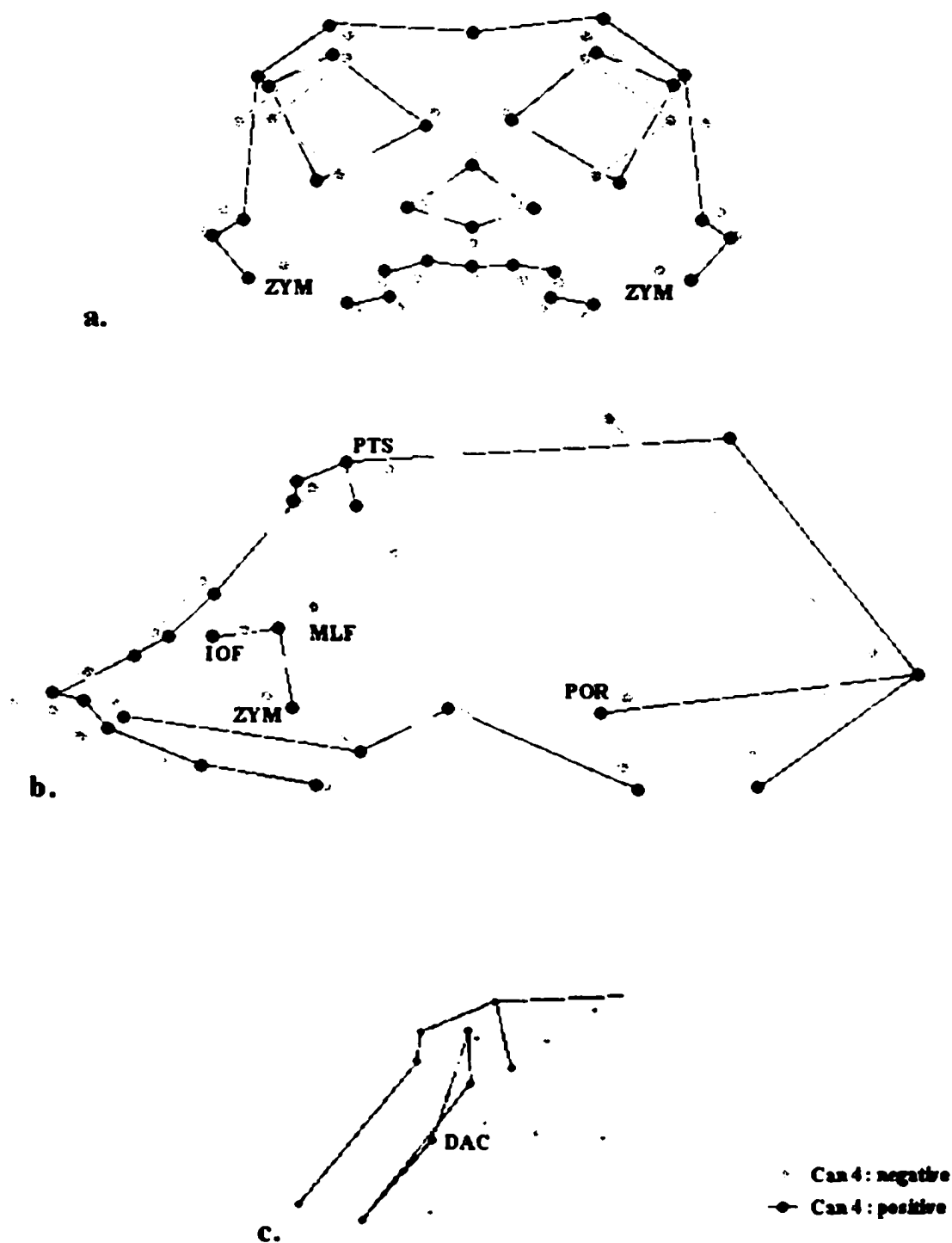


Figure 6-15 Shape change along CV 4. Black lines represent the positive loadings, gray lines show the negative loadings. (a) frontal view; (b) lateral view; (c) magnification of the orbital region (lateral view). See Figures 6-1 and 6-2 for additional landmark references.

MAHALANOBIS DISTANCE

To compare groups across the entire canonical space, unbiased Mahalanobis D^2 values were computed for each pair of genera. Hotelling's T^2 multivariate comparisons found highly significant ($p < 0.0001$) differences between all pairs of genus centroids—not entirely surprising for analyses conducted at the generic level. As described in Chapter 5, 10,000 equal-sample replicate CVAs were also performed and average D^2 values computed. Table 6-7 lists the Mahalanobis D^2 matrices for both whole-sample (lower triangle) and equal-sample (upper triangle) analyses. Relative distances between taxon pairs were similar in both analyses, suggesting that sample size differences did not greatly affect the distance metrics. The main difference between them was in *Cebus*: initially closest to *Gorilla*, the equal-sample values link *Cebus* with *Ateles*. *Pongo* also moves closer to the other apes in the equal-sample canonical space, while *Cercopithecus* becomes more distant.

Table 6-7 Matrix of unbiased Mahalanobis distance estimates between pairs of genera. Values in the lower triangle were computed from the whole sample; values in the upper triangle are mean distances computed from the equal-sample randomization procedure. Values from upper and lower triangles are not directly comparable, but relative differences within each should be similar if unequal sample size was not a significant factor determining distances.

Genus	Atel	Cebu	Cerc	Gori	Hylo	Pan	Pcol	Pong
Atel		278.5	414.4	260.1	276.3	265.9	381.7	312.2
Cebu	742.0		455.9	325.6	375.7	357.1	443.5	402.2
Cerc	768.6	1023.4		264.1	313.9	335.0	92.0	339.0
Gori	466.5	722.5	454.0		30.6	123.2	194.5	306.7
Hylo	497.1	794.2	518.4	46.6		81.4	249.9	214.0
Pan	530.2	800.3	511.0	218.8	138.5		277.2	216.4
Pcol	721.2	990.8	300.5	331.9	427.9	464.4		348.0
Pong	661.7	836.4	755.0	623.8	407.5	468.7	837.1	

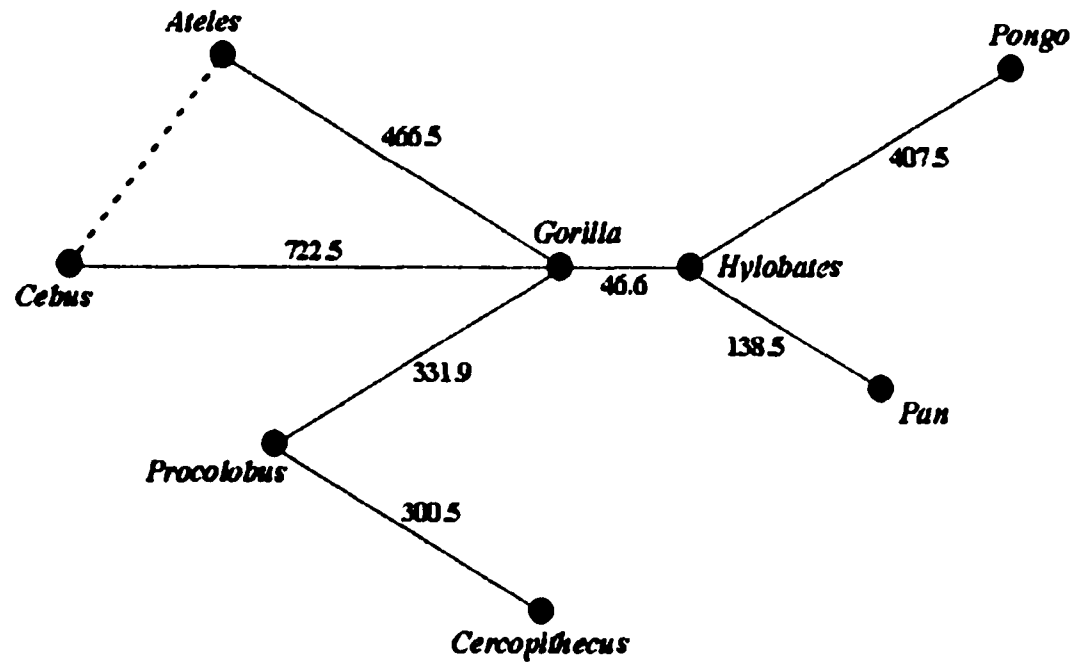


Figure 6-16 Minimum spanning tree showing the nearest-neighbor for each genus as measured by Mahalanobis D^2 . Relationships between connected taxa are drawn to scale; distances between un-joined genera are not to scale. Additional Mahalanobis distances are given in Table 6-8. The dotted line indicates the only proportionally different result of an equal-sample randomization test: the nearest neighbor to *Cebus* was *Ateles* rather than *Gorilla* (see text for discussion).

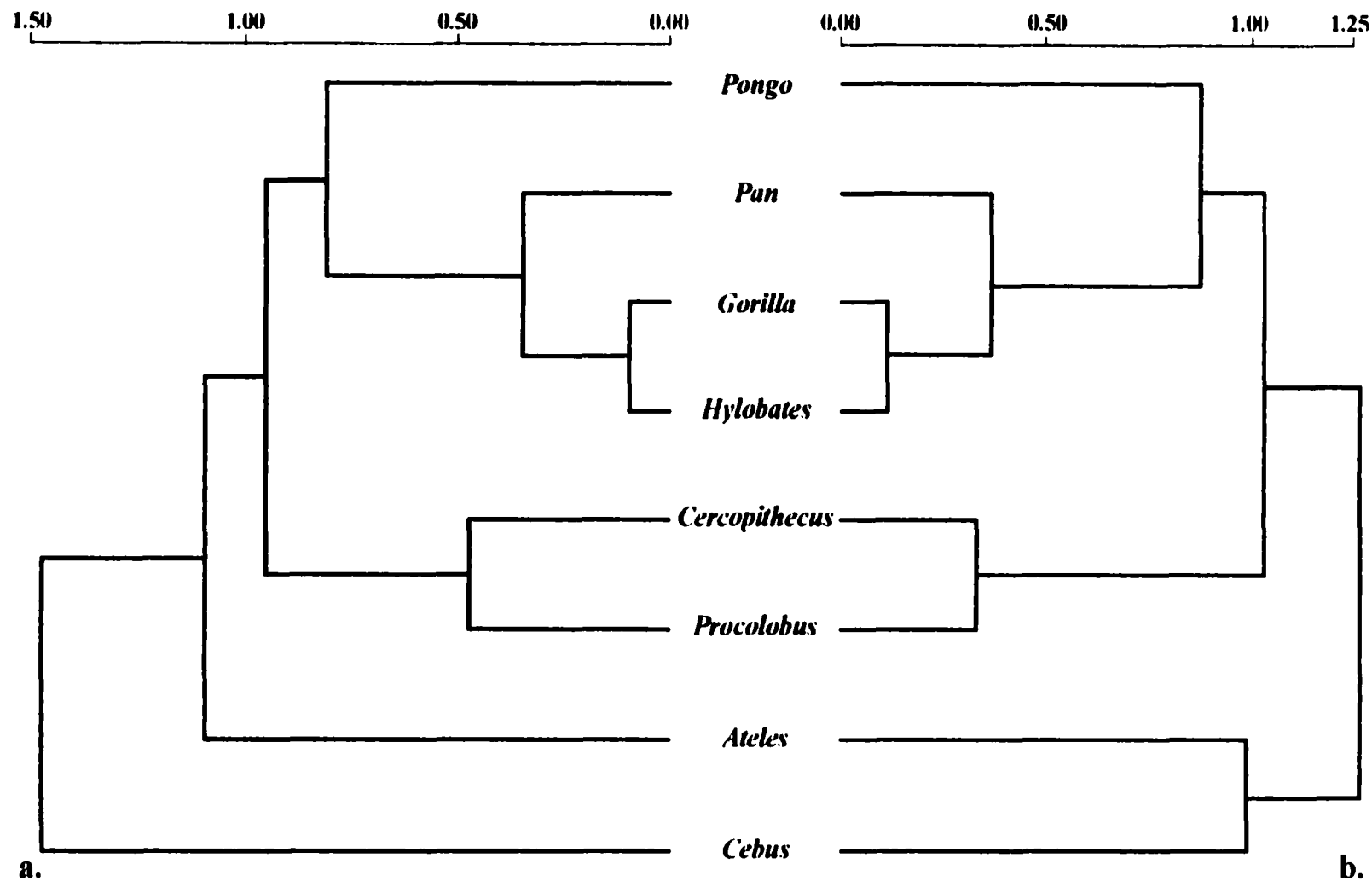


Figure 6-17 Results of UPGMA cluster analyses based on (a) Mahalanobis D^2 values from the whole sample, and (b) mean Mahalanobis D^2 values of equal-sample replicates ($n = 10,000$). The distance matrices are given in Table 8-8.

Figure 6-16 shows a minimum spanning tree (MST) based on whole-sample values displaying the shortest distances that link together all genera: the dashed line connecting *Cebus* and *Ateles* indicates the only topological difference that would result if equal-sample values were used instead. The MST shows distinct hominoid and cercopithecoid branches; platyrrhines also form a unique branch when equalized samples are used. *Cebus* is by far the most distinct genus, having both the greatest nearest-neighbor distance, as well as the highest average D^2 values; *Ateles* is somewhat closer to other taxa, but still fairly distinct. *Gorilla*, on the other hand, occupies a centralized location in this tree—linked closely to *Hylobates*. In fact, both of these genera cluster near the centroid of this canonical space, as demonstrated by average Mahalanobis D^2 values. *Pan* is somewhat centralized as well, and the distances between these three taxa are substantially shorter than all others in the distance matrix (see Table 6-7). *Pongo* is quite distant from all taxa, but closest to the other hominoids; this difference would be somewhat reduced using equal-sample values. The cercopithecoid taxa are exclusively each other's nearest neighbor, with *Procolobus* joining *Gorilla* as its second nearest neighbor.

To explore phenetic relationships hierarchically, a UPGMA cluster analyses was computed; the results are diagrammed in Figure 6-17. The tree on the left (Figure 6-17a) represents a cluster of values from the whole-sample analysis; on the right side (Figure 6-17b) is a cluster of mean D^2 values from the randomized equal-sample analysis. Relationships among most of the genera are similar in both trees. The three major anthropoid clades are clearly separated in both diagrams. Relationships among catarrhine genera are identical in both. As discussed above, equalizing the sample sizes brings

Cebus closer to *Ateles*. Thus, they form a distinct platyrrhine clade in Figure 6-17b, though the distance between them nearly equals that between hominoids and cercopithecoids. This dissimilarity may reflect the deep phylogenetic divergence and adaptational diversity among the major platyrrhine lineages (Delson & Rosenberger, 1984). Both cercopithecoids also cluster together. The substantial distance between them in the whole-sample analysis is likely an artifact of sample size inequality; indeed, when this is controlled for, *Cercopithecus* and *Procolobus* are closer than *Pan* and *Gorilla*. This is not surprising, however, as neither monkey is thought to be highly derived cranially (unlike, e.g., *Mandrillus* or *Rhinopithecus*). While detailed conclusions about relationships within and between the Platyrrhini and Cercopithecoidea are beyond the scope and sample of this project, it is clear that both taxa represent reasonable successive phenetic “outgroups” for the hominoids.

The hominoid superfamily also forms a distinct cluster, although relationships within this group do not conform to established taxonomy. *Gorilla*, *Hylobates*, and *Pan* form a fairly tight grouping, with minimal distances separating them; *Pongo*, on the other hand, is far removed. These results underscore the unique cranial morphology of the orangutan, but can be misleading with regard to its broader affinities. The phenograms in Figure 6-17 draw *Pongo* as the “outgroup” of the other apes and one can easily mistake this position as representing a more primitive morphology. What these results actually indicate is that the average distance between *Pongo* and the other apes is less than its distance to any other cluster; the relationship expressed is merely one of difference—neither derived, nor primitive. Comparing these cluster diagrams to the MST (see Figure 6-16), however, provides additional insight. The tight clustering of *Gorilla*, *Pan*, and the

more distantly related *Hylobates* suggests that the cranial morphology of *Pongo* may be derived relative to the other apes; while it is most similar to the other hominoids, the distance separating the orangutans is substantial.

Perhaps most interesting in these results is the close affinity between *Gorilla* and *Hylobates*. Indeed, the separation between these morphologies is the smallest pairwise distance in the sample—by a large margin. Moreover, the position of *Gorilla* near the centroid of the canonical space suggests that gorilla crania are the most generalized within this sample of taxa: in the differences that distinguish among cranial morphologies of these genera, *Gorilla* is closest to the mean. Thus, the highly distinct platyrrhines and cercopithecoids link to the hominoids through *Gorilla*. It is well established on both molecular and morphological grounds that hylobatids form the sister taxon to the hominids. If *Hylobates* is a good model of the basal hominoid cranium (e.g., Vogel, 1966; Delson, 1975, 1977; Delson & Andrews, 1975; Ward & Kimbel, 1983; Andrews, 1985; Harrison, 1987; Strasser & Delson, 1987), then these results suggest that the overall craniofacial morphology of *Gorilla* may be fairly primitive among apes. The proximity of *Pan* to these genera and to the canonical centroid would suggest that it is only slightly more derived from this basic pattern. The cranium of *Pongo*, then, is most likely derived among extant apes.

SHAPE DIFFERENCES BETWEEN CROWN CLADES

The consensus phylogeny of extant taxa is reiterated in Figure 6-18. Based on these relationships, shape differences distinguishing between crown clades deriving from each node were examined using a series of discriminant analyses (see Chapter 5). For

example, it was shown above that *Gorilla* and *Hylobates* are morphologically very similar when allometric effects are taken into consideration. If, however, one divides the apes into either hominids or hylobatids (node 3), then a discriminant analysis can be used to parse out the shared features by which all great apes differ from lesser apes. Cross-validation provides an estimate of the discriminant function's robusticity. Subsequent interpretations of shape differences along each discriminant axis demonstrate the morphological regions most affected by the cladogenesis—at least as preserved among crown clades.

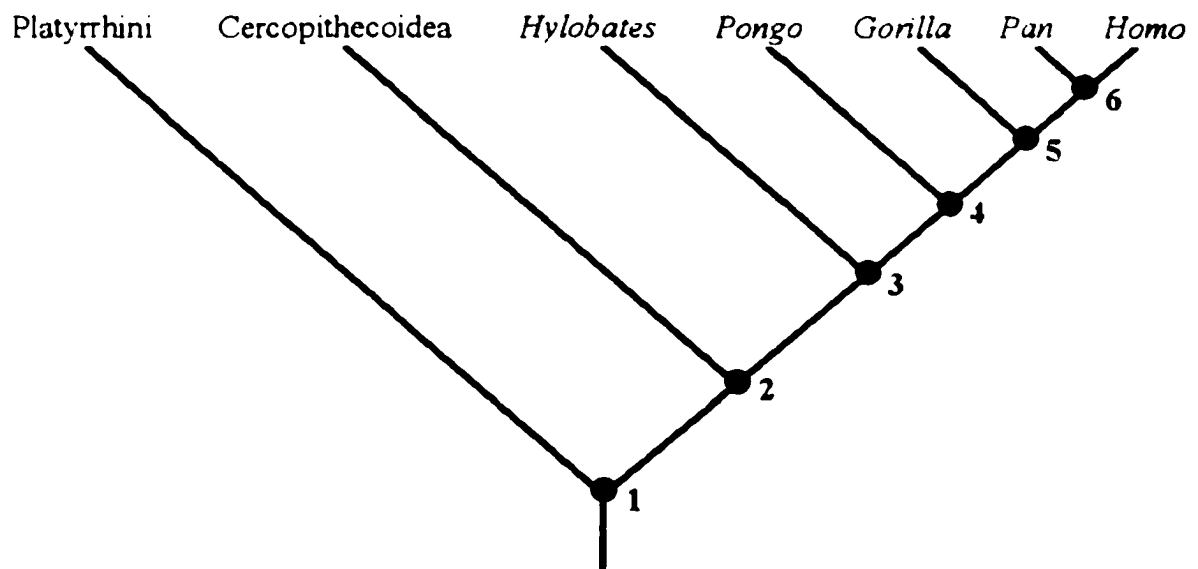


Figure 6-18 Consensus phylogeny of the relationships among extant apes and the main anthropoid clades. Nodes are referred to by number in the text.

Node 1: Platyrrhines vs. Catarrhines

Node 1 separates platyrrhine from catarrhine anthropoids. Sample sizes between the two groups were necessarily unequal in order to fairly represent all of the catarrhine taxa in this study. Table 6-8 shows the cross-validation results and Figure 6-19 plots the scores of each specimen (by genus) along the discriminant function. Given the small sample of platyrrhines (and cercopithecoids) used, these results must be regarded as preliminary. Nevertheless, they serve as an exploratory tool for developing hypotheses for future studies. And, despite the overall dissimilarity between *Ateles* and *Cebus* (see Table 6-7), the DA was very robust for separating these two groups.

Table 6-8 Cross-validation results for DA of cranial morphologies in catarrhines and platyrrhines. Each cell gives the number (n) and percent (%) of individuals from the taxa on the left assigned to the taxa across the top.

Taxon		Catarrhine	Platyrrhine
Catarrhine	n	32	
	%	100.00	
Platyrrhine	n		18
	%		100.00

Shape differences comprising the discriminant function are illustrated in Figure 6-20. Differences in the neurocranium are primarily reflected in a relative lengthening of the platyrrhine cranium, giving it a more dolichocephalic appearance compared to the catarrhine consensus. This antero-posterior expansion is most evident in the frontal bone (**PTS-BRE**) and the basi-occiput (**HOR-BAS**). Porion is placed well medial in the platyrrhines compared to catarrhines; it is also inferiorly displaced in conjunction with an inferior shift in the platyrrhine zygomatic arch. The platyrrhine face is slightly shorter than the catarrhine and has a more vertical profile. This is accomplished largely through

anterior rotation of the upper face and inferior truncation of the lower face in the platyrrhines. Beyond antero-posterior positioning, the differences in the upper face are minor: narrow facial breadth, taller orbital pillar, and larger orbits in the platyrrhines. Differences in the midface are primarily in the angle across the facial breadth. Zygomaxillare in platyrrhines is shifted posteriorly, aligning it with the orbital pillar. This makes the anterior zygomatic body nearly vertical, compared to the inclined catarrhine zygoma. However, when combined with an anterior shift in the platyrrhine infraorbital foramina, the lower midface becomes more angled about the midline. The lower face of the platyrrhine consensus is generally superiorly and posteriorly displaced from the catarrhine. The antero-inferior displacement of the catarrhine lower face seems to result from a combination of factors: increased subnasal clivus length, taller zygoma, and decreased cranial base flexion. The palate midline in catarrhines is longer than platyrrhines due to an expansion in the antero-posterior dimension of the palatine processes of the maxilla. Also of note, the configuration of anterior inter-dental landmarks in the platyrrhines slopes inferiorly from the canine toward the midline.

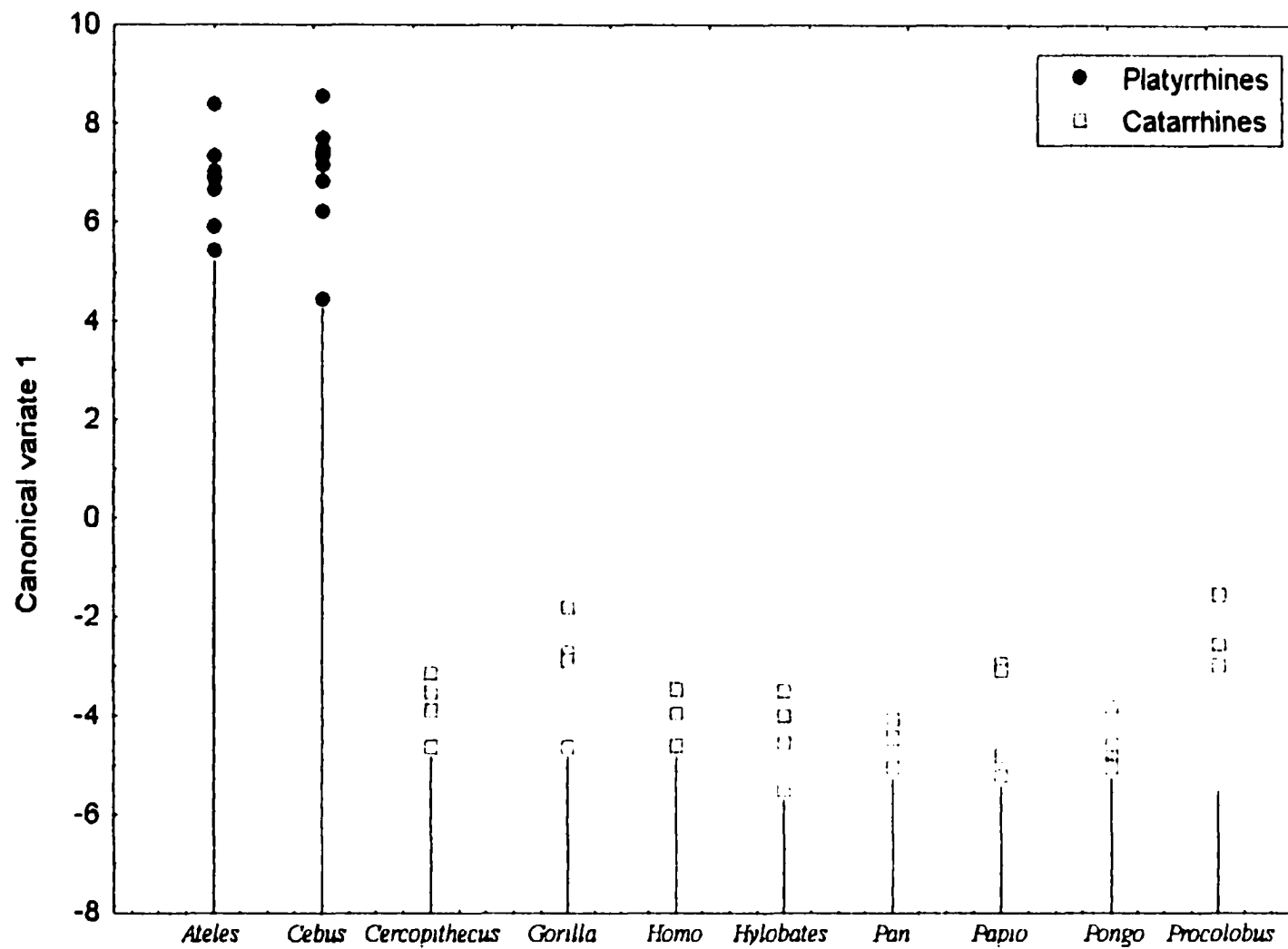


Figure 6-19 Plot of CV scores for the discriminant axis separating platyrrhines from catarrhines. Although only the two groups were used for class variables, these results are illustrated by genus to better depict the distribution of specimens on the axis.

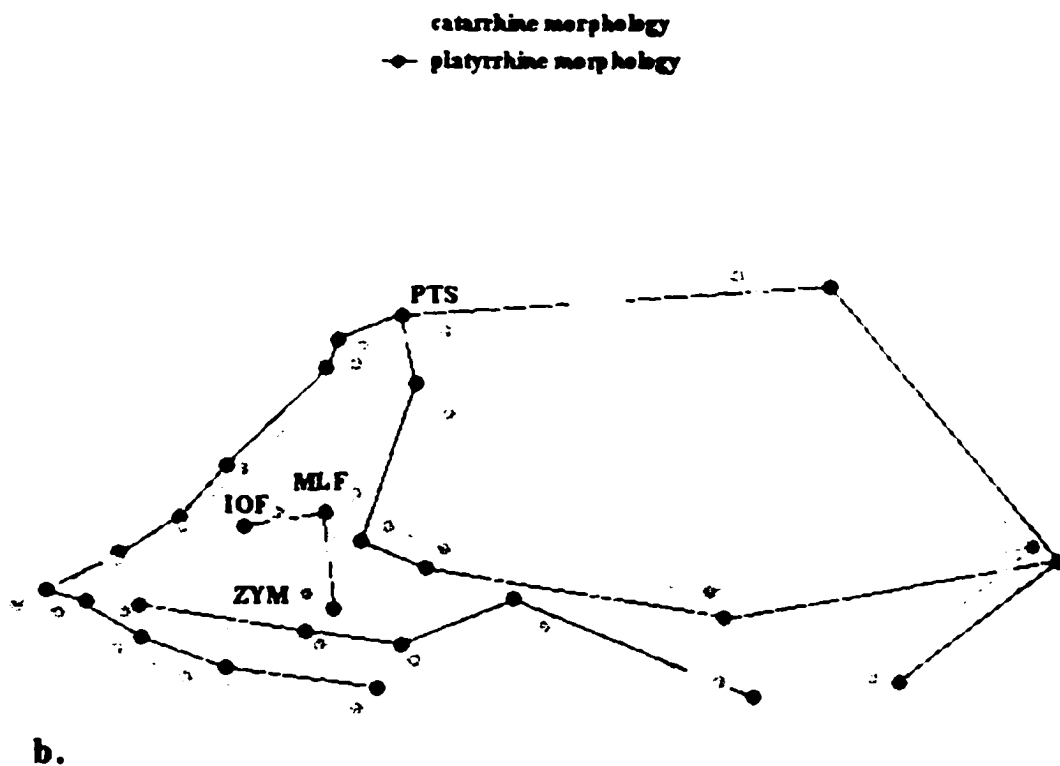
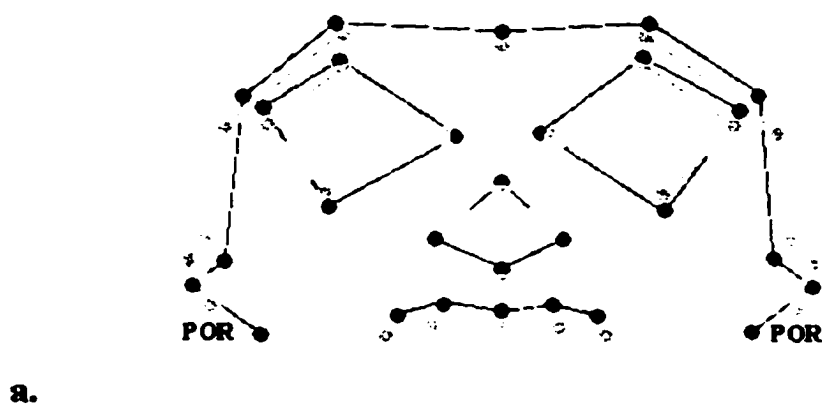


Figure 6-20 Shape change corresponding to the discrimination between catarrhines (gray) and platyrrhines (black) sampled for this project. (a) frontal view; (b) lateral view. See Figures 6-1 and 6-2 for additional landmark references.

Node 2: Cercopithecoids vs. Hominoids

Differences between cercopithecoids and hominoids were also easily detectable through discriminant analysis. Although only three cercopithecoid genera were used, colobines and cercopithecines are both represented as well as long- and short-faced forms. Cross-validation of specimens (Table 6-9) was completely successful for both groups and a plot of CV scores (Figure 6-21) illustrates the substantial separation between them.

Table 6-9 Cross-validation results for DA of cranial morphologies in cercopithecoids and hominoids. Each cell gives the number (n) and percent (%) of individuals from the taxa on the left assigned to the taxa across the top.

Taxon		Cercopithecoids	Hominoids
Cercopithecoids	n	30	
	%	100.00	
Hominoids	n		30
	%		100.00

Shape differences between cercopithecoids and hominoids are shown in Figure 6-22. The hominoid neurocranium shows expansion at all sagittal landmarks, as well as being broader across poria. The overall hominoid face is shorter than the cercopithecoid due mostly to an anterior rotation of the upper face and superior rotation of the anterior lower face. This is correlated with a steep upper- to mid-facial profile and a protruding lower face; in contrast, the cercopithecoid profile slopes fairly evenly along the protruding rostrum. The hominoid upper face is nearly vertical in profile and broad across the front. Orbital pillars are also vertical, making the upper face relatively planar. The hominoid orbits have shifted laterally within the broader face, increasing the interorbital distance. In cercopithecoids, the upper face is protruding, with the greatest difference

occurring in the length of the nasal bones. It is narrower than the hominoid, with lateral landmarks shifted posteriorly to create a sharper angle about the sagittal plane. The orbits are set closer together in the cercopithecoid and are slightly smaller. The hominoid nasal aperture is set relatively higher than in the cercopithecoid and is both shorter and broader. It also marks a greater protrusion, with the cercopithecoid aperture more vertical by comparison. Compared to the cercopithecoid subnasal region, hominoids evince a greatly expanded subnasal clivus, thicker palate, elongate incisive "foramen" (i.e., canal), and dissociation between clivus and nasal floor. Overall, the lower face in hominoids is broader and characterized by a dorsal rotation of the rostrum. This has the net effect of reducing kyphosis and producing a relatively airorhynch appearance. Interestingly, the inferior displacement of the posterior palate is accomplished through an inferior rotation of the basi-occiput and relative *shortening* of the vomer, rather than an increase in vomeral height.

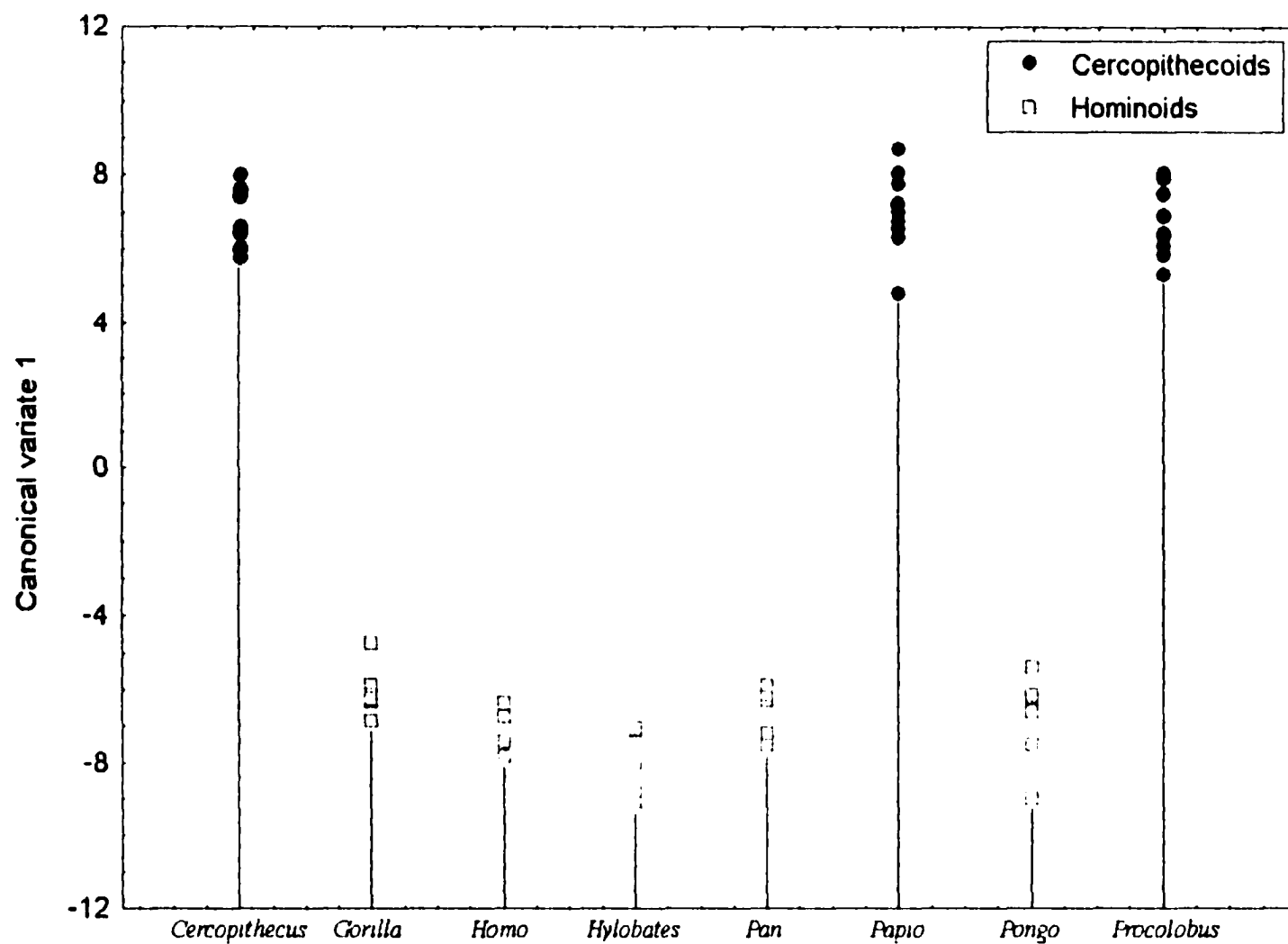


Figure 6-21 Plot of CV scores for the discriminant axis separating cercopithecoids from hominoids. Although only the two groups were used for class variables, these results are illustrated by genus to better depict the distribution of specimens on the axis.

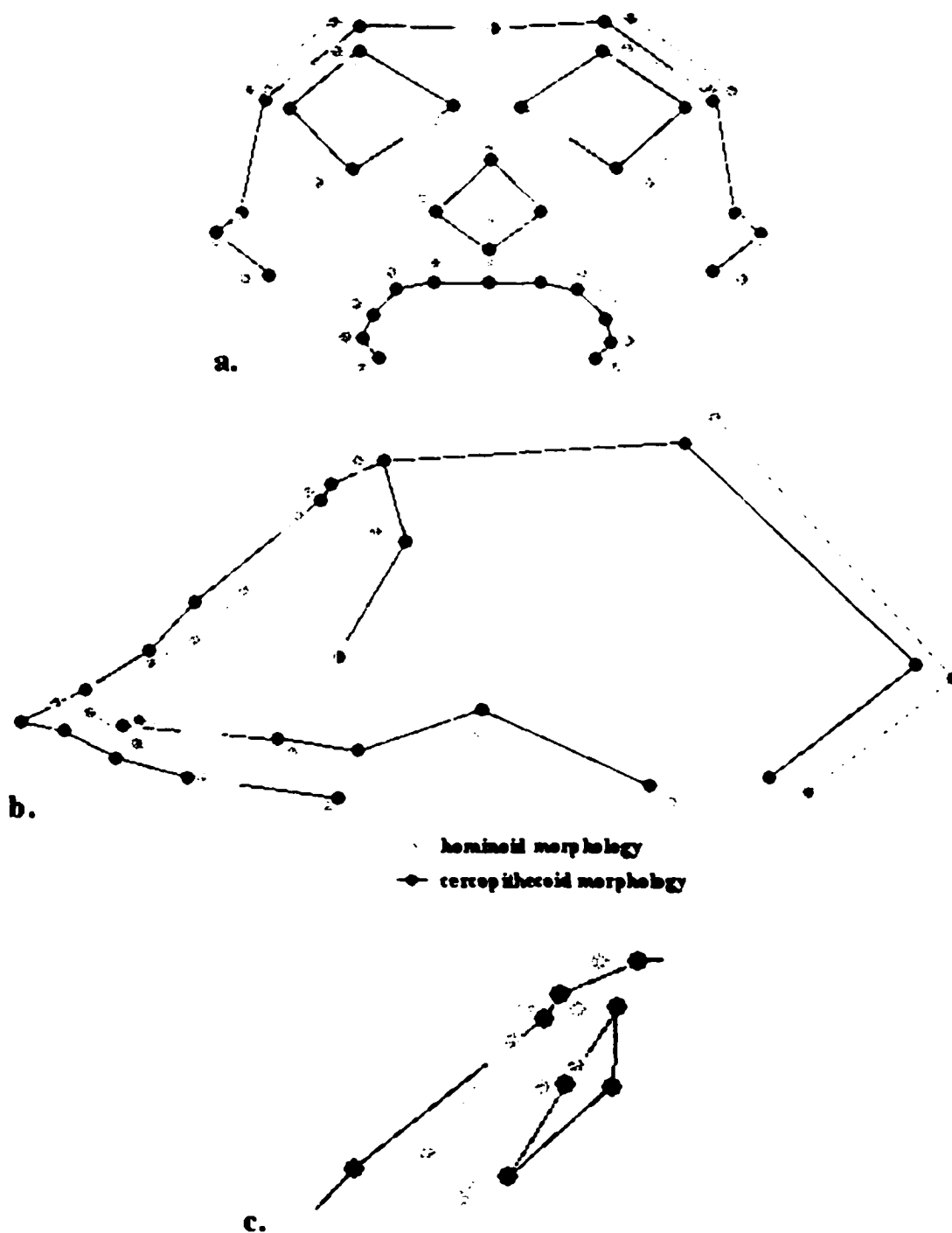


Figure 6-22 Shape change corresponding to the discrimination between hominoids (gray) and the cercopithecoid taxa (black) sampled for this project. (a) frontal view; (b) lateral view; (c) magnification of the orbital region (lateral view). See Figures 6-1 and 6-2 for additional landmark references.

Node 3: Hylobatids vs. Hominids

The split between lesser and great apes is slightly less distinct than earlier nodes due to the similarity between *Hylobates* and *Gorilla*. As shown in Table 6-10, all of the hylobatids were correctly classified, but four of the hominids (all male gorillas) were not. The plot of CV scores (Figure 6-23) illustrates a clear demarcation between the groups despite the misclassifications. It is also interesting to note that the axis of discrimination between hylobatids and hominids also tends to sort male from female gorillas—albeit with substantial overlap.

Table 6-10 Cross-validation results for DA of cranial morphologies in hylobatids and hominids. Each cell gives the number (n) and percent (%) of individuals from the taxa on the left assigned to the taxa across the top.

Taxon		Hylobatids	Hominids
Hylobatids	n	128	
	%	100.00	
Hominids	n	4	128
	%	3.13	96.88

Differences in shape between the two ape families are illustrated in Figure 6-24. The hominid cranium is markedly globular compared to the hylobatid due, in large part, to the antero-superior displacement of bregma. Great apes and humans also display a pronounced anterior shift of the foramen magnum, probably reflecting an increase in brain size. The hominid face is substantially longer than the hylobatid, notably in the nasal bones and subnasal clivus, as well as the vomer height. The degree of prognathism is comparable when this disparity is taken into account. In addition to a shorter face, gibbons and siamangs have a marked inferior displacement of the zygomatic arch, positioning it near the level of the palate roof. The upper face in hominids is narrower

with most features inclined posteriorly relative to the hylobatid configuration. The hominid orbits are also smaller due to a medial shift in **MTI** and **FMO** and a supero-medial shift in orbitale. Features in the hominid mid-face are generally postero-inferior to the hylobatid due to the inclination of the upper face and expansion of the nasal bones. The nasal aperture in great apes and humans is slightly shorter than the hylobatid and shifted posteriorly. There is also a great disparity between the hylobatid infraorbital foramen and zygomaxillare, indicating a sharper angling across the midline than in the hominid. Differences in the lower face largely reflect antero-inferior displacement in hominids. The subnasal inset (see Figure 6-24c) presents a better visualization of the morphology; to facilitate comparison, the two inset configurations were aligned by hand based on interdental landmarks. Chief differences occur in the expanded subnasal clivus, thickened palate, and elongate incisive canal of the hominids; this corroborates the work of Ward and colleagues (Ward & Kimbel, 1983; Ward & Pilbeam, 1983; Ward & Brown, 1986; Brown & Ward, 1988; McCollum & Ward, 1997) and suggests that the subnasal shape differences discussed above for PC 1 may have been driven more by *Hylobates* than *Gorilla*. This issue is taken up in greater detail in Chapter 8. Curiously, the hylobatids exhibit expansion of the mesio-distal canine dimension, suggesting that the gibbon canine is relatively broader than its hominoid counterparts; this is likely due to the “masculinization” of female hylobatid canines (Plavcan, 2001), which would drive up the average canine size.

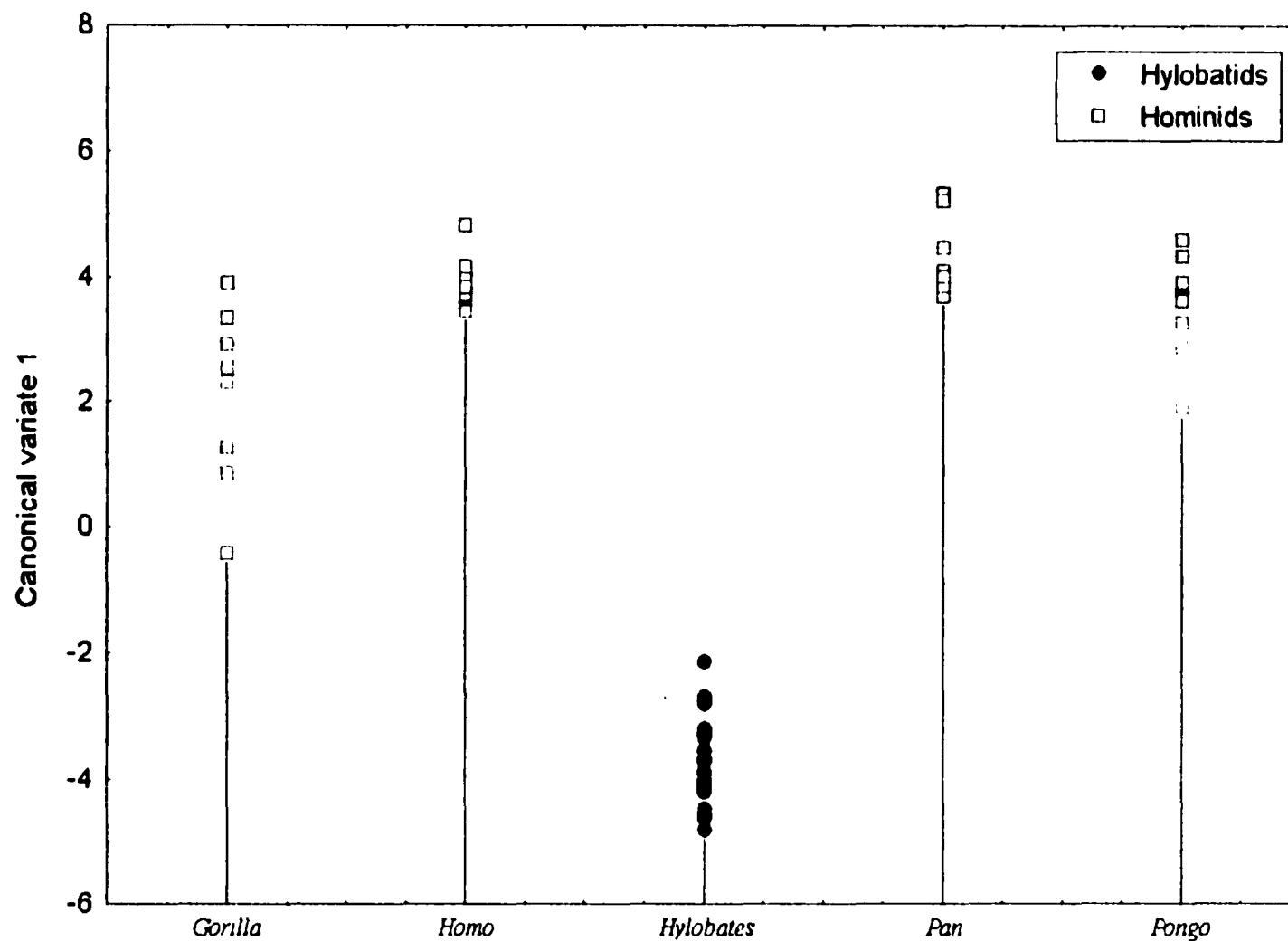


Figure 6-23 Plot of CV scores for the discriminant axis separating hylobatids from hominids. Although only the two groups were used for class variables, these results are illustrated by genus to better depict the distribution of specimens on the axis.

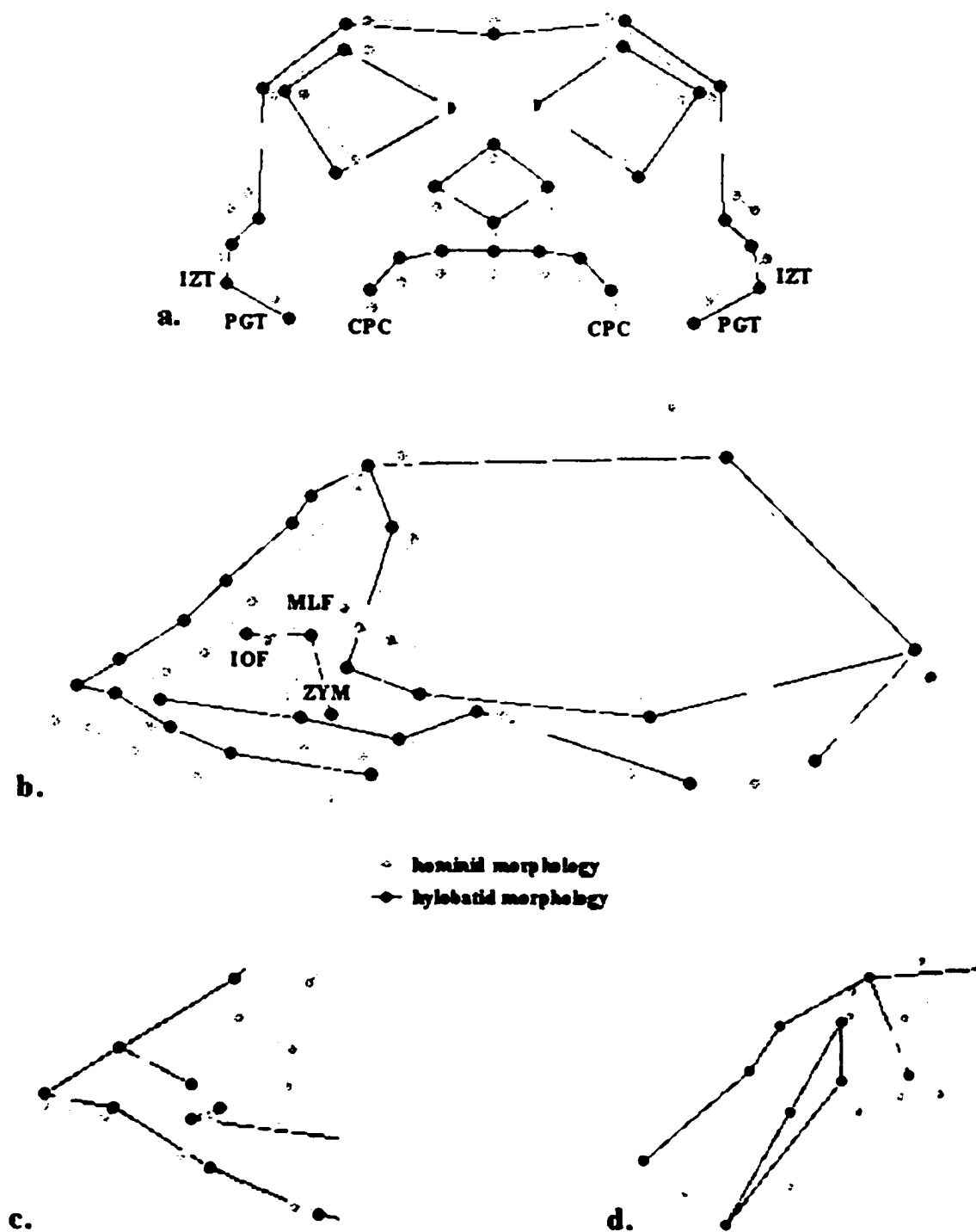


Figure 6-24 Shape change corresponding to the discrimination between hominids (gray) and hylobatids (black). (a) frontal view; (b) lateral view; (c) magnification of the subnasal region (lateral view); morphologies juxtaposed by hand to facilitate comparison; (d) magnification of the orbital region (lateral view). See Figures 6-1 and 6-2 for additional landmark references.

Node 4: Pongines vs. Hominines

There are clear morphological discriminators between pongines and hominines, as shown by both cross-validation results (Table 6-11) and the plot of CV scores (Figure 6-25). Shape differences represented by the discriminant axis are illustrated in Figure 6-26. Major differences in the neurocranium can be seen in overall size of the braincase and flexion of the basi-occiput. The orangutan brain case is substantially smaller than the hominine and appears to be rotated superiorly in relation to the face. The hominine upper face is anteriorly placed relative to the pongine, particularly toward the midline. Laterally this disparity is reduced, implying angularity in the hominine but a relatively planar pongine upper face. The upper face is also broader in hominines and this seems to extend through the midface. The pongine orbits are set much closer together than the hominine and there is an additional inferior displacement of dacryon. It is interesting to note that the tall, narrow orbits universally attributed to *Pongo* seem to derive primarily from a narrowing of the medial orbital morphology, rather than from significant expansion in height; this is particularly evident in the dacryon-orbitale chord.

Table 6-11 Cross-validation results for DA of cranial morphologies in hominines and pongines. Each cell gives the number (n) and percent (%) of individuals from the taxa on the left assigned to the taxa across the top.

Taxon		Pongines	Hominines
Pongines	n	56	
	%	100.00	
Hominines	n		60
	%		100.00

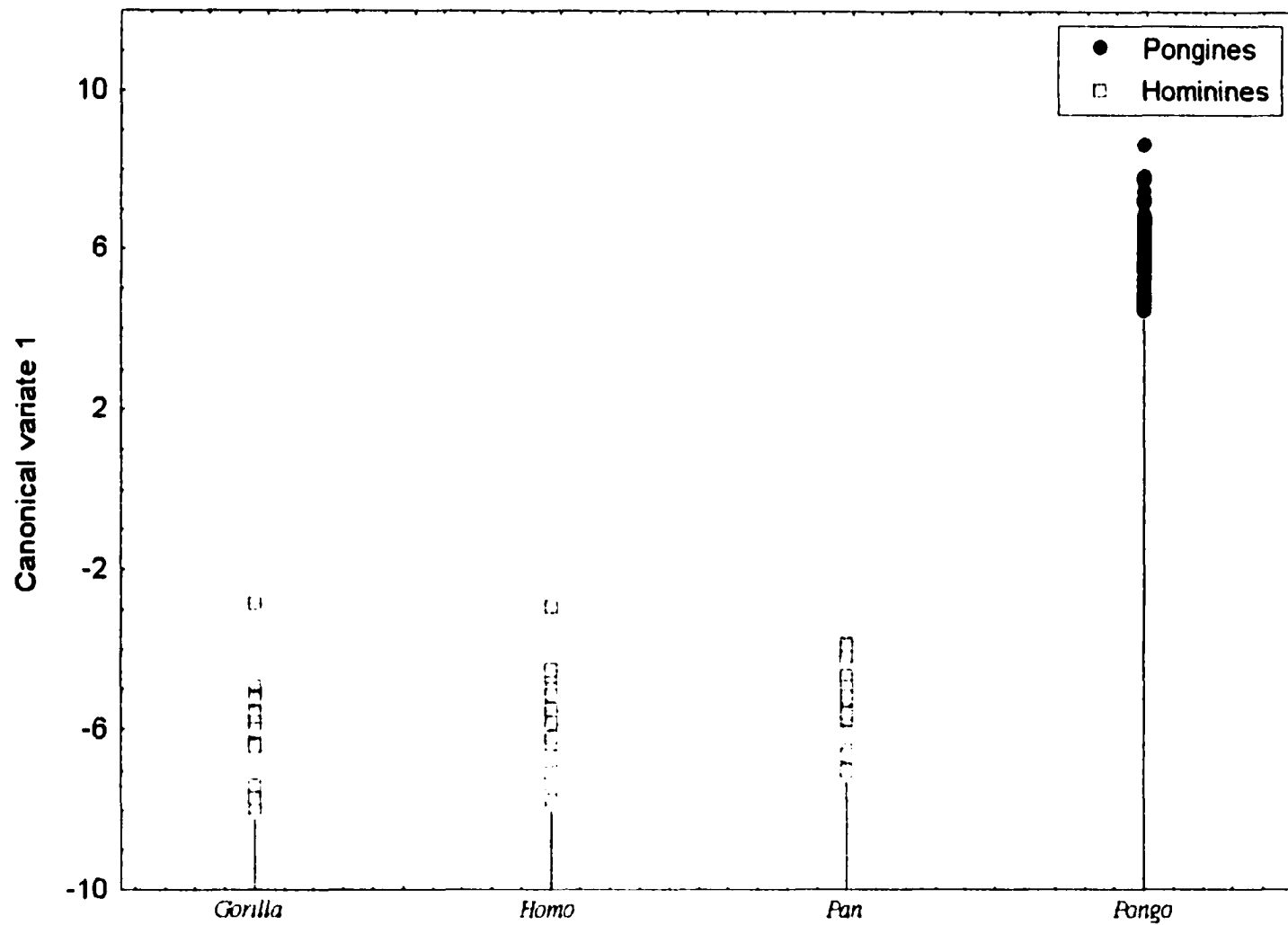


Figure 6-25 Plot of CV scores for the discriminant axis separating pongines from hominines. Although only the two groups were used for class variables, these results are illustrated by genus to better depict the distribution of specimens on the axis.

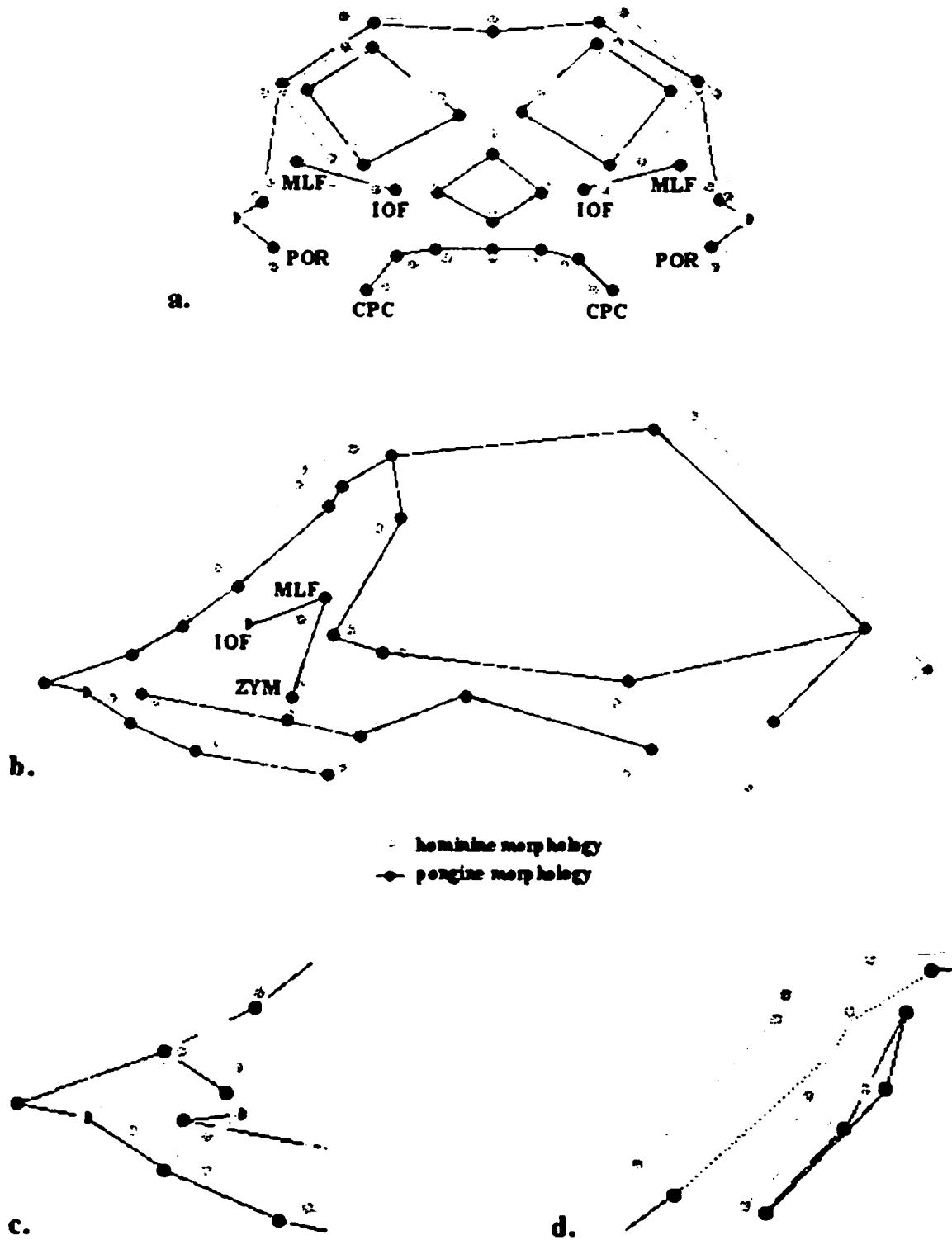


Figure 6-26 Shape change corresponding to the discrimination between hominines (gray) and pongines (black). (a) frontal view; (b) lateral view; (c) magnification of the subnasal region (lateral view); (d) magnification of the orbital region (lateral view). See Figures 6-1 and 6-2 for additional landmark references.

There is substantial difference between these subfamilies in the midfacial region. Hominines have strictly taller nasal apertures in Frankfurt horizontal plane, but this is primarily due to the retraction and consequential sloping of the pongine upper face. Lateral angling in both groups is equivalent by the level of alare. Infraorbital and zygomatic foramina are laterally displaced in hominines, coincident with the broader midface. At **SZT**, however, widths are equivalent. Below this, the pongine face becomes wider than the hominine in the palate. The posterior aspect of the palate is rotated inferiorly in the pongine, as indicated by increased distance between staphylion and hormion. Thus, it slopes more superiorly as it progresses forward until it reaches equivalence with the hominine in the premaxillary region. Here, however, there is a marked difference as the subnasal clivus in *Pongo* is greatly expanded anteriorly. This premaxillary protrusion causes the pongine palate to be relatively much longer than the hominine. There is also expansion in the posterior aspect of the pongine clivus, as can be noted at **CLI**. Palate thickness is similar between the groups, but the drop from nasal sill to floor is quite evident in hominines and absent from pongines.

Node 5: *Gorilla* vs. *Pan-Homo*

The node separating gorillas from a human-chimpanzee clade is the most controversial among hominoid phylogeneticists. Genetic analyses seem to unequivocally support a *Homo-Pan* clade, with *Gorilla* as the sister taxon. Few morphological studies have been able to replicate this result, however, (but see, e.g., Groves, 1986; Begun *et al.*, 1997; Strait *et al.*, 1997) and so some morphologists still regard the situation as an unresolved trichotomy (e.g., Andrews & Martin, 1987; Andrews, 1992; Andrews & Delson, 2000; Köhler, *et al.*, 2001). Here, *Homo* and *Pan* were treated as a single

taxonomic unit in order to discern their shared differences from *Gorilla*. Unfortunately, discriminant analysis of these landmarks was not sufficient to find a clear distinction, as demonstrated by cross-validation (see Table 6-12): of the 23 misclassified *Gorilla* specimens, 21 were male; all the misclassified *Homo-Pan* specimens were chimpanzees. Note, however, that an ANOVA found the centroids of these groups to be highly significantly different ($p < 0.0001$). The CV scores plotted in Figure 6-27 show *Gorilla* and *Homo* toward opposite extremes, with *Pan* bridging the gap between them. It is interesting to note that the function which best discriminates between these groups also separates male and female gorillas; male gorillas completely overlap with specimens of *Pan*, while females are more distinct. Sexes in *Pan* and *Homo* are mixed along this axis.

The substantial overlap between these groups makes irrelevant further discussion of the shape differences defining node 5 branches. The function separates—at the extremes—gorilla females from modern humans, with chimpanzees and male gorillas intermediate. Any interpretation of the corresponding shape coefficients, then, would reveal little about the shared features of *Homo* and *Pan*.

Table 6-12 Cross-validation results for DA of cranial morphologies in *Gorilla* and the *Homo-Pan* clade. Each cell gives the number (n) and percent (%) of individuals from the taxa on the left assigned to the taxa across the top.

Taxon		<i>Gorilla</i>	<i>Pan-Homo</i>
<i>Gorilla</i>	n	53	23
	%	69.74	30.26
<i>Homo-Pan</i>	n	21	55
	%	27.63	72.37

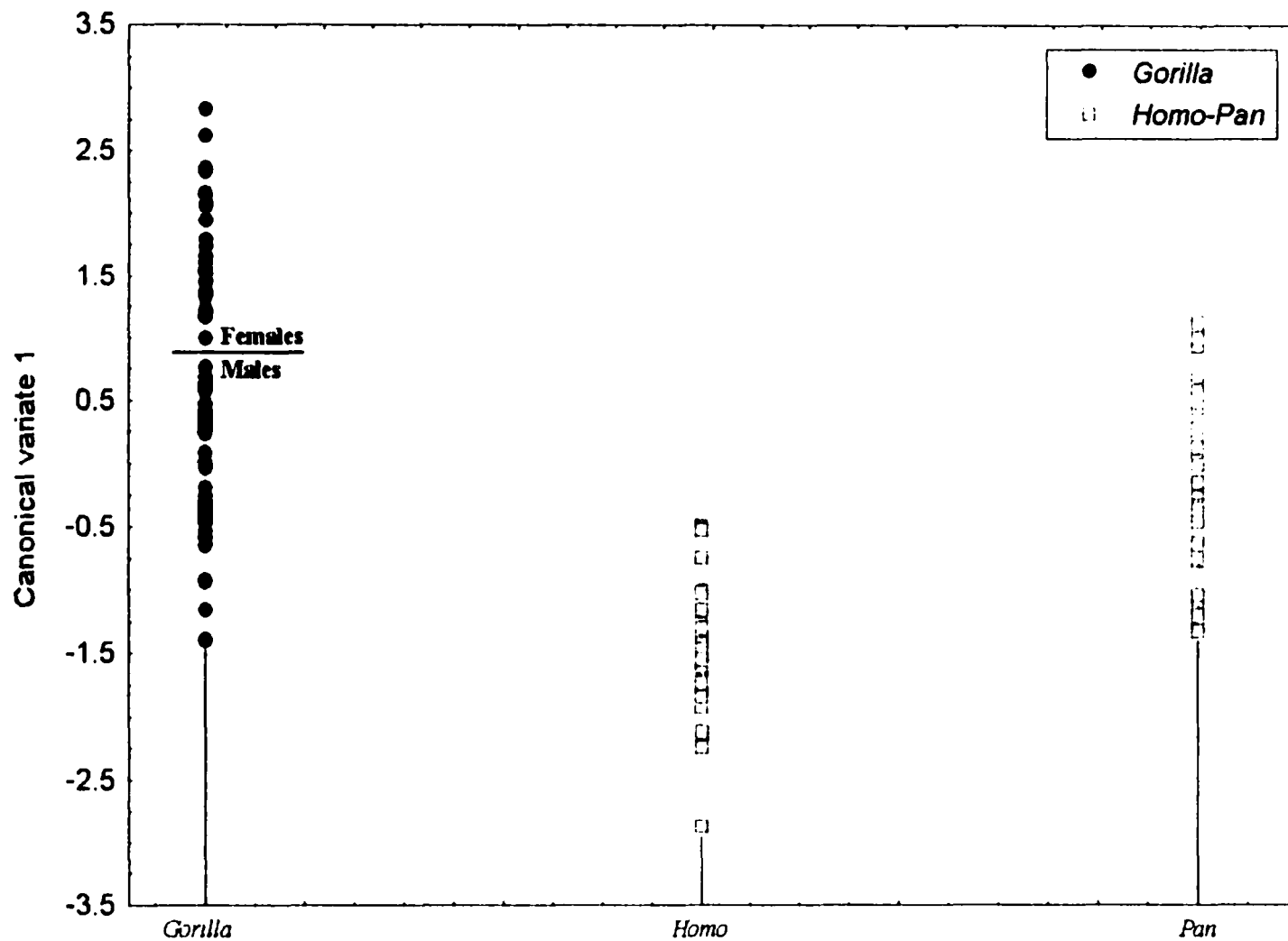


Figure 6-27 Plot of CV scores for the discriminant axis separating *Gorilla* from the *Pan-Homo* clade. Although only the two groups were used for class variables, these results are illustrated by genus to better depict the distribution of specimens on the axis. Note the complete overlap of *Pan* with *Gorilla*. Interestingly, this discriminant axis also separates male and female gorillas, with males scoring closer to humans and chimpanzees.

Node 6: *Pan* vs. *Homo*

The differences between *Pan* and *Homo* largely represent the distinctness of humans from all other apes. Such characteristics are routinely discussed in relation to fossil humans and the origin of the hominin clade, but are outlined briefly below. The distinction between human and chimpanzee is quite dramatic, as illustrated by a plot of CV scores (Figure 6-28). Interestingly, this axis of discrimination also separates the pygmy from common chimpanzees (ANOVA: $p < 0.0001$). Cross-validation of the discriminant analysis (Table 6-13) correctly assigned all specimens; this was true in every replicate and when the entire sample of *Pan* is included.

Shape changes corresponding to the discriminant function are illustrated in Figure 6-29. It is useful here to remember that the landmark configurations in the figures do not represent actual or “average” human and chimpanzee specimens; rather, they denote shape vectors corresponding to the discriminant function as applied to the consensus anthropoid configuration. In the neurocranium, the overwhelming difference is in brain size: all sagittal neurocranial landmarks show substantial expansion; biporionic width is also modestly increased. The human foramen magnum is well anterior to the chimpanzee; this corresponds to a reapportionment of the occipital bone from a relatively long basal but short squamous region in *Pan* to a shorter, flexed base and long squamous in *Homo*. The upper face in *Homo* is rotated anteriorly placing most of the landmarks in front of their counterparts in *Pan*. The differences in orbit size and placement are minor as is the change in width of the upper face. Perhaps the most significant distinction is the proximity of **PTS** and **MTS** in humans, but a pronounced difference (i.e., a post-toral sulcus) in *Pan*. The only major difference in the mid-face is in the superiorly placed nasal

aperture. From frontal view it appears that the human opening is substantially larger due to superior expansion. The profile view, however, shows this to be mostly a result of the anterior rotation of the entire upper face—with a gradual slope and shorter nasal bones contributing to a lesser degree. Thus, nasal apertures are approximately the same size, although the human's is less planar. Changes in the lower face are most evident in the subnasal region (see Figure 6-29c). The chimpanzee clivus is greatly expanded anteriorly, sloping sharply downward posteriorly; the human has a much shorter clivus. The anterior palate in *Homo* seems deflected superiorly, causing the major differences in the region of the incisive canal. The anterior dentition in *Pan* is broader than the human, particularly in the canine landmarks. It is interesting to note that the relationship of **STA** and **HOR** to the centroid is virtually the same in both genera.

Table 6-13 Cross-validation results for DA of *Pan* vs. *Homo*. Each cell gives the number (n) and percent (%) of individuals reclassified from the taxa on the left into the taxa across the top.

Taxon		<i>Pan</i>	<i>Homo</i>
<i>Pan</i>	N	38	
	%	100.00	
<i>Homo</i>	N		38
	%		100.00

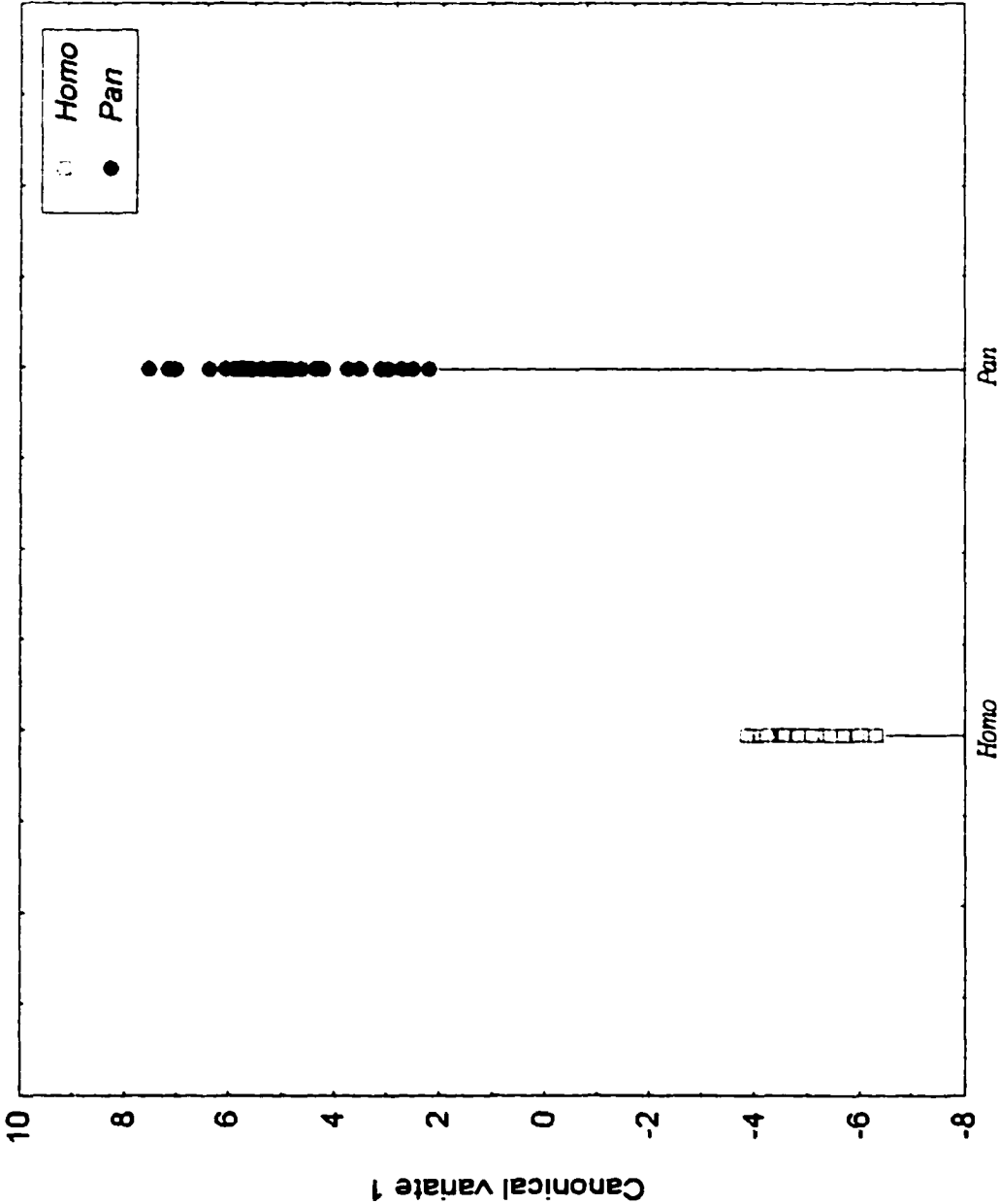


Figure 6-28 Plot of CV scores for the discriminant axis separating *Pan* and *Homo*.

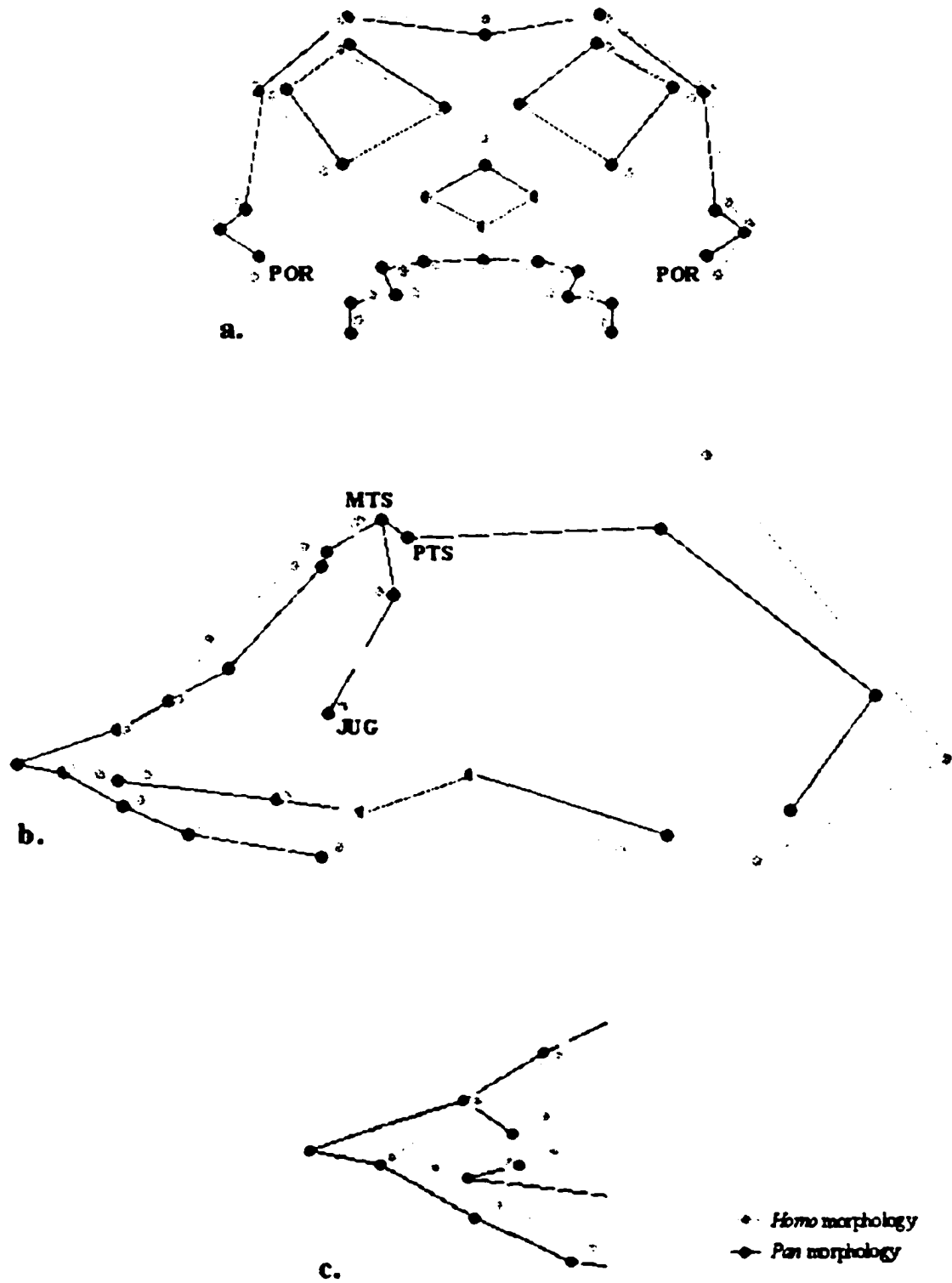


Figure 6-29 Shape change corresponding to the discrimination between *Homo* (gray) and *Pan* (black). (a) frontal view; (b) lateral view; (c) magnification of the subnasal region (lateral view). See Figures 6-1 and 6-2 for additional landmark references.

FOSSIL SPECIMENS

To conclude morphometric and statistical consideration of the entire cranium, I examined the phenetic affinities of several fossil hominoid specimens. While none of them retains all 65 landmarks, several are well enough preserved to warrant mention here. Discriminant analyses were performed on samples of the extant taxa in order to generate classification functions. These were done at the generic level and for each node of the consensus phylogeny (Figure 6-18). Discriminant functions were then used to place fossil specimens among extant taxa. Two-group and 3-group, as well as whole sample and equal-sample analyses were performed as described in Chapter 5. Due to varying degrees of preservation, analyses were done on two separate groups of fossils. The non-human group used 30 landmarks based on the shared morphology of *Afropithecus* (WK 16999), *Dryopithecus* (RUD 200), *Propithecus* (CGM 42842, DPC 2803, DPC 3161) and *Turkanapithecus* (WK 16950); analyses of the human group were based on 36 landmarks and used to classify *Australopithecus* (Sts 5), *Paranthropus* (WT 17000, ER 406), and early *Homo* (ER 1813, ER 3733) fossils. Landmarks used in each are listed in Table 6-14.

Non-human fossils were evaluated at the first four nodes of the consensus phylogeny; they were not evaluated at nodes 5 and 6, as it is highly unlikely that any is ancestral to the *Gorilla* or *Homo-Pan* clade. Human fossils were evaluated at nodes 4-6 using only 2-group analyses (see Chapter 5). Results of the generic classifications for all fossils are given in Table 6-15; node discrimination results are listed in Tables 6-16 (non-human) and 6-17 (human). In all three tables, cross-validation results are shown in the first row below each class variable. Boldface is used to denote the single assignment for

each specimen based on whole-sample discriminant analyses; numbers in the cells show the assignment distributions out of 1000 equal-sample replicates. These distributions were tested for significance using a χ^2 test for equal proportions, and *non-significant* results are designated by an asterisk.

Table 6-14 Landmarks used in discriminant analyses for assignment of fossils specimens. See Chapter 4 for definitions and discussion.

Non-human fossil group	Human fossil group
Jugale	Opisthocranium
Frontomale temporale	Porion
Frontomale orbitale	Jugale
Mid-orbit torus inferior	Frontomale temporale
Mid-orbit torus superior	Frontomale orbitale
Dacryon	Mid-orbit torus inferior
Orbitale	Mid-orbit torus superior
Zygoorbitale	Dacryon
Zygomaxillare	Orbitale
Malar root origin	Zygoorbitale
Glabella	Malar foramen
Nasion	Zygomaxillare
Lingual canine margin	Malar root origin
Canine-premolar contact	Post-toral sulcus
Premolar-molar contact	Glabella
Distal molar	Nasion
	Alare
	Anterior attachment of nasal septum
	Posterior glenoid tip
	Incisive
	Lingual canine margin

Table 6-15 Assignment of fossils to modern genera from discriminant analysis. Boldface indicates the single genus assignment for each fossil specimen based on the whole-sample analysis. Numbers show additional assignments out of 1000 randomized DAs using equal sample sizes. The first row beneath genus names lists the mean percentage of extant specimens correctly re-assigned in the replicate cross-validations. A χ^2 test for equal proportions ($\phi = 0.1$) found highly significant ($p < 0.0001$) deviations in the frequency distribution for each fossil.

		Atel	Cebu	Cerc	Papi	Pcol	Hylo	Pong	Gori	Pan	Homo
Mean reclassified in correct genus (%)		100.00	100.00	100.00	100.00	99.87	96.35	100.00	97.92	99.66	100.00
Proplio	DPC 2803	146	2	59	110	12	106	126	26	413	
	DPC 3161	124	19	270	11	311	3	88	28	146	
	CGM 42842	315		37	31	1	174	251	75	115	1
Afro	WK 16999			5		25	253	8	98	606	5
Turkana	WK 16950	16			1		338	19	162	464	
Dryo	RUD 200	190			6	46	180	51	407	20	95
Australo	STS 5									101	899
Paranth	WT 17000						2	2		30	966
	ER 406									6	994
Homo	ER 1813									26	974
	ER 3733										1000

Basal catarrhines

Propliopithecus

Genus level discriminations of *Propliopithecus* yielded a broad distribution of classifications. All three specimens placed in a variety of genera, with none receiving even 50% support from the replicates. DPC 2803 was the most consistent, classifying with *Pan* in the whole-sample analysis and in 41% of the replicates; *Ateles*, *Hylobates*, *Papio*, and *Pongo*, however, all saw better than 10% of the classifications. DPC 3161 was classified with *Procolobus* with 31% support from the replicate analyses; placement in *Cercopithecus* was only somewhat less frequent (27%), followed by *Pan* (15%) and *Ateles* (12%). CGM 42842 most resembled *Ateles* at this level, with 32% of the equal-sample classification; it placed with *Pongo* 25% of the time, and in *Hylobates* and *Pan* in better than 10% of the cases.

Table 6-16 Results from discriminant analyses and assignment of non-human catarrhine fossils at nodes 1-4 (see Figure 6-18). 2-group analyses forced fossils into one branch deriving from the node; 3-group analyses allowed the additional option of grouping with taxa external to the node ("primitive"). Boldface indicates the single classification for each specimen based on DA of the entire extant sample. Numbers show additional classifications of 1000 randomized tests using equal sample sizes. The first two rows beneath taxon names list the mean percentage of extant specimens correctly re-assigned in replicate series. * indicates a *lack of significance* from a χ^2 test for equal proportions.

Mean Cross-Validation %		NODE 1			NODE 2		
		platyrrhine	catarrhine		cercopithecoid	hominoid	primitive
2-group		98.67	95.94		100.00	99.53	
3-group					100.00	98.40	98.44
DPC 2803	2grp	681	319		454	546	
	3grp				230	245	525
DPC 3161	2grp	512*	488*		999	1	
	3grp				855	11	134
CGM 42842	2grp	850	150		408	592	
	3grp				59	154	787
WK 16999	2grp	21	979		53	947	
	3grp				36	942	22
WK 16950	2grp	189	811		0	1000	
	3grp				3	782	215
RUD 200	2grp	188	812		254	746	
	3grp				243	749	18
Mean Cross-Validation %		NODE 3			NODE 4		
		hylobatid	hominid	primitive	pongine	hominine	primitive
2-group		97.68	93.35		100.00	99.98	
3-group		95.57	96.88	94.77	99.04	95.53	94.49
DPC 2803	2grp	0	1000		996	4	
	3grp	0	48	952	410	204	386
DPC 3161	2grp	0	1000		964	36	
	3grp	0	0	1000	386	55	559
CGM 42842	2grp	1	999		994	6	
	3grp	0	115	885	447	32	421
WK 16999	2grp	372	628		0	1000	
	3grp	368	631	1	0	444	556
WK 16950	2grp	447	553		3	997	
	3grp	253	727	20	0	512	448
RUD 200	2grp	62	938		367	633	
	3grp	39	716	255	49	108	843

Looking only at generic assignments, there is not a strong consensus about the affinities of these specimens individually or as a group. *Ateles* and *Pan* received a number of assignments from all three. And, while the distribution profiles of DPC 2803 and CGM 42842 are remarkably similar (if not overwhelmingly discriminating), DPC 3161 seems to bear a closer affinity to the cercopithecoid genera. In the differences that separate catarrhines from platyrrhines (node 1), DPC 2803 and CGM 42842 placed largely within the latter; DPC 3161 placed equally in both, with a non-significant distribution. Node 2 results were significant in the 2-group analysis for all three specimens, but with a weak differential for DPC 2803 and CGM 42842: both classified among hominoids with little more than even support. It is not surprising, then, that these specimens placed predominantly in the “primitive” category in the 3-group analysis. DPC 3161 again demonstrated an affinity with cercopithecoids in both 2- and 3-group analyses. Interestingly, node 3 results were fairly uniform. In differences that distinguish hylobatids from hominids, *Propliopithecus* places decidedly among the latter: when the “primitive” option is added, however, all three specimens group there disproportionately. Results from node 4 indicate a clear lack of hominine features (relative to pongines). In the 3-group analyses, a substantial portion of the classifications land in the “primitive” group for all specimens. DPC 3161 and CGM 42842 classify there in the whole-sample DA, while DPC 2803 still groups among pongines.

The broad distribution of classifications renders interpretation of these results somewhat difficult. Yet, such results might be expected when analyzing catarrhines of primitive aspect (Harrison, 2002). It is clear that DPC 2803 and CGM 42842 have similar morphologies, while DPC 3161 is somewhat different. The first two bear stronger cranial

affinities to platyrrhines than any other group; the genus classification of DPC 2803 might hint at hominoid similarities, but the node 2 results make this suspect. DPC 3161, on the other hand, shows a strong similarity to cercopithecoids. Thus, there seems to be substantial variability within this sample. It is interesting that none of these specimens grouped with the hylobatids at node 3, all placing strongly with hominids; the abundance of “primitive” classifications, however, suggests that they do not bear a close affinity to hominids either. Finally, this analysis does not offer much support for the idea that *Pongo* shares a suite of ancestral catarrhine cranial features with *Propliopithecus* (e.g., McCrossin & Benefit, 1994). While *Pongo* received a moderate number of classifications at the genus level, neither these nor the 3-group results from node 4 were convincing.

Early Miocene putative hominoids

Afropithecus

In generic discrimination, WK 16999 placed most often in *Pan* (61%), including assignment there from the whole-sample analysis; it grouped with *Hylobates* in 25% of the replicates and *Gorilla* in almost 10%. In node discriminations, *Afropithecus* placed very strongly among both catarrhines and hominoids, unlike specimens of *Propliopithecus*. Node 3 results were less discriminating, with the specimen grouping among hominids 63% of the time in both 2- and 3-group analyses; it placed in the “primitive” category only once among the thousand replicates. At node 4, *Afropithecus* was demonstrably unlike the pongine morphology; when offered the “primitive” category, it was classified there in a weak majority (56%) of replicates—the balance was among hominines.

Alternative phylogenetic hypotheses for *Afropithecus* typically include it with stem catarrhines (e.g., Harrison, 2002), stem hominoids (e.g., Leakey & Walker, 1997), or primitive hominids (e.g., Andrews, 1992). Results from node analyses unambiguously confirm its catarrhine status and provide strong support for its membership in the Hominoidea. This last statement may be problematic, as Harrison (1987, 2002; Harrison & Rook, 1997) has argued that primitive catarrhine cranial morphology is more hominoid-like than cercopithecoïd. Thus, one might expect a basal catarrhine to obtain results similar to those of *Afropithecus*. Yet, the performance of WK 16999 in these tests was markedly different from that of any *Propliopithecus* specimen. *Afropithecus* genus classifications were strongly among hominoids, rather than widely distributed. And, unlike *Propliopithecus*, it did not classify in the “primitive” (or cercopithecoïd) category at node 2. One must bear in mind that these catarrhines of primitive aspect might be expected to differ from basal catarrhines of modern aspect—the latter being phenetically more similar to hominoids (see Harrison, 2002). Yet, as the superfamilial status of many or all of these advanced stem catarrhines is disputed (compare Andrews, 1992; Harrison, 2002), *Propliopithecus* remains the best available test subject. Using it as a benchmark, the evidence here supports the inclusion of *Afropithecus* in the hominoid superfamily.

The position of *Afropithecus* as a stem hominid is somewhat more ambiguous. In both 2- and 3-group analyses of node 3, *Afropithecus* was classified as a hominid, with 63% support from the replicates. This difference in proportion is highly significant ($p < 0.0001$), but fairly weak. Nevertheless, in the features that distinguish hominids from hylobatids, *Afropithecus* resembles the great apes. Finally, it is clear from node 4 that *Afropithecus* does not have overt affinities with *Pongo*. McCrossin & Benefit (1994)

have suggested that *Pongo* and *Afropithecus* share a number of characteristics that are primitive retentions of the ancestral catarrhine morphotype. While the results here do not dispute any particular character similarities (but see Chapter 7), it is clear that the morphology of *Afropithecus*—considered as a whole—is distinctly non-pongine. The 3-group analysis of node 4 splits fairly evenly between hominine and primitive, suggesting that *Afropithecus* is not particularly similar to either.

Turkanapithecus

Discrimination among genera assigned WK 16950 predominantly (46%) to *Pan*; 34% of the assignments were in *Hylobates* and 16% in *Gorilla*. *Turkanapithecus* placed with catarrhines in 81% of the node 1 replicates; it grouped with hominoids in all of the 2-group and 78% of the 3-group replicates at node 2. Results from node 3 are more puzzling. The difference between the frequency of assignments in hylobatids and hominids in the 2-group test was significant but negligible; the whole-sample analysis classified this specimen with the hylobatids. When the primitive category was added, however, support for its hominid affinity increased substantially. This is probably not strong evidence for naming *Turkanapithecus* a great ape. The 2-group results strongly indicate that in features distinguishing hominids from hylobatids, this specimen is like neither group. The addition of a third option—ostensibly to provide an alternative to the “either/or” of a 2-group analysis—in this case forced classifications among hominids proportionately higher than are probably warranted. Scrutiny of the CV scores for both 2-group and 3-group analyses supports this conclusion. Node 4 results are similar to *Afropithecus* in that there is no evidence of a pongine affinity for *Turkanapithecus*.

Phylogenetic hypotheses proposed for *Turkanapithecus* are similar to those put forth for *Afropithecus*: primitive catarrhine (Harrison, 2002), hominoid (Leakey & Leakey, 1988a), or hominid (e.g. Rae, 1993, 1997). The sum of these results supports the original designation of Leakey & Leakey (1986a) that *Turkanapithecus* is a stem hominoid; this conclusion, however, is more tentative than that of *Afropithecus*. WK 16950 shows clear hominoid affinities in those features that distinguish extant apes from cercopithecoids or platyrrhines. Moreover, its disposition in these analyses was decidedly different from those of *Propliopithecus* specimens: its genus classifications were largely confined to the hominoids. Yet, there is strong evidence (node 3, 2-group) that *Turkanapithecus* looks neither like a hylobatid nor a hominid in those features that distinguish them. Thus, WK 16950 is unlike hylobatids, hominids, cercopithecoids, or platyrrhines, yet seems to have some general hominoid affinities. This is the sort of pattern that might emerge for a basal catarrhine of modern aspect, as described by Harrison (1987, 1988, 2002). Nevertheless, without a better method to test this hypothesis, I will cautiously support the hominoid status of *Turkanapithecus*.

Late Miocene hominoids

Dryopithecus

RUD 200 had the greatest affinity to *Gorilla*, placing there in the whole-sample analysis and in 40% of the replicates. Surprisingly, it grouped with *Ateles* in 19% of the equal-sample randomizations and in *Hylobates* 18%. RUD 200 received fairly strong support in classifying as a catarrhine at node 1 and a hominoid at node 2; the addition of the “primitive” group did not significantly alter the node 2 results. At node 3, *Dryopithecus* grouped with hominids in 94% of the 2-group replicates and 72% of the 3-

group; in the features distinguishing hominids from hylobatids, it showed little affinity with the latter. At node 4, this specimen grouped with hominines in 63% of the 2-group replicates; it placed in the “primitive” category, however, in 84% of the 3-group tests.

Alternative hypotheses about the relationship of *Dryopithecus* to extant apes designate it as a stem hominoid (e.g. McCrossin & Benefit, 1997), primitive hominid (e.g. Andrews, 1992; Andrews *et al.*, 1996), basal hominine (Begun *et al.*, 1997), or stem pongine (e.g. Köhler *et al.*, 2001). Results from generic discrimination will not help to distinguish among three of these hypotheses, as *Gorilla* and *Hylobates* share similar cranial morphology (see above). They do, however, demonstrate the lack of affinity between RUD 200 and *Pongo*. In node discriminations, the status of *Dryopithecus* as a catarrhine and hominoid is well supported—and undisputed in the literature. 2-group results from node 3 are particularly strong in confirmation of *Dryopithecus* as a great ape; while the addition of the “primitive” group weakens this, it does not do so substantially. Node 4 results reiterate the dissimilarity between *Dryopithecus* and pongines in those features that separate the latter taxon from hominines. Nevertheless, it has no support as a hominine, based on the large number of “primitive” assignments at node 4. In summary, phenetic affinities of the most complete *Dryopithecus* cranium tend to rule out consideration of *Dryopithecus* as a stem hominoid, pongine, or hominine. There is, however, strong support for its position as a hominid.

Table 6-17 Results from discriminant analyses and assignments of fossil humans at phylogenetic nodes 4-6. Boldface indicates the classification for each specimen based on DA of the entire extant sample. Numbers show additional classifications from 1000 randomized tests using equal sample sizes. The first row beneath each taxon name gives the mean percentage of extant specimens correctly reclassified in the replicate series. Note the lack of robusticity in the node 5 discriminant function; replicate values are shaded to indicate their unreliability. * indicates a lack of significant difference from A χ^2 test for equal proportions. See text for further discussion.

Mean Cross-validation Percentage (%)	NODE 4		NODE 5		NODE 6	
	pongine	hominine	<i>Gorilla</i>	<i>Homo-Pan</i>	<i>Pan</i>	<i>Homo</i>
	100.00	100.00	65.55	70.82	100.00	100.00
Sts 5	39	961	191	809	1000	0
WT 17000	340	660	125	875	1000	0
ER 406	0	1000	112	888	1000	0
ER 1813	0	1000	177	823	488*	512*
ER 3733	0	1000	138	862	395	605

Plio-Pleistocene hominins

Australopithecus

In genus classifications, Sts 5 was placed in *Homo* based on the whole-sample analysis and in 90% of the replicates; remaining classifications were all in *Pan*. Among differences distinguishing pongines from hominines (node 4), *Australopithecus* placed strongly among the latter. Classifications at node 5 placed this specimen in the *Homo-Pan* sample, but cross-validation results indicate that the discriminant function is fairly weak in separating groups. Thus, node 5 results cannot be reliably used. Note, however, that Sts 5 grouped in *Homo-Pan* with substantially greater frequency (82%) than the clade cross-validation average (71%). Analysis of the extant taxa at node 5 (see Node 5 discussion above) demonstrated that misclassified specimens from the *Homo-Pan* sample were all chimpanzees. Therefore, the 81% classification here suggests that Sts 5 is somewhat closer to *Homo* on this discriminant function than is the chimpanzee centroid.

Having said that, this specimen was unanimously placed in *Pan* at node 6. Thus, while *Australopithecus* may have more human affinities than the “average” chimpanzee (from this sample), its cranial morphology is more chimpanzee-like in those features that distinguish *Pan* and modern *Homo*.

Paranthropus

Both WT 17000 and ER 406 placed in the genus *Homo* with overwhelming support (97% and 99%, respectively) from replicate tests; extraneous classifications were all in *Pan* excepting two (= 0.2%) classifications of WT 17000 in both *Hylobates* and *Pongo*. At node 4, ER 406 showed demonstrable hominine affinities. WT 17000, while classifying with great apes and humans in a significant ($p < 0.0001$) number of replicates, had fairly weak support at 66%. Thus, in features distinguishing African apes from pongines, *P. aethiopicus* had affinities with the latter in a third of the randomized samples. Node 5 results placed both specimens in a *Homo-Pan* clade, with better than 87% support from replicates. As noted above, this discriminant function is very weak for distinguishing node 5 crown clade morphologies; yet, by significantly outperforming the cross-validation average, these specimens demonstrate a more human-like affinity. As with *Australopithecus*, node 6 placed both specimens unanimously within *Pan*. Generic discrimination suggests that *Paranthropus* is more like modern *Homo* than it is any of the other extant taxa. In the specific features that separate *Pan* from *Homo*, however, they resemble the former. Note that there is no evidence here suggesting an affinity between *Paranthropus* and *Gorilla*.

Early *Homo*

Both fossil *Homo* specimens were strongly supported within this genus in discriminant analyses of extant genera; ER 3733, in fact, placed with modern humans in every replicate test. At node 4, these specimens were unanimously grouped within the hominine sample. Both were also strongly placed with a *Homo-Pan* group as opposed to *Gorilla*, but the cross-validation of this discriminant function shows it to be unreliable. As noted in discussions of *Australopithecus* and *Paranthropus* specimens, placement with the *Homo-Pan* sample at a higher rate than the cross-validation average suggests that these crania score closer to the modern human centroid on this discriminant function than was the chimpanzee centroid. Results at node 6 were inconclusive for ER 1813, as demonstrated by the non-significant χ^2 result. ER 3733 placed within *Homo* in the whole-sample test and in 60% of the replicates; while this distribution is significant ($p < 0.0001$), 60% support is fairly weak.

DISCUSSION

The work presented in this chapter can be broadly grouped into two types: data-driven and phylogeny-driven. Analyses conducted in the beginning sections were primarily designed to explore the morphological relationships among specimens and genera that are manifest within the data that were collected. This included principal components analysis, canonical variates analysis, and clustering of Mahalanobis distances for extant specimens. Thus, the goal was purely phenetic. Unburdened by evolutionary assumptions (except the minimal assumption [for CVA] that extant genera actually comprise natural groups), these analyses reveal patterns of similarity without

regard for pre-existing hypotheses of relationships or polarity. Results, then, were driven entirely by the structure of variation within the sample. Subsequent analyses in this chapter were designed to examine the morphological patterns that correlate with specific cladogenetic events. In these, data were constrained to vary along axes corresponding to the nodes of a consensus phylogeny of extant taxa (Figure 6-18). Such phylogenetic node discriminations were designed to estimate the amount of overlap between ranges of variation in crown clades, examine the shape differences between them, and test the affinities of fossil specimens according to these shape differences. Though still a phenetic analysis, this approach limits shape differences to those that are shared within clades but different between clades.

Data-driven analyses

Results from principal components, canonical variates, and cluster analyses of these non-human primates generally conformed to the consensus of anthropoid relationships with one major exception: the affinity between *Hylobates* and the African apes. If one accepts the hominoid relationships given in Figure 6-18, then the similarities demonstrated above among *Hylobates* and the African apes (and especially between *Hylobates* and *Gorilla*) could have two possible explanations: 1) they evolved convergently from a dissimilar ancestral morphology, or 2) they are retained homologously in African apes and *Hylobates* from a generalized crown ape pattern. Choosing between these alternatives is not so much a question of whether hylobatids are the sister taxon to great apes and humans. This is well accepted both among morphologists (e.g. Pilgrim, 1927; Simpson, 1945, 1949, 1953; Weidenreich, 1946; Delson & Andrews, 1975; Greenfield, 1979, 1980; Andrews, 1985; Harrison, 1987, 1993,

2002; Begun, 1992; 1994; Moyà Solà & Köhler, 1995; Andrews *et al.*, 1996; Begun, *et al.*, 1997; Rose, 1997; C. Ward, 1997; Singleton, 2000) and geneticists (Goodman, 1963; Sarich & Wilson, 1967; Sarich, 1971; Caccone & Powell, 1989; Ruvolo, 1994, 1997; Goodman *et al.*, 1998). The decision, rather, regards the craniofacial morphology of the ancestral hominoid.

The analyses presented in this work are not appropriate for reconstructing ancestral morphotypes. Nevertheless, a number of authors (Vogel, 1966; Delson, 1975, 1977; Delson & Andrews, 1975; Ward & Kimbel, 1983; Andrews, 1985; Harrison, 1987; Strasser & Delson, 1987) have proposed a hylobatid model for some or all aspects of ancestral catarrhine cranial morphology. If stem catarrhines of modern aspect were cranially similar to hylobatids, then we can infer, not unreasonably, that hylobatid crania are conservative among extant hominoids—as has been suggested by Pilbeam (2002). If so, the similarity shown between African ape and hylobatid morphologies would likely represent retention of this basic hominoid pattern. Alternatively, Benefit & McCrossin (1991, 1993) have argued that the ancestral catarrhine morphotype was more like *Propliopithecus* [= *Aegyptopithecus*], based on craniofacial similarities shared among this taxon, *Victoriapithecus*, *Afropithecus*, and to a lesser extent *Dryopithecus* and *Sivapithecus* (see also Leakey & Leakey, 1986a; Simons, 1987; Leakey *et al.*, 1988b, 1991). In this case, the cranial morphology of *Hylobates* is regarded as more derived from the ancestral catarrhine morphology. These authors, however, do not preclude hylobatids from representing the primitive hominoid condition, though gibbons do not exhibit all of the features they ascribe to the morphotype.

Based on phenetic results presented here, these data support a hylobatid model of ancestral hominoid craniofacial morphology. The Mahalanobis distance values for both *Hylobates* and *Gorilla* place them at near the centroid of the overall taxon distribution. Thus, in a very literal sense, these can be considered generalized morphologies among this sample. If Harrison (1987, 1988, 1993, 2002; Harrison & Rook, 1997) is correct in suggesting that hominoid cranial morphology is phenetically similar to the ancestral catarrhine morphotype, then the relative proximity of cercopithecoid (and platyrrhine) genera to *Gorilla* in the minimum spanning tree (see Figure 6)—indeed the placement of *Gorilla* and *Hylobates* at the heart of this tree—is additional evidence that the morphology of these apes is phenetically conservative. Preliminary analyses by the author have also suggested that African apes and *Hylobates* may share a similar pattern of craniofacial ontogeny. Such evidence provides some justification (e.g., Reidl, 1978; Wood, 1988; Lieberman, 1995; Lieberman *et al.*, 1996; McCollum, 1999; Collard & O'Higgins, 2001; but see Lieberman, 2000) for concluding that these phenetic similarities among adults result from an inherited pattern of growth.

It is patent that all taxa contain a mixture of plesiomorphic and apomorphic features, and these results do not dispute this. They do suggest, however, that the degree to which African ape crania are apomorphic may have been overestimated, perhaps greatly. A survey of hominoid phylogenetic literature from the past few decades finds no researchers arguing the close affinity of *Hylobates* and *Gorilla* crania, nor that *Gorilla* retains a primitive *hominoid* (as opposed to great ape; see Pilbeam, 1979; Wolpoff, 1982) morphology. Yet, this work clearly supports the former supposition, and leads to inference of the latter (see above). In theory, the presence or absence of plesiomorphies

might not hinder the successful reconstruction of hominoid phylogeny: a properly coded and polarized cladistic analysis ignores primitive retentions. That previous studies have not recognized the degree similarity between hylobatids and African apes, however, suggests a more fundamental problem at the level of character coding. This is almost certainly related to size.

The extant sister taxon to Hominidae is markedly smaller than the great apes. This size difference greatly exacerbates two problems that can potentially confound character coding: 1) mistaking size difference for shape difference, and 2) conflating allometric effects with phylogenetic effects. In qualitative analyses, these errors would manifest as separate character states for hylobatid features that are merely smaller versions of a great ape morphology. It is difficult to qualitatively assess isometric differences across diverse body sizes: qualitatively assessing allometric differences is nigh to impossible. Yet, importantly, the erroneous creation of additional character states for *Hylobates* would largely go unnoticed, *because phylogenetic results derived from such data would likely conform to the consensus phylogeny*. In other words, one can easily reconstruct the “correct” extant phylogeny from a systemically erroneous character matrix. This is because the bifurcation of hominoid family lineages is superimposed over a dichotomy in body size. Such errors, while yielding a correct extant phylogeny, would result in an inflated impression of African ape autapomorphy. This has serious consequences for placing the myriad of fossil hominoids in a phylogenetic context: miscoded characters would yield relationships among similar body sizes rather than evolutionary branches. Moreover, if the hylobatid model is accepted for the ancestral hominoid cranium, then

many features treated as derived in phylogeny reconstruction may be, in fact, primitive traits—and therefore cladistically meaningless—scaled to a larger body size.

In quantitative analyses, body size must be standardized in order to compare data. A common approach for size correction is the use of ratios (see Jungers *et al.*, 1995): scaling one measurement by another. However, unless the relationships among variables are isometric, simple ratios can actually confound isometry and allometry (Neff & Marcus, 1980). For example, if one were to scale bi-zygomatic width by cranium length across several taxa, the resulting ratios would not describe a single dimension, but a *relationship* between two dimensions. If that relationship varies allometrically, then differences between different-sized taxa could result from size alone—having nothing to do with phylogeny. The outcome would mirror that in qualitative analysis: *Hylobates* would typically be given a separate character state. Thus, again one can easily achieve the correct phylogenetic result in apes for reasons that may be spurious.

The analyses presented here, with isometric and allometric adjustments to the data, suggest a strong overall affinity between crania of *Hylobates* and *Gorilla* (and *Pan* to a lesser extent). I conclude, therefore, that many of the purported differences between them may derive from scaling patterns. The implication of this is that we may need to rethink the character coding of some hominoid cranial features. Collard & Wood (2000) have concluded that cranial morphology is a poor vehicle for constructing phylogenetic hypotheses for the Hominoidea. While there are several flaws in their reasoning (Alba *et al.*, 2001; see McNulty, 2002), results here indicate that part of the problem may lie in our perception and coding of these features. A better understanding of cranial

plesiomorphies and apomorphies would indeed give us potentially stronger phylogenetic hypotheses.

Phylogenetic node discrimination

Analyses based on the consensus phylogeny helped to determine areas of the cranium that correspond to particular cladistic events in anthropoid history. This is not to say that characters from outside these regions should simply be dropped from phylogenetic analyses. Rather, this method provides a tool for studying the morphological correlates of evolution and a framework for judging the relative usefulness of some characters and character states (see Pilbeam, 1997). It can also serve as a starting point for research into the developmental, functional, and structural factors that underlie the stability or lability of particular morphological regions. Table 6-18 summarizes the shape differences that correspond to discriminations between crown clade morphologies in the consensus phylogeny. Note that these methods were very robust for distinguishing between morphologies of these crown clades in every case except node 5 (*Gorilla* vs. *Homo-Pan*).

The classification of fossil specimens by this approach offers a useful heuristic device for assessing their phenetic affinities based on the shape differences separating crown clades. While not a cladistic method, it places fossils according to those differences that are shared within one group and differ from the other group.

Table 6-18 Summary of shape differences determined from discriminant analyses between crown clades in the extant phylogeny (Figure 6-18). For each discrimination, the characteristics listed describe differences between the taxon in boldface with respect to the taxon in parentheses. Note that the discriminant analysis between *Gorilla* and the *Homo-Pan* group was not resolved, and so no characteristics are listed here.

Catarrhines (vs. platyrrhines)

more globular, wider (bi-porionic) neurocranium
 shorter basi-occiput
 greater protrusion of profile
 broad upper face rotated dorsally on the neurocranium
 low fronto-malar suture
 superiorly placed zygomatic arch
 anteriorly placed lateral zygoma
 longer, inferiorly expanded lower face

Hominoids (vs. cercopithecoids)

larger brain
 broad, flat (planar) upper face, rotated ventrally on the neurocranium
 short nasal bones
 nasal aperture short and broad, set higher on the face
 prognathism largely subnasal
 more airorhynch
 greatly elongated and taller subnasal clivus
 thick palate
 lateral shift in orbits

Hominids (vs. hylobatids)

neurocranium taller and slightly longer
 anterior shift in foramen magnum
 flat upper face, rotated dorsally on the neurocranium
 small orbits
 long nasal bones
 short orbital pillar and superiorly-placed anterior zygomatic arch
 anteriorly placed zygoma (especially lateral zygoma)
 nasal aperture short, set lower on the face
 elongated and taller subnasal clivus
 thick palate and elongate incisive canal
 narrower (mesio-distal) canines

Table 6-18 (cont.)

Hominines (vs. pongines)

larger brain (especially antero-posteriorly)
 flexed basi-occiput
 long occipital squamous (OPI-OPC)
 broad upper face angled across midline, rotated
 ventrally on the neurocranium
 lateral shift in orbits
 shorter, vertical profile
 markedly shorter (antero-posteriorly) subnasal clivus
 shorter incisive canal
 dissociation of nasal sill and nasal floor

Homo-Pan (vs. *Gorilla*): not resolved. See text for discussion

Homo (vs. *Pan*)

greatly expanded neurocranium
 anteriorly placed foramen magnum
 long occipital squamous, short basi-occiput
 upper face rotated ventrally on neurocranium
 lack of a post-toral sulcus
 short, protruding nasal bones
 less protruding profile
 reduced (antero-posterior) subnasal clivus length
 maxillary palatine process rotated dorsally
 reduced overall palate length

Both *Afropithecus* and *Turkanapithecus* were shown to share affinities with extant hominoid crania, the former having some similarity to hominids. Harrison's (1987, 1988, 2002) observation that ape crania are phenetically similar to the ancestral catarrhine morphotype cannot be directly addressed from these analyses. Instead, the use of *Propliopithecus* as a surrogate for basal catarrhine morphology demonstrated that both *Afropithecus* and *Turkanapithecus* have stronger hominoid affinities than do these Fayum specimens. This supports their designation as hominoids to the extent that

Propliopithecus actually does exhibit the ancestral features of a crown catarrhine; as a catarrhine of primitive aspect (e.g., Harrison, 2002) such an assumption may be unwarranted. Nevertheless, a better alternative is not available. European *Pliopithecus* is also considered to be a conservative catarrhine (Harrison, 1987; 2002; Benefit & McCrossin, 1993; Andrews *et al.*, 1996) and too incomplete to include here; the other likely candidates are the very specimens in question. Therefore, cranially both *Afropithecus* and *Turkanapithecus* are grouped with the Hominoidea, bearing in mind all of the caveats discussed above. *Afropithecus* may tentatively be placed with the hominids, although the evidence here is weak. Similarities between these two fossils and *Propliopithecus* specimens (Leakey & Leakey, 1986a,b; Leakey *et al.*, 1988a, b; Benefit & McCrossin, 1991, 1993; Leakey *et al.*, 1991), as measured by their discrimination results, were not readily apparent.

The cranial morphology of *Dryopithecus* was strongly endorsed as hominid. There was no support here for recognizing pongine affinities for RUD 200 (*contra* Moyà Solà & Köhler, 1993, 1995; Köhler *et al.*, 2001). And, although more similar to the hominines by comparison, its preference for the “primitive” category at node 4 strongly argues against a link to African ape and human morphology (*contra* Begun, 1992, 1994, 2002; Begun & Kordos, 1997; Begun *et al.*, 1997). The position of *Dryopithecus* as a stem catarrhine (Benefit & McCrossin, 1995; McCrossin & Benefit, 1997) is more difficult to assess. RUD 200 was not greatly similar to *Hylobates*—one model for the ancestral hominoid cranium (e.g., Pilbeam, 2002)—particularly in those features separating gibbons from great apes. Nor were its results like those of *Propliopithecus*, which resembles Benefit & McCrossin’s (1991, 1993) ancestral catarrhine morphotype.

On the other hand, the specimen that performed most similarly to RUD 200 was the cranium of *Afropithecus*. *Dryopithecus* had stronger, though not overwhelming, support grouping it with the hominids than did *Afropithecus* and so it is placed there with somewhat more confidence. Nevertheless, these cranial data argue strongly against its position as a pongine or hominine, but cannot entirely rule out the possibility that *Dryopithecus* is a stem hominoid.

All of the human fossils grouped strongly with *Homo* in the generic classification. Results were fairly consistent at node 4, placing each specimen with the hominines. Interestingly, however, WT 17000 showed a moderate affinity with *Pongo* in those features that discriminate between extant pongines and hominines. Though still grouped with the African apes, this affinity suggests that some aspects of the pongine cranial configuration may have evolved independently (but see Schwartz, 1984). These analyses were not able to discriminate between *Gorilla* and *Homo-Pan* with any degree of confidence. At node 6, specimens of *Australopithecus* and *Paranthropus* grouped unanimously with *Pan*; this suggests a stronger affinity with chimpanzee crania relative to modern humans and *could* be indicative of a more primitive morphology—providing that *Pan* is a reasonable model of the common ancestor (see Pilbeam, 2002; but see also, Martin, 1998). ER 1813 was statistically equidistant from *Pan* and *Homo*, while ER 3733 was placed in *Homo* with only moderate support. These results, while not unexpected, highlight the difficulty in classifying members of a highly autapomorphic clade.

CHAPTER 7: MORPHOMETRIC ANALYSIS OF SUPRAORBITAL MORPHOLOGY

This chapter discusses the morphometric and statistical analyses that were performed on the supraorbital landmarks and resampled supraorbital ridge curve data (semi-landmarks). Basic principal components and canonical variates analyses are detailed first, in order to examine variability across all specimens and among specified genera. Hierarchical relationships are then discussed in the context of a cluster analysis of Mahalanobis distances. The chapter concludes with a series of discriminant analyses used to demonstrate patterns of shape change that define the branches of a consensus phylogeny of extant anthropoids. Fossil specimens with preserved supraorbital morphologies are then tested at each node on this tree in order to determine their best placement.

LANDMARK CONFIGURATIONS

Landmarks used in this chapter are listed in Table 7-1 (see chapter 4 for landmarks definitions) along with their abbreviations. The supraorbital ridge curve was resampled to eleven, equally spaced semi-landmarks. This line is bounded on both ends by frontomale temporale. The nine semi-landmarks between them are referred to as L1-L9. Figure 7-1 shows the consensus configuration of all specimens in frontal (Figure 7-1a) and lateral (Figure 7-1b) views. Labels in this figure serve as a reference for all subsequent figures in this chapter that illustrate shape differences.

Table 7-1 Landmarks and semi-landmarks used in analyses of supraorbital morphology. See Chapter 4 for definitions and discussion. * denotes semi-landmarks

Landmark	Abbreviation
Midline:	
Glabella	GLA
Nasion	NAS
Bilateral:	
Frontomale temporale	FMT
Frontomale orbitale	FMO
Mid-orbit torus inferior	MTI
Mid-orbit torus superior	MTS
Ridge curve:	
Resampled points*	L1-L9

SAMPLE TAXA AND SIZE CORRECTION

All ten extant genera were included in the analyses in this chapter. Fossil taxa that preserve enough supraorbital morphology to warrant inclusion here are: *Afropithecus* (WK 16999), *Australopithecus* (Sts 5), *Dryopithecus* (RUD 77, RUD 200, CLI 18000), *Graecopithecus* (XIR 1), *Homo* (ER 1470, ER 1813, ER 3732, ER 3733, ER 3883), *Paranthropus* (ER 406, ER 732, ER 13750 WT 17000), *Propliopithecus* (DPC 2803, DPC 3161, CGM 42842), *Sivapithecus* (GSP 15000), and *Turkanapithecus* (WK 16950). This list includes specimens that preserve only half of the supraorbital morphology (e.g., GSP 15000), as missing data were reconstructed in data processing (see Chapter 4). Because these fossil configurations include all landmarks and semi-landmarks analyzed in this chapter, all were included in the initial principal components analysis

Unlike the previous analyses on the entire cranial landmark set, body size could not be shown to contribute to variation in supraorbital morphologies once taxonomic and sex differences were accounted for (see Chapter 5 for discussion). Therefore,

superimposed coordinate data—rather than residuals of coordinates regressed against centroid size—were used in statistical analyses.

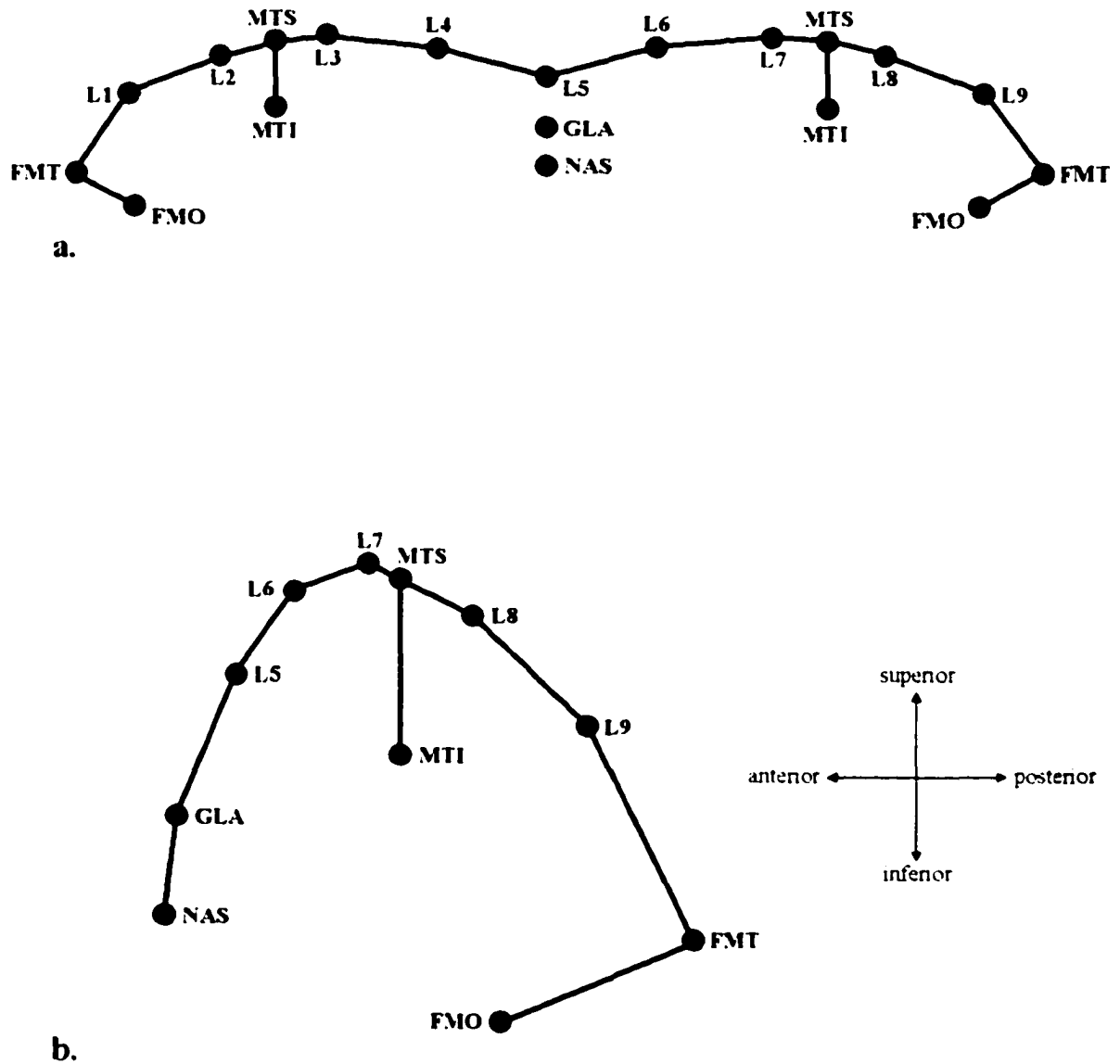


Figure 7-1 Consensus configuration of the supraorbital landmarks and semi-landmarks. (a) frontal view; (b) lateral view with orientation compass. Names corresponding to the landmark and semi-landmark abbreviations are given in Table 7-1. Subsequent shape diagrams all depict landmarks in the same views.

PRINCIPAL COMPONENTS ANALYSIS

A principal components analysis was performed on the covariance matrix of superimposed coordinate data from the supraorbital region. Analyses of variance (ANOVAs) were done on PC scores in order to test for statistical differences among extant genera for each axis; fossil specimens were not tested in this manner. Results of the PCA and ANOVAs are shown in Table 7-2 for the first 15 PCs; subsequent axes—comprising less than 1% each of the total group variability—were examined but are not listed here. ANOVA results indicate highly significant ($p < 0.0001$) differences among the mean PC scores for each axis except PC 10—it shows a significant difference ($p = 0.0185$). Pairwise t-tests with a Bonferroni adjustment were performed on the least-squares adjusted means for each genus (see Table 7-3) in order to examine differences between pairs of taxa. The first four principal component axes are discussed in detail below; variation on subsequent axes was examined and found to overlap to such a degree as to preclude any meaningful interpretation regarding taxonomic, phylogenetic, body size, or sex differences.

Principal component 1

The first principal component represents nearly 40% of the total variability among supraorbital morphologies. T-test results are displayed in Table 7-3 and a graph of specimen scores on PC 1 and PC 2 is shown in Figure 7-2. The greatest difference along this axis separates most of the catarrhines (*Cercopithecus*, *Gorilla*, *Homo*, *Pan*, *Papio*, and *Procolobus*) from a group of platyrrhines (*Ateles* and *Cebus*) and *Hylobates*; *Pongo* falls out largely between them, although overlapping more with the platyrrhine-hylobatid range. T-test results tend to confirm these groups: *Pongo* is significantly different from

all taxa excepting *Cebus*; *Ateles*, *Cebus*, and *Hylobates* are mutually distinct from all other taxa and not significantly different from each other. Among the other catarrhines, the African apes were not shown to be different from each other or from *Papio* and *Cercopithecus*; *Papio* was not distinct from *Cercopithecus* or *Procolobus*, but the means of these latter two were significantly different from each other.

Table 7-2 Summary of PCA and ANOVA results for the first fifteen principal component axes. PCA results give statistics for the latent roots of the sample variance (eigenvalues), the proportion of variance explained by each component, and the cumulative proportion of the variance summarized by each PC and those preceding it. One-way ANOVAs were performed on each component to test for significant differences among genera; F-values and probabilities are given for tests of the null-hypothesis that all genera share a common mean.

	PRINCIPAL COMPONENTS ANALYSIS			ANALYSIS OF VARIANCE	
	Eigenvalue	Proportion	Cumulative	F Value	Pr > F
PC 1	0.01016723	0.3951	0.3951	226.09	<.0001
PC 2	0.00408855	0.1589	0.5540	180.99	<.0001
PC 3	0.00214938	0.0835	0.6375	86.26	<.0001
PC 4	0.00164794	0.0640	0.7016	59.41	<.0001
PC 5	0.00159114	0.0618	0.7634	31.56	<.0001
PC 6	0.00115384	0.0448	0.8082	8.84	<.0001
PC 7	0.00060782	0.0236	0.8318	7.13	<.0001
PC 8	0.00055621	0.0216	0.8535	7.17	<.0001
PC 9	0.00045563	0.0177	0.8712	10.61	<.0001
PC 10	0.00037046	0.0144	0.8856	2.24	0.0185
PC 11	0.00029566	0.0115	0.8971	6.17	<.0001
PC 12	0.00027260	0.0106	0.9076	3.84	<.0001
PC 13	0.00024744	0.0096	0.9173	13.00	<.0001
PC 14	0.00022527	0.0088	0.9260	4.75	<.0001
PC 15	0.00020661	0.0080	0.9340	7.13	<.0001

Table 7-3 Results of pairwise t-tests between genera for PCs 1-4. Bonferroni adjusted p-values are given in the lower triangle. * indicates significance at $\alpha=0.05$

P C	1	Genus	Atel	Cebu	Cerc	Gori	Homo	Hylo	Pan	Papi	Pcol	Pong
		Atel			*	*	*		*	*	*	*
P C	1	Cebu	0.2939		*	*	*		*	*	*	
		Cerc	<.0001	<.0001				*			*	*
		Gori	<.0001	<.0001	1.0000			*			*	*
		Homo	<.0001	<.0001	0.6561	0.0504		*				*
		Hylo	1.0000	0.0880	<.0001	<.0001	<.0001		*	*	*	*
		Pan	<.0001	<.0001	1.0000	1.0000	0.0678	<.0001			*	*
		Papi	<.0001	<.0001	1.0000	1.0000	1.0000	<.0001	1.0000			*
		Pcol	<.0001	0.0002	0.0244	0.0015	1.0000	<.0001	0.0038	1.0000		*
		Pong	0.0003	1.0000	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	
		Genus	Atel	Cebu	Cerc	Gori	Homo	Hylo	Pan	Papi	Pcol	Pong
P C	2	Atel					*					*
		Cebu	1.0000				*					*
		Cerc	1.0000	1.0000		*						*
		Gori	1.0000	1.0000	<.0001		*	*	*			*
		Homo	<.0001	<.0001	0.4374	<.0001		*	*	*	*	*
		Hylo	0.1465	0.1415	1.0000	<.0001	0.0005		*			*
		Pan	1.0000	1.0000	0.7086	<.0001	<.0001	<.0001				*
		Papi	1.0000	1.0000	1.0000	0.4692	0.0001	0.4199	1.0000			*
		Pcol	1.0000	1.0000	1.0000	1.0000	<.0001	0.0673	1.0000	1.0000		*
		Pong	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	
P C	3	Atel			*	*			*	*		
		Cebu	1.0000		*	*			*	*	*	
		Cerc	<.0001	<.0001		*	*	*	*			*
		Gori	0.0462	0.0091	0.0032		*	*	*	*		*
		Homo	0.1471	0.5053	<.0001	<.0001			*	*	*	
		Hylo	0.7027	1.0000	<.0001	<.0001	1.0000		*	*	*	
		Pan	<.0001	0.0001	<.0001	<.0001	0.0166	<.0001		*	*	*
		Papi	<.0001	<.0001	1.0000	<.0001	<.0001	<.0001	<.0001		*	*
		Pcol	0.0545	0.0169	1.0000	1.0000	<.0001	<.0001	<.0001	0.0208		*
		Pong	1.0000	1.0000	<.0001	<.0001	0.0641	0.3880	<.0001	<.0001	<.0001	
P C	4	Atel		*	*	*		*	*		*	*
		Cebu	<.0001		*	*	*	*	*	*	*	*
		Cerc	<.0001	<.0001		*	*					
		Gori	<.0001	<.0001	1.0000		*	*				
		Homo	0.1455	<.0001	<.0001	<.0001		*	*	*	*	*
		Hylo	<.0001	<.0001	1.0000	0.0006	<.0001		*	*		*
		Pan	0.0009	<.0001	0.5579	1.0000	<.0001	<.0001				
		Papi	0.6239	<.0001	0.5835	1.0000	<.0001	0.0389	1.0000			
		Pcol	0.0027	<.0001	1.0000	1.0000	<.0001	1.0000	1.0000	1.0000		
		Pong	0.0164	<.0001	0.1333	0.3044	<.0001	<.0001	1.0000	1.0000	1.0000	

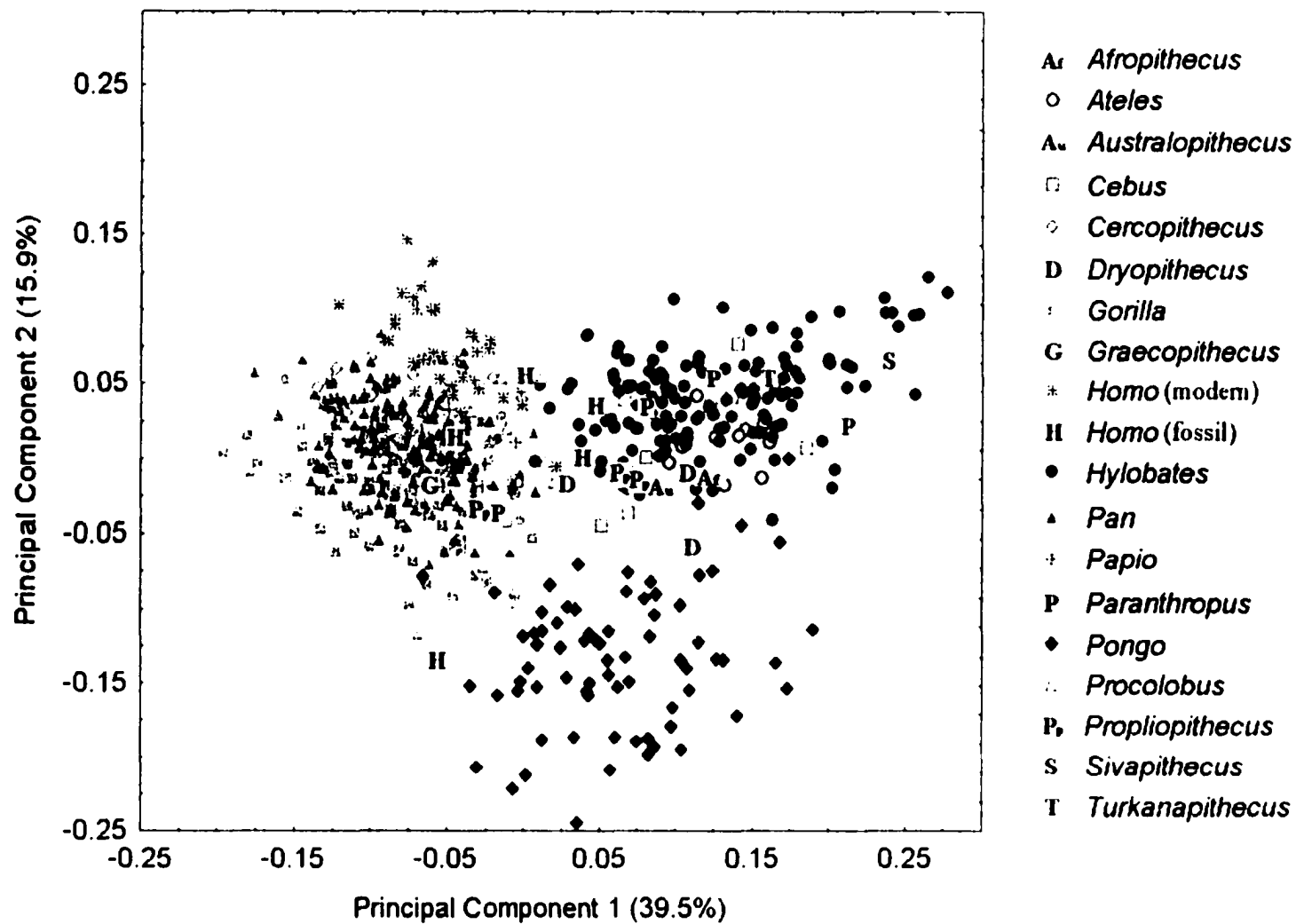


Figure 7-2 Plot of principal component scores for PC 1 and PC 2. PC 1 separates *Ateles*, *Cebus*, and *Hylobates* from the cercopithecoids and hominines. *Pongo* ranges between these groups, but is closer to the platyrrhine-*Hylobates* cluster. PC 2 separates *Pongo* from all other taxa.

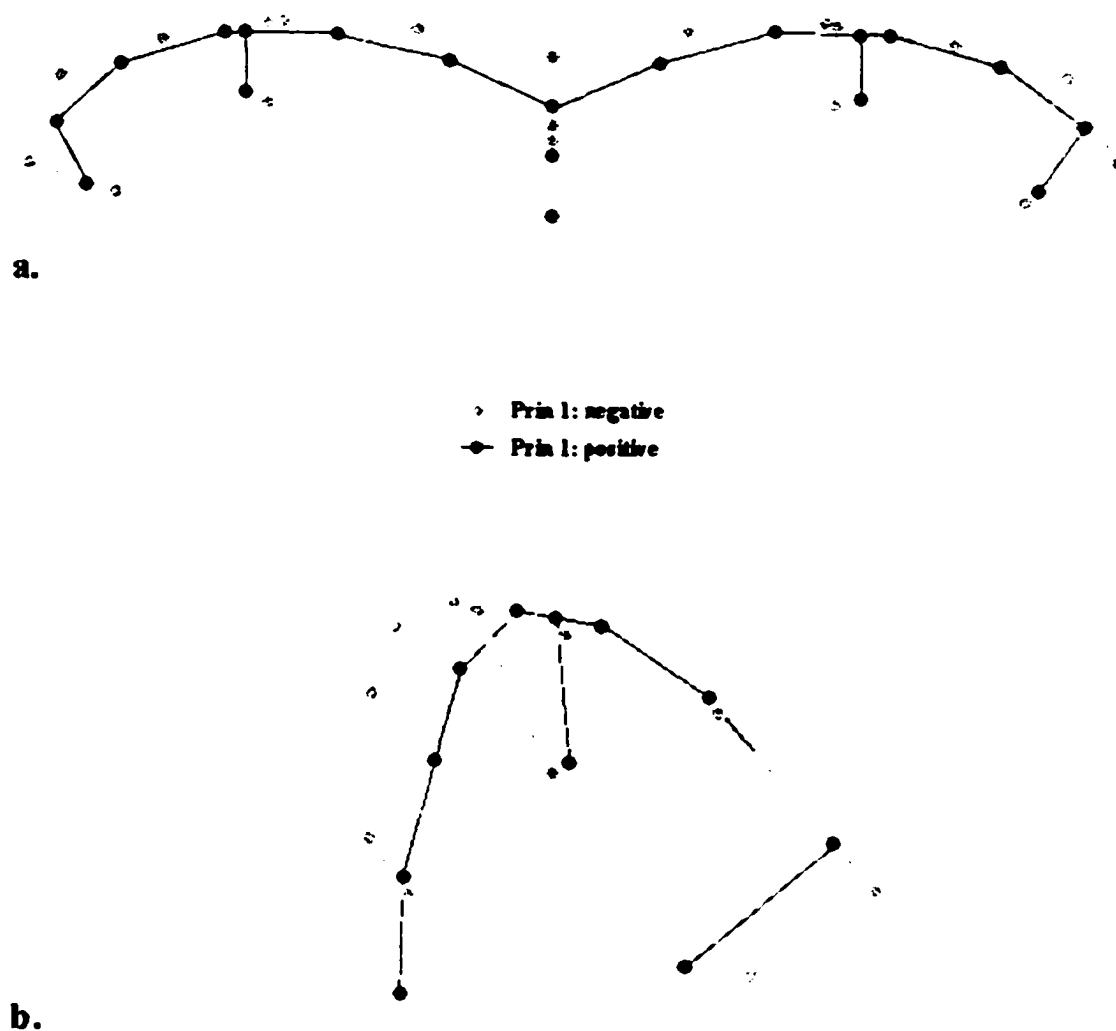


Figure 7-3 Shape change along PC 1. Black lines represent the positive loadings, gray lines show the negative loadings. (a) frontal view; (b) lateral view. See Figure 7-1 for landmark references.

The fossil specimens are widely scattered along this axis. *Graecopithecus* (XIR 1), with the most negative score on PC 1, is placed among the hominines and cercopithecoids. Specimens of *Homo* generally cluster here as well. ER 1813 and ER 3732 have scores similar to XIR 1; ER 3883 is more central on this axis, while ER 1470 and ER 3733 placed just within the hylobatid-platyrrhine range. *Paranthropus* specimens

are broadly distributed along PC 1. ER 732 has the only negative PC score, placing it beyond the hylobatid-platyrrhine range; ER 406 and ER 13750, on the other hand, group near the densest concentration of hylobatids; WT 17000 has the largest score for this genus, placing it beyond the ranges of all the extant taxa except *Hylobates*. One specimen of *Propliopithecus* (DPC 2803) scored among the hominines, while the other two (DPC 3161, CGM 42842) fell among *Hylobates*, *Pongo*, and the platyrrhines. *Dryopithecus* specimens fall beyond the African ape-cercopithecoid ranges, grouping with the hylobatids and platyrrhines on PC 1. This is only just true for RUD 200, while RUD 77 and CLI 18000 are near the centroid of the hylobatid-platyrrhine cluster. *Afropithecus*, *Australopithecus*, and *Turkanapithecus* also fall in the thick of this group, though the hominin is just beyond the range of *Ateles*. GSP 15000 has the greatest PC score among fossils, placing near the positive edge of the hylobatid range, but beyond the ranges of all other taxa. It should be noted that scores for *Pongo*, falling between the two extremes and having a wide distribution, encompassing all of the fossil specimens except WT 17000 and GSP 15000.

Figure 7-3 illustrates shape change along the first principal component axis. It is clear that PC 1 comprises substantial variability at most of the data points, with **MTI** the one exception. Towards the negative pole of PC 1, supraorbital morphology is wider and more “squared” in the lateral extremes, and the midline region depresses inferiorly only modestly. There is, however, a substantial anterior displacement of the midline morphology, tapering off lateral to **MTS**. This expansion is largely confined to the morphology above the orbit, however, as **MTI** is barely affected and **NAS** not at all. The latter, however, is displaced sharply superiorly. While the midline is placed anteriorly,

the most lateral aspect of the negative morphology is actually posterior to its positive counterpart. At the positive pole, the supraorbital region is more rounded, starting inferiorly in the midline and curving gradually down in the lateral aspect. The morphology is flatter across the front, lacking a prominent glabellar eminence, with NAS situated substantially inferiorly.

Principal component 2

The second principal component comprises almost 16% of the total variation. As shown by the t-test results (Table 7-3) and a graph of PC scores (see Figure 7-2), this axis largely separates *Pongo* from the other taxa; while *Homo* is also separated from all taxa except *Cercopithecus*, its range of values is not as distinct as that of the orangutan. Mean scores for all of the hominoids are significantly different from each other on the second principal component. There is substantial overlap, however, among the ranges of *Gorilla*, *Hylobates*, and *Pan*.

Nearly all of the fossil specimens group with the main cluster of extant taxa. The one exception to this is ER 1813, which is placed exclusively in the range of *Pongo*; all of the other specimens of fossil *Homo* fall beyond the orangutan scores, overlapping with all other taxon ranges (including *Homo*). CLI 18000 falls in the overlap between *Gorilla*-*Pan* and *Pongo*. The other two specimens of *Dryopithecus*, however, are more comfortably within the main cluster. Specimens of *Afropithecus*, *Australopithecus*, *Graecopithecus*, and one member of *Paranthropus* (ER 732) all technically fall within the range of *Pongo* (because of a single outlier), but are much closer to the centroids of the other taxon clusters. Other *Paranthropus* specimens, as well as *Sivapithecus* and *Turkanapithecus*, are completely beyond the orangutan range. Unlike the first principal

component, *Propliopithecus* specimens scored similarly on this axis, falling near the African ape centroid, but not within the range of *Pongo*. It is interesting to note that a major PC axis separating *Pongo* from the other taxa also separates *Sivapithecus* from *Pongo*. This runs contrary to the oft-published similarities between the supraorbital morphologies of the two (e.g., Pilbeam, 1982; Ward & Brown, 1986; Brown & Ward, 1988).

The shape change represented along the second PC axis is shown in Figure 7-4. Perhaps the most notable difference is in the lateral supraorbital morphology. At the negative pole, **FMT** is substantially displaced supero-laterally, resulting in a substantial vertical displacement between it and **FMO**. This may seem counterintuitive, as *Pongo* is usually thought to have narrow, rounded supraorbital costae (e.g., Ward & Brown, 1986; Schwartz, 1997). Unlike the other taxa, however, the fronto-malar suture in *Pongo* travels vertically across the orbital pillar. Thus, orangutan supraorbital costae have a significant malar component which rounds off the lateral extreme. The unique, rounded brow of *Pongo*, then, is not evident here as the supraorbital line is delimited by **FMT**. This is replaced, however, by the unique sutural morphology of *Pongo* as shown in Figure 7-4 by negative deformation of the consensus. It is curious to note that the negative pole represents a thicker brow between **MTI** and **MTS**. Both this feature and the lateral flattening may explain the relatively negative placement of *Gorilla* on this axis. In the midline, the negative pole displays an inferior depression of the supraorbital line and of glabella. This is a rather abrupt change, as the negative morphology lies superior to the positive in the glabellar portion of the supraorbital line (**L4** and **L6**). From lateral view, it is clear that the negative morphology is largely flat across the front: midline landmarks

are well posterior to their positive counterparts, while lateral ones are anterior. It is also clear from this view that the sutures between **FMO** and **FMT** are largely equal in length at both extremes. The major difference, then, is in the vertical component.

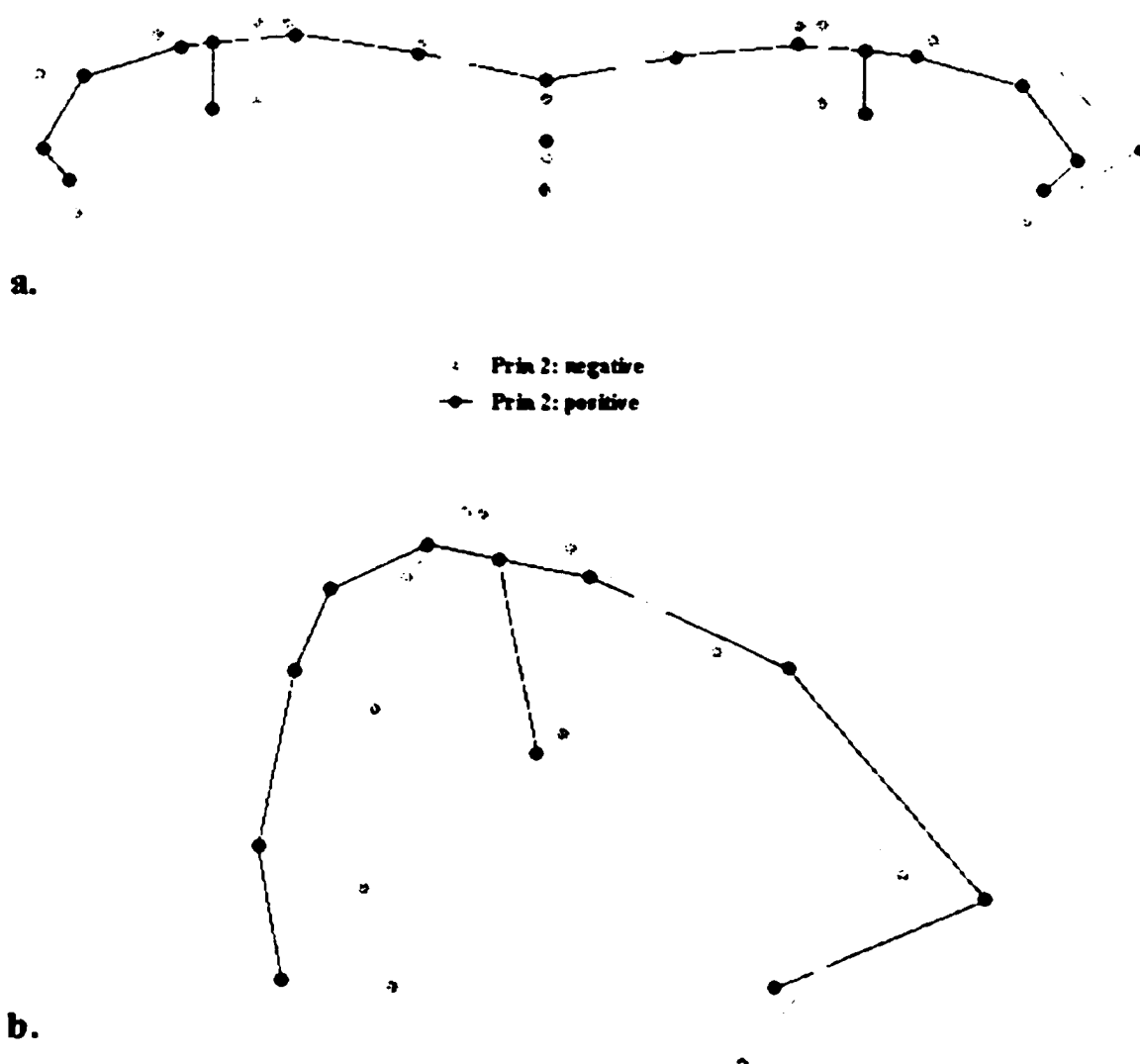


Figure 7-4 Shape change along PC 2. Black lines represent the positive loadings, gray lines show the negative loadings. (a) frontal view; (b) lateral view. See Figure 7-1 for landmark references.

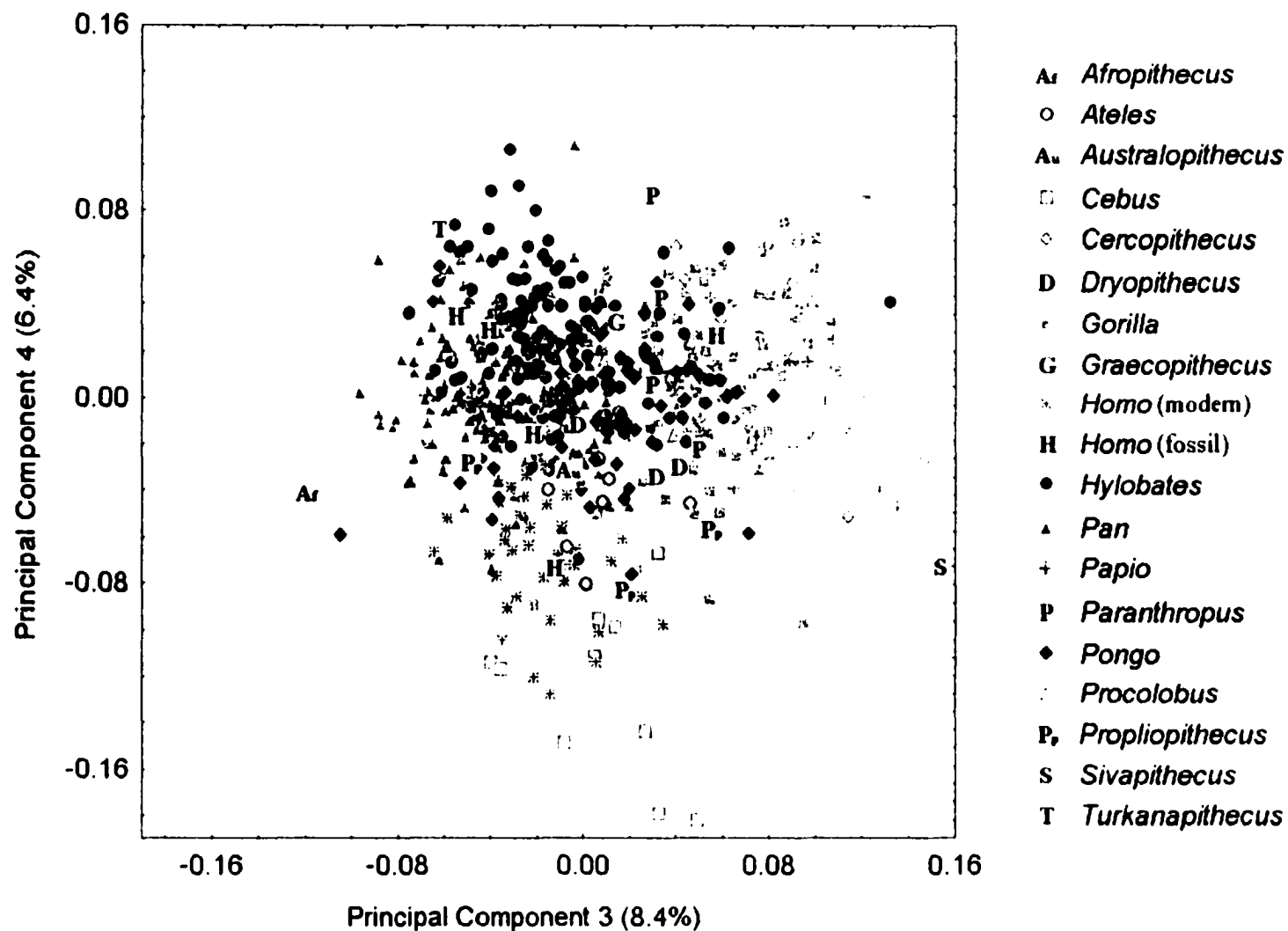


Figure 7-5 Plot of principal component scores for PC 3 and PC 4. PC 3 largely separates the cercopithecoids and *Gorilla* from the other taxa. PC 4 sorts platyrrhine and modern human specimens from the rest of the sample.

Principal component 3

Principal component 3 summarizes only 8% of the variability among supraorbital morphologies. The t-test results listed in Table 7-3 show a complex pattern of differences. A plot of PC scores, given in Figure 7-5, more clearly shows a demarcation between a cercopithecoid-*Gorilla* group and the other taxa. *Gorilla*, however, occupies a somewhat intermediate position, being significantly different from all taxa except *Procolobus*. The other hominoids cluster more negatively on this axis.

An alternate way to interpret this axis is that it represents the difference in shape between *Afropithecus* and *Sivapithecus*. *Afropithecus* has the most negative score on PC 3 of all specimens. *Turkanapithecus* has the second most negative score, placing just within the ranges of all of the hominoids. Four of the five fossil *Homo* specimens and the one *Australopithecus* group on the negative end. The fifth fossil *Homo* (ER 1813), while technically still within the ranges of *Hylobates* and *Pongo*, is much closer to the mean values of the cercopithecoid-*Gorilla* group. Once again DPC 2803 falls away from the other *Propliopithecus* specimens, placing near the lower range of the hominoid specimens; CGM 42842 sits between the main clusters, while DPC 3161 is near the *Gorilla*-cercopithecoid centroid. In *Dryopithecus*, CLI 18000 is the only specimen with a negative score on PC 3; RUD 77 and RUD 200 fall in the overlap among *Gorilla*, *Hylobates*, and *Pongo*. *Graecopithecus* is situated near the mean value for all PC 3 scores. It is closest to the main cluster of taxa, falling only within the range of *Gorilla* among the cercopithecoid-*Gorilla* cluster. The four specimens of *Paranthropus* all fall in roughly the same region: closest to the cercopithecoid-*Gorilla* group, but still within the

range of *Hylobates* and *Pongo*. At the positive extreme, *Sivapithecus* falls beyond the range of all other taxa.

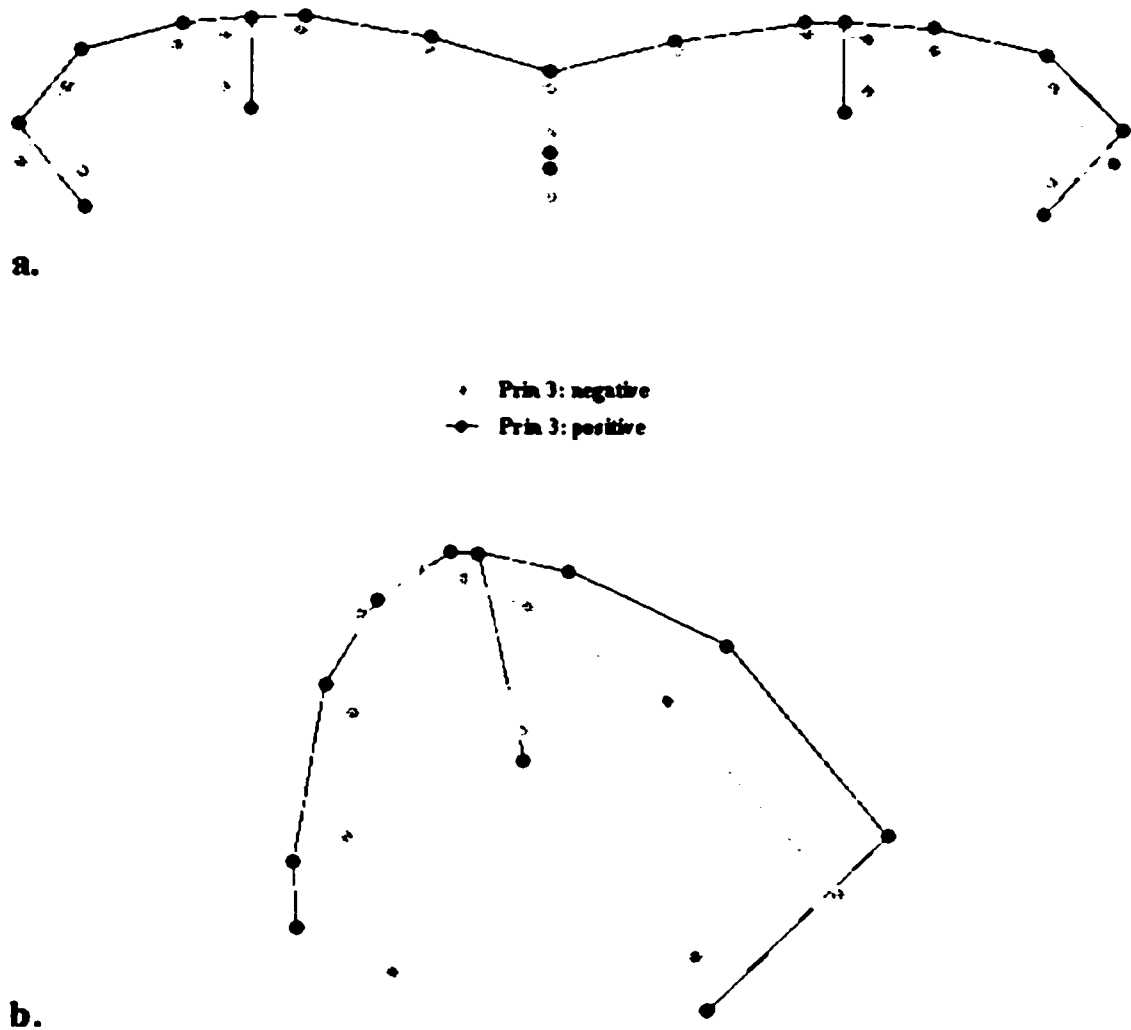


Figure 7-6 Shape change along PC 3. Black lines represent the positive loadings, gray lines show the negative loadings. (a) frontal view; (b) lateral view. See Figure 7-1 for landmark references.

Shape differences along PC 3 are illustrated in Figure 7-6. Morphology at the negative end is largely compressed vertically: the supraorbital line is everywhere inferior and the thickness substantially reduced (**MTI—MTS; GLA—L5**). Laterally, the suture across the orbital pillar is largely horizontal, running antero-medial and only slightly inferior from **FMT** to **FMO**. In the midline, **GLA** and **NAS** are closely approximated at the positive pole, but more spaced at the negative. From the lateral view, there is a clear angling across the front in the positive morphology. This is largely effected in the lateral landmarks, however, as **L5** and **L6 (L4)** are similarly placed in negative and positive morphologies. Inferior to **L5**, then, the positive morphology extends anteriorly relative to the negative.

Principal component 4

The fourth principal component represents just over 6% of the total variability in the sample. The main difference along this axis (see Figure 7-6) is between a platyrrhine-*Homo* group and the other taxa. Differences between genus pairs are listed with the t-test results in Table 7-3. Most notable among these, the mean PC score for *Hylobates* is significantly different from all of the taxa except *Cercopithecus*.

Among fossil specimens, CGM 42842 has the lowest score on PC 4 falling within the lower ranges of *Homo* and *Ateles* and the upper range of *Cebus*; the other two *Propliopithecus* specimens scored near the lower range of the non-human catarrhine taxa. ER 3883 placed near the mean value for modern *Homo*, while ER 1470 fell just beyond the modern human range among the main cluster; the other fossil *Homo* specimens are well within the main cluster, situated toward the higher end of the range. *Sivapithecus* is placed among the lower scores, grouping most closely with *Cebus* and *Homo*.

Afropithecus, *Australopithecus*, and *Dryopithecus* all sit within the overlap between the two groups, although CLI 18000 is just within the largest *Ateles* scores. *Paranthropus* specimens vary widely along this axis, from ER 406 just overlapping the range of *Ateles*, to WT 17000 among the largest *Gorilla*, *Hylobates*, and *Pan* scores. Both *Graecopithecus* and *Turkanapithecus* are situated within the main cluster, although the latter is placed toward the high end of the range.

The differences in supraorbital morphology along PC 4 are shown in Figure 7-7. At the negative pole, midline landmarks are substantially displaced superiorly. As the supraorbital line extends beyond **MTS**, the morphology tapers inferiorly, with a sharp inferior drop between **FMT** and **FMO**. This gives the negative morphology a rounded appearance from frontal view, while the positive morphology is more squared. In lateral view, both morphologies are approximate in their angling across the face. The negative pole, however, is displaced anteriorly, superior to **FMO** and **NAS**. This results, among other things, in a prominent glabella.

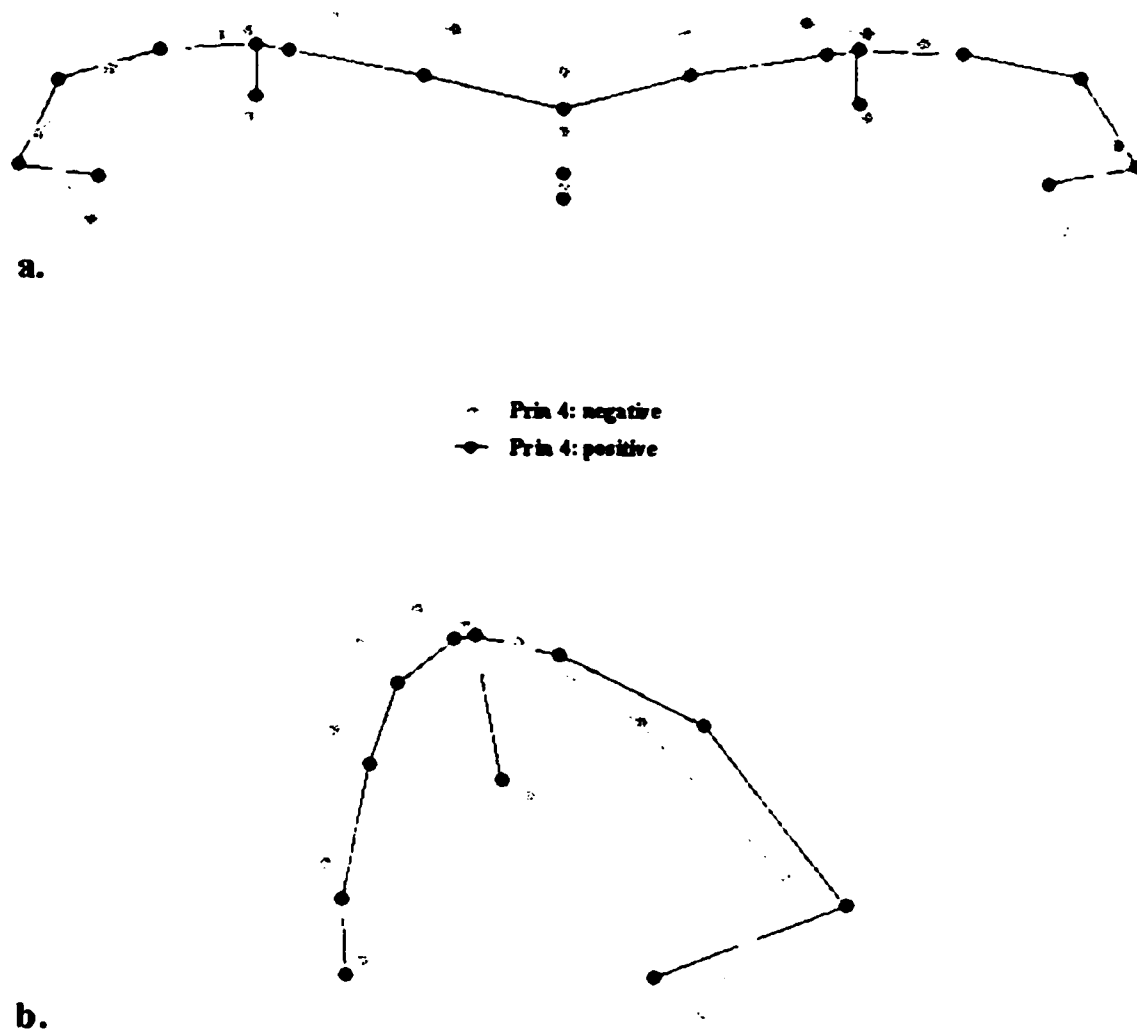


Figure 7-7 Shape change along PC 4. Black lines represent the positive loadings, gray lines show the negative loadings. (a) frontal view; (b) lateral view. See Figure 7-1 for landmark references.

CANONICAL VARIATES ANALYSIS

To explore shape differences among genera, canonical variates analysis (CVA) was performed on the non-zero principal component scores (see Chapter 5). ANOVAs were performed on scores for each CV to test for statistical differences among genus

means. CVA and ANOVA results are listed in Table 7-4. Cross-validation results (see Table 7-5) indicate that the CVA was very successful at correctly assigning extant specimens. Re-assignment was better than 95% for all genera except *Ateles*, *Cebus*, and *Cercopithecus*. Interestingly, the two misclassified platyrrhines remained grouped within the platyrrhines, and misidentified *Cercopithecus* specimens were put into the other cercopithecoid genera. Among hominoids, misclassified *Gorilla* specimens were put into *Pan*, and vice versa; *Homo* specimens were grouped with *Pan*. Specimens of *Pongo* and *Hylobates* that were misidentified fell in with *Ateles*. *Papio* and *Procolobus* achieved 100% correct classification.

All canonical axes were examined for differences, but only the first six are discussed in detail below. ANOVA results demonstrated highly significant differences ($p < 0.0001$) among genera on each CV; pairwise differences were determined using t-tests, with results shown in Table 7-6.

Table 7-4 Summary of CVA and ANOVA results for all nine canonical variate axes. CVA results give statistics for the latent roots of the among-groups variance (eigenvalues), the proportion of variance explained by each variate, and the cumulative proportion of the variance summarized by that CV and those preceding it. One-way ANOVAs were performed on each axis to test for significant differences among genera; F-values and probabilities are given for tests of the null-hypothesis that all genera share a common mean.

	CANONICAL VARIATES ANALYSIS			ANALYSIS OF VARIANCE	
	Eigenvalue	Proportion	Cumulative	F Value	Pr > F
CV 1	11.3128	0.4033	0.4033	692.99	<0.0001
CV 2	7.2447	0.2583	0.6616	486.96	<0.0001
CV 3	3.7656	0.1343	0.7959	238.85	<0.0001
CV 4	2.0133	0.0718	0.8677	127.66	<0.0001
CV 5	1.7258	0.0615	0.9292	107.82	<0.0001
CV 6	1.0345	0.0369	0.9661	66.89	<0.0001
CV 7	0.3944	0.0141	0.9802	24.86	<0.0001
CV 8	0.3048	0.0109	0.9910	19.10	<0.0001
CV 9	0.2515	0.0090	1.0000	16.29	<0.0001

Table 7-5 Cross-validation results from CVA of extant specimens. Each cell gives the number (n) and percent (%) of individuals from the genus on the left assigned to the genus across the top.

Genus		Atel	Cebu	Cerc	Gori	Homo	Hylo	Pan	Papi	Pcol	Pong
Atel	n	9	1								
	%	90.00	10.00								
Cebu	n	1	9								
	%	10.00	90.00								
Cerc	n			8					1	1	
	%			80.00					10.00	10.00	
Gori	n				109			5			
	%				95.61			4.39			
Homo	n					36		2			
	%					94.74		5.26			
Hylo	n	1					141				
	%	0.70					99.30				
Pan	n				2			164			
	%				1.20			98.80			
Papi	n								10		
	%								100		
Pcol	n									10	
	%									100	
Pong	n	1									71
	%	1.39									98.61

Table 7-6 Results of pairwise t-tests between genera for CVs 1-6. Bonferroni adjusted p-values are given in the lower triangle. * indicates significance at $\alpha=0.05$.

1	C V	Genus	Atel	Cebu	Cerc	Gori	Homo	Hylo	Pan	Papi	Pcol	Pong
		Atel		*	*	*	*		*	*	*	*
		Cebu	<0.0001			*		*	*			*
		Cerc	<0.0001	1.0000		*		*	*			*
		Gori	<0.0001	<0.0001	<0.0001		*	*	*	*	*	*
		Homo	<0.0001	1.0000	1.0000	<0.0001		*	*			*
		Hylo	1.0000	<0.0001	<0.0001	<0.0001	<0.0001		*	*	*	*
		Pan	<0.0001	<0.0001	0.0151	<0.0001	<0.0001	<0.0001			*	*
		Papi	<0.0001	0.0743	1.0000	<0.0001	1.0000	<0.0001	1.0000			*
		Pcol	<0.0001	1.0000	1.0000	<0.0001	1.0000	<0.0001	0.0002	0.1057		*
		Pong	0.0002	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	
2	C V	Genus	Atel	Cebu	Cerc	Gori	Homo	Hylo	Pan	Papi	Pcol	Pong
		Atel			*	*	*	*		*	*	*
		Cebu	1.0000		*	*	*	*		*	*	*
		Cerc	<0.0001	<0.0001			*	*	*			*
		Gori	<0.0001	<0.0001	1.0000		*	*	*		*	*
		Homo	<0.0001	<0.0001	<0.0001	<0.0001		*	*	*	*	*
		Hylo	0.0049	0.0145	<0.0001	<0.0001	<0.0001		*	*	*	*
		Pan	1.0000	1.0000	<0.0001	<0.0001	<0.0001	<0.0001		*	*	*
		Papi	<0.0001	<0.0001	1.0000	1.0000	<0.0001	<0.0001	<0.0001			*
		Pcol	0.0019	0.0008	0.2168	0.0021	<0.0001	<0.0001	<0.0001	0.3182		*
		Pong	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	
3	C V	Genus	Atel	Cebu	Cerc	Gori	Homo	Hylo	Pan	Papi	Pcol	Pong
		Atel		*		*	*	*			*	
		Cebu	0.0133		*	*	*	*	*		*	
		Cerc	1.0000	0.0025		*	*	*			*	
		Gori	<0.0001	<0.0001	<0.0001		*		*	*		*
		Homo	<0.0001	<0.0001	<0.0001	<0.0001		*	*	*	*	*
		Hylo	<0.0001	<0.0001	<0.0001	1.0000	<0.0001		*	*		*
		Pan	1.0000	<0.0001	1.0000	<0.0001	<0.0001	<0.0001			*	*
		Papi	1.0000	0.0535	1.0000	<0.0001	<0.0001	<0.0001	1.0000		*	
		Pcol	0.0003	<0.0001	0.0020	0.9171	<0.0001	1.0000	<0.0001	<0.0001		*
		Pong	0.3242	1.0000	0.0548	<0.0001	<0.0001	<0.0001	<0.0001	1.0000	<0.0001	

Table 7-6 (cont.)

	Genus	Atel	Cebu	Cerc	Gori	Homo	Hylo	Pan	Papi	Pcol	Pong
C V 4	Atel			*		*		*	*	*	*
	Cebu	1.0000		*		*		*	*		*
	Cerc	<0.0001	<0.0001		*	*	*	*		*	*
	Gori	1.0000	1.0000	<0.0001		*	*	*	*	*	*
	Homo	<0.0001	0.0043	<0.0001	<0.0001		*	*			*
	Hylo	1.0000	0.5902	<0.0001	0.0344	<0.0001		*	*	*	*
	Pan	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001		*	*	*
	Papi	<0.0001	0.0014	0.0857	<0.0001	1.0000	<0.0001	<0.0001			*
	Pcol	<0.0001	0.2453	0.0003	<0.0001	1.0000	<0.0001	<0.0001	1.0000		*
	Pong	1.0000	0.0013	<0.0001	<0.0001	<0.0001	0.0022	<0.0001	<0.0001	<0.0001	
C V 5	Genus	Atel	Cebu	Cerc	Gori	Homo	Hylo	Pan	Papi	Pcol	Pong
	Atel			*				*	*	*	
	Cebu	0.2720		*			*	*	*	*	*
	Cerc	<0.0001	<0.0001		*	*	*	*			*
	Gori	1.0000	0.2092	<0.0001			*	*	*	*	*
	Homo	1.0000	1.0000	<0.0001	0.2648		*	*	*	*	*
	Hylo	0.9876	<0.0001	<0.0001	<0.0001	<0.0001		*	*	*	*
	Pan	0.0010	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001		*	*	*
	Papi	<0.0001	<0.0001	1.0000	<0.0001	<0.0001	<0.0001	<0.0001		*	*
	Pcol	<0.0001	<0.0001	0.0701	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001		*
	Pong	1.0000	0.0001	<0.0001	0.0008	<0.0001	0.3960	<0.0001	<0.0001	<0.0001	
C V 6	Genus	Atel	Cebu	Cerc	Gori	Homo	Hylo	Pan	Papi	Pcol	Pong
	Atel		*	*	*	*	*	*	*	*	*
	Cebu	<0.0001		*	*	*	*	*	*	*	*
	Cerc	0.0011	<0.0001		*	*	*	*			*
	Gori	<0.0001	<0.0001	0.0033		*					
	Homo	<0.0001	<0.0001	<0.0001	<0.0001		*	*	*	*	*
	Hylo	<0.0001	<0.0001	0.0046	1.0000	<0.0001					
	Pan	<0.0001	<0.0001	0.0139	1.0000	<0.0001	1.0000				
	Papi	<0.0001	<0.0001	0.2800	1.0000	0.0495	1.0000	1.0000			
	Pcol	<0.0001	<0.0001	0.7766	1.0000	0.0095	1.0000	1.0000	1.0000		
	Pong	<0.0001	<0.0001	0.0017	1.0000	<0.0001	1.0000	1.0000	1.0000	1.0000	

Canonical variate 1

The first canonical axis comprises 40% of the variation in supraorbital morphology among groups. CV scores are plotted in Figure 7-8. The majority of pairwise comparisons between taxon means were significantly different (see Table 7-6); the greatest difference, however, separates *Ateles*, *Hylobates*, and *Pongo* from the other taxa. Among these three, means of *Hylobates* and *Ateles* were not different from each other, but both differed from *Pongo*. *Gorilla*, *Homo*, and *Pan* were all significantly different from each other, but with substantial overlap, especially between the latter two. Cercopithecoid genera were not different from each other or from *Homo*. Unlike the other taxa, *Cebus* did not cluster tightly; its widely distributed CV scores overlap the ranges of every other genus. This dispersal indicates that the pattern of variation among *Cebus* supraorbital morphologies is different from the variation within other genera.

Figure 7-9 illustrates shape variation along CV 1 between a positively loading *Ateles-Hylobates-Pongo* group and the more negative scores of the African apes and cercopithecoids. Morphology at the negative pole is nearly flat across the supraorbital line with little interruption at the midline, but a sharp inferior drop between **L1 (L9)** and **FMT**. At the positive end, the supraorbital line is much more rounded, inferiorly displaced in the midline, rising up toward **MTS** and then rounding inferiorly towards **FMT**. The negative morphology is also characterized by a thicker (supero-inferiorly) brow and superiorly displaced **NAS** and **GLA**. This displacement is especially true of **NAS**, which closely approximates **GLA**. From the lateral view, the negative morphology projects anteriorly at the midline and slightly posteriorly at **FMT**; this results in a greater angling across the front of the face.

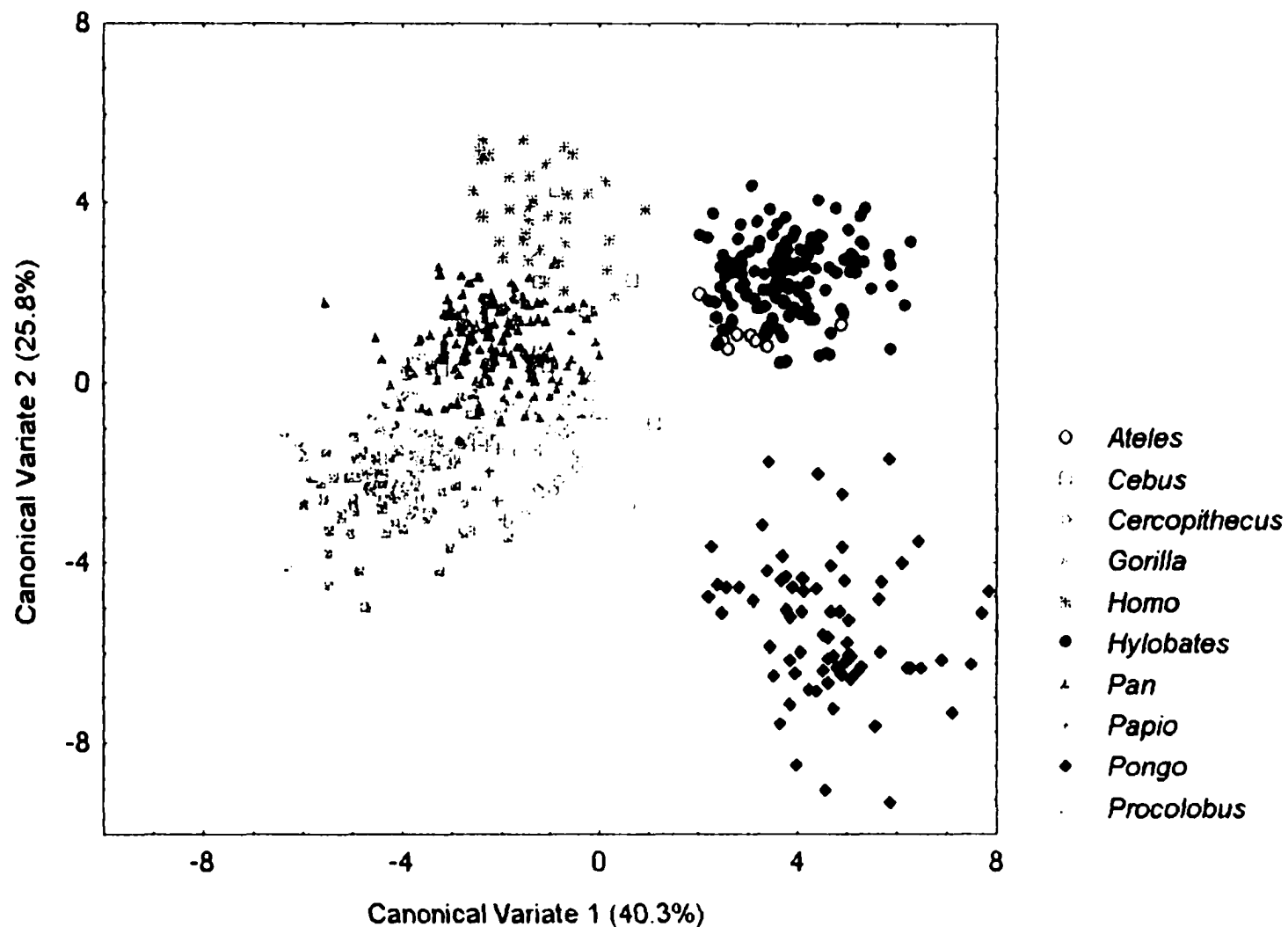
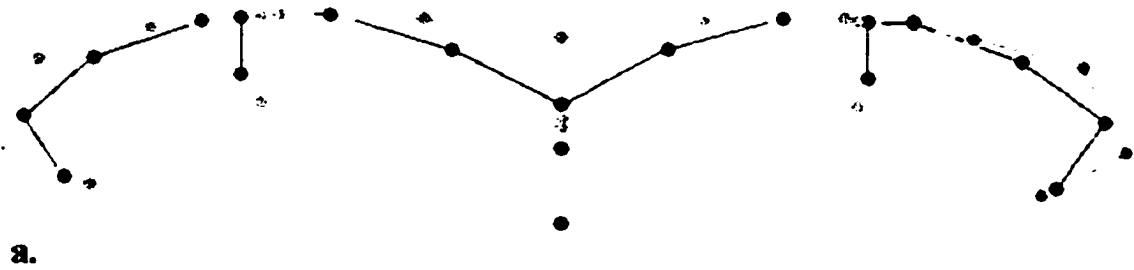
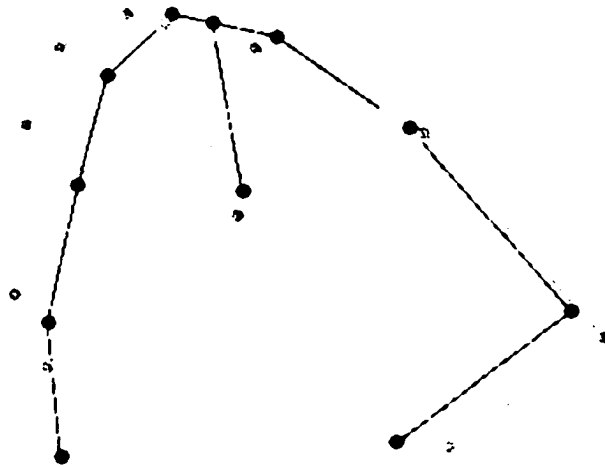


Figure 7-8 Plot of canonical variate scores for CV 1 and CV 2. CV 1 separates *Pongo*, *Hylobates*, and *Ateles* from the cercopithecoids and hominines; *Cebus* spans the gap between these groups, but does not cluster tightly as a genus. CV 2 distinguishes *Pongo* from *Hylobates*, *Ateles*, and *Homo*; *Gorilla*, *Pan*, and the cercopithecoids form a third intermediate group. *Cebus* again does not cluster as a genus on this axis.



a.

+ Can 1: negative
 — Can 1: positive



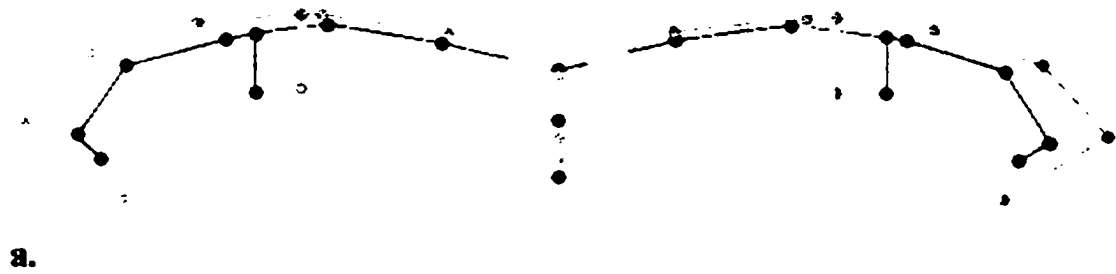
b.

Figure 7-9 Shape change along CV 1. Black lines represent the positive loadings, gray lines show the negative loadings. (a) frontal view; (b) lateral view. See Figure 7-1 for landmark references.

Canonical variate 2

CV 2 represents nearly 26% of the total among-groups variation; these CV scores are plotted in Figure 7-8. As depicted in the graph, the second canonical variate separates *Pongo* at the negative end from *Homo* and *Hylobates* at the positive; means of all three genera are significantly different from every other taxon. Between these extremes are *Gorilla*, *Pan*, the cercopithecoid genera and *Ateles*. Again, *Cebus* is widely distributed across the axis, though mainly in the positive half.

Shape change along CV 2 is illustrated in Figure 7-10. Both positive and negative extremes represent a somewhat rounded supraorbital morphology. The negative, however, is much broader, extending substantially lateral to the positive morphology. It is interesting to note that the mid-torus landmarks (**MTI** and **MTS**) are closer to the midline in the negative morphology, yet the brow extends further laterally. This is indicative of a narrow interorbital breadth in *Pongo*. Other features of the negative morphology include a greater distance between **MTI** and **MTS**, between **FMO** and **FMT** with a substantial vertical component, and the approximation of **NAS** and **GLA**. From lateral perspective, the negative morphology is slightly reduced in the antero-posterior dimension, making it flatter across the front.



→ Can 2: negative
 —●— Can 2: positive

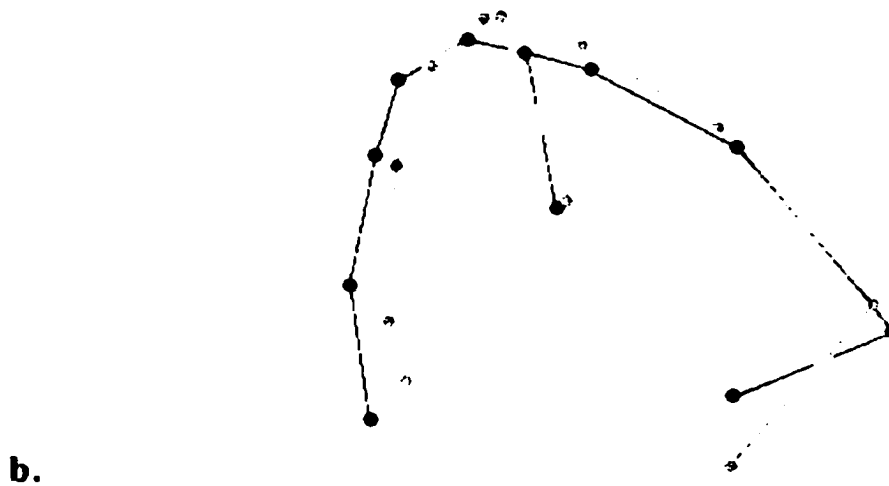


Figure 7-10 Shape change along CV 2. Black lines represent the positive loadings, gray lines show the negative loadings. (a) frontal view; (b) lateral view. See Figure 7-1 for landmark references.

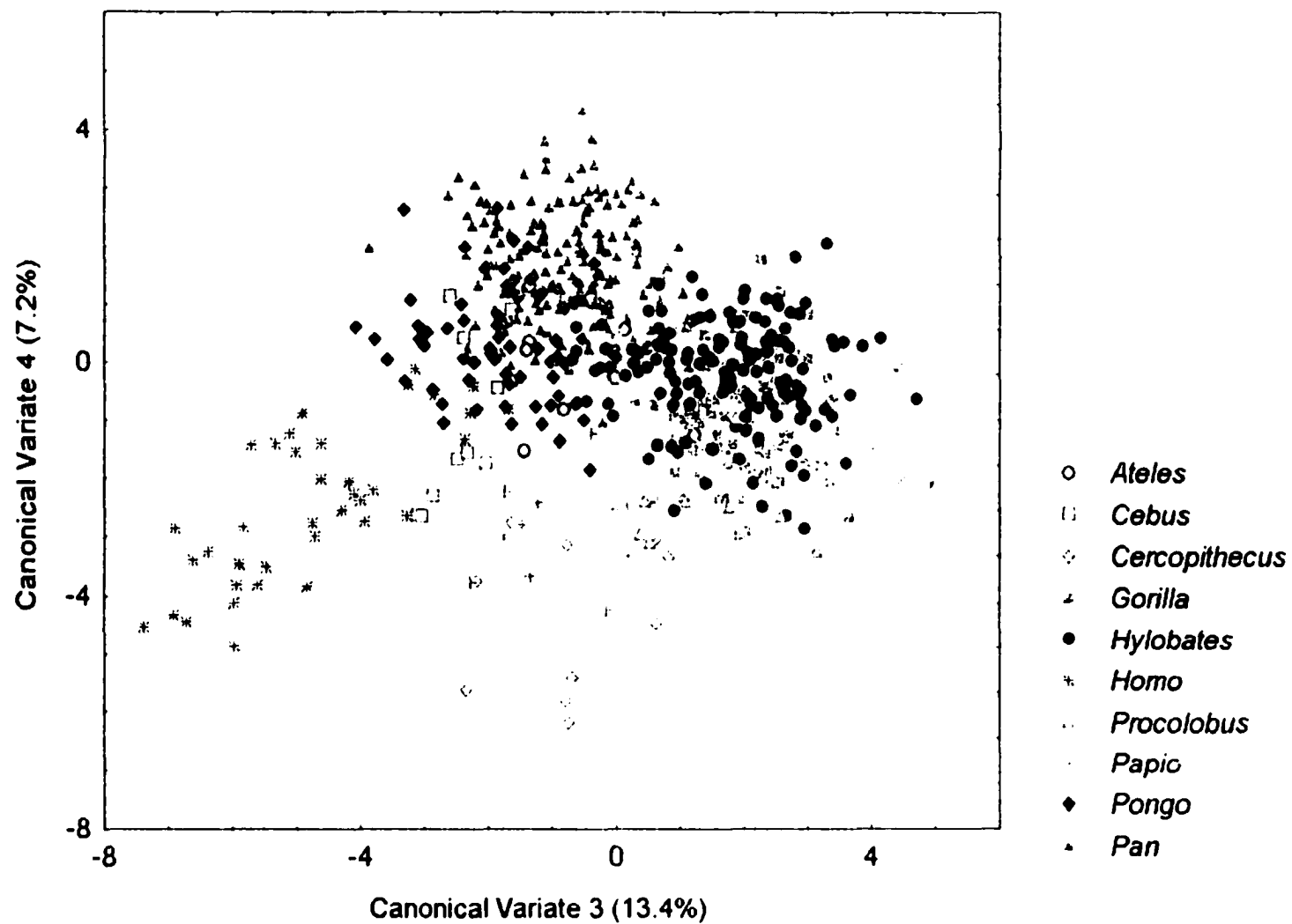


Figure 7-11 Plot of canonical variate scores for CV 3 and CV 4. CV 3 discriminates between *Homo* and the other African apes, with the remaining genera falling in the middle. CV 4 distinguishes cercopithecoids and *Homo* from the other taxa.

Canonical variate 3

Canonical variate 3 summarizes about 13% of the among-groups variability. Figure 7-11 plots the CV scores for each specimen. There are three main groups that fall out along this axis: *Homo* at the negative end, *Gorilla-Hylobates-Procolobus* at the positive end, and the other six taxa in between. The mean value of CV scores for *Homo* is significantly different from all other genera. Similarly, *Gorilla*, *Pan*, and *Procolobus* are each significantly different from the other taxa, but not from each other.

Figure 7-12 shows the differences in shape between the negative and positive poles of CV 3. The negative morphology has a greater vertical component than the positive. This is particularly true in the medial region; both negative and positive **NAS** are similarly placed, but the negative **GLA** and **L5** are superior to their positive counterparts. Lateral to **L5**, the negative supraorbital line arches superior to the positive line—coming back to the same level near **L2 (L8)**. From the lateral perspective, the negative midline morphology is sharply anterior above **GLA**; **NAS**, however, is set posterior to its positive counterpart. The lateral morphology at the negative extreme is also anteriorly placed except for **FMO**.

Canonical variate 4

The fourth canonical variates axis represents 7% of the among-groups variation. As shown in Figure 7-11, this dimension separates *Cercopithecus* at the negative pole and *Pan* at the positive. While CV 4 tends to pull out the cercopithecoids from the other taxa, there is substantial overlap among taxon ranges. Shape change along CV 4 is fairly minimal, as shown in Figure 7-13. Perhaps the greatest distinctions from the frontal view are the thicker brow overall (**MTI-MTS**) and obliquely angled suture between **FMT** and

FMO. From the lateral view, the negative morphology is slightly more angled with midline landmarks anteriorly placed and lateral landmarks slightly posteriorly placed relative to the positive. This makes a more acute the angle of the supraorbital line across the front of the face.

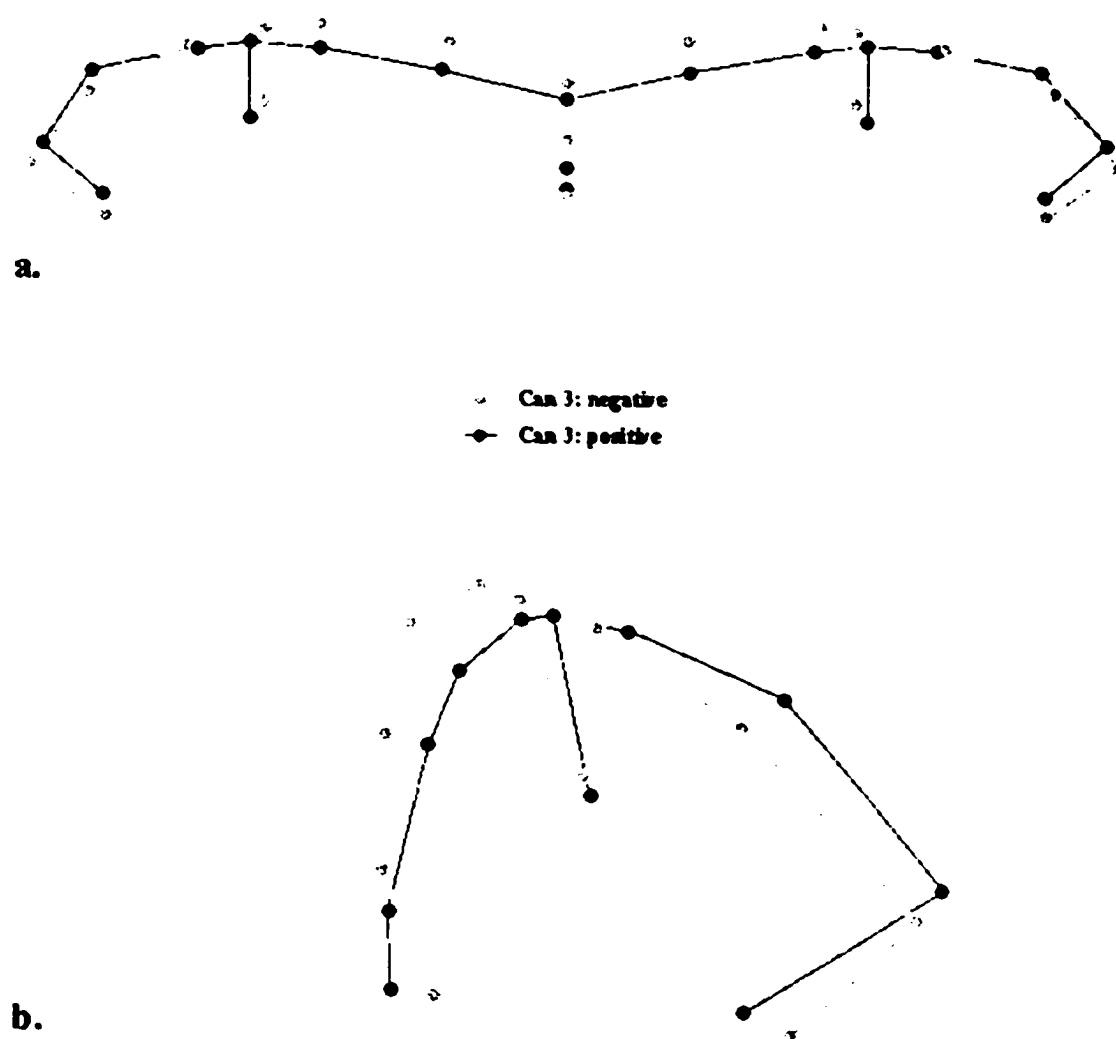
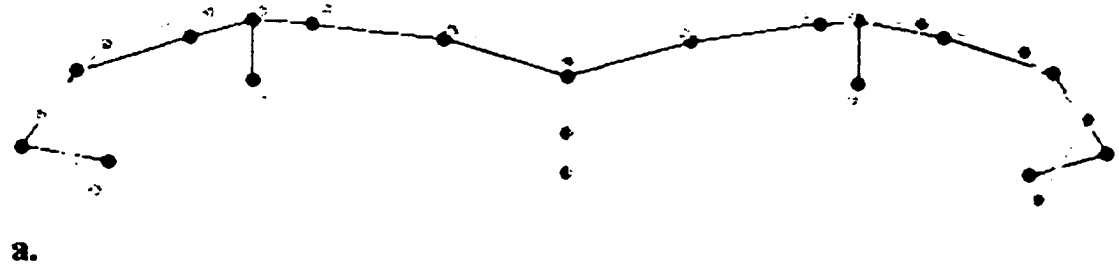


Figure 7-12 Shape change along CV 3. Black lines represent the positive loadings, gray lines show the negative loadings. (a) frontal view; (b) lateral view. See Figure 7-1 for landmark references.



• Can 4: negative
 — Can 4: positive

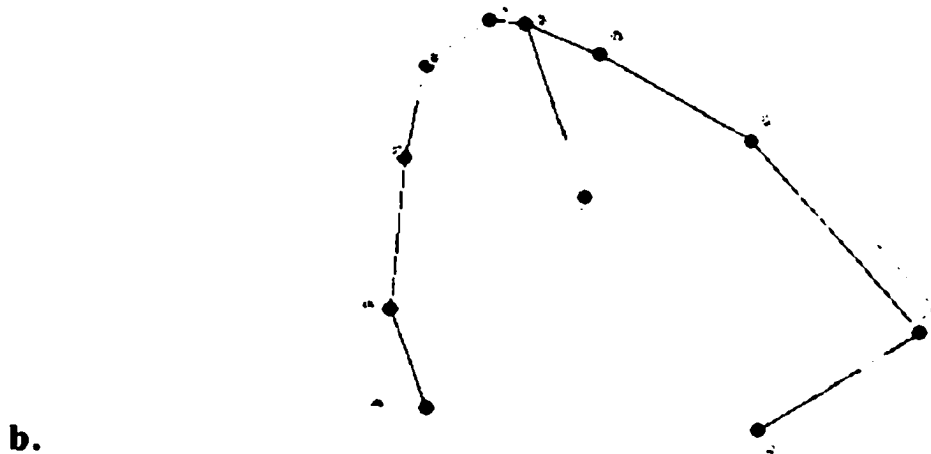


Figure 7-13 Shape change along CV 4. Black lines represent the positive loadings, gray lines show the negative loadings. (a) frontal view; (b) lateral view. See Figure 7-1 for landmark references.

Canonical variate 5

CV 5 comprises just over 6% of the total variability among genera. As demonstrated in the plot of CV scores (Figure 7-14) and the t-test results (Table 7-6), the greatest distinction along this axis separates cercopithecoids from all other taxa. The means of *Cercopithecus*, *Papio*, and *Procolobus* are significantly different from other genera; the latter two are significantly different from each other as well, but not from *Cercopithecus*. While significant differences were found between non-cercopithecoid taxon pairs, there is substantial overlap among the ranges of them all.

Figure 7-15 shows the shape change represented by CV 5; in this case, the positive pole is indicative of cercopithecoid supraorbital morphology. While both supraorbital lines are somewhat arched and dip inferiorly at the midline, the positive morphology corners sharply just lateral to **L1 (L9)** heading towards **FMT**. In the midline positive morphology, **L5** and **GLA** are slightly superior. **NAS**, however, is well inferior to its negative counterpart. The angle of the supraorbital line across the face is more acute at the positive extreme, owing to the anterior extension of midline landmarks and the posterior displacement of lateral landmarks. The suture between **FMT** and **FMO** runs at a strong diagonal in the negative morphology, but is more horizontal in the positive.

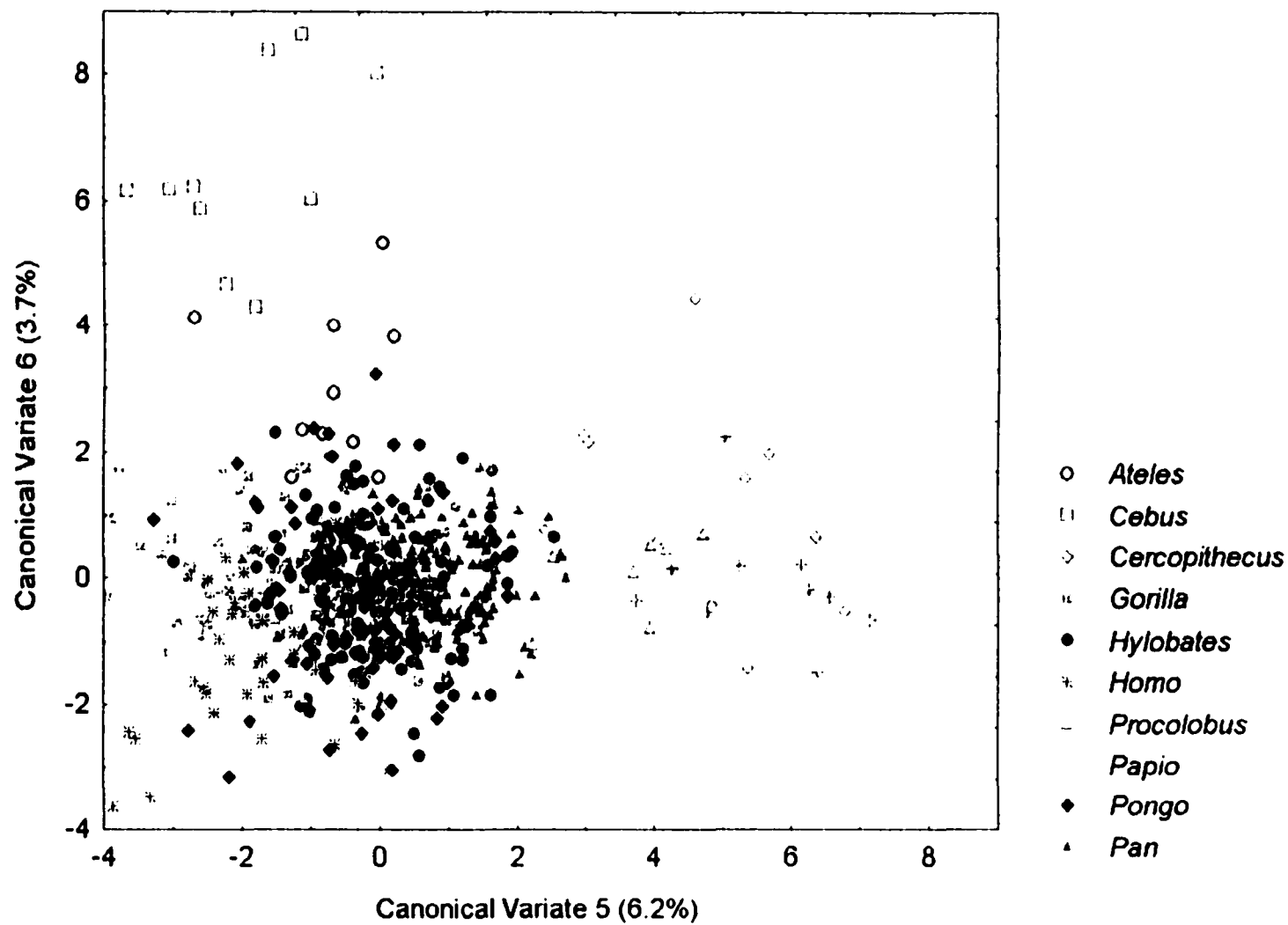


Figure 7-14 Plot of canonical variate scores for CV 5 and CV 6. CV 5 clearly discriminates between a hominoid-platyrrhine group and the cercopithecoids. CV 6 distinguishes catarrhines from platyrrhines.

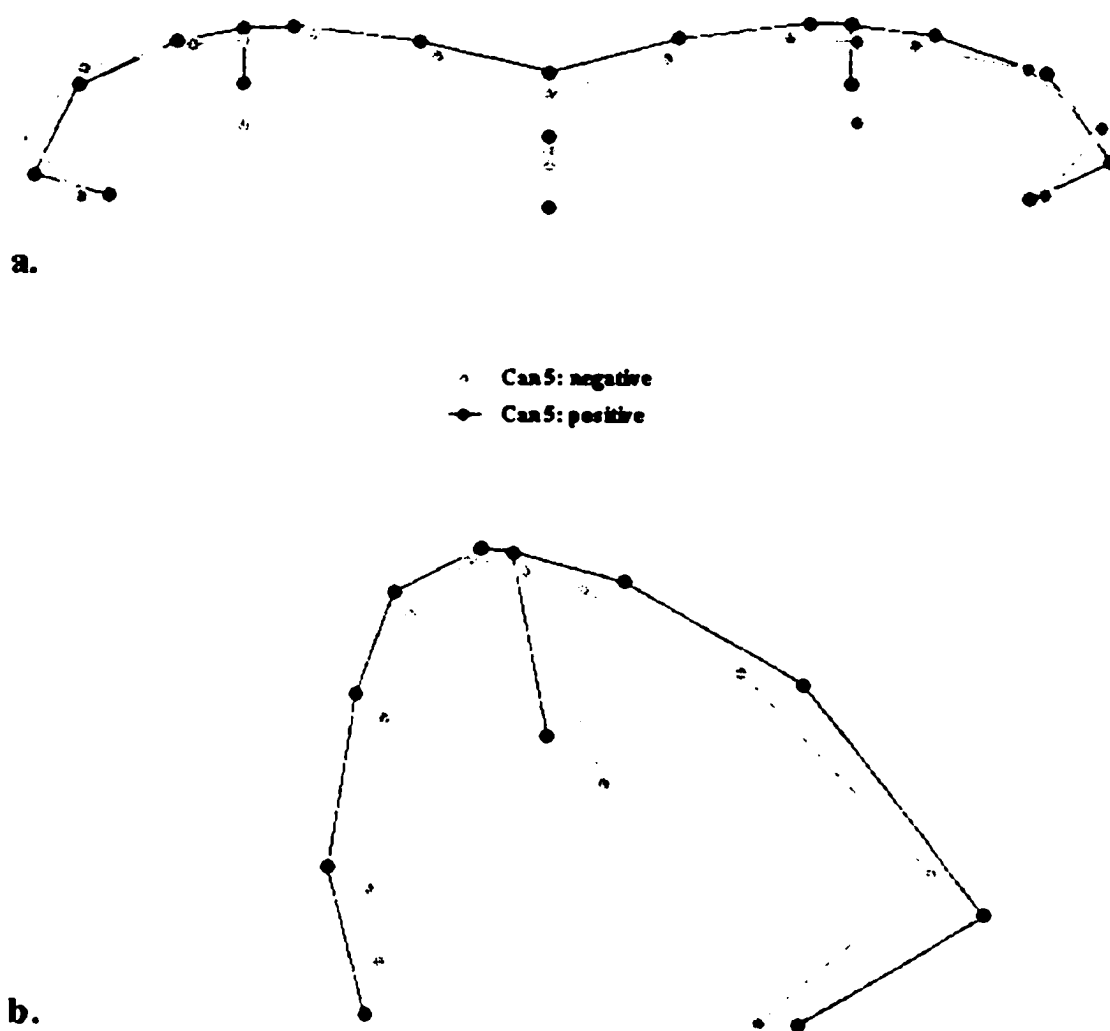


Figure 7-15 Shape change along CV 5. Black lines represent the positive loadings, gray lines show the negative loadings. (a) frontal view; (b) lateral view. See Figure 7-1 for landmark references.

Canonical variate 6

The sixth canonical variates axis summarizes only 3.7% of the variability among the supraorbital morphologies of these genera. Yet, it clearly distinguishes the platyrrhine genera from all others. This is evident from plots of the CV scores (Figure 7-14). T-test results (see Table 7-6) generally tell the same story, although both platyrrhine genera are significantly different from each other as well as the other taxa. *Homo* is also significantly different from the other taxa, placing at the most negative end of this axis. The only additional differences are between *Cercopithecus* and the hominoid taxa; none of the cercopithecoid genera was found to be distinct from another.

Differences in shape along CV 6 (Figure 7-16) are subtle. In the positive (platyrrhine) extreme, the supraorbital line is slightly shorter, with **FMT** situated superomedial to its negative counterpart. The suture between this landmark and **FMO**, however, drops sharply in the positive, with a more horizontal line in the negative. At the midline, **GLA** and **NAS** are somewhat inferior in the positive extreme—especially the latter. The angling of the supraorbital line across the front is nearly identical at both poles until **FMT**; in the negative morphology, this landmark is well posterior to its positive counterpart. Overall, the platyrrhine morphology is taller than the others, extending inferior to the negative morphology both in the midline and laterally.

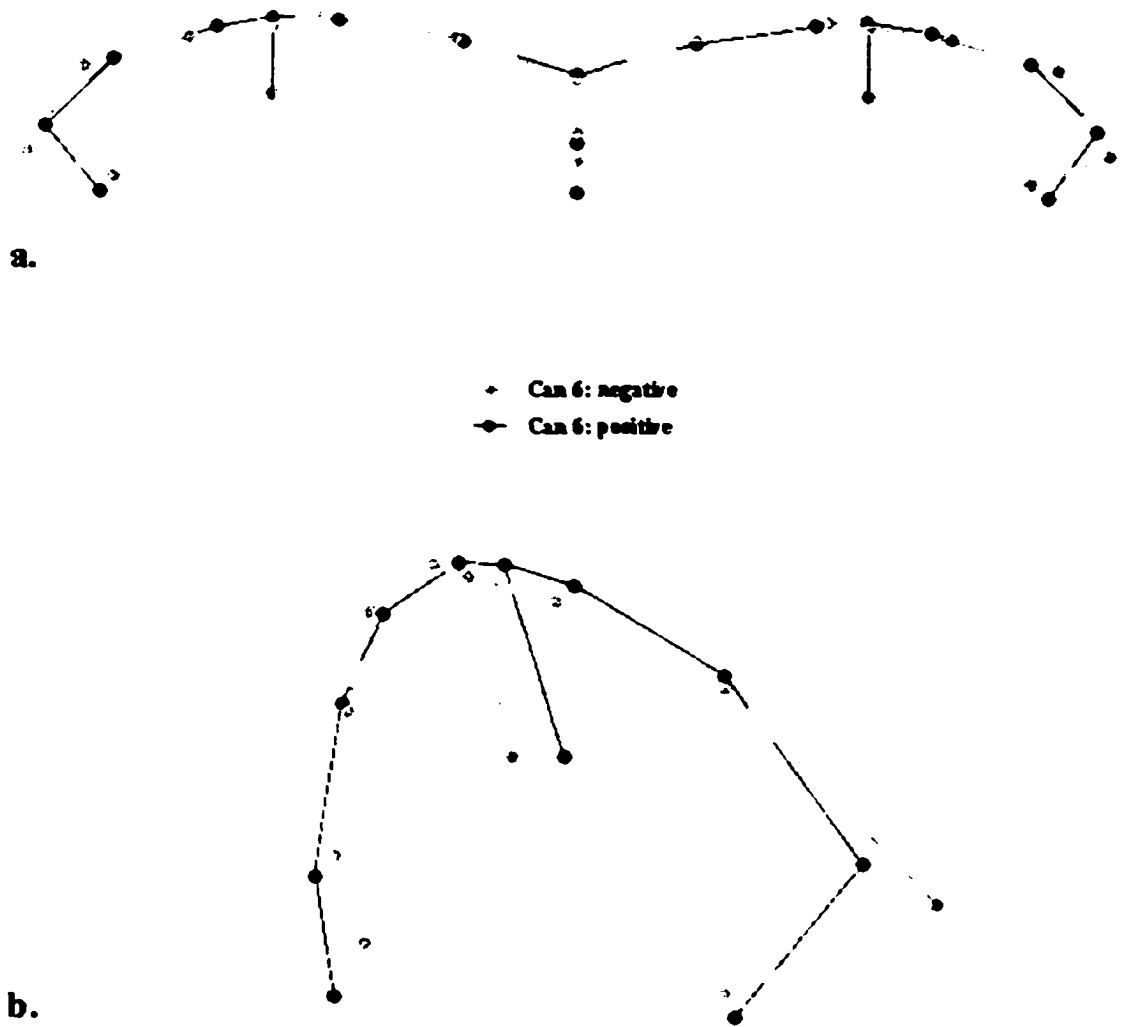


Figure 7-16 Shape change along CV 6. Black lines represent the positive loadings, gray lines show the negative loadings. (a) frontal view; (b) lateral view. See Figure 7-1 for landmark references.

MAHALANOBIS DISTANCE

Unbiased Mahalanobis distance estimates were computed for each pair of genera and used to compare groups within the canonical space. The multivariate extension of pairwise t-tests, Hotelling's T^2 , yielded significant differences ($p < 0.0001$) between every pair of genera. To assess the effects of sample size differences among taxa, 10,000 randomized Mahalanobis D^2 values were computed using equal sample sizes, as described in Chapter 5. Table 7-7 lists the D^2 values for each pairwise comparison: values in the lower triangle are distances computed from the whole sample; values in the upper triangle are mean distances obtained from the randomization procedure. Whole-sample D^2 values are not directly comparable to those derived from the randomization, as they originate from differently scaled canonical spaces. One can compare, however, the relative values between pairwise comparisons. If the sample size had no effect, then these relative distances should be similar. For example, the whole-sample *Ateles-Cebus* distance (53.0) is close to one-half of the *Ateles-Cercopithecus* distance (101.4). A similar ratio holds for the *Ateles-Cebus* (89.7) and *Ateles-Cercopithecus* (180.6) randomized average distances, suggesting that sample size was not a significant factor in these pairs. This is hardly unexpected, given that these non-hominoid taxa all had equal sample sizes from the beginning.

Table 7-7 Matrix of unbiased Mahalanobis distance estimates between pairs of genera. Values in the lower triangle were computed from the whole sample; values in the upper triangle are mean distances computed in the randomization procedure. Values from upper and lower triangles are not directly comparable, but relative differences within each should be similar if unequal sample size was not a significant factor determining distances.

Genus	Atel	Cebu	Cerc	Gori	Homo	Hylo	Pan	Papi	Pcol	Pong
Atel		89.7	180.6	192.5	136.3	78.9	124.0	178.9	128.6	164.1
Cebu	53.0		166.9	168.1	134.0	169.5	127.4	199.9	132.0	235.4
Cerc	101.4	100.2		129.2	173.9	213.5	124.3	83.9	87.0	198.8
Gori	85.1	77.3	70.2		156.5	187.2	78.0	149.0	107.6	232.3
Homo	75.3	73.1	102.1	83.7		166.2	74.5	165.6	139.0	277.3
Hylo	32.1	78.7	93.1	74.8	73.7		123.6	237.8	128.5	198.7
Pan	54.4	57.4	69.4	25.3	46.3	46.7		125.2	96.8	211.2
Papi	105.1	117.0	39.1	67.7	101.2	102.7	61.3		103.2	223.5
Pcol	72.1	86.2	40.6	45.8	84.6	55.9	42.0	43.9		206.2
Pong	68.8	113.4	100.6	94.5	131.9	70.5	85.6	110.7	87.0	

The main difference between the whole-sample distances and the randomized mean distances occurred among the most similar taxa. Computed from the whole sample, the shortest distance in the matrix connects *Gorilla* and *Pan*. In the randomized analysis, however, the smallest D^2 value is between *Homo* and *Pan*. This suggests that the relatively smaller sample of modern humans (38 adult specimens) affected the Mahalanobis distance computation (despite the bias correction). McNulty (in press) examined these supraorbital data in a sample limited to hominoids and also found the sample size of *Homo* to affect the outcome. In that analysis, however, *Gorilla* and *Pan* were shown to be the most similar, with *Homo* linked to them. This results reinforces the similarity among hominine brows, but suggests that details within this clade may be obscure. Beyond the re-evaluation of *Homo*, other taxon pairs were broadly similar in whole-sample and equal-sample analyses.

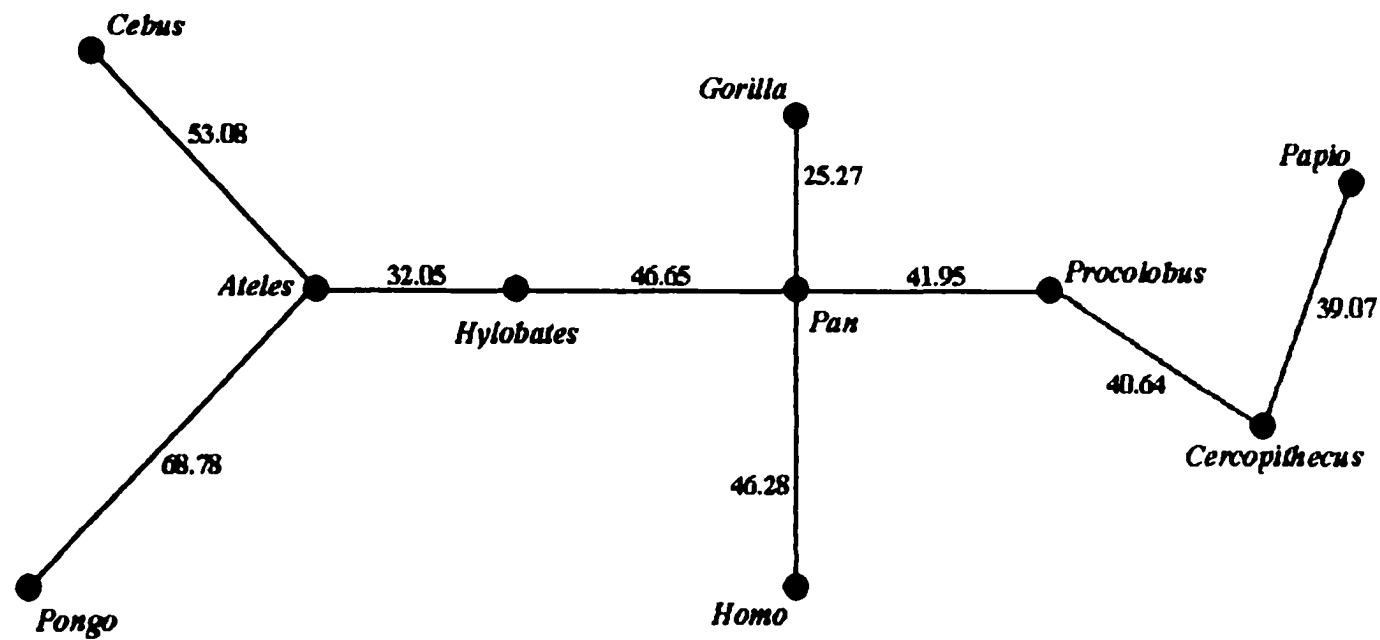


Figure 7-17 Minimum spanning tree showing the nearest-neighbor for each genus as measured by Mahalanobis D^2 values from the whole-sample analysis. Relationships between connected taxa are drawn to scale; distances between un-joined genera are not to scale. Additional Mahalanobis distances are given in Table 7-7 for both whole-sample and equal-sample analyses (see text for discussion).

To help visualize Mahalanobis D^2 relationships, the whole-sample values from Table 7-7 were used to construct a minimum spanning tree (Figure 7-17); a tree constructed from mean replicate distances yielded an identical topology, with only slightly different branch proportions (see above). There are three basic clusters shown on the MST. As already noted, the closest taxa among this sample are the hominines. *Pan*, in fact, occupies the most central region in this canonical space, having the lowest average Mahalanobis D^2 values in both analyses. The second nearest cluster is *Ateles-Hylobates*, the latter of which links with *Pan* to join these clusters. The third group is a cluster of the cercopithecoids. The *Cercopithecus-Papio* distance is the next smallest; *Procolobus* is closest to *Cercopithecus* in morphology, but only slightly further from *Pan*. It is interesting that the two cercopithecines group together despite the presence of a “torus” in *Papio*, but not *Cercopithecus*. This suggests that they share a similar overall configuration of landmarks despite having differences in traditionally recognized character states. *Cebus* is most closely linked to *Ateles*, and this value is substantially less than its distances to other genera; it is not terribly close to *Hylobates* in morphology. *Pongo* has the most unique supraorbital morphology, generating the largest Mahalanobis distances in the sample. While its nearest neighbor is *Ateles*, the high D^2 value suggests that this probably not indicative of a strong affinity.

UPGMA cluster diagrams are shown in Figure 7-18 to illustrate hierarchical relationships among genera. The left tree (Figure 7-18a) represents a cluster of Mahalanobis distance estimates calculated in the whole sample analysis; the right (Figure 7-18b) is a cluster of the mean D^2 values from the randomized equal-sample analyses.

The trees are broadly similar, and largely recapitulate the relationships seen in the minimum-spanning tree. *Pongo* has the most unique supraorbital morphology, grouping with none of the other genera. The next major split is between a platyrrhine-*Hylobates* group and the other catarrhines; *Homo* clusters with the former in the whole-sample analysis, but links closely to *Pan* when sample size is accounted for. Both trees contain a cercopithecoid cluster and a platyrrhine-*Hylobates* cluster. In fact, the only major difference between them is in the placement of *Homo*. *Gorilla* and *Pan* group together in both cluster analyses, but an equal-sample approach results in a cluster of hominines.

Interpreting these results in a broader evolutionary context is difficult. It is clear from both the MST (Figure 7-17) and the cluster diagrams (Figure 7-18) that these methods of analysis are able to detect fairly subtle phylogenetic information. Indeed, the results presented here go beyond traditional descriptive diagnoses of supraorbital “torus” or “rim.” For example, the supraorbital tori found in *Gorilla* and *Pan*, as well as in *Papio* were here recognized as distinct morphologies. Moreover, the landmark configuration describing the supraorbital rim of *Cercopithecus* was more similar to that of *Papio*’s torus than the rim of *Procolobus*. It is also interesting that the supraorbital morphology of *Homo* was linked closely to *Pan*—the shortest distance in the equal-sample analysis. This suggests that, despite the autapomorphic morphology of modern human crania, they still retain a supraorbital configuration similar to that of *Pan*. This is particularly important as many researchers assign a unique character state (“superciliary arches”) to modern human supraorbital morphology. These data, however, suggest that the visible differences between *Pan* and *Homo* likely have little to do with the “brow” itself, but result from expansion of the frontal lobe and development of a supra-toral forehead.

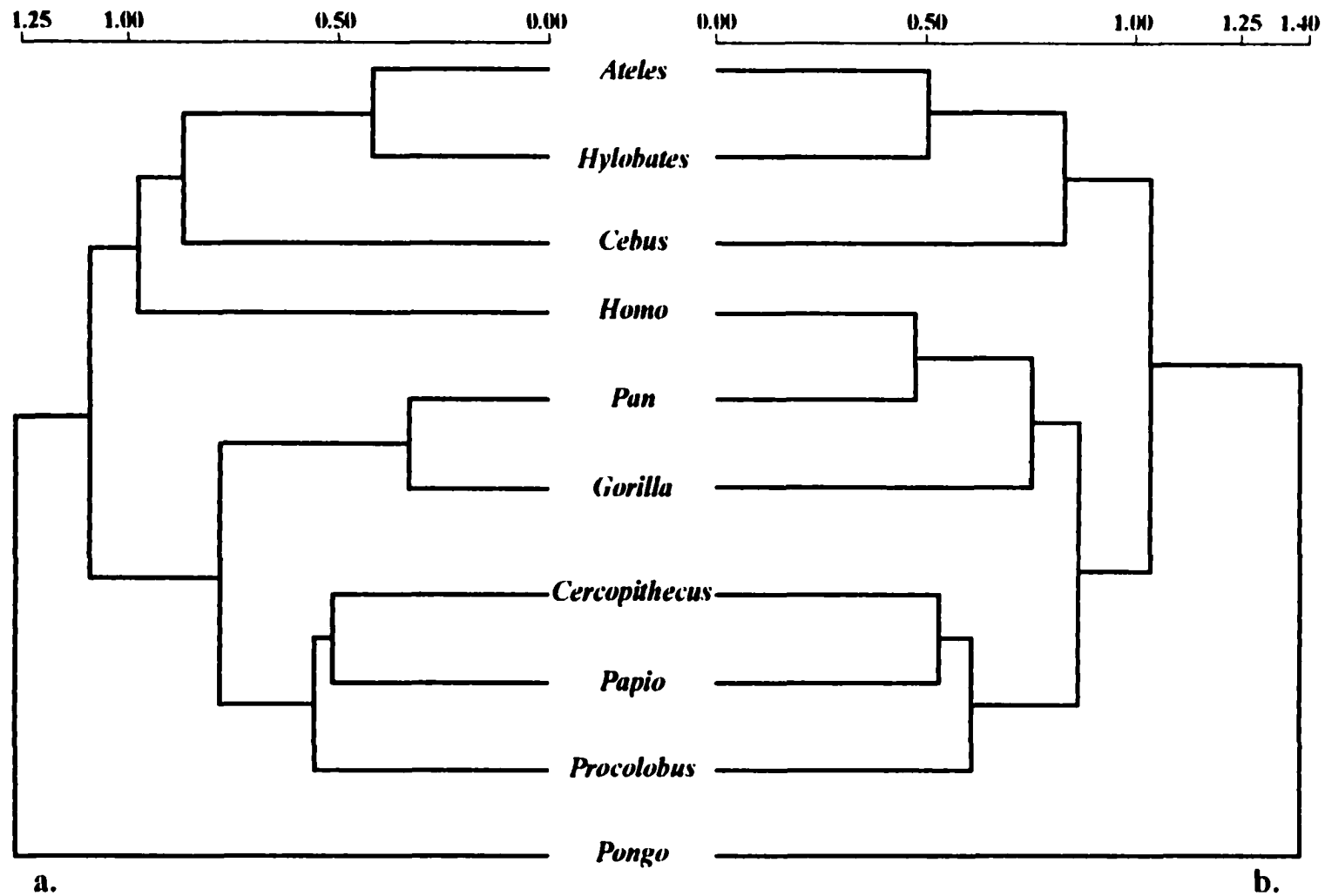


Figure 7-18 Results of UPGMA cluster analyses based on (a) Mahalanobis D^2 values from the whole sample, and (b) mean Mahalanobis D^2 values of equal-sample replicates ($n=10,000$). The input matrices for both are given in Table 7-7.

Overall, the branching pattern of the equal-sample cluster diagram is similar to that of a phylogeny for these taxa. The two exceptions to this are *Hylobates* (grouping with the platyrrhines) and the very distinct *Pongo*. It is impossible to assess from these data whether or not the similarity between *Hylobates* and *Ateles* is a shared primitive anthropoid condition or a convergent acquisition. Nevertheless, it is interesting to note that when sample size is controlled, the hylobatid morphology is revealed to be quite distinct among these genera; its average D^2 values were second only to *Pongo* in length. Thus, its morphology is not generalized in a phenetic sense relative to the other taxa. Orangutan supraorbital morphology is the most autapomorphic among these genera. Again, it is difficult to infer any evolutionary meaning from this result. Phenetically, however, this would seem to argue against the hypothesis that *Pongo* shares supraorbital morphology similar to the primitive catarrhines (e.g., Benefit & McCrossin, 1991, 1993); while *Pongo* is most similar to *Ateles*, the actual distance is too great to imply a strong affinity. Phenetically speaking, *Pan* and *Procolobus* are the most generalized in this sample and may serve as better models for conservative catarrhine supraorbital morphology.

SHAPE DIFFERENCES BETWEEN CROWN CLADES

Results of the above analyses demonstrate that phenetic relationships among these samples do not entirely correspond to their phylogenetic relationships. Specifically, *Hylobates* and *Pongo* were shown to differ in their supraorbital morphologies from the other hominoids and from each other. Alternatively, morphologies of the hominines and of the sample of cercopithecoids were relatively distinct. This suggests that, based on

supraorbital morphology, one might reasonably be able to classify a specimen as a cercopithecoid or hominine, but not necessarily as a hylobatid or hominid. A better way to address this, however, is to examine the shape differences represented by the crown clades in this sample. A series of two-group discriminant analyses were performed to test for differences in supraorbital morphology at each node of the consensus phylogeny (see Figure 7-19). The exact procedure used here is detailed in Chapter 5. Cross-validations were used to assess the ability of discriminant functions to assign sample specimens; coefficients of the functions were then applied to the consensus landmark configuration to visualize the shape difference at each node.

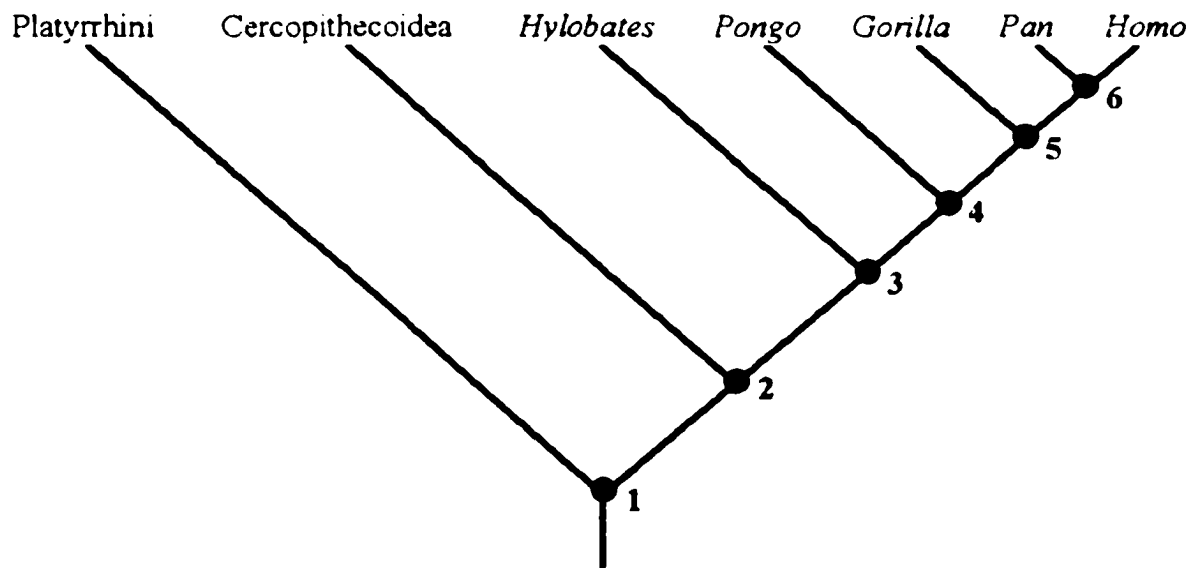


Figure 7-19 Consensus phylogeny of the relationships among extant apes and the main anthropoid clades. Nodes are referred to by number in the text.

Node 1: Platyrrhines vs. Catarrhines

The first node in Figure 7-19 separates catarrhines and platyrrhines. Table 7-8 shows the cross-validation results of the discriminant analysis; Figure 7-20 shows a plot of the scores for each specimen (by genus) on the discriminant function. This analysis was quite successful at distinguishing between catarrhine and platyrrhine supraorbital morphologies. Platyrrhines were correctly reclassified every time; among catarrhines, one hylobatid was incorrectly grouped with the platyrrhines. In fact, of all the catarrhine genera, *Hylobates* is the most similar to the platyrrhines. In analyses of genera, *Ateles* and *Hylobates* were shown to be quite similar (see above). Results from node 1 discrimination show that *Hylobates* and *Procolobus* tend to be centralized in those features specifically separating these platyrrhines from catarrhines. Nevertheless, these data still provide a robust discrimination between the two groups. The other cercopithecoids and *Gorilla* occupy the negative end of this function—being most distinct from platyrrhines in those features distinguishing these infraorders. These results broadly agree with generic-level analyses discussed above.

Table 7-8 Cross-validation results for DA of supraorbital morphologies in catarrhines and platyrrhines. Each cell gives the number (n) and percent (%) of individuals from the taxa on the left assigned to the taxa across the top.

Taxon		Catarrhine	Platyrrhine
	N	31	1
Catarrhine	%	96.88	3.13
Platyrrhine	N		20
	%		100.00

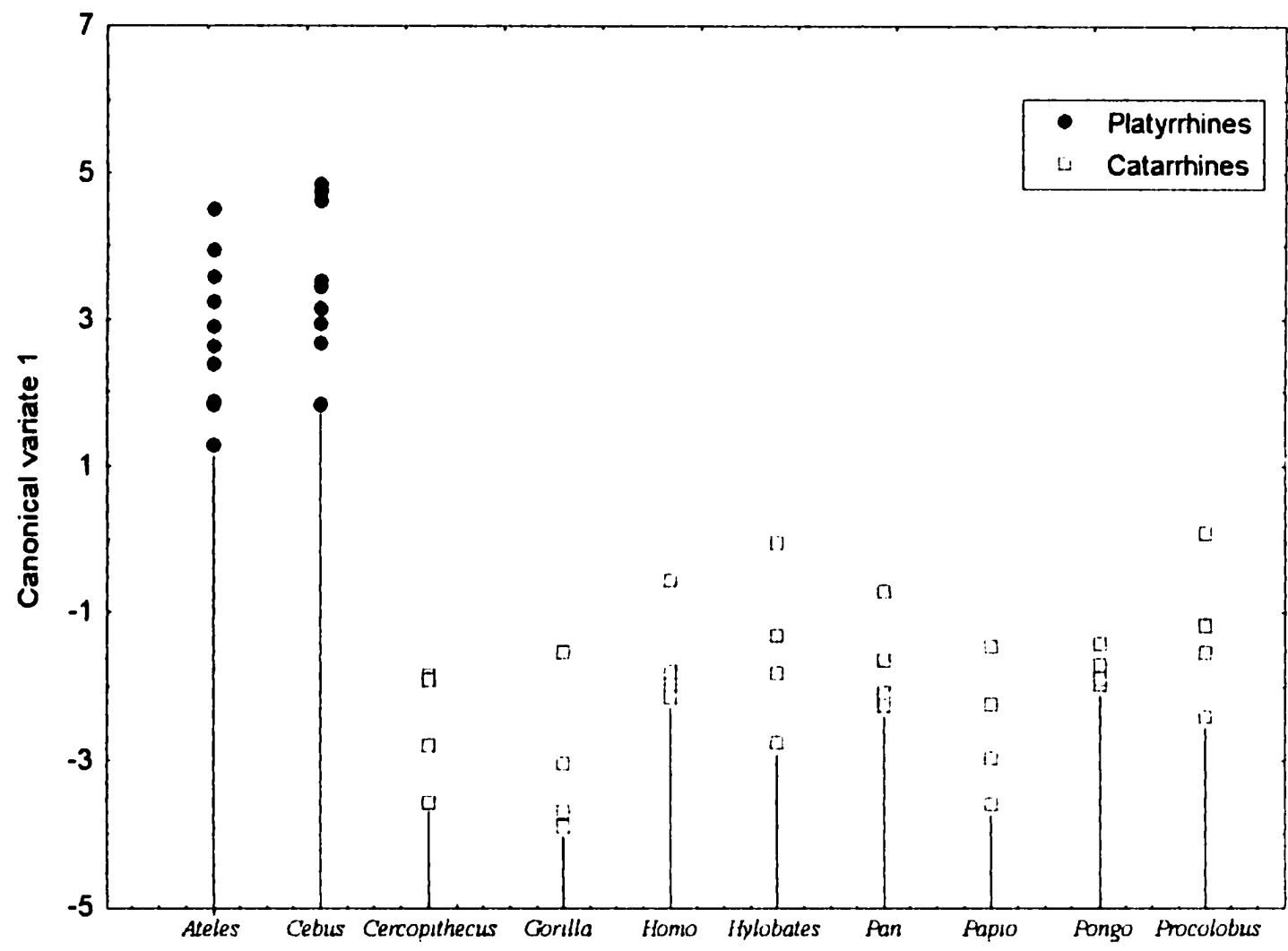


Figure 7-20 Plot of CV scores for the discriminant axis separating platyrrhines from catarrhines. Although only the two groups were used for class variables, these results are illustrated by genus to better depict the distribution of specimens on the axis.

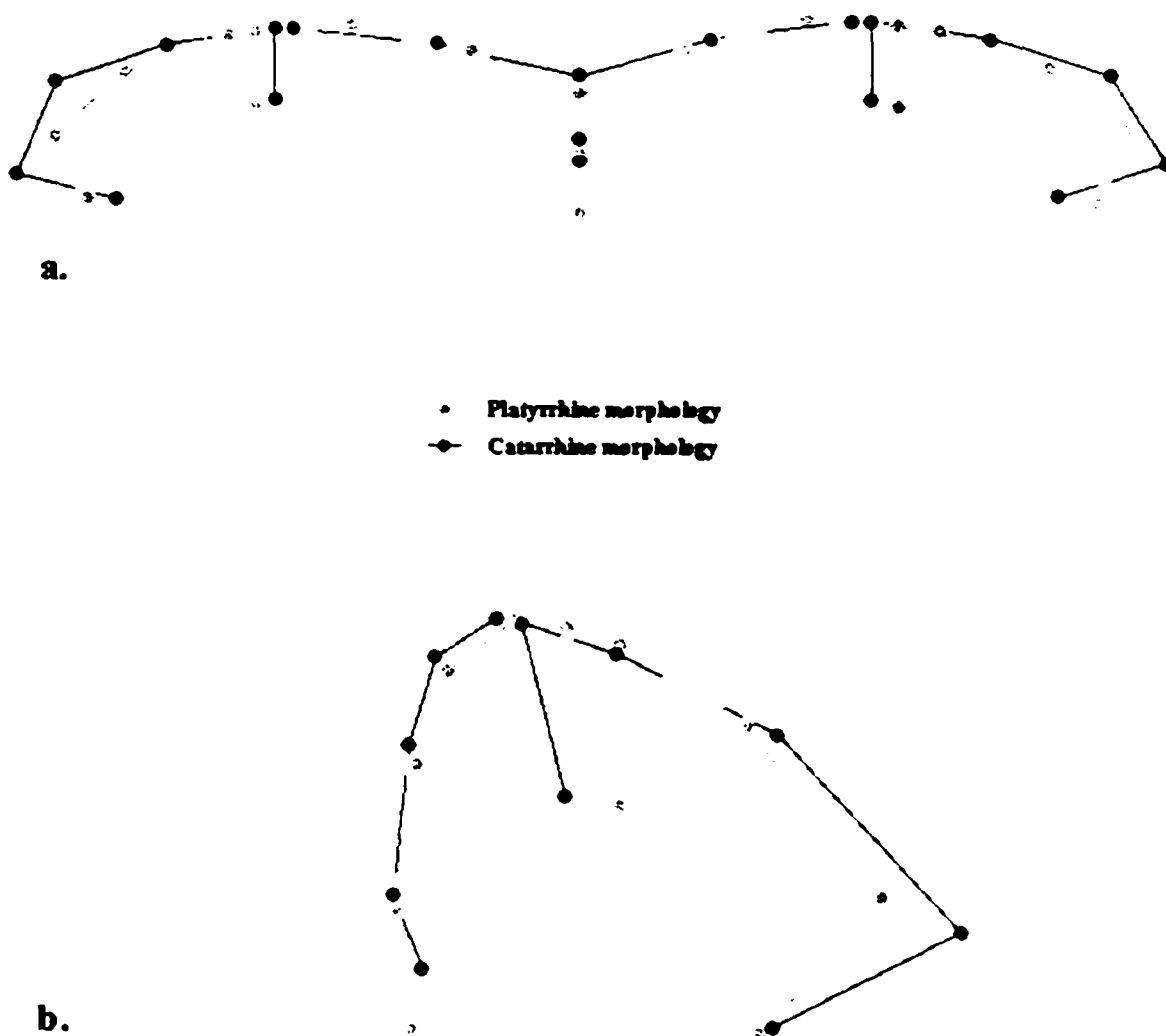


Figure 7-21 Shape change corresponding to the discrimination between platyrrhines (gray) and catarrhines (black) sampled for this project. (a) frontal view; (b) lateral view. See Figure 7-1 for landmark references.

The difference in shape between these platyrrhines and catarrhines is illustrated in Figure 7-21. The greatest region of difference is in the lateral extremes. The platyrrhine morphology tapers inferiorly at a steeper rate, terminating at **FMT** antero-medial to its catarrhine counterpart. Thus, the catarrhine morphology is more angled across the front of the supraorbital region. It also has a thicker lateral orbital pillar relative to the platyrrhine, with **FMO** well medial, inferior, and anterior to **FMT**. In platyrrhines, **FMO** is antero-inferior to **FMT**, but only slightly medial. The other region of difference is among the midline landmarks. The catarrhine **L5** and **GLA** are slightly superior to those in the platyrrhine morphology; **NAS**, however, is superiorly and posteriorly displaced in the catarrhine, describing a pronounced glabella.

Node 2: Cercopithecoids vs. Hominoids

A discriminant analysis of these data was also robust for distinguishing between the cercopithecoids and hominoids sampled here. Cross-validation (Table 7-9) correctly reassigned all of the hominoids and all but one of the cercopithecoids—a specimen of *Papio*. Scores of each specimen are plotted in Figure 7-22.

Table 7-9 Cross-validation results for DA of cercopithecoid and hominoid supraorbital morphologies. Each cell gives the number (n) and percent (%) of individuals from the taxa on the left assigned to the taxa across the top.

Taxon		Cercopithecoids	Hominoids
Cercopithecoids	n	29	1
	%	96.67	3.33
Hominoids	n		30
	%		100.00

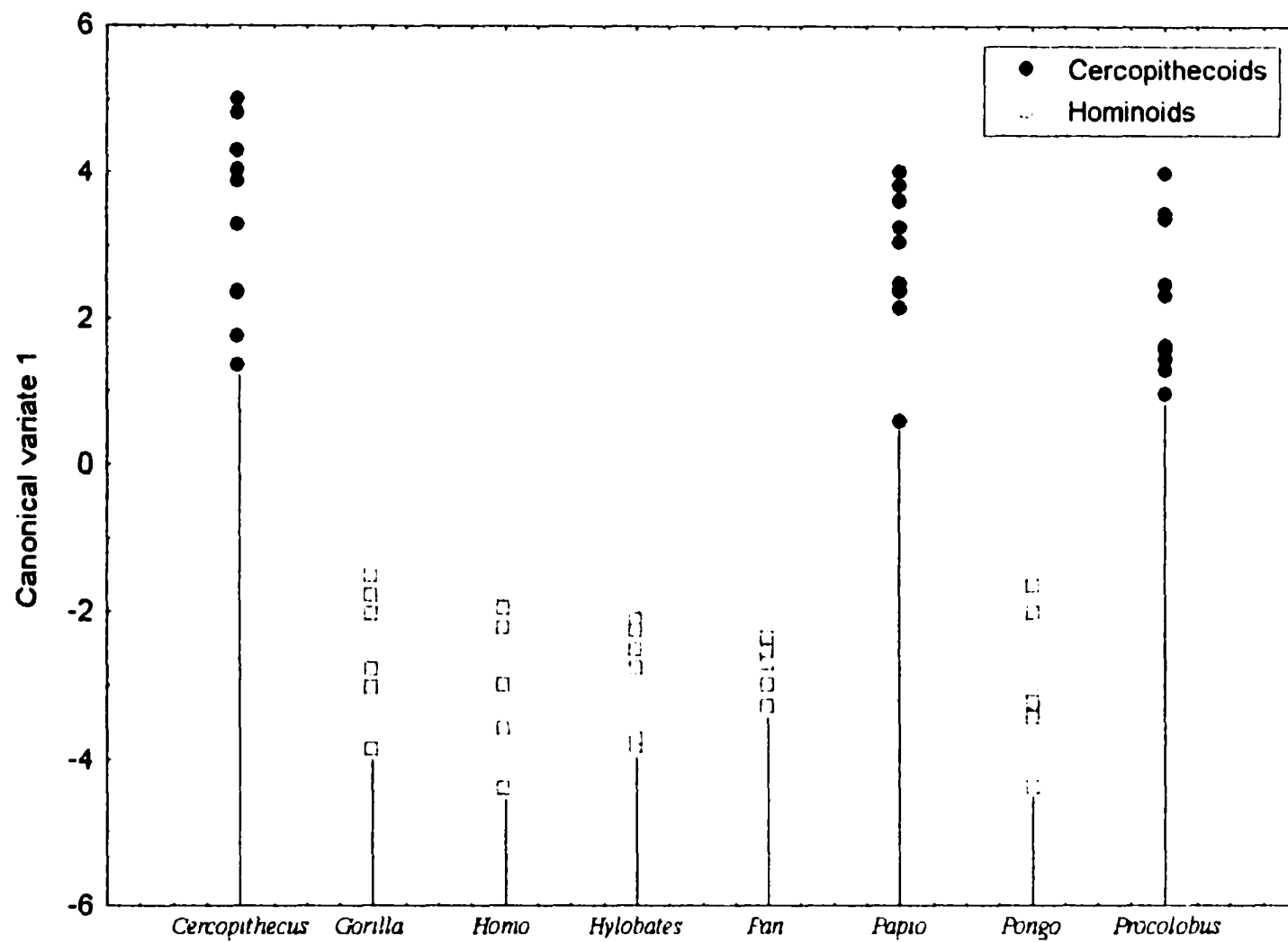
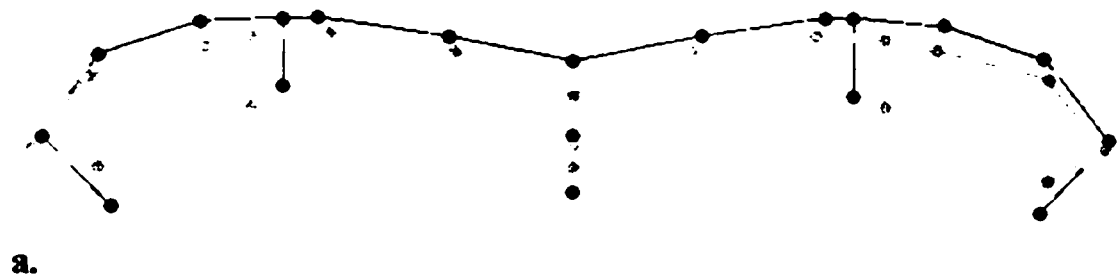


Figure 7-22 Plot of CV scores for the discriminant axis separating cercopithecoids from hominoids. Although only the two groups were used for class variables, these results are illustrated by genus to better depict the distribution of specimens on the axis.



• Hominoid morphology
 • Cercopithecoïd morphology

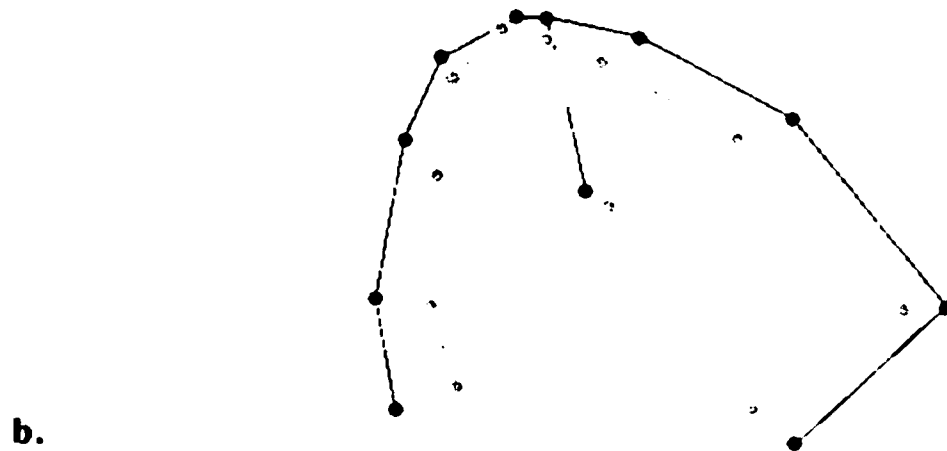


Figure 7-23 Shape change corresponding to the discrimination between hominoids (gray) and the cercopithecoïd taxa (black) sampled for this project. (a) frontal view; (b) lateral view. See Figure 7-1 for landmark references.

Figure 7-23 illustrates the shape differences represented by the discriminant function. The relative width of both hominoid and cercopithecoid morphologies are nearly the same. The cercopithecoid, however, has substantially greater infero-superior and antero-posterior components. Thus, the supraorbital ridge curve is relatively superior. **FMO** and **NAS** are substantially inferior, and the angle across the front is more acute in the Old World monkey specimens. Beyond this, the hominoid supraorbital ridge curve has a moderate inferior displacement towards the midline.

Node 3: Hylobatids vs. Hominids

The difference between supraorbital morphologies of the lesser apes and the great apes was also easily detected in a discriminant analysis. Two of the hylobatids were incorrectly reclassified as hominids, while only a single specimen of *Pongo* was mistaken for a hylobatid. Still, better than 98% of both groups were correctly placed. A plot of specimen scores, by genus, is given in Figure 7-24.

Table 7-10 Cross-validation results for DA of hylobatid and hominid supraorbital morphologies Each cell gives the number (n) and percent (%) of individuals from the taxa on the left assigned to the taxa across the top.

Taxon		Hylobatids	Hominids
Hylobatids	n	126	2
	%	98.44	1.56
Hominids	n	1	127
	%	0.78	99.22

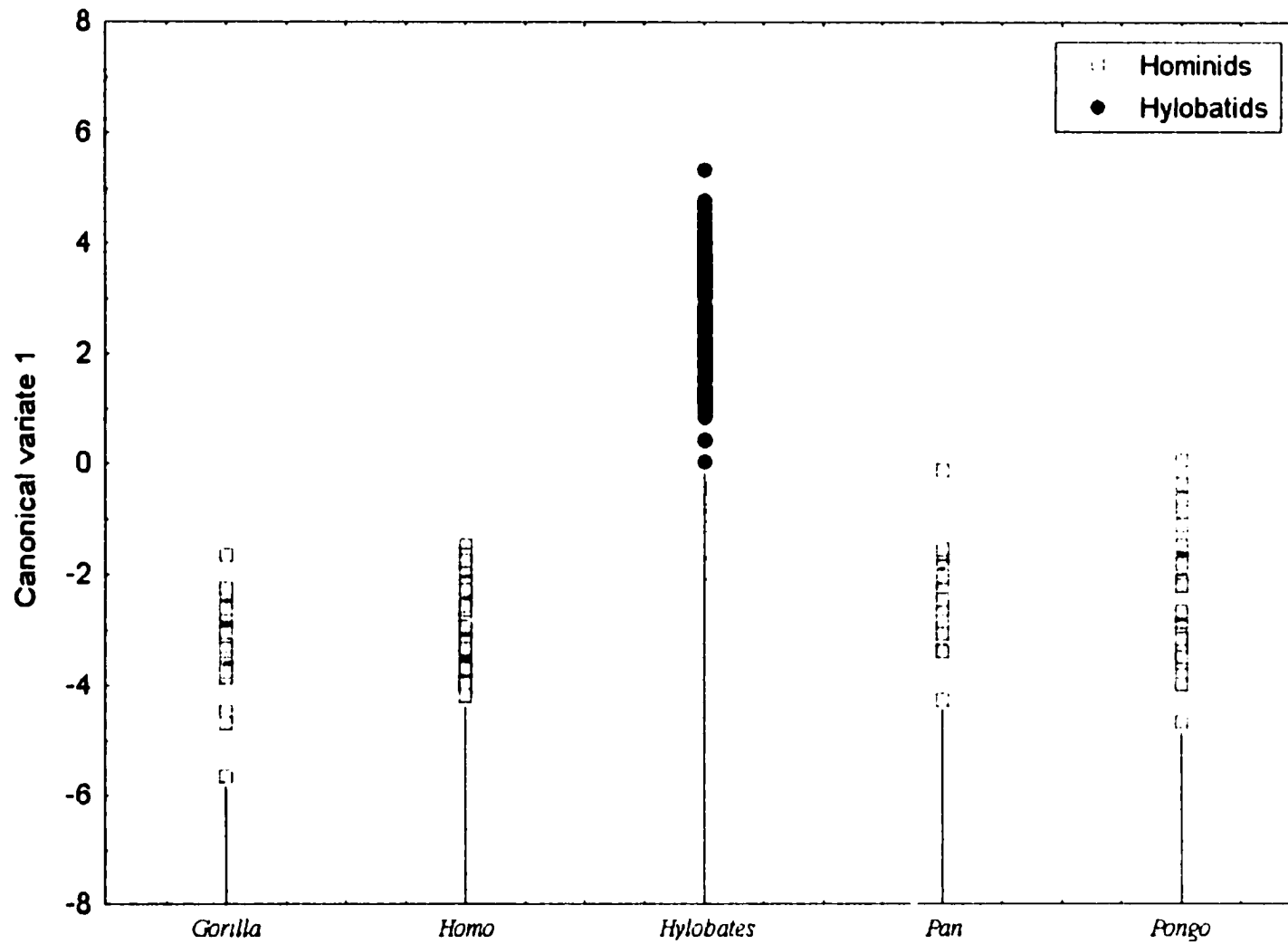
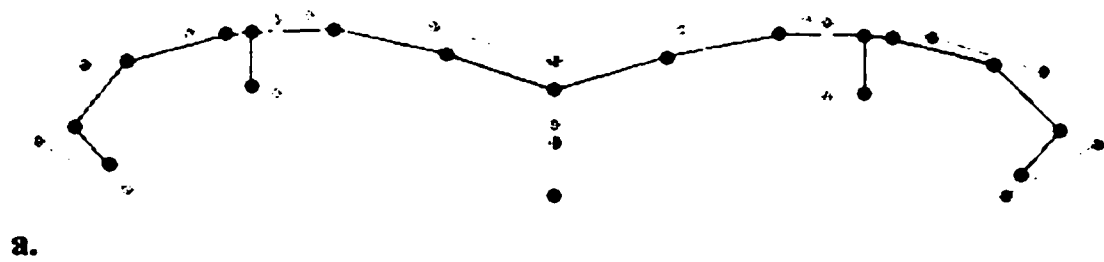


Figure 7-24 Plot of CV scores for the discriminant axis separating hylobatids from hominids. Although only the two groups were used for class variables, these results are illustrated by genus to better depict the distribution of specimens on the axis.



~ Hominid morphology
 — Hylobatid morphology

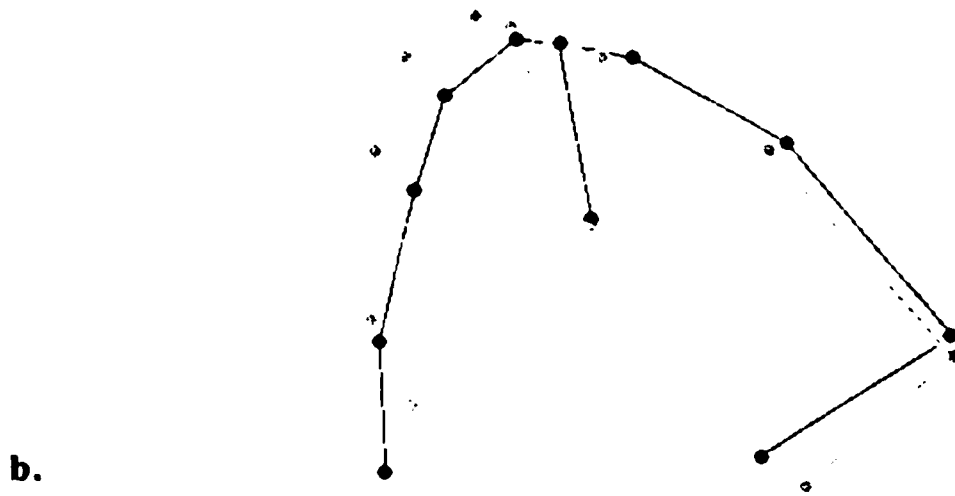


Figure 7-25 Shape change corresponding to the discrimination between hominids (gray) and hylobatids (black). (a) frontal view; (b) lateral view. See Figure 7-1 for landmark references.

Differences between the supraorbital morphologies of hylobatids and hominids are shown in Figure 7-25. In *Hylobates*, the middle of the ridge curve (**L5**) dips inferiorly contributing to a more rounded appearance. Laterally, the hylobatid brow terminates medially with a narrower orbital pillar. Again, there is a distinct difference at **NAS**, as the hominid landmark is set substantially superior and posterior compared to the hylobatid. Despite a narrower width across the front, the mid-torus landmarks in *Hylobates* are well lateral of those in the great apes. That indicates a substantially broader interorbital region among lesser apes. Finally, the angle across the front is similar if measured at the height of glabella, but more acute in the hominid supraorbital ridge curve. This results from a nearly vertical relationship between **GLA** and **L5** in the great apes.

Node 4: Pongines vs. Hominines

Discriminant analysis of supraorbital data from pongines and hominines was highly successful at separating the two. Cross-validation indicated a correct re-assignment of all specimens. This is not surprising, given the results from analyses of Mahalanobis distances: *Pongo* was the most distinct genus among the sample (see Table 7-7. This is also evident in the plot of discriminant scores (Figure 7-26), which shows the substantial gap between the subfamilies.

Table 7-11 Cross-validation results for DA of pongine and hominine supraorbital morphologies. Each cell gives the number (n) and percent (%) of individuals from the taxa on the left assigned to the taxa across the top.

Taxon		Pongines	Hominines
Pongines	n	72	
	%	100.00	
Hominines	n		72
	%		100.00

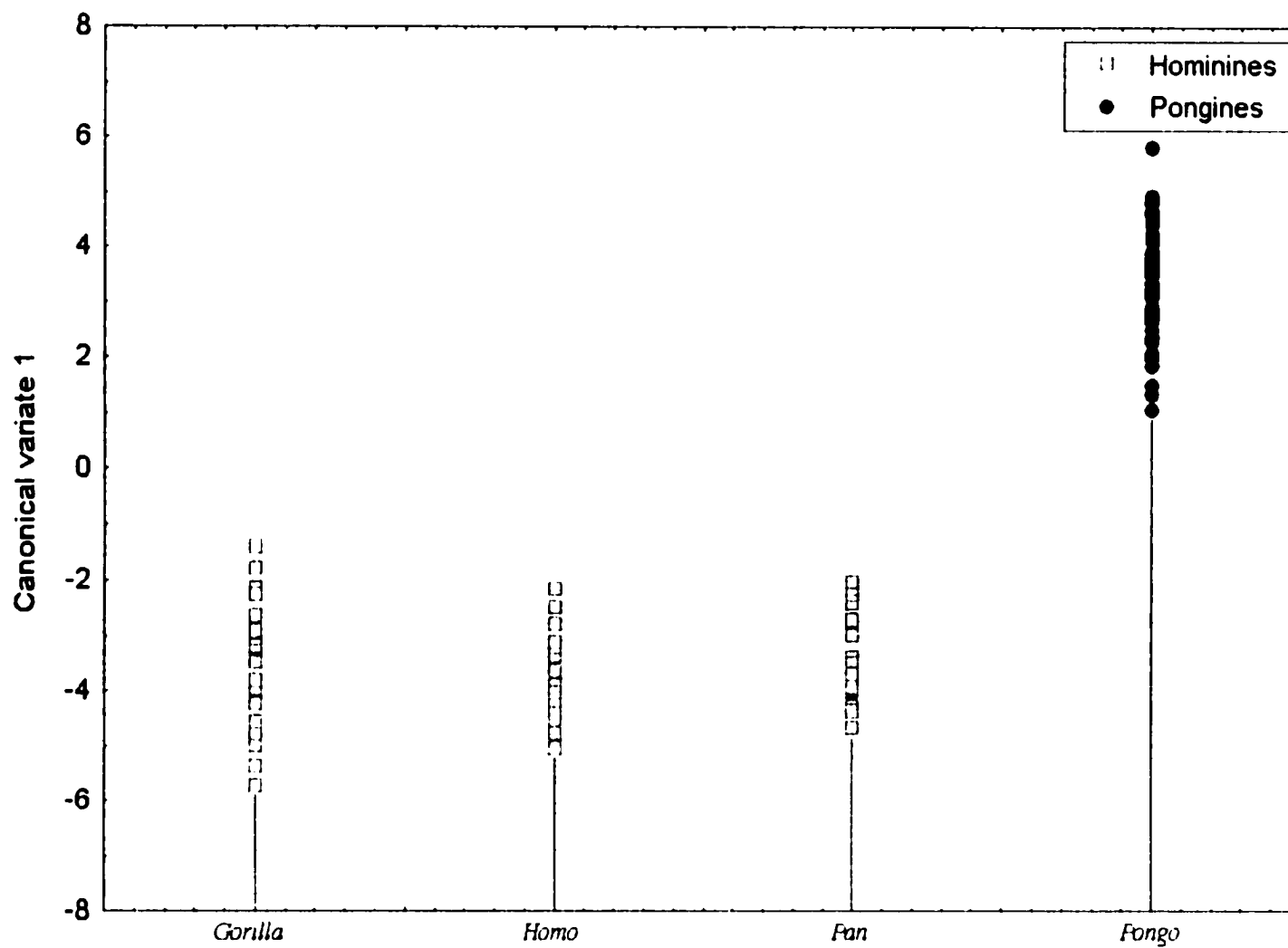
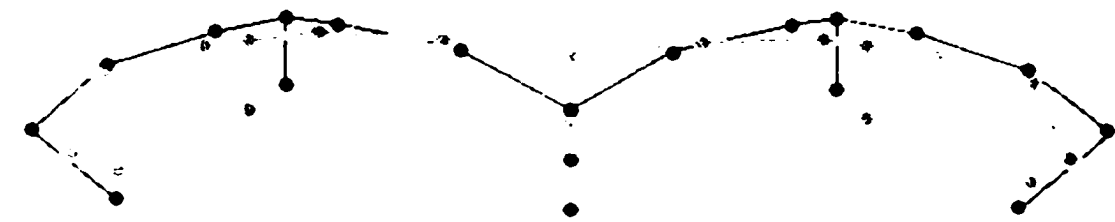
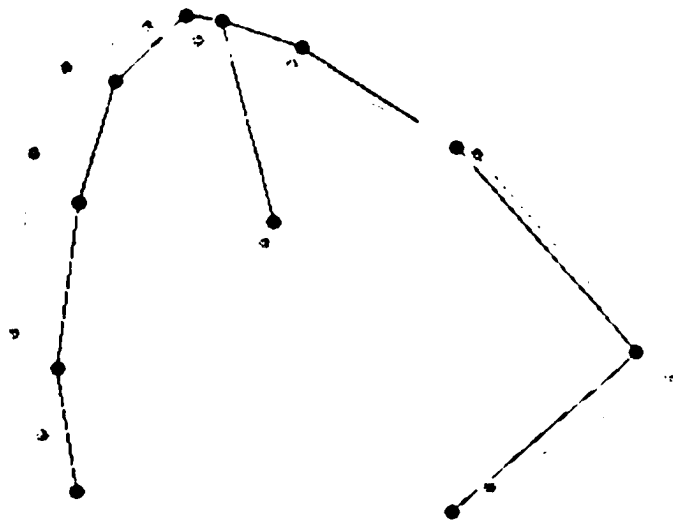


Figure 7-26 Plot of CV scores for the discriminant axis separating pongines from hominines. Although only the two groups were used for class variables, these results are illustrated by genus to better depict the distribution of specimens on the axis.



a.

+ Hominine morphology
 — Pongine morphology



b.

Figure 7-27 Shape change corresponding to the discrimination between hominines (gray) and pongines (black). (a) frontal view; (b) lateral view. See Figure 7-1 for landmark references.

Figure 7-27 illustrates shape differences between pongines and hominines. The supraorbital ridge curve in African apes is nearly horizontal, dropping inferiorly just medial to **FMT**; inferior displacement at **L5** is only slight. In *Pongo*, **L5** is well inferior to **L4** and **L6**; the supraorbital ridge curve arches superiorly to **MTS** and then gradually inferiorly towards **FMT**. The fronto-malar suture is long in pongines, with **FMO** set far inferior to **FMT**. All of the midline landmarks are substantially inferior and posterior compared to their hominine counterparts. Moreover, the medial position of **MTI-MTS**, despite the greater breadth of the supraorbital ridge curve, reflects the characteristic narrow interorbital breadth of *Pongo*. In lateral view, the relatively straight angle across the front of the pongine supraorbital ridge curve is evident from the posterior placement of medial landmarks.

Node 5: *Gorilla* vs. *Pan-Homo*

Unlike the node 5 analysis of the entire cranium, there is a clear distinction between supraorbital morphologies of *Gorilla* and a *Homo-Pan* group. Cross-validation (Table 7-12) correctly re-assigned specimens from both groups with greater than 98% success—missing only one gorilla and one chimpanzee. The distinction between these groups is illustrated in Figure 7-28 by the plot of discriminant scores. It is generally recognized (e.g., Simpson, 1945, 1949, 1953; Weidenreich, 1946; Delson & Andrews, 1975; Kluge, 1983; Schwartz, 1984; Shae, 1985; Andrews & Martin, 1987; Collard & Wood, 2000, 2001) that the overall morphology of *Pan* is more similar to that of *Gorilla* than to *Homo* (but see Groves, 1986; Begun *et al.*, 1997; Strait *et al.*, 1997); examinations of the entire cranial dataset certainly confirmed this. Yet, this analysis suggests that the modern humans and chimpanzees share similarities in their supraorbital landmark

configurations to the exclusion of *Gorilla*. This was also demonstrated above by both whole-sample and equal-sample Mahalanobis distances. Here, these shape differences can be visualized (Figure 7-29).

Table 7-12 Cross-validation results for DA of *Gorilla* and *Pan-Homo* morphologies. Each cell gives the number (n) and percent (%) of individuals from the taxa on the left assigned to the taxa across the top.

Taxon		<i>Gorilla</i>	<i>Pan-Homo</i>
<i>Gorilla</i>	n	77	1
	%	98.72	1.28
<i>Pan-Homo</i>	n	1	77
	%	1.28	98.72

The shape of the supraorbital ridge curve is very similar between these groups; the *Homo-Pan* morphology, however, is somewhat less broad, with the lateral extreme terminating medial to that of *Gorilla*. Beyond that, the configuration of midline landmarks is very different. While **L5** is similar in both, glabella is inferior in *Gorilla* suggesting a relatively thicker (inferior-superior) supraorbital torus. Nasion, on the other hand, is well superior and somewhat anterior in *Gorilla* relative to *Homo-Pan*. The configurations of mid-torus landmarks are also interesting. The thickening of the gorilla torus is clearly illustrated. Surprisingly, however, the lateral placement of the mid-torus landmarks indicates that *Homo* and *Pan* have relatively broader interorbital regions than *Gorilla*.

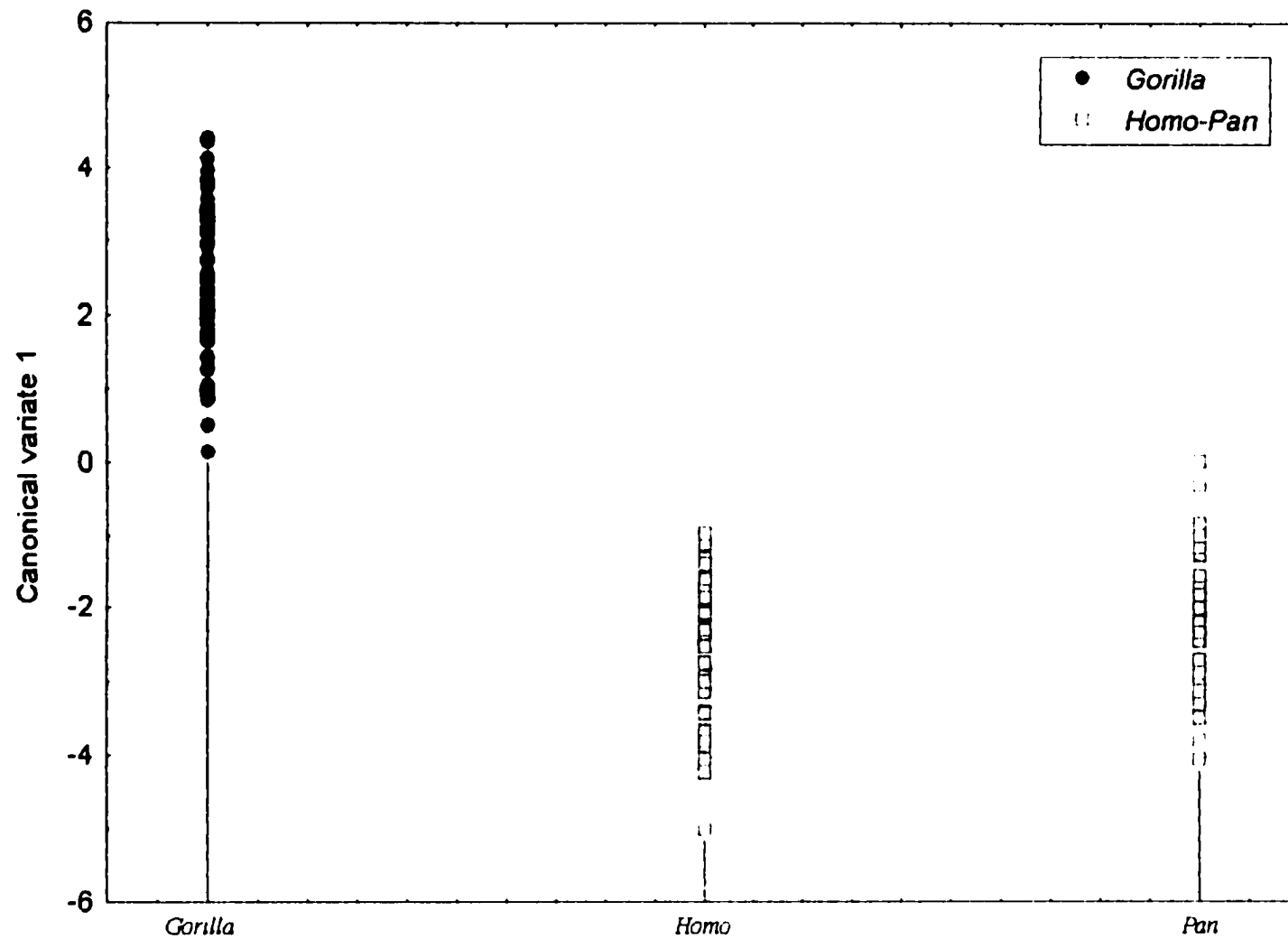
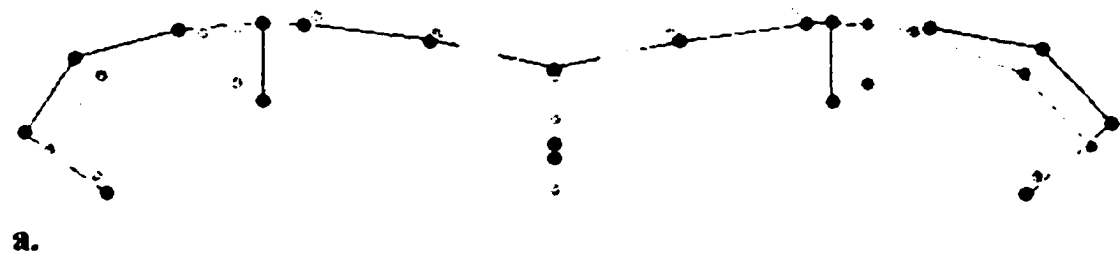


Figure 7-28 Plot of CV scores for the discriminant axis separating *Gorilla* from the *Pan-Homo* clade. Although only the two groups were used for class variables, these results are illustrated by genus to better depict the distribution of specimens on the axis.



• *Homo-Pan morphology*
 • *Gorilla morphology*

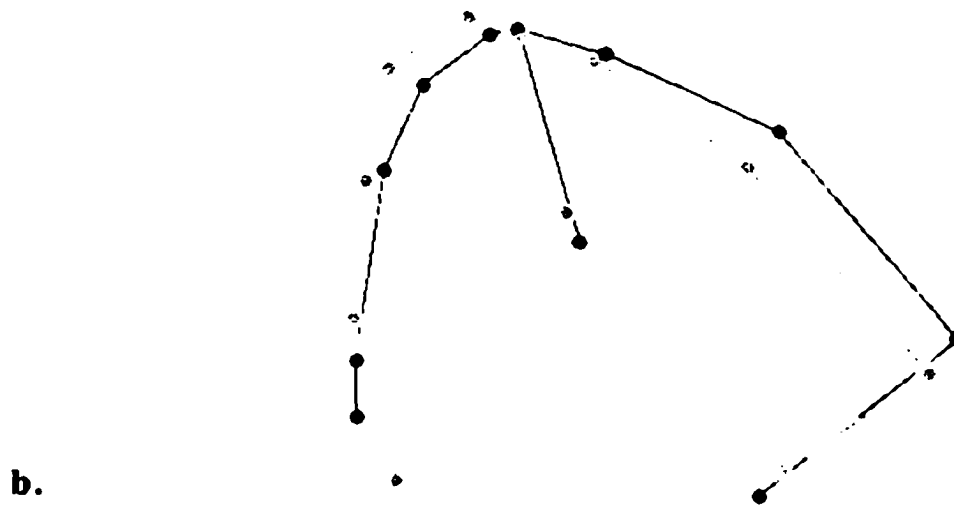


Figure 7-29 Shape change corresponding to the discrimination between *Homo-Pan* (gray) and *Gorilla* (black). (a) frontal view; (b) lateral view. See Figure 7-1 for landmark references.

Node 6: *Pan* vs. *Homo*

The differences between *Homo* and *Pan* are quite sharp. Cross-validation (Table 7-13) successfully grouped every specimen into the correct genus: a plot of the discriminant scores (Figure 7-30) illustrates this divide between the groups. These differences, however, are largely the differences between modern humans and the other African apes. To demonstrate this, a discriminant analysis was also performed with *Gorilla* and *Pan* in one group, and *Homo* in another. Results were similar, with the exception that one *Pan* specimen was misclassified as a human. Shape differences for both analyses are illustrated in Figure 7-31. It is fairly obvious from inspection that most of the variation between *Homo* and *Pan* is the same as that between *Homo* and *Pan-Gorilla*.

Table 7-13 Cross-validation results for DA of *Pan* and *Homo* morphologies. Each cell gives the number (n) and percent (%) of individuals from the taxa on the left assigned to the taxa across the top.

Taxon		<i>Pan</i>	<i>Homo</i>
<i>Pan</i>	N	38	
	%	100.00	
<i>Homo</i>	N		38
	%		100.00

The supraorbital ridge curve in *Homo* is more arched than in *Pan*. Unlike any of the morphologies discussed above, however, this curve is not accomplished through the inferior displacement of **L5** and **GLA**. *Homo* retains the superiorly placed glabella and midline segment of the brow that separates the African apes from the other hominoids.

The arching contour is achieved through superior placement of semi-landmarks just lateral to the midline, followed by a gradual inferior tapering beyond **MTS**. The result is a reduction in the breadth of the supraorbital ridge curve in *Homo*. In *Pan*, the supraorbital ridge curve is similar to that of *Gorilla* (see Figure 7-29), being mostly horizontal with a sharp inferior drop just medial to **FMT**. All of the midline landmarks in *Homo* are anteriorly placed relative to *Pan*. Only **GLA**, however, differs in its vertical placement, being inferiorly situated in *Pan*. One of the few differences between the *Homo* vs. *Pan* comparison and the *Homo* vs. *Gorilla-Pan* comparison is in the position of nasion; it is equivalent in both *Homo* and *Pan*, but displaced superiorly in *Gorilla* (see also Figure 7-29). The other major difference is in the mid-torus landmarks, bearing on both brow thickness and interorbital breadth. Again, the width of the overall morphology is reduced in *Homo*, yet the mid-torus landmarks are laterally displaced. Combined with the results from node 5 (see Figure 7-29) and from the *Homo* vs. *Gorilla-Pan* comparison (Figure 7-31b), it is clear that *Homo* has the broadest interorbital region relative to its size. In brow thickness, *Homo* is greater than *Pan*, but less than *Gorilla*.

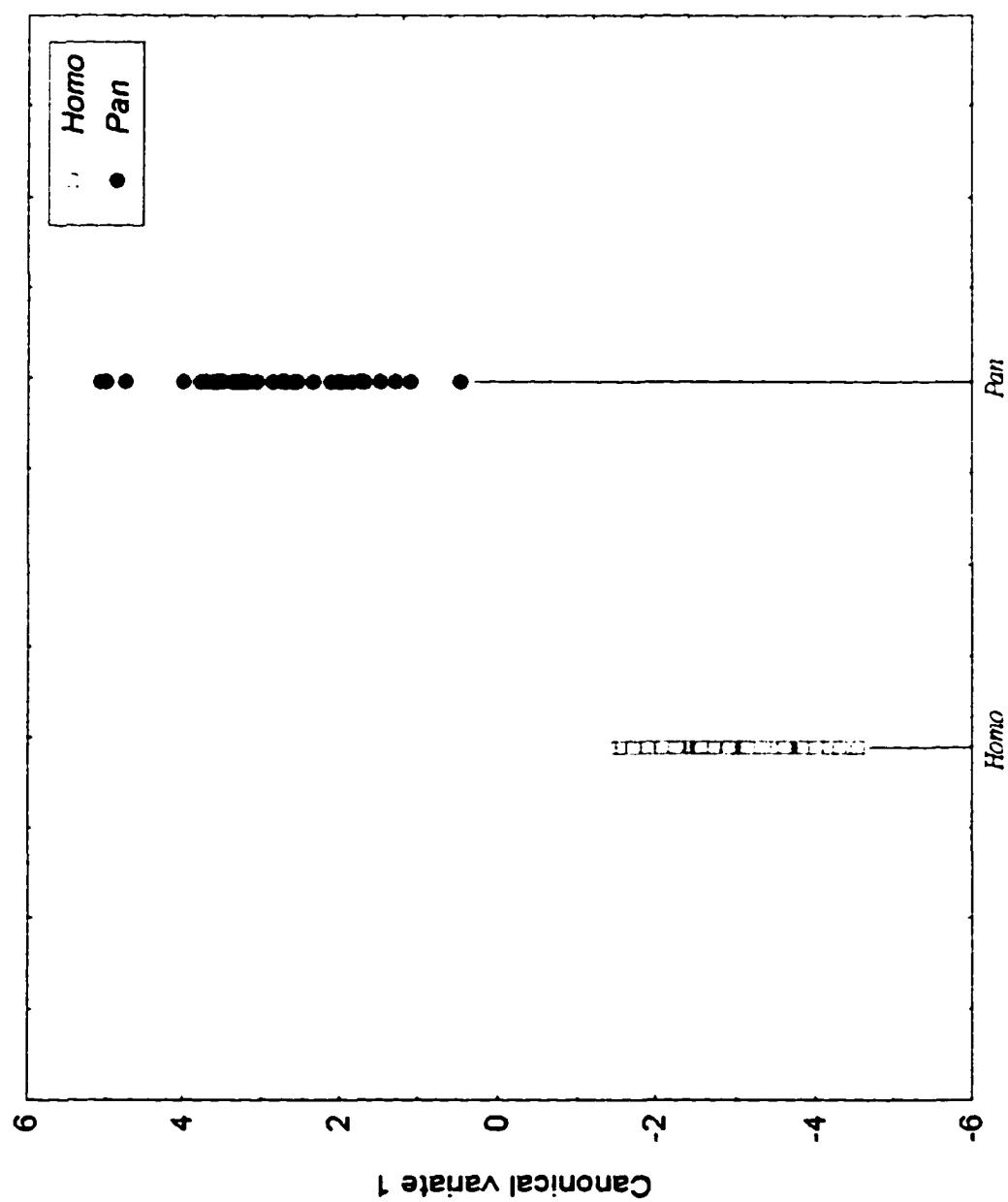


Figure 7-30 Plot of CV scores for the discriminant axis separating *Pan* and *Homo*.

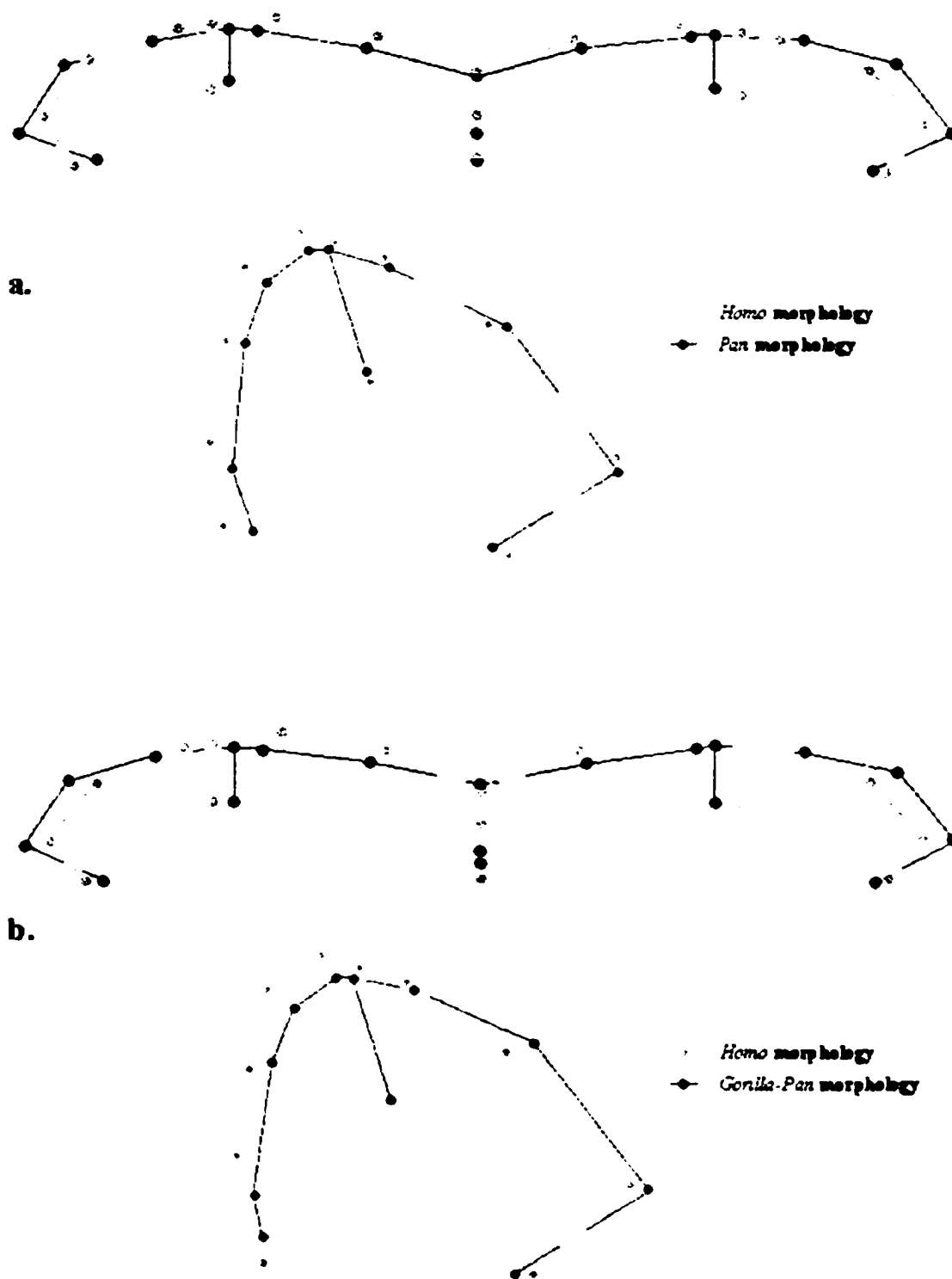


Figure 7-31 Frontal and lateral views of the shape change corresponding to discriminations between (a) *Homo* (gray) and *Pan* (black), and (b) *Homo* and *Gorilla-Pan*. Note that the shape differences in both are similar. See Figure 7-1 for landmark references.

FOSSIL SPECIMENS

Workers in hominoid morphology typically recognize two or three character states among the supraorbital morphologies of non-human extant apes. Supporters of the former (e.g., Moyà Solà & Köhler, 1993, 1995) have argued that development of a supraorbital torus is a derived character state, while lack of one is primitive. Clarke (1977), however, introduced the term *costa supraorbitalis* to differentiate the morphology of *Pongo* (and *Paranthropus*). Thus, many workers (e.g., Kelly & Pilbeam, 1986; Ward & Brown, 1986; Brown & Ward, 1988; Benefit & McCrossin, 1993, 1995; Köhler *et al.*, 2001) now recognize three supraorbital conditions among living apes. Typically, these are referred to as supraorbital rims (hylobatids), costae (*Pongo*), and tori (*Gorilla* and *Pan*). Begun *et al.* (1997), however, identified an alternative set of three character states: the lack of, presence of, or strong development of a supraorbital torus. Most workers also apply these same labels to fossil specimens, representing hypotheses of similarity between extinct and extant morphologies.

These affinities were tested using a series of discriminant analyses among genera and at each node of the consensus phylogeny. As in the principal components analysis, the fossil sample included specimens of *Afropithecus* (WK 16999), *Australopithecus* (Sts 5), *Dryopithecus* (RUD 77, RUD 200, CLI 18000), *Graecopithecus* (XIR 1), *Homo* (ER 1470, ER 1813, ER 3732, ER 3733, ER 3883), *Paranthropus* (ER 406, ER 732, ER 13750, WT 17000), *Propliopithecus* (DPC 2803, DPC 3161, CGM 42842), *Sivapithecus* (GSP 15000), and *Turkanapithecus* (WK 16950). Separate analyses were computed for the whole sample and for equal-sample replicates using both 2-group and 3-group models; assignment distributions were tested for significant differences using a χ^2 test for

equal proportions. The exact methods used here are described in detail in Chapter 5.

Results from both whole-sample and randomization analyses are shown in Tables 7-14,

7-15, and 7-16. The row immediately below class variables (e.g., genus, node) lists the

mean correct re-assignment percentages for extant taxa. The numbers in each cell show

the assignment distribution from replicate tests, while boldface indicates the single.

whole-sample assignment. An asterisk denotes *non*-significance in the proportion of

fossil assignments.

Table 7-14 Assignment of fossils to modern genera from discriminant analysis. Boldface indicates the single genus assignment for each fossil specimen based on the whole-sample analysis. Numbers show additional assignments out of 1000 randomized DAs using equal sample sizes. The first row beneath genus names lists the mean percentage of extant specimens correctly re-assigned in the replicate cross-validations. A χ^2 test for equal proportions ($\phi = 0.1$) found highly significant ($p < 0.0001$) deviations in the frequency distribution for each fossil.

		Atel	Cebu	Cerc	Papi	Pcol	Hylo	Pong	Gori	Pan	Homo
Mean reclassified in correct genus (%)		99.85	99.91	97.29	100.00	99.99	99.68	100.00	99.06	99.60	99.07
Proplio	DPC 2803	2	100		10	168	185			285	250
	DPC 3161		1			995	1	3			
	CGM 42842	30	265			9	124			281	291
Turkana	WK 16950	2					984	11		3	
Afro	WK 16999		3			44	863	1		86	3
Siva	GSP 15000	155				1	40	804			
Dryo	CLI 18000	2				7	609		251	131	
	RUD 77	57	27		31		335		23	478	2
	RUD 200	75	42		44	38		9	759	80	
Graeco	XIR 1			23	36	45	12	1	805	78	
Australo	Sts 5				4	60	97			518	321
Paranth	WT 17000								446	424	130
	ER 406								744	17	239
	ER 732		32	49	19		4	49	578	168	101
	ER 13750	5			15				403	249	328
Homo	ER 1470	71					77			49	803
	ER 1813				7			3	1	24	965
	ER 3732							10	114	414	462
	ER 3733				1		13	2		309	675
	ER 3883				1		1			21	977

Specimens of *Propliopithecus*, *Afropithecus*, *Turkanapithecus*, *Dryopithecus*, *Sivapithecus*, and *Graecopithecus* were placed into extant genera (see Table 7-14) and along branches deriving from nodes 1-4 (see Table 7-15). With the exception of *Graecopithecus*, most authors have not hypothesized that the supraorbital morphology of these taxa corresponds to that of a specific clade branching from nodes 5 or 6. Dean (see Dean & Delson, 1992), however, suggested that aspects of the morphology of *Graecopithecus* are shared specifically with *Gorilla*. XIR 1, therefore, was also evaluated at nodes 5 and 6 (see Table 7-16). Using this approach, it was possible to test alternative hypotheses about the character states of these brow morphologies.

Basal Catarrhines

Propliopithecus

In the first detailed description of these fairly complete *Propliopithecus* specimens, Simons (1987) interpreted their supraorbital morphology as “a raised supraorbital rim” like those of hylobatids (p. 276). Other researchers have variously described *Propliopithecus* as having a weakly developed (Szalay & Delson, 1979; Leakey & Leakey, 1986a, 1988b) or no supraorbital torus (Leakey et al 1988b; Shea, 1988), without specifically linking this morphology to any extant character state. Alternatively, Benefit & McCrossin (1993, 1995; McCrossin & Benefit, 1994) view the brow region of these specimens as corresponding to those of several catarrhines: *Pongo*, *Afropithecus*, *Dryopithecus*, *Sivapithecus*, and *Victoriapithecus*. Naming all of these morphologies costae, they argue that it is representative of the ancestral catarrhine morphotype (Benefit & McCrossin, 1991, 1993; McCrossin & Benefit, 1994).

Table 7-15 Results from discriminant analyses and classification of non-human catarrhine fossils at phylogenetic nodes (see Figure 7-19). 2-group analyses forced fossils into one branch deriving from the node; 3-group analyses allowed the additional option of grouping with taxa preceding the node ("primitive"). Boldface indicates the single assignment for each specimen based on DA of the entire extant sample. Numbers show additional assignments of 1000 randomized tests using equal sample sizes. The first two rows beneath taxon names list the mean percentage of extant specimens correctly re-assigned in the replicate series. * indicates a *lack of significance* from a χ^2 test for equal proportions.

Mean Cross-Validation %		NODE 1			NODE 2		
		platyrrhine	catarrhine		cercopithecoid	hominoid	primitive
2-group		99.92	99.65		99.02	99.35	
3-group					98.77	98.83	99.30
DPC 2803	2grp	202	798		348	652	
	3grp				324	656	20
DPC 3161	2grp	123	877		885	115	
	3grp				867	133	0
CGM 42842	2grp	127	863		17	983	
	3grp				1	892	107
WK 16950	2grp	3	997		43	957	
	3grp				25	953	22
WK 16999	2grp	2	998		191	809	
	3grp				188	810	2
GSP 15000	2grp	198	802		167	833	
	3grp				58	720	222
CLI 18000	2grp	17	983		81	919	
	3grp				5	986	9
RUD 77	2grp	21	979		0	1000	
	3grp				1	993	6
RUD 200	2grp	150	850		8	992	
	3grp				57	943	0
XIR 1	2grp	0	1000		98	902	
	3grp				93	907	0

Table 7-15 (cont.)

Mean Cross-Validation %		NODE 3			NODE 4		
		hylobatid	hominid	primitive	pongine	hominine	primitive
2-group		99.93	99.35		100.00	100.00	
3-group		99.52	96.32	95.45	100.00	100.00	100.00
DPC 2803	2grp	44	956		0	1000	
	3grp	55	190	755	0	64	954
DPC 3161	2grp	2	998		122	878	
	3grp	0	194	806	35	1	964
CGM 42842	2grp	175	825		5	995	
	3grp	163	232	605	0	102	898
WK 16950	2grp	996	4		529*	471*	
	3grp	1000	0	0	3	0	997
WK 16999	2grp	509*	491*		451	549	
	3grp	998	1	1	3	87	910
GSP 15000	2grp	634	366		931	69	
	3grp	306	406	288	983	0	17
CLI 18000	2grp	524*	476*		15	985	
	3grp	947	41	12	0	16	984
RUD 77	2grp	351	649		46	952	
	3grp	135	713	152	0	0	1000
RUD 200	2grp	149	851		23	977	
	3grp	60	916	24	0	354	646
XIR 1	2grp	88	912		30	970	
	3grp	37	959	4	0	971	29

Generic discrimination of *Propliopithecus* demonstrated two distinct patterns among the three specimens. DPC 2803 and CGM 42842 had remarkably similar classification distributions, spread broadly through a number of extant taxa. Both were classified with *Pan* in the whole-sample analysis and in 28% of the replicates. They also grouped frequently (> 25%) in *Homo*—this being the most frequent placement of CGM 42842 at 29%—and among *Cebus* and *Hylobates* in at least 10% of the replicates. DPC 2803, unlike CGM 42842, classified with *Procolobus* in 17% of the randomizations. This broad pattern of classification is starkly contrasted by the results for DPC 3161, which

grouped with *Procolobus* in more than 99% of the replicates. The cluster analysis of Mahalanobis D^2 values performed above demonstrated a distinct separation between cercopithecoid supraorbital morphologies and those of the other taxa. DPC 3161 seems to share this morphology with the Old World monkeys sampled here. The other two specimens of *Propliopithecus* do not have strong affinities with any of these genera, although *Pan* and *Homo* received the most classifications. Node analyses tended to be more uniform, with one notable exception. All three specimens placed fairly strongly among catarrhines at node 1. At node 2, however, DPC 2803 and CGM 42842 were well supported among hominoids, even in 3-group analyses. DPC 3161, however, placed with cercopithecoids in better than 85% of both 2- and 3- group replicates. This is not surprising given its performance in genus discriminations. Nevertheless, it indicates that at least one specimen of *Propliopithecus* has a brow more like an Old World monkey in those features which distinguish them from apes. Other results were fairly uniform, with all three specimens grouping with hominids (at node 3) and hominines (at node 4) in 2-group analyses, but placing strongly in the "primitive" category in 3-group tests.

Given the disparity between assignment distributions here, it seems counterproductive to ascribe to this genus a single phylogenetic interpretation. Nevertheless, the character state hypotheses described above are not really supported by *either* pattern of classification. A moderate affinity between the morphologies of *Propliopithecus* and *Hylobates* was found in generic discriminations. Yet, the two specimens for which this is true are more similar to both *Pan* and *Homo*; CGM 42842 is also more similar to *Cebus*. The third specimen demonstrated no affinity to the lesser ape brow morphology. This conclusion was reinforced by node 3 results, where

Propliopithecus was decidedly more like hominids in 2-group tests, but placed in the “primitive” group when given the opportunity. Thus, Simons (e.g., 1987) referral of this character to the gibbon morphology is not supported here. The hypothesized similarity between these specimens and *Pongo* (Shea, 1988; Benefit & McCrossin, 1993, 1995; McCrossin & Benefit, 1994) found even less support in these tests: only one specimen classified with the orangutans in genus discriminations, and that in only 3 of the thousand replicates. In the features separating pongines from hominines, all three specimens were accorded to hominines in 2-group tests, but placed strongly in the “primitive” category in 3-group analyses.

Thus, neither hylobatid nor pongine affinities were evident in these *Propliopithecus* specimens. Surprisingly, two of the fossils seem most similar to the hominines, although low replicate support among genera and the recurring classifications of “primitive” at node 4 do not evince the strength of this affinity. The broad distribution of generic assignments for DPC 2803 and CGM 42842 suggest that they do not bear a strong resemblance to any of these genera. DPC 3161, on the other hand, demonstrates a clear affinity to the cercopithecoids—in particular *Procolobus*. In fact, looking specifically at node 2 one could characterize the morphology of *Propliopithecus* as either ape-like (DPC 2803, CGM 42842) or monkey-like (DPC 3161). In using this genus to represent basal catarrhines, such polymorphism presents somewhat of a hindrance. Nevertheless, having two models for basal catarrhines can still be useful in discarding some hypotheses, as shown above. Alternatively, perhaps there is a more fundamental question that should be asked. Is it possible that these three specimens of *Propliopithecus* comprise more than one taxon (*contra* Simons, 1987)?

Early Miocene putative hominoids

Afropithecus

The supraorbital morphology of *Afropithecus* was originally described (Leakey & Leakey, 1986a) as a thin torus (see also Leakey *et al.*, 1988b, 1991). One can infer that their usage of the term “torus” was one of convenience (see, e.g., Szalay & Delson, 1979), rather than a specific character state hypothesis. And, indeed, Leakey & Walker (1997) described this morphology as supraorbital costae, specifically linking it to a model of the ancestral catarrhine morphology (see Benefit & McCrossin, 1993, 1995; McCrossin & Benefit, 1994; see above). Alternatively, Moyà Solà & Köhler (1993, 1995) identify the *Afropithecus* morphology as primitive among hominoids. Note that, despite appearances, this is a substantively different hypothesis from that proposed by Benefit & McCrossin (e.g., 1993). Moyà Solà & Köhler (e.g., 1995) treat hominoid supraorbital morphology as a binary character (presence/absence of a torus) and do not recognize costae as a distinct character state. Thus, while both models conclude that the brow of *Afropithecus* is primitive, one does so because of shared morphology with (among others) *Pongo*—the other due to a lack of shared morphology with African apes. Pickford *et al.* (1997) and Köhler *et al.* (2001) recognize the brow of *Afropithecus* as primitive among hominoids, but differentiate it from the morphology of *Pongo*. See below (i.e., *Sivapithecus*) for a complete discussion of this discrepancy (compare, e.g., Moyà Solà & Köhler, 1995; Pickford, Moyà Solà & Köhler, 1997).

Results from my analyses argue against some of these hypotheses, but do not provide strong support for an alternative. Discriminant analyses among genera placed the *Afropithecus* morphology with hylobatids in both the whole-sample test and in 86% of

the replicates (see Table 7-14). At node 1, this specimen grouped almost unanimously with the catarrhines. Node 2 results strongly supported grouping this specimen with the apes in those features which distinguish hominoids from cercopithecoids (see Table 7-15). The results at node 3, however, were somewhat different. In the 2-group analysis, *Afropithecus* morphology was demonstrably ambiguous—grouping with the great apes in the whole-sample analysis, but splitting evenly (χ^2 : $p = 0.5692$) in the replicate tests (see Table 7-15). On the other hand, when the primitive category was added, WK 16999 placed strongly with *Hylobates*. In such a case, the 2-group result takes precedence (see discussion in Chapter 5), indicating that *Afropithecus* morphology is similar to neither hylobatids nor hominids in the features that distinguish them: if this specimen clearly belongs in neither group, then the question as to whether it should be classified into one of them (vs. a third) becomes moot. Note, this result does not necessarily imply that *Afropithecus* morphology is the “average” of a gibbon and great ape features. Node 4 results were nearly equal in the 2-group tests, but placed *Afropithecus* strongly in the “primitive” group in the 3-group.

There is no support in these analyses for grouping *Afropithecus* supraorbital morphology with *Pongo* (cf. Benefit & McCrossin, 1993, 1995). Of a thousand replicate discriminations among genera, only one supported such a link. In the 2-group analysis at node 4, *Afropithecus* grouped fairly equally with hominines and pongines; in the 3-group, it was overwhelmingly placed in the “primitive” category. Both results suggest that the brow morphology of *Afropithecus* is dissimilar to those of both great ape subfamilies. While these data cannot adequately address Benefit & McCrossin’s (1993, 1995) hypothesis about the morphology of the ancestral catarrhine morphotype, they argue

strongly for the exclusion of *Afropithecus* from any typology that includes *Pongo*. Whether or not this morphology is primitive for hominoids or catarrhines is more difficult to assess. At a generic level, *Afropithecus* was strongly similar to *Hylobates*, contrasting markedly with either pattern of *Propliopithecus* classifications. Conversely, their results in the node discriminations were very similar. Of interest, however, is the fact that specimens of *Propliopithecus* failed to classify at node three because they fell heavily into the “primitive” category; *Afropithecus* did not classify as if failed the χ^2 test for significance—and was demonstrably different from the “primitive” group. If *Propliopithecus* is a good model for the ancestral eucatarrhine brow morphology (e.g., Simons, 1987; Benefit & McCrossin, 1993, 1995; Leakey & Walker, 1997; but see Harrison, 1987 for a general critique of this model), then the *Afropithecus* supraorbital morphology might reasonably be grouped with hominoids based in its overall similarity to *Hylobates*. Alternatively, if this region evolved substantially between *Propliopithecus* and catarrhines of modern aspect, then it is possible that this morphology is not indicative of a hominoid pattern.

Turkanapithecus

The initial descriptions of WK 16950 ascribed to it a distinct (Leakey & Leakey, 1986b) or thick (Leakey *et al.*, 1988a) supraorbital torus, though Kordos & Begun (1997) argue that it is less well developed than that of RUD 77. Often referred to in the literature, few studies have directly analyzed the morphology of *Turkanapithecus* in a systematic manner. Those that have (e.g., Rae 1993, 1997), primarily dealt with the middle and lower face in order to include other small-bodied Miocene catarrhines in the

analyses. In general, most authors concur with the original description of thickened supraorbital tori (e.g., Rae, 1993; Harrison, 2002).

Results here strongly support the affinity between the supraorbital morphologies of *Turkanapithecus* and *Hylobates*. This was demonstrated in the whole-sample discrimination among genera, with 98% support from equal-sample replicates. At nodes 1 and 2, the *Turkanapithecus* brow grouped strongly with catarrhines (99% support) and hominoids (95% support), respectively. At node 3, WK 16950 placed overwhelmingly among the hylobatids in both 2-group and 3-group analyses. Note that this is very different from results in *Propliopithecus* and *Afropithecus*. At node 4, the whole-sample discrimination assigned *Turkanapithecus* to the pongines, but replicates demonstrated this to be spurious—classifications split evenly (χ^2 : $p = 0.0666$) between pongines and hominines; this was further demonstrated by 91% placement among the “primitive” category in 3-group tests.

Thus, all of the evidence reported here supports allocation of the *Turkanapithecus* morphology to the same character state as that of *Hylobates*. There is also a distinction between these results and those shown for *Propliopithecus* (either model). To wit, the results at node 3 show a marked affinity between hylobatids and WK 16950 in those features that separate gibbons from great apes. Thus, one might reasonably suggest that *Turkanapithecus* displays a hominoid supraorbital morphology. On the other hand, several authors (e.g., Vogel, 1968; Delson, 1975, 1977; Delson & Andrews, 1975; Szalay & Delson, 1979; Andrews, 1985; Harrison, 1987; Strasser & Delson, 1987) have suggested that hylobatid faces are similar to the ancestral catarrhine morphotype. Tabulated lists provided by Andrews (1985) and Harrison (1987), however, do not list

supraorbital morphology as part of the model. Ironically, Simons (1987), arguing that *Propliopithecus* is similar to the ancestral hominoid morphotype, specifically listed a gibbon-like brow for stem hominoids. It was shown here, of course, that *Turkanapithecus* and *Propliopithecus* have very different affinities and that the latter is not greatly similar to hylobatids.

Late Miocene Hominoids

Sivapithecus

Since its discovery in 1979, most researchers have agreed that the craniofacial morphology of *Sivapithecus* most resembles that of *Pongo*. Many have suggested that this affinity is indicative of a close evolutionary relationship (e.g., Pilbeam, 1982; Ward & Kimbel, 1983; Shea, 1985; Ward & Brown, 1986; Andrews & Martin, 1987; Brown & Ward, 1988; Andrews, 1992; Moya Solà & Köhler, 1993, 1995; Andrews, *et al.*, 1996; Begun & Kordos, 1997; Pickford *et al.*, 1997; Köhler *et al.*, 2001). Others, however, have argued that its overall morphology may represent retention of a more primitive hominoid *Bauplan* (Corrucini & McHenry, 1980; Kelley & Pilbeam, 1986; Pilbeam *et al.*, 1990; Pilbeam & Young, 2001). Referring specifically to the brow morphology, the supraorbital costae are typically thought to be shared with pongines (Shea, 1985, 1988; Kelley & Pilbeam, 1986; Ward & Brown, 1986; Andrews & Martin, 1987; Brown & Ward, 1988; Pickford *et al.*, 1997; Köhler *et al.*, 2001), primitive catarrhines (e.g., Leakey *et al.*, 1988b, 1991; Benefit & McCrossin, 1993, 1995), or primitive hominoids (Moya Solà & Köhler, 1993, 1995).

It is important to note a fundamental shift in argumentation here. Moya Solà & Köhler (1993, 1995) regard the lack of a supraorbital torus as primitive for hominoids.

thus linking *Sivapithecus* and *Pongo* brows with those of all known fossil and extant apes except *Pan* and *Gorilla*. Pickford, Moyà Solà, & Köhler (1997) and Köhler, Moyà Solà, & Alba (2001), however, specifically use supraorbital costae as a derived character to unite a clade of Eurasian pongines. This represents both a change in their opinion (perhaps based on more recent fossil discoveries) and recognition that the supraorbital costae of *Pongo* are a derived character. Their position is somewhat confused, however, by inclusion of *Hylobates* in this pongine character state (Pickford *et al.*, 1997: 464), rather than in their category for primitive hominoid morphology ("superciliary arches thin"). By linking hylobatids to a defining feature of their pongine clade, one can infer that either *Hylobates* is a pongine (supraorbitally derived from a more primitive hominoid morphotype; Pickford *et al.*, 1997), or that this feature is not exclusively diagnostic of pongines (Moyà Solà & Köhler, 1993, 1995). Both of these conclusions cannot be true (*contra* Pickford *et al.*, 1997).

Discriminant analyses performed here confirm the similarity between *Sivapithecus* and *Pongo* brow morphologies. Analyses at the genus level assigned GSP 15000 to orangutans based on the entire sample and in more than 80% of the replicates; *Ateles* scored the second most assignments with 16% of the total. Similar levels of support placed *Sivapithecus* among catarrhines (node 1) and hominoids (node 2), in agreement with the whole-sample tests. At node 3, however, *Sivapithecus* was assigned to hylobatids in the 2-group whole-sample analysis, with moderate support from replicates. 3-group analyses, however, placed *Sivapithecus* among the hominids, with corroboration from replicate series. χ^2 tests show both of these results to be significant, but support—particularly for the 3-group analysis—was generally weak. Of the features

that separate the morphologies of hominids from hylobatids. GSP 15000 resembles the latter in the majority of random samples. Such results can be interpreted in support of the hypothesis that *Sivapithecus* retains some aspects of the primitive hominoid morphology (following, e.g., Moyà Solà & Köhler, 1993, 1995). However, generic-level and node 4 analyses give strong evidence of its pongine affinities—it placed with the genus *Hylobates* in only 4% of the replicates.

The majority of evidence here supports the affinity between supraorbital morphologies of *Pongo* and *Sivapithecus*. Contradicting evidence from node 3 is fairly weak in the 2-group analyses and non-existent in the 3-group analyses. And, there is strong support linking GSP 15000 to *Pongo* both in features that discriminate between pongines and hominines, and those that separate extant genera. If the brow configuration of *Hylobates* is a good model of the stem hominid supraorbital condition (e.g., Simons, 1987), then such results at node 3 might be expected (McNulty, in press). This is especially true given the highly unique nature of the pongine configuration (see Table 7-7; Figure 7-18). The inclusion of *Sivapithecus* within Benefit & McCrossin's (1993, 1995) model of ancestral catarrhine supraorbital morphology does not follow from these results. There is no evidence of similarity between GSP 15000 and any of the *Propliopithecus* specimens, as measured by their performance here.

Dryopithecus

Recent discoveries of *Dryopithecus* cranial remains (Kordos, 1987; Begun & Moyà Solà, 1992; Kordos & Begun, 2001) have greatly added to our knowledge of—and contention over—this genus. One of the key areas of disagreements among researchers regards the condition of the supraorbital morphology. Begun (1992, 1994) and colleagues

(e.g. Andrews, 1992; Begun & Kordos, 1993; Andrews *et al.*, 1996; Begun & Kordos, 1997; Begun *et al.*, 1997; Kordos & Begun, 2001) have ascribed to *Dryopithecus* an incipient supraorbital torus, indicative of African ape affinities. Others have attributed to this genus a pongine-like supraorbital condition, based on RUD 44 (Clarke, 1977; Martin & Andrews, 1982; Ward & Brown 1986; Brown & Ward, 1988; Shea, 1988) or the new cranial specimens (e.g., Pickford *et al.*, 1997; Köhler *et al.*, 2001). Benefit & McCrossin (1993, 1995) also identified similarities between *Dryopithecus* and *Pongo* morphologies, including both in a group displaying the ancestral catarrhine condition. Kelley & Pilbeam (1986) argued that RUD 44 (retained by them in *Rudapithecus*) exhibits neither a distinct supraorbital torus, nor the morphology present on GSP 15000 (and, by inference, *Pongo*).

Results from generic analyses grouped CLI 18000 most frequently (61%) with *Hylobates*, but placed it with *Gorilla* in 25% of the replicates. RUD 77 was classified as *Pan*, but with weak support (48%) and a significant showing (34%) in *Hylobates*. RUD 200 had the most biased assignment distribution, grouping with *Gorilla* in more than 75% of the replicates. All three fossils scored similarly at nodes 1 and 2: their catarrhine and hominoid affinities were well supported. Node 3 results revealed differences among them, however. Results of the 2-group analysis indicated that CLI 18000 is similar to neither hominids nor hylobatids, but the addition of a third group caused it to cluster with *Hylobates*—nearly identical to results for WK 16999. RUD 77 grouped with the hominids at node 3, with moderate support from both 2-group (65%) and 3-group (71%) analyses. RUD 200 had a much stronger showing among the hominids, with 85% support in the 2-group discrimination and 92% support in the 3-group.

The most salient conclusion regarding *Dryopithecus* is evident in results from node 4. These analyses provide no support for grouping any *Dryopithecus* supraorbital morphology with that of *Pongo*. In the 2-group analysis, all three fossils classified with hominines in better than 95% of the replicates. For the 3-group discrimination, CLI 18000 and RUD 77 placed almost entirely in the primitive category; RUD 200 grouped there as well, but had a moderate showing (35%) with the African apes. Placement among the pongines happened in fewer than 5% of the replicates of any fossils—and happened not at all when the “primitive” option was available. These results were corroborated in the generic-level discrimination (see Table 7-14), where the three specimens placed with *Pongo* a combined 9 times (out of 3000).

Such results argue against the affinities of *Dryopithecus* and *Pongo* supraorbital morphologies either as a derived pongine (Pickford *et al.*, 1997; Köhler *et al.*, 2001), primitive hominoid (e.g., Moyà Solà & Köhler, 1993, 1995), or primitive catarrhine (Benefit & McCrossin, 1993, 1995) feature. While other characters have been cited in support of a distinct Eurasian pongine clade (see Köhler *et al.*, 2001), the supraorbital shape, as represented by these data, does not support allocation of *Dryopithecus* to this group. In the same vein, this evidence weakens the support justifying a pongine supraorbital morphology in the ancestral catarrhine (e.g., Benefit & McCrossin, 1993). Indeed, despite substantial variation among these three fossils, none of them displays a supraorbital morphology similar to *Pongo*. The hypothesis that *Dryopithecus* morphology is undifferentiated into a modern morphology (Kelley & Pilbeam, 1986; Moyà Solà & Köhler, 1993, 1995) is not corroborated here based on comparisons with *Propliopithecus*. In fact, both fossils from Rudabánya have morphology that is reasonably placed among

the Hominidae. Within this group, they are most similar to African ape genera (see Table 7-14), but do not place within the hominines as a whole when given the option of “primitive.” Similarly, McNulty (in press) has shown that neither specimen bears a close affinity to the *Gorilla* or *Pan-Homo* clade when analyzed in a 2-group discrimination. The conclusion, then, must be that this morphology is somewhat different from the African ape torus.

The Spanish specimen (CLI 18000) displayed results that were substantially different from the Rudabánya specimens. In nearly all of the pertinent analyses, its morphology was most similar to that of hylobatids. Results of the replicate analyses, however, suggest that this may not be indicative of a close affinity—among genera, it grouped with *Hylobates* only 61% of the time. Moreover, the 2-group analysis at node 3 suggests that CLI 18000 has affinities with neither hylobatid nor hominid morphology. As discussed for *Afropithecus* (see above), the 3-group results here likely reflect this specimen’s *dissimilarity* from the hominid-primitive pole of the canonical axis. The overall results of this specimen were most similar to those of *Afropithecus*. Yet, in this case there was not a strong affinity with the hylobatid morphology. It is possible that the differences between CLI 18000 and the Hungarian specimens represent specific differences within *Dryopithecus*, or a higher-level taxonomic distinction (see Cameron, 1999). Indeed, such results might be expected for a stem hominid (e.g. Andrews, 1992) that does not share any particular features with extant apes. Alternatively, one must also consider the possibility that these results reflect poor preservation. While this specimen was assumed to retain the entire left zygomatic process of the frontal (Begun, 1994; Moyà Solà & Köhler, 1995), it is possible that the lateral termination of the CLI 18000

frontal is a break, rather than a suture. If so, morphometric data from this specimen would not be comparable to those from other specimens. In any case, these supraorbital data align this specimen best with hylobatids, but only tentatively.

Table 7-16 Results from discriminant analyses and assignments of human fossils and *Graecopithecus* at phylogenetic nodes 4-6. Boldface indicates the assignment for each specimen based on DA of the entire extant sample. Numbers show additional assignments from 1000 randomized tests using equal sample sizes. The first row beneath each taxon name gives the mean percentage of extant specimens correctly re-assigned in the replicate series. * indicates a *lack of significant difference* from χ^2 tests for equal proportions. See text for further discussion.

Mean Cross-validation Percentage (%):	NODE 4		NODE 5		NODE 6	
	pongine	hominine	<i>Gorilla</i>	<i>Homo-Pan</i>	<i>Pan</i>	<i>Homo</i>
	100.00	100.00	98.39	98.63	100.00	100.00
XIR 1	30	970	670	330	805	195
Sts 5	0	1000	0	1000	573	427
WT 17000	69	931	41	959	655	345
ER 406	3	997	2	998	187	813
ER 732	8	992	194	806	258	742
ER 13750	17	983	0	1000	479*	521*
ER 1470	0	1000	0	1000	1	999
ER 1813	36	964	4	996	534	466
ER 3732	45	955	112	888	603	397
ER 3733	26	974	0	1000	144	856
ER 3883	12	988	0	1000	65	935

Graecopithecus

The Late Miocene hominoid from Greece (Bonis & Koufos, 1993) is generally regarded as more derived in supraorbital morphology than its *Dryopithecus* contemporaries (but see Moyà Solà & Köhler, 1993, 1995). Pickford *et al.* (1997) and Köhler *et al.* (2001) have described this region as pongine-like—more advanced than the costae of *Dryopithecus*, but less so than those of *Sivapithecus* and *Pongo*. Others (e.g., Begun, 1992, 1994; Dean & Delson, 1992; Benefit & McCrossin, 1995; Andrews *et al.*,

1996) have likened the *Graecopithecus* morphology to that of the African apes, or specifically to *Gorilla* (see Dean & Delson, 1992). De Bonis and colleagues (Bonis & Koufos, 1993, 1994, 1997, 2001), alternatively, argue that the particular morphology of the *Graecopithecus* supraorbital torus is a derived condition shared with the hominin lineage.

In generic-level analyses, XIR 1 was assigned to *Gorilla* based on the entire sample, and supported there in more than 80% of the equal-sample replicates. *Pan* was its second most frequent assignment (8%), while all other genera received fewer than 5%. Results from each analysis at nodes 1-4 (see Table 7-15) were fairly straightforward: the *Graecopithecus* morphology was strongly (> 90%) supported as similar to catarrhines, hominoids, hominids, and hominines. At node 5, XIR 1 grouped with *Gorilla* over the *Pan-Homo* clade, receiving moderate support (67%) from replicates. In discrimination between *Pan* and *Homo* (node 6), this specimen was demonstrably more similar to the morphology of the former.

Based on these data, one cannot conclude that *Graecopithecus* and *Pongo* share a common supraorbital morphology (*contra* Pickford *et al.*, 1997; Köhler *et al.*, 2001). In only one out of a thousand generic-level replicates was XIR 1 classified with the orangutans. At node 4, 3% of the 2-group replicates grouped it among pongines; none of the 3-group replicates did. Similarly, the affinities between XIR 1 and humans (e.g., Bonis & Koufos, 2001) found no support here. This specimen did not group once with *Homo* in generic level analyses, and placed with *Pan* more frequently at node 6. Alternatively, these analyses result in clear support for grouping the *Graecopithecus* morphology with the hominines. Among the hominines, XIR 1 shows a closer affinity to

Gorilla than to other genera or the *Pan-Homo* clade (see Dean & Delson, 1992). Support for this is not overwhelming, however (cf. node 5 results). In terms of character coding, analyses of these data provide strong evidence of the similarities between African ape and *Graecopithecus* supraorbital morphologies.

Plio-Pleistocene hominins

Fossil human specimens were evaluated at nodes 4-6 on the phylogenetic tree (see Figure 7-19) using 2-group discriminant analyses (see Chapter 5 for discussion). Results from the generic-level discriminant analyses are given in Table 7-14; node analysis results are presented in Table 7-16. The similarities among *Gorilla*, *Pan*, and *Homo* supraorbital morphologies make moot a discussion of character coding at nodes 5 and 6 (at least in regard to Miocene hominoid fossils). The *Pan-Homo* distance is the shortest in the equal-sample matrix (see Table 7-7); the *Pan-Gorilla* distance is only slightly longer (and the shortest distance in the whole-sample matrix). This supports the recognition of a single character state for the three hominine supraorbital morphologies. In fact, the brows of *Australopithecus* and early *Homo* are often grouped with the other African apes (e.g., Clarke, 1977; Ward & Brown, 1986; Begun *et al.*, 1997). Yet, Clarke (1977) has descriptively linked the morphology of *Paranthropus* to that of *Pongo*. Kimbel *et al.* (1984) suggested that, while early *Homo* specimens have morphologies similar to those of *Gorilla* and *Pan*, *Australopithecus* morphology is somewhat different. And finally, Leakey *et al.* (1964), in their revision of the genus *Homo*, ascribed to it a diversity of supraorbital morphologies, "ranging from a massive and very salient supra-orbital torus to a complete lack of any supra-orbital projection and a smooth brow region" (p. 7). The results below, then, examine these suppositions.

Australopithecus

The supraorbital morphology of Sts 5 was classified with *Pan* in the whole-sample analysis of genera, but received weak (52%) support from the replicates—it grouped with *Homo* in 32% of them. At nodes 4 and 5, the Sts 5 morphology was classified among hominines and the *Pan-Homo* clade (respectively) with complete agreement from replicate tests. Node 6 analyses were less decisive. The whole-sample discrimination classified Sts 5 with *Homo*. Results from replicate series showed a significant difference (χ^2 : $p < 0.0001$), but similar distribution in both genera provided only weak support. It is tempting to interpret such results as evidence of the transition from a chimpanzee-like ancestral morphology towards a modern human morphology. Yet, they could equally be interpreted (see Neff & Marcus, 1980) as indicating that Sts 5 morphology is dissimilar from both *Pan* and modern *Homo* (Kimbel *et al.*, 1984).

Paranthropus

Three of the four brow morphologies of *Paranthropus* specimens were classified with *Gorilla* in the whole-sample analysis. Of these, WT 17000 had the least support (45%) in replicate analyses, with 42% placement in *Pan* and 13% in *Homo*. ER 732 grouped with *Gorilla* in 58% of the replicates, *Pan* in 17%, and *Homo* 10%. ER 406 had the strongest support in *Gorilla* at 74%; it placed with *Homo* in 24% of the replicates and *Pan* in fewer than 2%. Unlike the other *Paranthropus* specimens, the brow morphology of ER 13750 grouped with *Homo* in the whole sample analysis. Replicate tests, however, suggest that this results stems from the differences in sample sizes (see above). Even accounting for that, however, this specimen had similar representation in all three hominine genera: 40%-*Gorilla*, 33%-*Homo*, 25%-*Pan*.

All specimens grouped in both hominine and *Pan-Homo* clades, with strong backing from the replicate tests. Results from node 6 were interesting in that the whole-sample and replicates tests differed for every specimen but WT 17000—it grouped in *Pan* with 66% support. The other three specimens were also classified with *Pan* from the whole-sample discrimination, but placed more frequently in *Homo* when sample sizes were equal. The difference was negligible for ER 13750, as its classifications split evenly (χ^2 : $p = 0.1841$). The morphologies of ER 406 and ER 732, however, were placed with *Homo* in 81% and 74% (respectively) of the replicates (χ^2 : $p < 0.0001$). The results from randomized equal-sample analyses are likely to be more useful than those from the whole-sample analysis, as the small sample size of *Homo* was shown (see above) to affect the outcome of such tests.

Regarding the differences that separate these genera, the supraorbital morphology of *Paranthropus* specimens is most similar to *Gorilla*. Each, however, also has a significant number of classifications with the other hominines. The differences between a *Gorilla* and a *Pan-Homo* clade, however, sort these specimens towards the latter. What there is no evidence of here, though, is an affinity between the *Paranthropus* configurations and those of *Pongo*. Only ER 732 grouped with the orangutans in generic discriminations—at a frequency of just under 5%. At node 4, the WT 17000 morphology was grouped with the pongines in only 7% of the replicates; the others placed there in fewer than 2%. While the descriptive criteria for supraorbital “costae” (see Clarke, 1977) are visible (to varying degrees) in *Paranthropus*, the overall shape of this region is very different from *Pongo*. Regarding them as the same, then, adds potentially misleading information to any evolutionary analysis.

Early *Homo*

The supraorbital morphologies of these East African early *Homo* specimens were mostly classified in the genus *Homo*; the one exception was ER 3732, which placed in *Pan*. In replicate tests, there was strong support for the classifications of ER 1470, ER 1813, and ER 3883. ER 3733 had moderate support, with 68% of the replicates placed in *Homo*. ER 3732 had more replicate classifications in *Homo* (46%) than in *Pan* (41%), but the difference was minor; it also had 11% placement within the genus *Gorilla*. Results from nodes 4 and 5 demonstrated strong affinities between these morphologies and the hominine and *Pan-Homo* configurations. At node 6, the two specimens of early *Homo* were classified with *Pan* in the whole-sample discrimination. Replicate series showed a significant difference (χ^2 : $p = 0.0315$) for ER 1813, but the similarity in assignment distributions made such support weak; ER 3732 had somewhat better support (60% *Pan*, 40% *Homo*). The other specimens of fossil *Homo* were classified with the modern *Homo* morphology at node 6. ER 1470 had the most support from the replicates, receiving only 1 classification (out of 1000) among the chimpanzees. ER 3733 and ER 3883 were strongly supported within *Homo* at (86%) and (94%), respectively.

DISCUSSION

Like the previous one, this chapter can be divided into two sections. The first employed analyses guided purely by exploratory phenetics, with a goal of examining structures manifest within the data. This included principal components analysis, canonical variates analysis, taxon clustering, and other considerations of Mahalanobis distances. The second section was based upon an underlying phylogenetic assumption of

relationships within the Hominoidea, and among hominoids, cercopithecoids, and platyrrhines. Using this framework, discriminant analyses were used to explore shape differences distinguishing supraorbital morphologies from these clades and to test hypotheses regarding the affinities of fossil brow morphologies. Overall results from both sections are discussed below.

Data-driven analyses

Principal components, canonical variates, and cluster analyses provided some interesting insights into the phenetic relationships of these extant adult supraorbital morphologies. The greatest difference among these specimens separates the two platyrrhines, *Hylobates*, and *Pongo* from the rest of the catarrhines. Indeed, the supraorbital morphologies of *Ateles* and *Hylobates* were demonstrably similar in most analyses. *Pongo*, on the other hand, displays the most unique supraorbital configuration. While most similar to *Ateles*, it has the largest Mahalanobis distances among all taxa (see Table 7-7; Figure 7-18). *Cebus* is also most similar to *Ateles*, but fairly distinct in its morphology. In the minimum spanning tree (Figure 7-17), the branch between these two genera is second only to *Pongo-Ateles* in length. Moreover, the distance between *Cebus* and the *Ateles-Hylobates* cluster (Figure 7-18) is similar to the distance between the cluster of cercopithecoids and African apes. It should also be reiterated that *Cebus* specimens, unlike those of other taxa, did not cluster together on the first two canonical variate axes (see Figure 7-8). This suggests that the structure of intrageneric variation within *Cebus* is largely different from that of the other taxa. In fact, the axes that comprise the majority of *among*-group differences here also represent substantial *within*-

group differences for *Cebus*. Overall, these data show a clear affinity between *Ateles* and *Hylobates*. *Pongo* and *Cebus*, however, appear to be separately unique among these taxa.

The effects of sample size differences were tested using randomized replicate canonical variates analyses. The most significant difference between whole-sample and equal-sample replicate analyses was in the distance relationships of *Homo*. When the entire sample of extant specimens was used to compute Mahalanobis D^2 values, *Homo* clustered with a group of *Ateles*, *Hylobates*, and *Cebus*. This was misleading, however, as the configuration of *Homo* supraorbital morphology was most similar to that of *Pan* (see Table 7-7: lower triangle; Figure 7-17). When sample size was controlled, *Homo* was still closest morphologically to *Pan*, but their separation became the shortest in the distance matrix (Table 7-7: upper triangle); this, in turn, was reflected in the UPGMA cluster (Figure 7-18b).

Aside from *Ateles*, *Hylobates*, *Cebus*, and *Pongo*, there were two distinct clusters of supraorbital morphology: cercopithecoids and hominines (including *Homo* in equal-sample analyses). Among extant hominoids, then, there is ample morphometric evidence for recognizing three distinct character states, corresponding to the morphologies of *Pongo*, *Hylobates*, and the hominines; this conclusion supports the descriptive distinctions drawn by many researchers (e.g., Clarke, 1977; Shea, 1985; Kelly & Pilbeam, 1986; Ward & Brown, 1986; Brown & Ward, 1988; Benefit & McCrossin, 1993, 1995; Köhler *et al.*, 2001). One could further divide living apes into 4 morphologies. Yet, the difference between D^2 values of *Gorilla-Pan* and *Homo-Pan* is minimal (Table 7-7). There is no evidence here to support a separate character state for modern human supraorbital morphology, as captured by these data. The phenetic distance

between *Homo* and *Pan* is the shortest value in the equal-sample distance matrix; if those are not recognized as a single state, then no clusters would be. The close affinity between these two is actually somewhat surprising. Despite the highly autapomorphic nature of modern human crania (see, e.g., results in Chapter 6), there is clear metric evidence here demonstrating retention of a hominine supraorbital configuration.

The final group of extant morphologies is the cluster of cercopithecoids. It is interesting to note the mixing of seemingly different morphologies here: a bar-like torus in *Papio* clustered with the simple superciliary arches or rims of *Cercopithecus*.

Traditional descriptive labels for these morphologies crosscut the metric affinities described by their landmark configurations; indeed, *Papio* would group with the African apes under descriptively defined character states. Yet, the morphometric evidence points to a clearly demarcated cercopithecoid cluster. A comparison of among cluster distances (Figure 7-18) argues for the recognition of a unique character state for these monkeys.

Phylogenetic node discrimination

Analyses based on the assumed consensus phylogeny (Figure 7-19) were performed with three goals in mind. First, the supraorbital morphologies represented by members of crown clades were tested to determine their robusticity for delineating between branches at each node. Discriminations correctly reclassified specimens with better than 95% frequency at every node; the pongine/hominine (node 4) cross-validation achieved 100% reclassification. Having demonstrated this, the second aim was to determine differences in morphology that correspond to each discriminant axis. Therefore, the shape differences at each node were visualized by adding (and subtracting)

the discriminant vectors to the consensus coordinates. These shape differences are summarized in Figure 7-17.

Table 7-17 Summary of shape differences determined from discriminant analyses between crown clades in the extant phylogeny (Figure 7-19). For each discrimination, the characteristics listed describe differences between the taxon in boldface with respect to the taxon in parentheses.

Catarrhines (vs. platyrrhines)

laterally expanded brow
 supraorbital angle more acute across front
 lateral orbital pillar thicker
 inferiorly placed fronto-malar suture
 nasion markedly superior and somewhat posterior; prominent glabella

Hominoids (vs. cercopithecoids)

reduced supero-inferior and antero-posterior dimensions
 supraorbital line more depressed medially
 broader interorbital region
 nasion more superiorly displaced

Hominids (vs. hylobatids)

brow expanded laterally
 Inferiorly placed fronto-malar suture, especially laterally
 midline and medial morphology displaced superiorly
 nasion also displaced posteriorly
 glabellar portion of supraorbital line displaced anteriorly
 lateral orbital pillar thicker
 narrower interorbital region

Hominines (vs. pongines)

midline landmarks displaced substantially superior and anterior
 supraorbital angle more acute across the front
 supraorbital line nearly flat—"bar-like"
 rapid inferior drop just medial to **FMT**
 lateral orbital pillar narrower
 broader interorbital region

Table 7-17 (cont.)

***Homo-Pan* (vs. *Gorilla*)**

brow reduced in lateral dimension

GLA-NAS expanded

reduced toral thickness

broader interorbital region

***Homo* (vs. *Pan*)**

brow reduced in lateral dimension

supraorbital line arches superiorly between the midline and MTS

midline landmarks anteriorly displaced

GLA superiorly displaced

lateral orbital pillar narrower

broader interorbital region

expanded toral thickness

The third goal was to examine the affinities of fossil supraorbital morphologies with extant genera and at each of these nodes. Fossils were treated as unknowns and then assigned to a group based on discriminant functions derived from extant taxa. This was done both on the whole sample, and with randomized equal-sample replicates.

Results of the fossil classifications clearly did not support hypothesized affinities by some researchers. Both *Afropithecus* and *Turkanapithecus* morphologies were strongly supported within catarrhines over the platyrrhine sample, and in hominoids over the cercopithecoid sample. The *Turkanapithecus* brow was very similar to *Hylobates*, both among genera and at node 3. Compared to *Propliopithecus*, this specimen was reasonably grouped with hominoids rather than stem catarrhines. The morphology of *Afropithecus* was also most similar to *Hylobates*, but node 3 results suggest that it may be fairly unique among these taxa. A comparison with *Propliopithecus* provided some

support that this morphology is more like extant apes rather than basal catarrhines; this evidence was tentative, however, compared to results from *Turkanapithecus*. There was no support here for uniting the supraorbital morphologies of *Propiropithecus*,

Afropithecus, *Dryopithecus*, *Sivapithecus*, and *Pongo* in a single, supraorbital morphology (*contra* Benefit & McCrossin, 1993, 1995). Interestingly, the three specimens of *Propiropithecus* exhibited two distinct morphologies in these analyses.

Specimens of *Dryopithecus* behaved somewhat differently from each other in these analyses. CLI 18000 was most similar to *Hylobates* among extant taxa; its overall results were remarkably like those of *Afropithecus*, but without as strong an affinity to hylobatids. An unambiguous classification for the Spanish *Dryopithecus* specimen was not forthcoming from these analyses. It is tentatively group with *Hylobates* based on its strongest affinity, but bearing in mind a possible bias due to poor preservation.

Dryopithecus specimens from Rudabánya (RUD 77, RUD 200) demonstrated stronger affinities to hominids: the RUD 77 morphology classified with *Pan*, RUD 200 grouped in *Gorilla*, and both placed with hominids at statistically significant frequencies. The hominine affinities of *Dryopithecus* were not supported here, as demonstrated by assignments to the “primitive” category of all three specimens as node 4. Thus, while the Hungarian specimens show the greatest affinity to extant hominine genera, they are not demonstrably similar to African apes and humans as a group. Above all, there was no evidence linking the supraorbital morphology of any *Dryopithecus* specimen with that of *Pongo*. The morphology of XIR 1 (*Graecopithecus*) was very well supported within the hominines, showing the greatest affinity to *Gorilla*. Like *Dryopithecus*, there was no evidence grouping this specimen with *Pongo*.

All of the human fossils placed strongly among the hominines and among the *Pan-Homo* group. The brow of Sts 5 was classified with *Pan* in generic-level and node 6 analyses, but with only weak support. The morphologies of *Paranthropus* specimens were generally most similar to *Gorilla*; at node 6, WT 17000 was closer to *Pan*, while results for WT 13750 were statistically equivocal. ER 406 and 732, however, grouped with *Homo* in a significant number of replicates. There was little evidence suggesting that *Paranthropus* morphology is similar to *Pongo* (*contra* Clarke, 1977). All of the fossil *Homo* specimens placed with modern humans at the generic level, except ER 3732 (*Pan*). At node 6, the two specimens of *Homo habilis* grouped more frequently with *Pan*, although support was weak for ER 1813. Others strongly grouped among the modern human supraorbital morphologies.

CHAPTER 8: MORPHOMETRIC ANALYSIS OF PALATAL MORPHOLOGY

Chapter 8 reviews the analyses that were performed on landmarks from the palatal morphology. As with previous chapters, principal components and canonical variates analyses are used to explore, respectively, variation among specimens and among genera. Unbiased Mahalanobis distance estimates are then discussed regarding pairwise distances between taxa in canonical space; hierarchical relationships are examined through cluster analysis. The second half of the chapter looks at the phylogenetic node discriminations used to find and test patterns of palatal variation that distinguish extant clades on a consensus phylogeny. Fossils are tested at each node to determine their best fit within this phylogeny.

Table 8-1 Landmarks used in analyses of palatal morphology. See Chapter 4 for definitions and discussion.

Landmark	Abbreviation
Midline:	
Posterior clivus	CLI
Anterior attachment of nasal septum	ANS
Alveolare	ALV
Staphylion	STA
Midline anterior palatine	MAP
Incisivion	INC
Bilateral:	
Malar root origin	MRO
I ¹ -I ² contact	I12
Inferior premaxillo-maxillary suture	IPM
Posterior incisive canal	PIC
Lingual canine margin	LCM
Canine-premolar contact	CPC
Premolar-molar contact	PMC
Distal molar	DM3

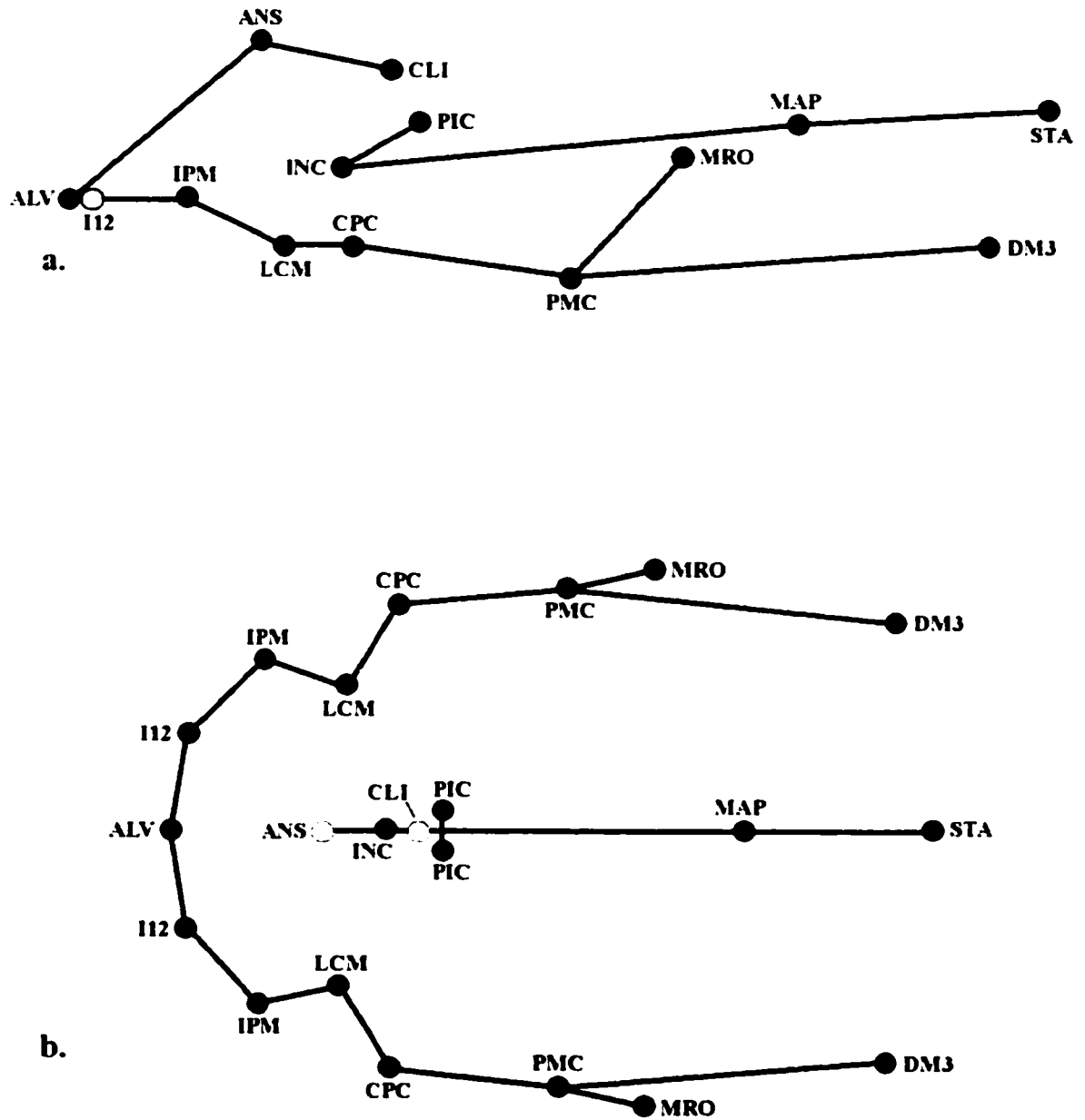


Figure 8-1 Consensus configuration of the palatal landmarks. (a) lateral view; (b) superior view. Landmark names correspond to the abbreviations given in Table 8-1. Open circles indicate landmarks that were used in analyses, but not depicted in shape diagrams. Lines connecting landmarks are provided solely to aid in visualizing shape differences.

LANDMARK CONFIGURATIONS

Landmarks used to describe the palate are listed in Table 8-1 along with their abbreviations. Figure 8-1 illustrates the consensus configuration for these landmarks from both lateral and superior views. Abbreviations shown in this figure serve as reference for all subsequent illustrations of shape deformation. Note that the contact point between medial and lateral incisors (**I12**) will not be shown in lateral view—its antero-posterior position closely tracks alveolare (**ALV**) in every case. All other landmarks will be included throughout the illustrations of shape differences in this chapter.

SAMPLE TAXA AND SIZE CORRECTION

All ten extant anthropoid genera were included in analyses of the palate. Specimens of *Morotopithecus* (UMP 62-11), *Proconsul* (RU 16000), *Propithecus* (DPC 2803, DPC 3161), and *Sivapithecus* (GSP 15000) retain the entire set of palate landmarks and were therefore included directly in principal components analysis, and classified as unknowns in discriminant analyses. Additional specimens attributed to *Rangwapithecus* (SO 700) and *Graecopithecus* (RPI 128, XIR 1) could not be included in PCA, but were analyzed in phylogenetic node discriminations using a reduced data set that did not include the posterior incisive canal (**PIC**) and staphylion (**STA**) landmarks.

There was not a clear allometric effect demonstrable in these palatal data. While several PCs were significantly correlated with centroid size, it could not be demonstrated that this correspondence resulted from allometric effects beyond those associated with taxonomic and sex differences. When these effects were factored out of the data, none of the PCs was significantly correlated with centroid size (see Chapter 5 for a full discussion

of this). Therefore, a size adjustment was not applied to palatal data; superimposed coordinate data—rather than residuals of coordinates regressed against centroid size—were therefore used in statistical analyses. See the discussion of PC 2 below regarding possible size effects in these data.

PRINCIPAL COMPONENTS ANALYSIS

A principal components analysis was performed on the covariance matrix of superimposed coordinate data from the palate. All specimens from extant taxa and most of the fossil specimens listed above were included here. ANOVAs were performed on the scores of resulting PC axes in order to test for differences among genera. Both PCA and ANOVA results are shown in Table 8-2 for the first 15 principal components, comprising more than 92% of the total sample variability. Higher-level axes were examined but are not shown here. ANOVA results indicate highly significant ($p < 0.0001$) differences among genera on these first 15 PCs. To test for differences between genera, pairwise t-tests were performed and a Bonferroni adjustment applied. T-test results are shown in Table 8-3. The first four PCs are discussed in detail below.

Table 8-2 Summary of PCA and ANOVA results for the first fifteen principal component axes. PCA results give statistics for the latent roots of the sample variance (eigenvalues), the proportion of variance explained by each component, and the cumulative proportion of the variance summarized by each PC and those preceding it. One-way ANOVAs were performed on each component to test for significant differences among genera; F-values and probabilities are given for tests of the null-hypothesis that all genera share a common mean.

	PRINCIPAL COMPONENTS ANALYSIS			ANALYSIS OF VARIANCE	
	Eigenvalue	Proportion	Cumulative	F Value	Pr > F
PC 1	0.01245742	0.4902	0.4902	493.61	<0.0001
PC 2	0.00386700	0.1522	0.6423	364.63	<0.0001
PC 3	0.00158999	0.0626	0.7049	134.24	<0.0001
PC 4	0.00113715	0.0447	0.7496	118.91	<0.0001
PC 5	0.00104652	0.0412	0.7908	47.72	<0.0001
PC 6	0.00063767	0.0251	0.8159	6.58	<0.0001
PC 7	0.00060673	0.0239	0.8398	20.67	<0.0001
PC 8	0.00046686	0.0184	0.8581	16.24	<0.0001
PC 9	0.00037344	0.0147	0.8728	6.64	<0.0001
PC 10	0.00028439	0.0112	0.8840	16.22	<0.0001
PC 11	0.00024533	0.0097	0.8937	9.47	<0.0001
PC 12	0.00022444	0.0088	0.9025	11.45	<0.0001
PC 13	0.00020774	0.0082	0.9107	20.11	<0.0001
PC 14	0.00019080	0.0075	0.9182	4.30	<0.0001
PC 15	0.00016327	0.0064	0.9246	3.87	<0.0001

Principal component 1

The first principal component represents nearly 49% of the total variability among specimens. Table 8-3 shows the results of pairwise t-tests; specimen scores for PC 1 are graphed in Figure 8-2. This axis clearly distinguishes hominids from the rest of the anthropoids. In fact, there is only minimal overlap between groups: one specimen of *Gorilla* falls within the ranges of *Cebus* and *Procolobus*. Among the hominids, means of *Homo*, *Pan*, and *Pongo* were significantly different from all other taxa, but not from each other. The mean of *Gorilla* specimens was significantly different from all taxa; although falling near the center of this axis, the range of *Gorilla* substantially overlapped those of the other hominid genera. Among the non-hominid cluster, *Papio* had the most negative mean value, while *Cebus* and *Procolobus* placed closest to zero. The means of *Ateles*, *Cercopithecus*, and *Hylobates* fell near the center of this cluster. While t-test results show

significant differences between particular pairs within this aggregate, the ranges of all non-hominid taxa overlap substantially.

Fossil specimens scored broadly across the first principal component. Specimens of *Morotopithecus* and *Proconsul* were very similar, placing near the mean of the non-hominid cluster. Both fall within the ranges of *Ateles*, *Cercopithecus*, *Hylobates*, and *Papio*, but beyond the limits of *Cebus* and *Procolobus*. Both specimens of *Propliopithecus* placed more negatively, falling only within the ranges of *Hylobates* and *Papio*. Unlike these African taxa, *Sivapithecus* placed with the hominids along PC 1. Even so, it was fairly close to the center of the axis, falling only within the range of *Gorilla*.

The difference in morphology represented by PC 1 is illustrated in Figure 8-3. Most of these differences are concentrated in the anterior midline of the palate. The morphology represented by the positive pole of PC 1 (hominid genera) is much longer in the subnasal clivus. Therefore, the premaxillary inter-dental landmarks are antero-inferior to their negative counterparts, while the anterior attachment of the nasal septum and the posterior pole of the clivus are placed postero-superiorly to theirs. This coincides with a substantial lengthening of the incisive foramen into a canal and relative thickening of the anterior palate. These differences in premaxillary morphology were accomplished largely through postero-superior extension of the nasal morphology (**ANS**, **CLI**, and **PIC**) relative to the rest of the palate. Other differences between negative and positive morphologies were relatively minor with the exception of the malar root origin. In hominids this is set more posteriorly relative to the premolar-molar contact than in non-hominids.

Table 8-3 Results of pairwise t-tests between genera for PCs 1-4. Bonferroni adjusted p-values are given in the lower triangle. * indicates significance at $\alpha=0.05$

	Genus	Atel	Cebu	Cerc	Gori	Homo	Hylo	Pan	Papi	Pcol	Pong
		Atel	Cebu	Cerc	Gori	Homo	Hylo	Pan	Papi	Pcol	Pong
P C 1	Atel		*		*	*		*			*
	Cebu	0.0220			*	*	*	*	*		*
	Cerc	1.0000	0.6256		*	*		*			*
	Gori	<.0001	<.0001	<.0001		*	*	*	*	*	*
	Homo	<.0001	<.0001	<.0001	<.0001		*	*	*	*	*
	Hylo	1.0000	0.0002	1.0000	<.0001	<.0001		*	*	*	*
	Pan	<.0001	<.0001	<.0001	<.0001	1.0000	<.0001		*	*	*
	Papi	1.0000	<.0001	0.2522	<.0001	<.0001	0.4893	<.0001		*	*
	Pcol	0.4458	1.0000	1.0000	<.0001	<.0001	0.0401	<.0001	0.0008		*
	Pong	<.0001	<.0001	<.0001	<.0001	1.0000	<.0001	1.0000	<.0001	<.0001	
P C 2	Atel				*	*	*	*	*	*	*
	Cebu	1.0000		*	*	*	*	*	*	*	*
	Cerc	0.3328	0.0156		*	*		*	*	*	*
	Gori	<.0001	<.0001	<.0001		*	*	*	*	*	*
	Homo	<.0001	<.0001	<.0001	<.0001		*	*	*	*	*
	Hylo	0.0009	<.0001	1.0000	<.0001	<.0001		*	*	*	*
	Pan	<.0001	<.0001	0.5827	<.0001	<.0001	<.0001		*	*	*
	Papi	<.0001	<.0001	<.0001	1.0000	<.0001	<.0001	<.0001		*	*
	Pcol	<.0001	<.0001	0.1734	<.0001	<.0001	0.0458	1.0000	<.0001		*
	Pong	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	1.0000	
P C 3	Atel		*		*	*			*		
	Cebu	<.0001		*	*	*	*	*	*	*	*
	Cerc	1.0000	<.0001			*		*	*		
	Gori	<.0001	<.0001	0.4915		*	*	*	*		*
	Homo	<.0001	<.0001	<.0001	<.0001		*	*	*	*	*
	Hylo	1.0000	<.0001	1.0000	<.0001	<.0001		*	*		
	Pan	0.2184	<.0001	<.0001	<.0001	<.0001	<.0001		*	*	*
	Papi	<.0001	<.0001	<.0001	<.0001	1.0000	<.0001	<.0001		*	*
	Pcol	0.3784	<.0001	1.0000	1.0000	<.0001	0.4371	<.0001	<.0001		*
	Pong	1.0000	<.0001	1.0000	<.0001	<.0001	1.0000	<.0001	<.0001	1.0000	
P C 4	Atel		*		*	*	*	*	*	*	*
	Cebu	<.0001		*			*	*	*	*	*
	Cerc	1.0000	<.0001		*	*	*	*	*	*	*
	Gori	<.0001	1.0000	<.0001			*	*	*	*	*
	Homo	<.0001	1.0000	<.0001	1.0000		*	*	*	*	*
	Hylo	<.0001	0.0140	<.0001	<.0001	<.0001		*	*		*
	Pan	<.0001	0.7795	<.0001	<.0001	0.0006	0.0245		*		*
	Papi	0.4662	<.0001	0.0179	<.0001	<.0001	<.0001	<.0001		*	*
	Pcol	0.0002	0.0139	0.0118	<.0001	0.0002	1.0000	0.4412	<.0001		*
	Pong	1.0000	<.0001	1.0000	<.0001	<.0001	<.0001	<.0001	0.0677	<.0001	

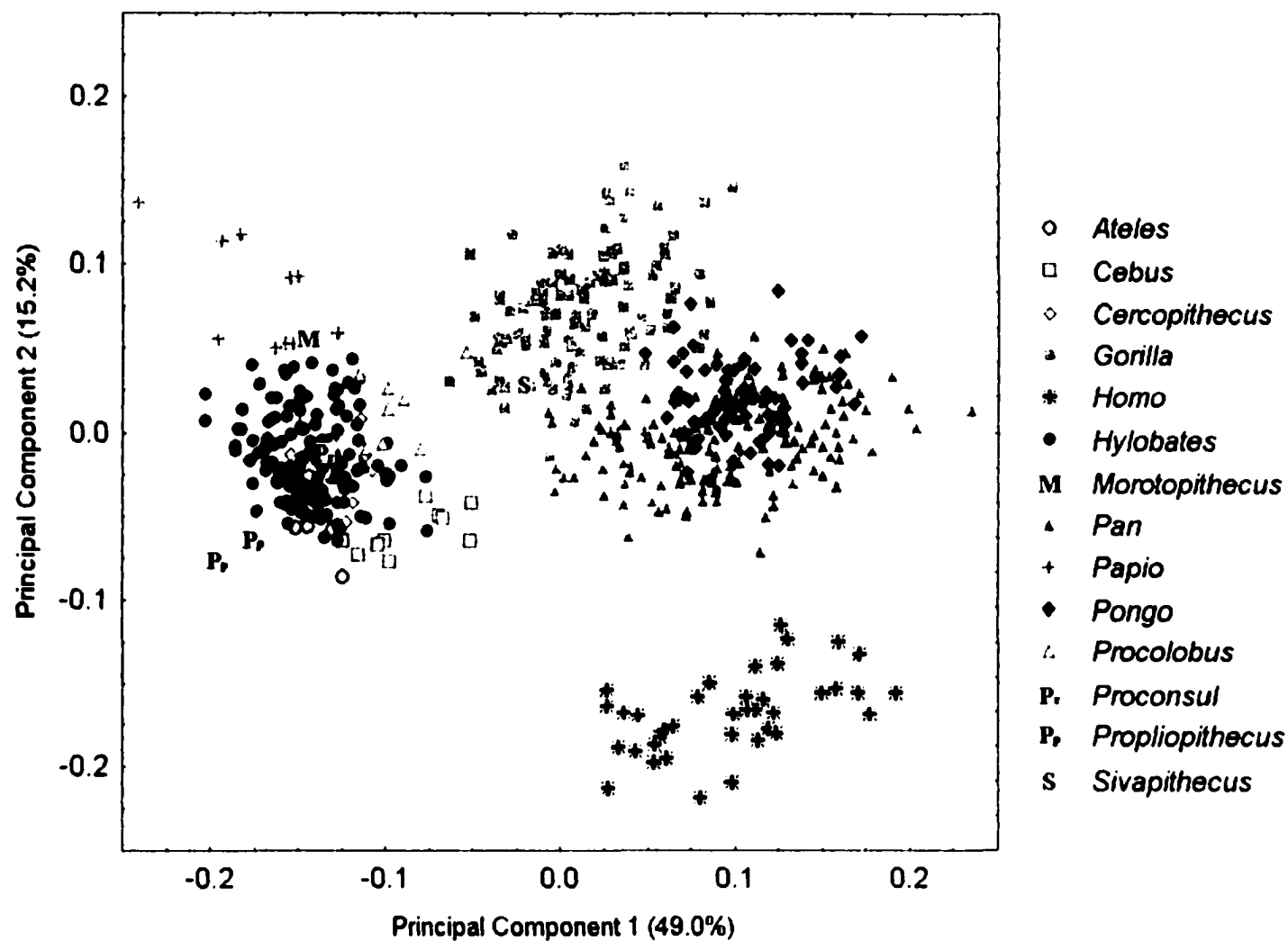


Figure 8-2 Plot of principal component scores for PC 1 and PC 2. PC 1 separates hominid from non-hominid taxa. PC 2 separates humans from all other taxa, as well as sorting males (positive) and females (negative) of *Cercopithecus*, *Gorilla*, *Pan*, *Papio*, *Procolobus*, and *Pongo*; gibbons (negative) from siamangs (positive); and chimpanzees (positive) from bonobos (negative).

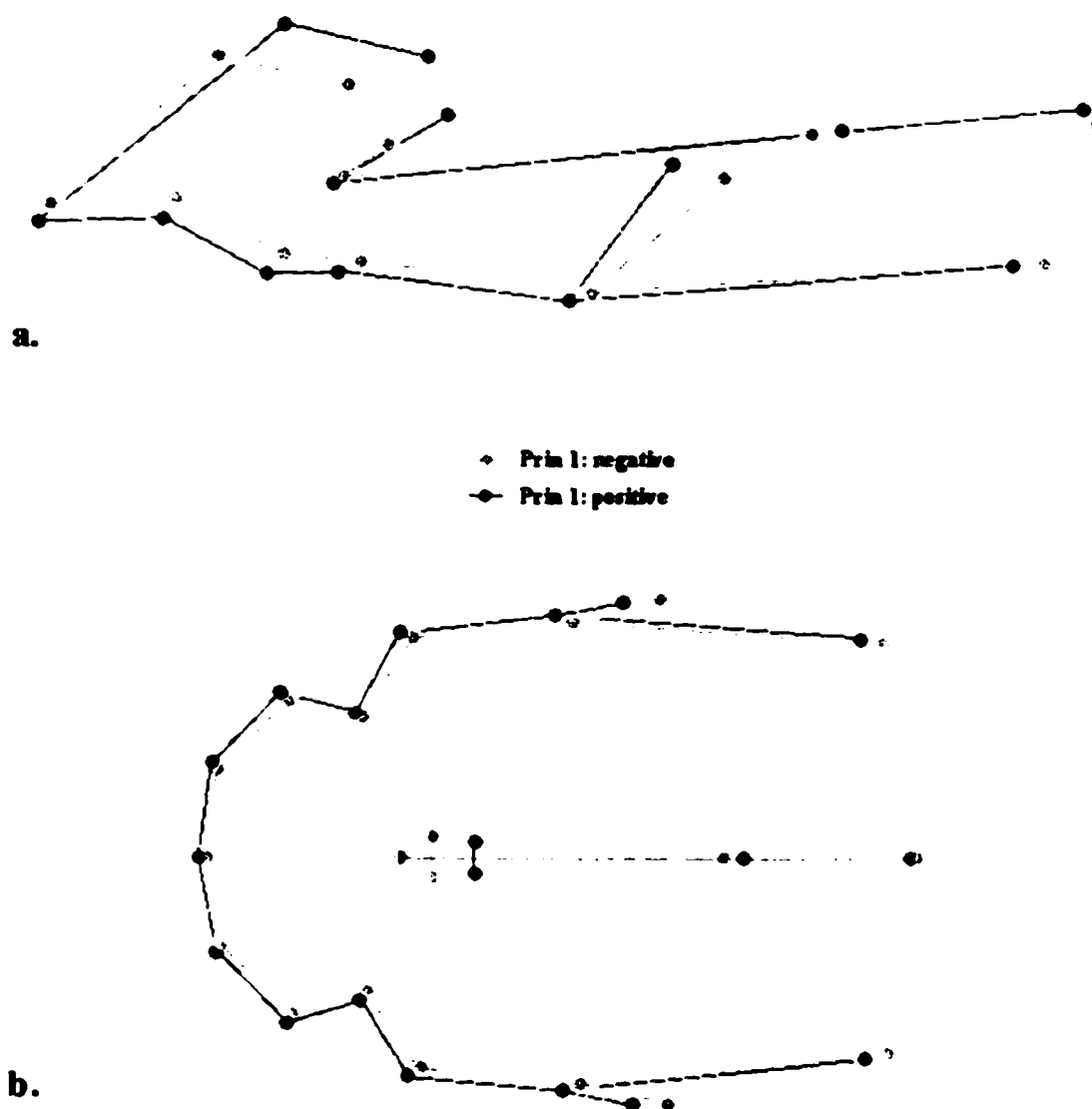


Figure 8-3 Shape change along PC 1. Black lines represent the positive loadings, gray lines show the negative loadings. (a) lateral view; (b) superior view. See Figure 8-1 for landmark references.

Results from PC 1 support the work of Ward and colleagues (Ward & Kimbel, 1983; Ward & Pilbeam, 1983; Ward & Brown, 1986; Brown & Ward, 1988; McCollum *et al.*, 1993; McCollum, 1997; McCollum & Ward, 1997; McCollum, 1999), which showed that great apes and humans have a substantively different subnasal morphology from *Hylobates* and other catarrhines. Note, however, that among hominids *Gorilla* is

significantly different, being somewhat closer to the non-hominid condition. This clarifies results from the PCA of the entire set of cranial landmarks (see Chapter 6). In that analysis, PC 1 tended to separate *Hylobates* and *Gorilla* from the other hominoids in a number of features including subnasal differences (see Figure 6-5). It is clear from this analysis that gorillas—although most similar to other hominids—have a relatively shorter subnasal clivus and thinner palate. The first PC from this analysis does not sort male and female gorillas, as did PC 1 for the entire cranium. This suggests that those sex differences were not related to palatal morphology.

Principal component 2

The second principal component comprises 15% of the palatal variation among these specimens. T-test results (Table 8-3) show significant differences between most of the taxon-pairs. Yet, the greatest difference along the second PC axis is between *Homo* and the other taxa (see Figure 8-2). The modern human mean is by far the most negative here, and its range overlaps with none of the others. This is in contrast to *Gorilla* and *Papio*, which have the largest mean values and are significantly different from all taxa except each other. The range of *Gorilla* on PC 2 substantially overlaps most of the other ranges, excepting *Ateles*, *Cebus*, and *Homo*. In contrast, *Papio*'s range overlaps only *Hylobates* and *Pongo* (and, of course, *Gorilla*). The other taxa are arranged between *Homo* and *Gorilla/Papio* clusters. Interesting among this cluster is the negative tendency of the two platyrrhine genera.

Fossil taxa were somewhat scattered along this axis. *Morotopithecus* placed most positively, near the mean of *Gorilla*, but overlapping with the lower range of *Papio* and the upper range of *Pongo*. *Sivapithecus* was situated near the mean of *Pongo*, but within

the ranges of *Gorilla*, *Hylobates*, *Pan*, and *Procolobus*. *Proconsul* placed near the means of *Cercopithecus*, *Hylobates*, and *Pan*, but within the ranges of all catarrhine genera except *Homo* and *Papio*. The most negative scores among fossil were in *Propliopithecus*, with both specimens situated near the mean of *Ateles* and *Cebus*. While DPC 2803 scored within the lower range of *Hylobates* and *Pan*, DPC 3161 placed only among the platyrrhines.

Beyond generic differences, PC 2 shows substantial sorting between sexes and among certain species. Males and females from all three cercopithecoid genera sort perfectly along this axis, with males scoring more positively than females. *Gorilla*, *Pan*, and *Pongo* sexes tend to sort on PC 2 as well. Parametric t-tests comparing sex means within these three genera found them all to be significantly different (*Gorilla*: $p < 0.0001$; *Pan*: $p < 0.0001$; *Pongo*: $p = 0.0061$); there is, however, considerable overlap between the male and female scores in each. Platyrrhine and modern human specimens do not sort by sex on PC 2. This axis also sorts gibbons and siamangs (but not their sexes), as well as chimpanzees and bonobos (by taxon and sex). Again, t-tests between the means of these groups found the differences to be highly significant ($p < 0.0001$), but the ranges overlap substantially.

Given these sorting patterns, it is tempting to think of PC 2 as representing allometric change: significant size differences, whether between sexes or congeneric species, sort differently. Such a clear-cut distinction, however, is not warranted for several reasons. Firstly, genera do not sort strictly by size here. The placement of *Homo* specimens clearly shows this. Moreover, *Ateles*, *Cebus*, *Cercopithecus*, *Hylobates*, and *Procolobus* all range with the substantially larger specimens of *Pan*, while *Papio* places

at the high end of the much larger *Gorilla* range. Building on the size-correlation analyses discussed in Chapter 5, a regression of PC 2 versus the log of centroid size was performed separately for each sex in each genus. The results showed that size was not significantly correlated with PC 2 except among males of *Gorilla* ($p = 0.0029$; $R^2 = 0.1304$) and *Pan* ($p = 0.0041$; $R^2 = 0.1559$)—and these with very weak explanatory power. Size, therefore, explains only a fraction of the shape variation within sexes, and none of the variation within species. This indicates that any allometric effects summarized by this component are intimately related to taxonomic and sex differences.

In any case, the shape differences represented along this axis do coincide with differences between the sexes of all catarrhine genera except *Homo* and *Hylobates*, and with differences between gibbons and siamangs, and chimpanzees and bonobos. These differences are illustrated in Figure 8-4. Morphology toward the negative pole (represented by *Homo*) shows an antero-posterior shortening of the premaxilla. Premaxillary inter-dental landmarks are set posteriorly to their positive-tending counterparts. Conversely, nasal premaxillary landmarks (ANS, CLI, and PIC) are anteriorly and superiorly placed relative to the positive morphology. Consequently, the negative pole is characterized by relatively taller (supero-inferiorly) subnasal morphology, a more vertical subnasal clivus, and a thicker anterior palate. These shape differences can largely be summarized by a ventral rotation of the negative subnasal morphology relative to the positive. The post-canine dentition also shows differences along this axis, with inter-dental landmarks laterally expanded at the negative pole; these differences are suggestive of the characteristic parabolic shape of the modern human

palate. Finally, the horizontal plate of the palatine bone is substantially shorter and angled slightly anteriorly in the negative morphology.

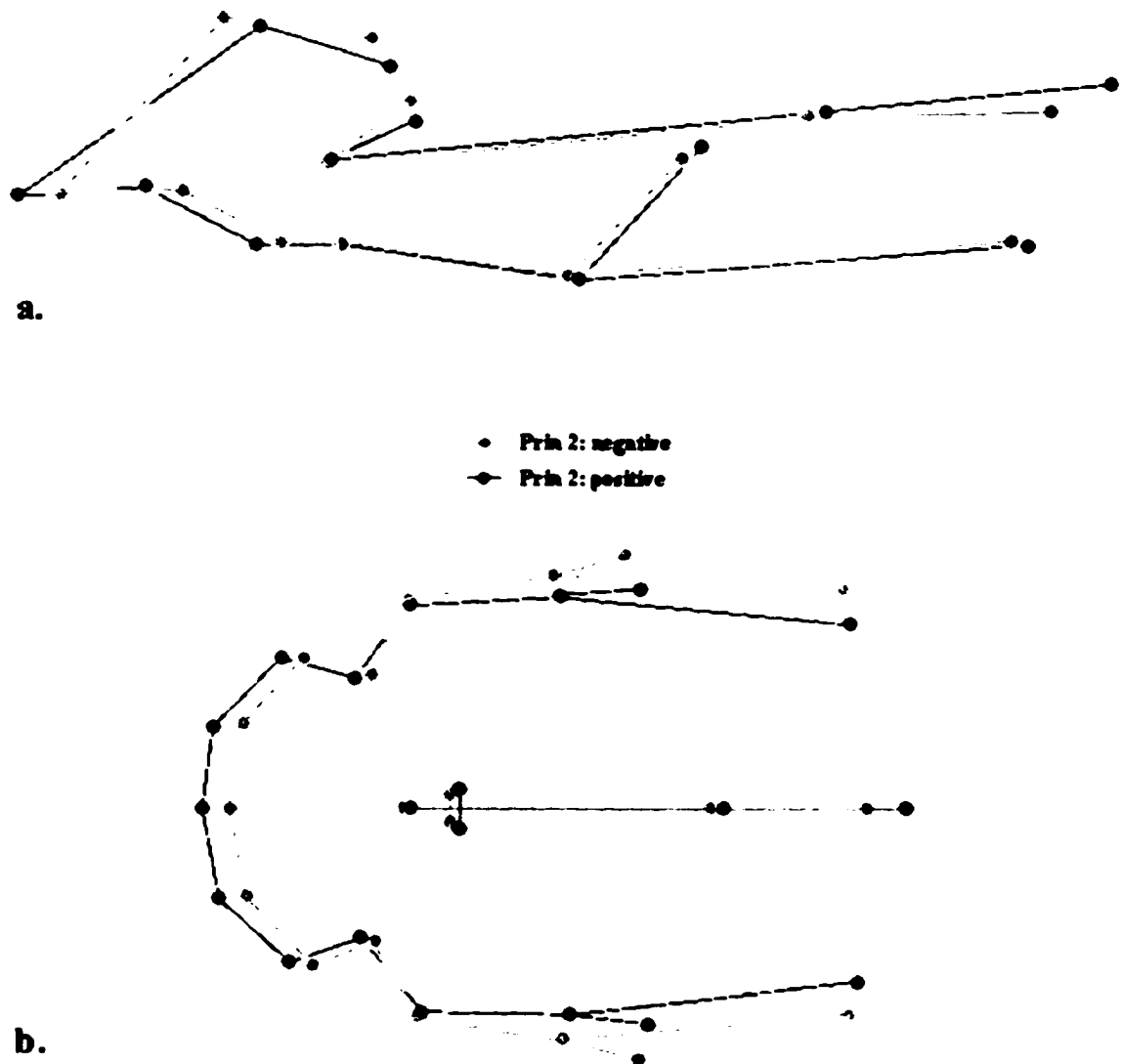


Figure 8-4 Shape change along PC 2. Black lines represent the positive loadings, gray lines show the negative loadings. (a) lateral view; (b) superior view. See Figure 8-1 for landmark references.

Principal component 3

The third principal component summarizes only 6% of the variation among these palatal morphologies. As such, there is substantial overlap among most of the genus ranges. T-test results (Table 8-3) and a graph of PC scores (Figure 8-5) show that PC 3 largely represents the difference between *Cebus* on the negative end, and *Homo-Papio* on the positive end. The mean of *Cebus* scores is significantly different from all other genus means; its range overlaps only with the most negative specimens of *Pan*. *Homo* and *Papio* means are significantly different from all genera except each other. *Papio* specimens overlap with the upper range of *Gorilla*, while *Homo* specimens overlap all of the other taxa except *Cebus*. Indeed, *Homo* shows the most variability along this axis. The other seven taxa cluster between the extremes of *Cebus* and *Homo/Papio*. While there are some differences between taxon-pairs (see Table 8-3), all ranges overlap substantially.

Specimens of *Morotopithecus*, *Sivapithecus*, and *Propliopithecus* (DPC 3161) were very similar on PC 3, placing just on the positive side of zero. This situated them near the mean values of most extant genera, but beyond the ranges of *Cebus*, *Homo*, and *Papio*. DPC 2803, however, scored more positively, falling near the mean of *Gorilla*, but in ranges of all the hominoids. *Proconsul* was the only fossil with a negative score on PC 3. Though not within the range of *Cebus*, this specimen fell only amid the lower ranges of *Pan* and *Pongo*.

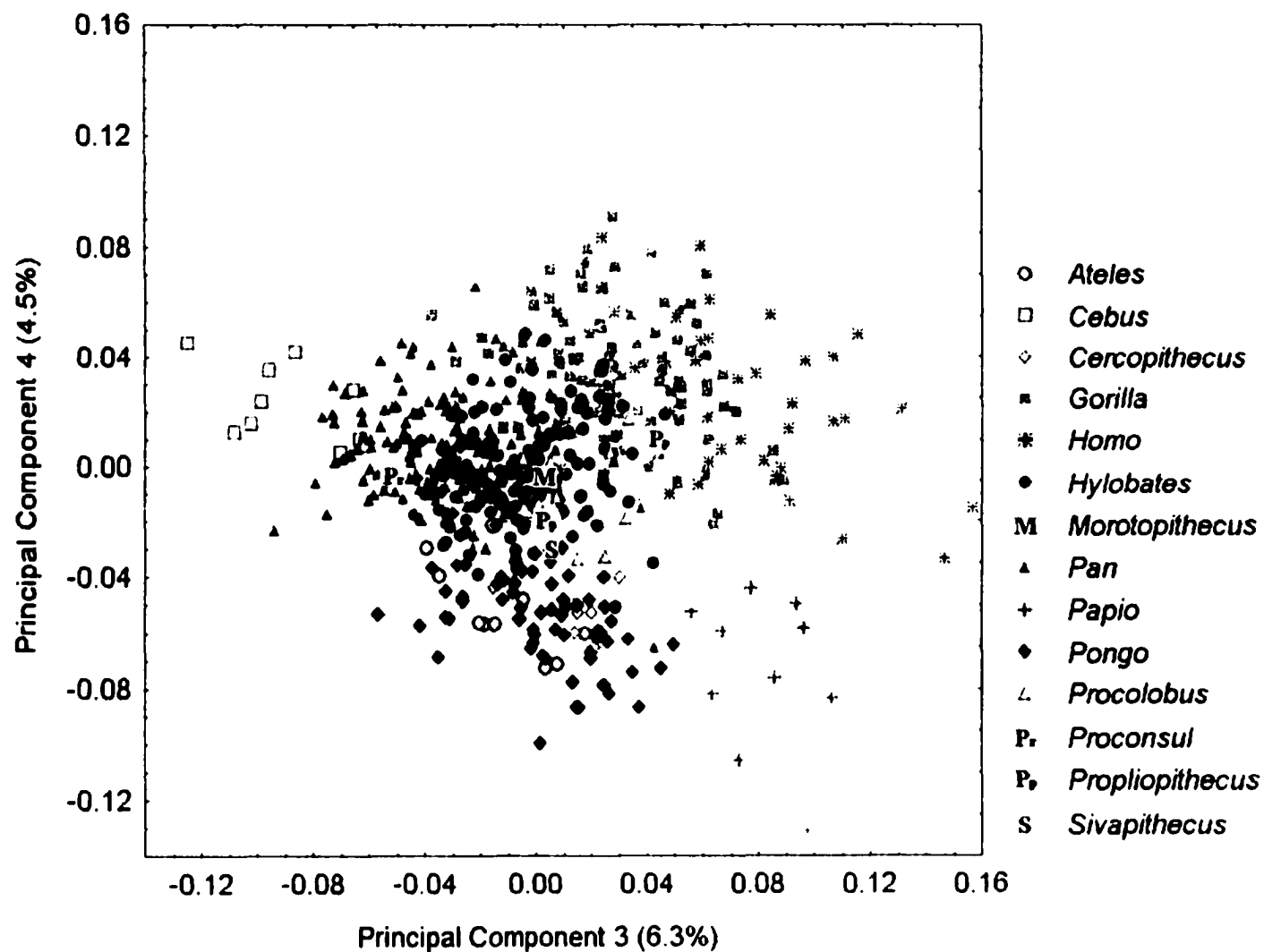


Figure 8-5 Plot of principal component scores for PC 3 and PC 4. PC 3 largely separates *Cebus* on the negative end from *Homo* and *Papio* on the positive; it also sorts males and females of both platyrrhine genera. PC 4 tends to separate African apes and *Cebus* from a group of *Ateles*, *Cercopithecus*, *Papio*, and *Pongo*.

Where PC 2 sorted sexes of many catarrhine genera. PC 3 sorted males and females of both *Ateles* and *Cebus*, with females scoring more positively. *Ateles* sexes were completely separated here, while those of *Cebus* displayed some overlap. PC 3 also distinguished among species of *Hylobates*, with *H. agilis* and *H. muelleri* scoring more negatively than *H. concolor* and *H. syndactylus*. Pairwise parametric t-tests with a Bonferroni adjustment were used to compare the mean scores for these species. Results (Table 8-4) bear out the differences discussed above: *H. agilis* and *H. muelleri* are significantly different from the other two species, but not from each other; similarly, *H. concolor* and *H. syndactylus* are not significantly different from each other. Scores from all four species do overlap, however.

Table 8-4 Results of pairwise t-tests with a Bonferroni adjustment testing for differences among hylobatid species on PC 3. Corrected p-values are given in the lower triangle. * indicates significance at $\alpha=0.05$.

Species	<i>H. agilis</i>	<i>H. concolor</i>	<i>H. muelleri</i>	<i>H. syndactylus</i>
<i>H. agilis</i>		*		*
<i>H. concolor</i>	0.0013		*	
<i>H. muelleri</i>	1.0000	0.0016		*
<i>H. syndactylus</i>	<0.0001	1.0000	<0.0001	

Shape differences represented by PC 3 are shown in Figure 8-6. The negative extreme (represented by *Cebus*) is characterized by an anterior expansion in the premaxillary inter-dental landmarks, but posterior retraction of the anterior nasal spine and a sharply inferior displacement of posterior subnasal landmarks. In conjunction with this, the morphology anterior to the molars is expanded laterally relative to the positive morphology. This combination yields a longer, shallower subnasal clivus, with a broad

but shallow anterior palate at the negative pole. Differences in the posterior morphology include more anterior placement of the malar root origin, supero-medial displacement of the distal end of the dental arcade, and a shortening of the horizontal plate of the palatine.

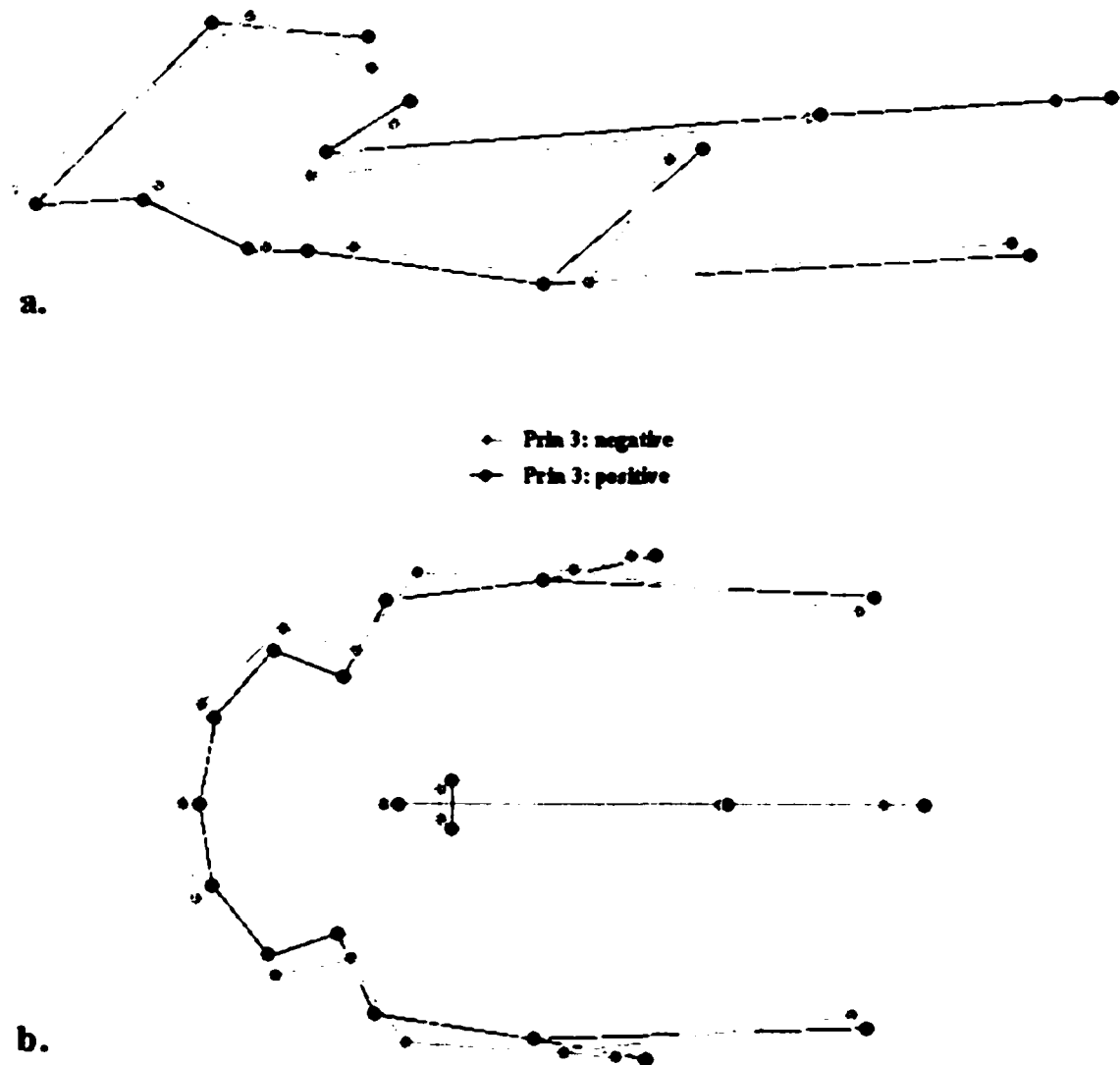


Figure 8-6 Shape change along PC 3. Black lines represent the positive loadings, gray lines show the negative loadings. (a) lateral view; (b) superior view. See Figure 8-1 for landmark references.

Principal component 4

PC 4 represents 4% of the among-specimens palatal variability. Sorting among taxa on this axis was fairly indistinct (see Figure 8-5), but t-tests (Table 8-3) did find some significant pairwise differences. The fourth principal component generally represents the difference between a cluster of African apes and *Cebus* and one of *Ateles*, *Cercopithecus*, *Papio*, and *Pongo*; *Hylobates* and *Procolobus* are situated near the center. None of these groups is exclusive and there is substantial overlap among all ranges. Specimens of *Morotopithecus* and *Proconsul* placed just on the negative side of zero, falling within the ranges of all hominoid genera, as well as that of *Procolobus*: *Propliopithecus* specimens scored somewhat more negatively (DPC 3161) or positively (DPC 2803), but still within ape ranges. The score of *Sivapithecus* on PC 4 was the most negative among fossils, yet still within the ranges of all genera except the African apes and *Papio*. Other taxonomic or sex differences were not found along this axis.

Differences in morphology represented by PC 4 (Figure 8-7) are confined largely to the premaxillary and midline landmarks. The negative morphology (represented best by *Papio* and *Pongo*) is characterized by anterior expansion of the incisor alveoli, inferior displacement of the anterior septal attachment and posterior clivus, and superior deflection of the anterior palate. This results in a substantial subnasal protrusion, shorter (supero-inferior) clivus height, proximity of the nasal sill and floor, and a deep anterior palate. Distal to the incisors, there is little change in the dental arcade. The midline palate, however, is more horizontal at the negative pole, with a greatly shortened horizontal palatine. Finally, the malar root origin at the negative extreme is set substantially posterior relative to the positive.

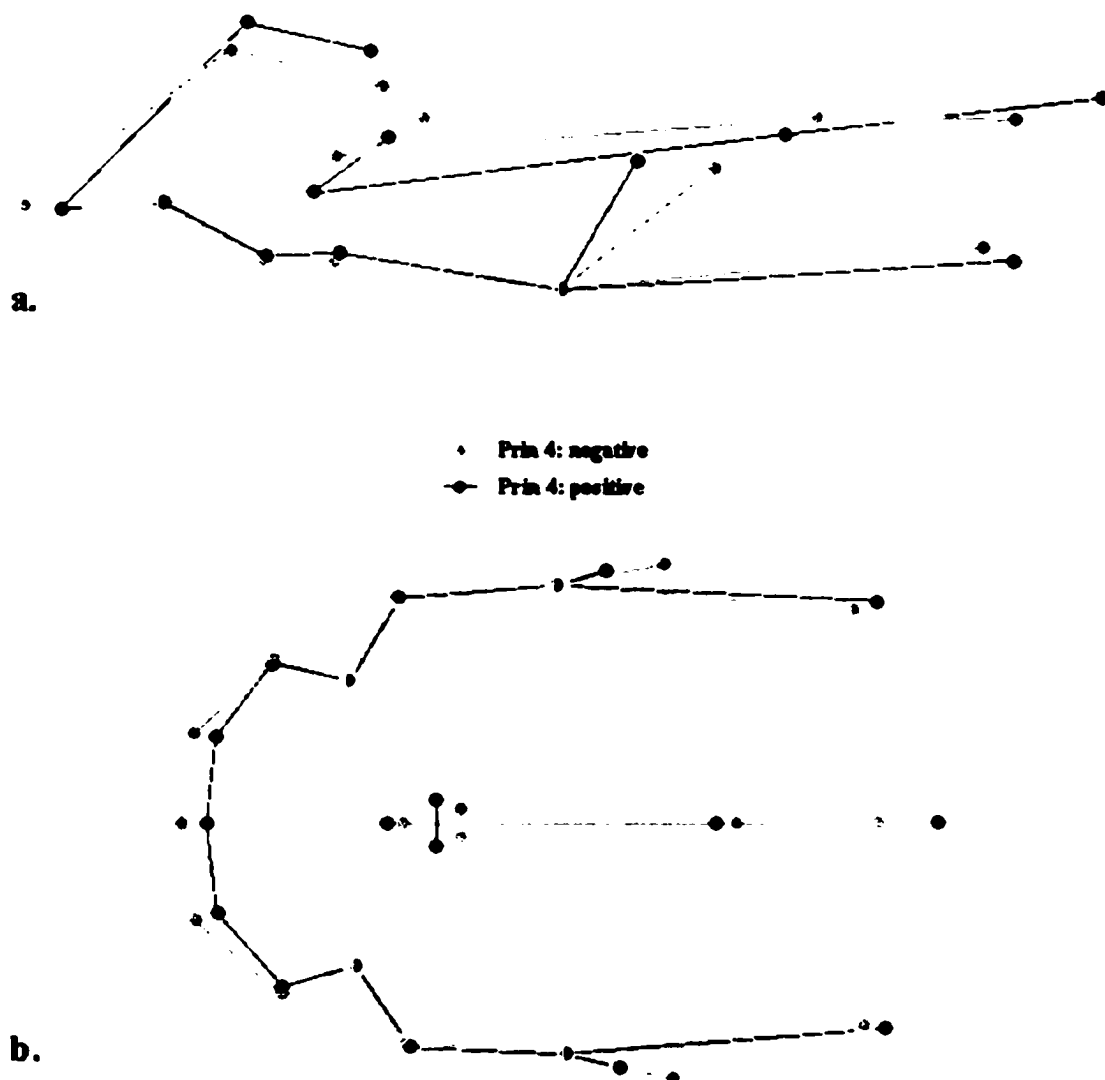


Figure 8-7 Shape change along PC 4. Black lines represent the positive loadings, gray lines show the negative loadings. (a) lateral view; (b) superior view. See Figure 8-1 for landmark references.

CANONICAL VARIATES ANALYSIS

Canonical variates analysis was used to examine shape differences among known, extant genera; fossil genera were not included, as their sample sizes preclude the calculation of within-group variation. Analyses of variance were performed on CV scores to test for differences among genera; these were highly significant ($p < 0.0001$) on every canonical variate. Both CVA and ANOVA results are listed in Table 8-5. Cross-validations were also performed to test the robusticity of the calculated discriminant functions. These results, shown in Table 8-6, show perfect re-assignment of every specimen in the sample, suggesting that these data are robust for distinguishing among these genera. Though all canonical axes were examined for differences, only the first six are discussed in detail below. Pairwise parametric t-tests with a Bonferroni correction were performed to indicate particular differences on each canonical axis. These results are shown in Table 8-7.

Table 8-5 Summary of CVA and ANOVA results for all nine canonical variate axes. CVA results give statistics for the latent roots of the among-groups variance (eigenvalues), the proportion of variance explained by each variate, and the cumulative proportion of the variance summarized by that CV and those preceding it. One-way ANOVAs were performed on each axis to test for significant differences among genera; F-values and probabilities are given for tests of the null-hypothesis that all genera share a common mean.

	CANONICAL VARIATES ANALYSIS			ANALYSIS OF VARIANCE	
	Eigenvalue	Proportion	Cumulative	F Value	Pr > F
CV 1	21.4302	0.4350	0.4350	1236.49	<0.0001
CV 2	11.4863	0.2332	0.6681	754.13	<0.0001
CV 3	5.9417	0.1206	0.7888	357.81	<0.0001
CV 4	4.0221	0.0816	0.8704	246.11	<0.0001
CV 5	2.8684	0.0582	0.9286	181.13	<0.0001
CV 6	1.8653	0.0379	0.9665	117.47	<0.0001
CV 7	0.8393	0.0170	0.9835	51.51	<0.0001
CV 8	0.5489	0.0111	0.9947	26.46	<0.0001
CV 9	0.2631	0.0053	1.0000	5.21	<0.0001

Table 8-6 Cross-validation results from CVA of extant specimens. Each cell gives the number (n) and percent (%) of individuals from the genus on the left assigned to the genus across the top.

Genus		Atel	Cebu	Cerc	Gori	Homo	Hylo	Pan	Papi	Pcol	Pong
Atel	n	10									
	%	100									
Cebu	n		10								
	%		100								
Cerc	n			10							
	%			100							
Gori	n				110						
	%				100						
Homo	n					38					
	%					100					
Hylo	n						146				
	%						100				
Pan	n							165			
	%							100			
Papi	n								10		
	%								100		
Pcol	n									10	
	%									100	
Pong	n										71
	%										100

Table 8-7 Results of pairwise t-tests between genera for CVs 1-6. Bonferroni adjusted p-values are given in the lower triangle. * indicates significance at $\alpha=0.05$.

CV 1	Genus	Atel	Cebu	Cerc	Gori	Homo	Hylo	Pan	Papi	Pcol	Pong
	Atel		*	*	*	*	*	*	*		*
	Cebu	0.0260		*	*	*	*	*	*		*
	Cerc	0.0398	<.0001		*	*		*	*	*	*
	Gori	<.0001	<.0001	<.0001		*	*	*	*	*	*
	Homo	<.0001	<.0001	<.0001	<.0001		*	*	*	*	*
	Hylo	0.0002	<.0001	1.0000	<.0001	<.0001		*	*	*	*
	Pan	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001		*	*	*
	Papi	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001		*	*
	Pcol	1.0000	0.0856	0.0113	<.0001	<.0001	<.0001	<.0001	<.0001		*
	Pong	<.0001	<.0001	<.0001	<.0001	0.0224	<.0001	<.0001	<.0001	<.0001	
CV 2	Genus	Atel	Cebu	Cerc	Gori	Homo	Hylo	Pan	Papi	Pcol	Pong
	Atel				*	*			*		*
	Cebu	1.0000			*	*	*				*
	Cerc	1.0000	1.0000		*	*			*		*
	Gori	<.0001	<.0001	<.0001		*	*	*		*	
	Homo	<.0001	<.0001	<.0001	<.0001		*	*	*	*	*
	Hylo	0.8461	0.0139	1.0000	<.0001	<.0001		*	*	*	*
	Pan	1.0000	1.0000	1.0000	<.0001	<.0001	<.0001		*		*
	Papi	0.0366	0.6905	0.0004	0.1906	<.0001	<.0001	<.0001			
	Pcol	1.0000	1.0000	1.0000	<.0001	<.0001	0.0291	1.0000	0.4585		*
	Pong	<.0001	<.0001	<.0001	1.0000	<.0001	<.0001	<.0001	1.0000	<.0001	
CV 3	Genus	Atel	Cebu	Cerc	Gori	Homo	Hylo	Pan	Papi	Pcol	Pong
	Atel		*		*	*	*	*	*	*	*
	Cebu	0.0003		*	*	*	*	*	*	*	
	Cerc	1.0000	0.0007		*	*	*	*	*	*	*
	Gori	<.0001	<.0001	<.0001		*	*	*	*	*	*
	Homo	<.0001	<.0001	<.0001	<.0001		*	*	*	*	*
	Hylo	<.0001	<.0001	<.0001	<.0001	<.0001					*
	Pan	<.0001	<.0001	<.0001	<.0001	<.0001	1.0000				*
	Papi	0.0012	<.0001	0.0005	<.0001	0.0029	1.0000	1.0000			*
	Pcol	0.0008	<.0001	0.0003	<.0001	0.0045	1.0000	1.0000	1.0000		*
	Pong	<.0001	1.0000	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	

Table 8-7 (cont.)

C V 4	Genus	Atel	Cebu	Cerc	Gori	Homo	Hylo	Pan	Papi	Pcol	Pong
	Atel		*	*			*	*	*		
	Cebu	<.0001		*	*	*	*	*	*	*	*
	Cerc	<.0001	<.0001		*	*			*	*	*
	Gori	0.9047	<.0001	<.0001			*	*	*		*
	Homo	1.0000	<.0001	<.0001	0.9860		*	*	*		
	Hylo	<.0001	<.0001	1.0000	<.0001	<.0001		*	*	*	*
	Pan	<.0001	<.0001	1.0000	<.0001	<.0001	<.0001		*	*	*
	Papi	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001		*	*
	Pcol	0.0644	<.0001	0.0001	1.0000	0.0959	<.0001	<.0001	<.0001		*
	Pong	1.0000	<.0001	<.0001	<.0001	1.0000	<.0001	<.0001	<.0001	0.0009	
C V 5	Genus	Atel	Cebu	Cerc	Gori	Homo	Hylo	Pan	Papi	Pcol	Pong
	Atel		*	*	*	*	*	*	*	*	*
	Cebu	<.0001		*	*	*	*	*	*	*	*
	Cerc	<.0001	<.0001		*		*	*	*		
	Gori	<.0001	<.0001	0.0010		*	*	*	*	*	*
	Homo	<.0001	<.0001	1.0000	0.0001		*	*	*		*
	Hylo	<.0001	<.0001	<.0001	<.0001	<.0001		*	*	*	*
	Pan	<.0001	<.0001	<.0001	<.0001	<.0001	0.5598		*	*	*
	Papi	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001		*	*
	Pcol	<.0001	<.0001	1.0000	0.0020	1.0000	<.0001	<.0001	<.0001		
	Pong	<.0001	<.0001	1.0000	<.0001	0.0001	<.0001	<.0001	<.0001	1.0000	
C V 6	Genus	Atel	Cebu	Cerc	Gori	Homo	Hylo	Pan	Papi	Pcol	Pong
	Atel		*		*	*	*	*	*	*	*
	Cebu	<.0001		*	*	*	*	*	*	*	*
	Cerc	1.0000	<.0001		*	*	*	*	*	*	*
	Gori	<.0001	0.0015	<.0001			*		*	*	*
	Homo	<.0001	0.0019	<.0001	1.0000		*		*	*	*
	Hylo	<.0001	<.0001	<.0001	<.0001	<.0001		*	*	*	
	Pan	<.0001	0.0117	<.0001	1.0000	1.0000	<.0001		*	*	*
	Papi	0.0004	0.0014	<.0001	<.0001	<.0001	<.0001	<.0001			*
	Pcol	<.0001	0.0100	<.0001	<.0001	<.0001	<.0001	<.0001	1.0000		*
	Pong	<.0001	<.0001	<.0001	<.0001	0.0008	1.0000	<.0001	<.0001	<.0001	

Canonical variate 1

The first canonical axis comprises nearly 44% of the total variation among genera. Specimen scores on this axis are plotted in Figure 8-8. Results from pairwise t-

tests (Table 8-7) demonstrate that the mean CV scores for almost every pair of genera are significantly different; the only exceptions are *Cercopithecus-Hylobates*, *Ateles-Procolobus*, and *Cebus-Procolobus*. As with PC 1, however, the major distinction along this axis was between the hominid and non-hominid genera—in this case, with no overlap between the groups. Ranges of all hominid genera overlapped with each other. Non-hominid genera, however, were somewhat more distinct. *Papio* had the most negative scores, and overlapped only with *Cercopithecus* and *Hylobates*. *Cebus* scores were the least negative and fell only within the range of *Procolobus*. Ranges of *Ateles*, *Cercopithecus*, *Hylobates*, and *Procolobus* all overlapped.

Figure 8-9 illustrates the shape differences represented by CV 1. These differences, however, are the same as those discussed for PC 1 (see Figure 8-3). The distribution of specimens along the first canonical axis is nearly identical to their distribution on PC 1. This suggests that the greatest axis of variability among *specimens* is nearly coincident with the greatest axis of variation among *genera*. This was demonstrated statistically with a regression analysis of CV 1 scores onto PC 1 scores. The results ($p < 0.0001$; $R^2 = 0.8897$) indicate that most of the variability on the first canonical axis can be explained by the variation on the first PC axis. Discussion of the shape differences represented by PC 1 (see above) holds equally for the differences along this canonical axis and is not repeated here.

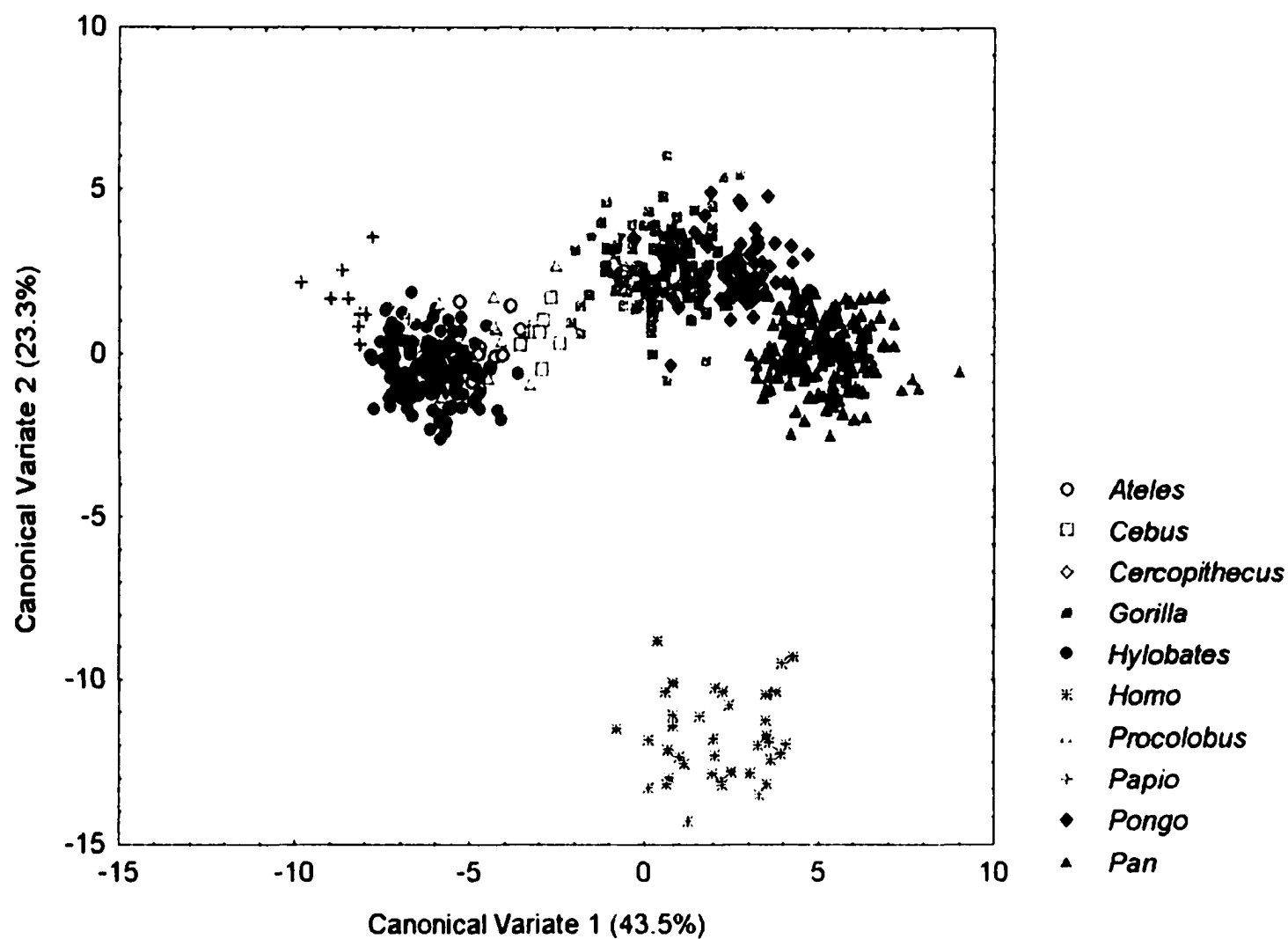


Figure 8-8 Plot of canonical variate scores for CV 1 and CV 2. CV 1 separates hominid from non-hominid genera. CV 2 largely distinguishes *Homo* from all other taxa; this axis also sorts male and female specimens of the cercopithecoid genera.

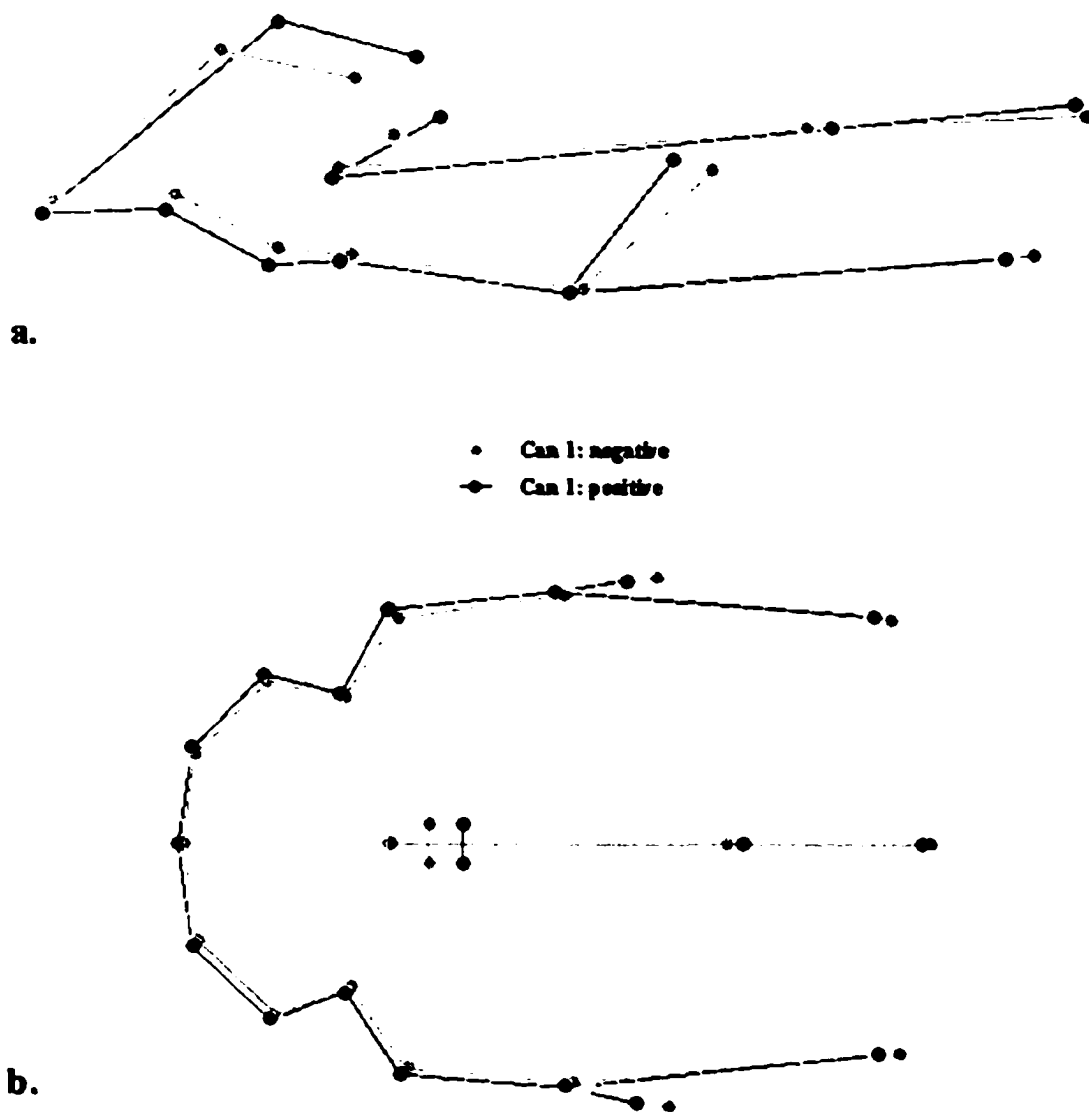


Figure 8-9 Shape change along CV 1. Black lines represent the positive loadings, gray lines show the negative loadings. (a) lateral view; (b) superior view. Differences in this axis are nearly identical to those on PC 1. See Figure 8-1 for landmark references.

Canonical variate 2

CV 2 represents 23% of the among-groups variation in palate morphology. Figure 8-8 shows a plot of specimen scores along this axis; Table 8-7 lists the results of pairwise t-tests between genera. As with PC 2, the greatest distinction on CV 2 is between the negatively scoring *Homo* and the other taxa. This is contrasted by a group of *Gorilla*, *Papio*, and *Pongo*, which have significantly different means from other taxa but not from each other; their ranges overlap those of the other non-human genera, however. Taxa between these extremes show some differences but have substantially overlapping ranges.

Although this axis bears a strong resemblance to PC 2, it is not entirely the same. Differences between species of *Hylobates* and *Pan* were not evident here. Similarly, there was no sorting of male and female specimens of *Gorilla*, *Pan*, and *Pongo* on CV 2. This is not surprising, perhaps, given that intra-generic differences are minimized through CVA. Nevertheless, sexes do sort among cercopithecoid scores for this axis: *Papio* males and females separate completely, while *Cercopithecus* and *Procolobus* sexes show some overlap. In these cases, males scored more positively than females on CV 2.

Shape changes summarized by the second canonical variate are illustrated in Figure 8-10. As with CV 1, deformations on this axis were nearly identical to those of PC 2. Regression of CV 2 scores onto PC 2 scores again demonstrates a strong correlation ($p < 0.0001$; $R^2 = 0.7695$). Although there are differences between the two axes (as just described), they are not manifest in a descriptive treatment of shape deformation: both describe the difference between *Homo* and the other taxa. That discussion, therefore, is not repeated here.

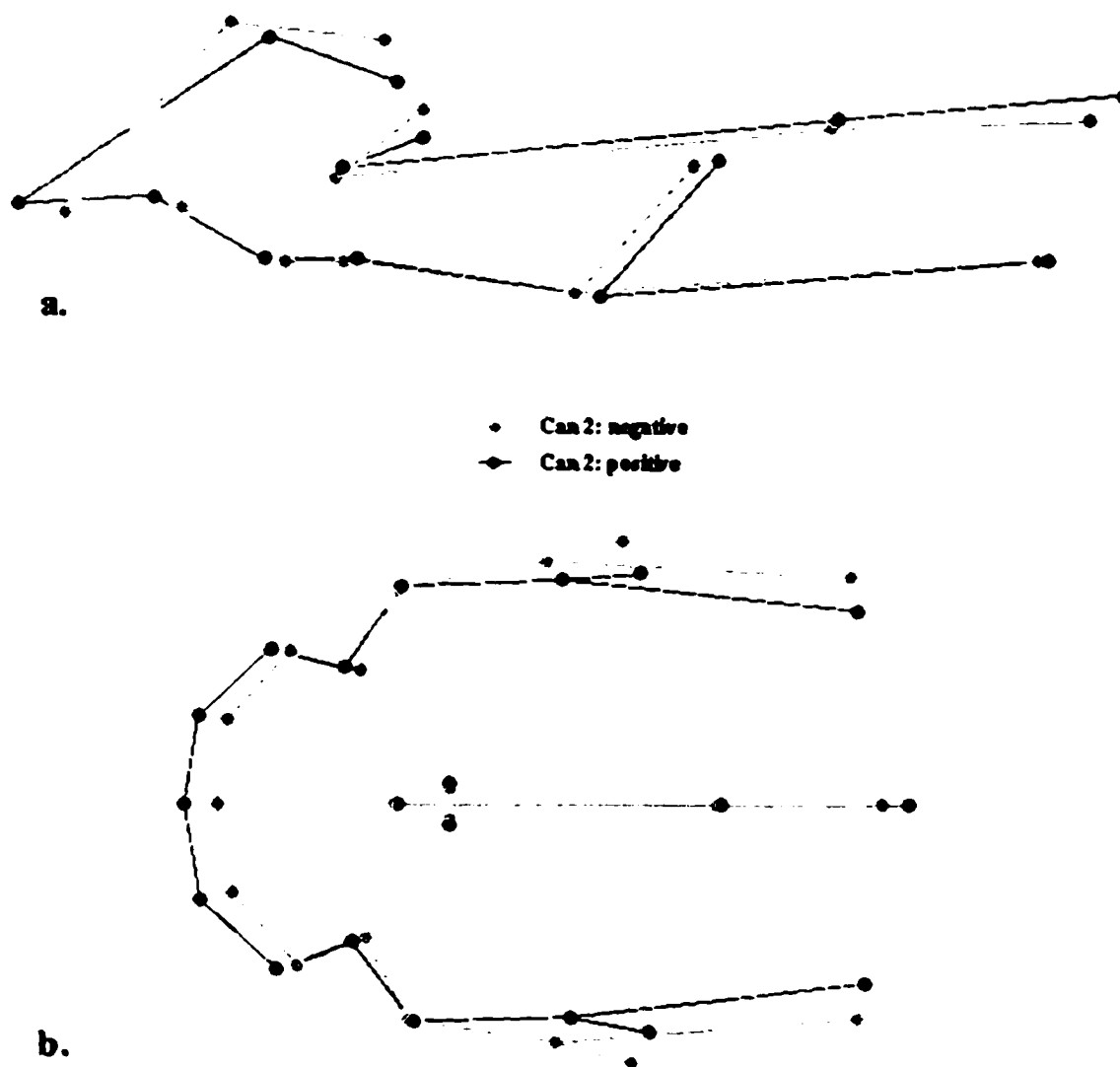


Figure 8-10 Shape change along CV 2. Black lines represent the positive loadings, gray lines show the negative loadings. (a) lateral view; (b) superior view. See Figure 8-1 for landmark references.

Canonical variate 3

Canonical variate 3 summarizes 12% of the variability among extant genera. A plot of the CV scores is shown in Figure 8-11; t-test results are given in Table 8-7. The extremes of this axis are defined by *Cebus* and *Pongo* on the negative end, and *Gorilla* on the positive. The means of both *Cebus* and *Pongo* are significantly different from all genera except each other. The range of *Cebus* scores, however, overlaps those of *Ateles*, *Cercopithecus*, and *Hylobates*, while the *Pongo* range overlaps all others except *Gorilla*. The *Gorilla* mean was significantly different from all taxa, with a range that overlapped only *Homo*, *Hylobates*, and *Papio*. *Homo* also had a significantly different mean from all other genera, its mean falling towards *Gorilla*; its specimen scores, however, ranged among those of every genus except *Cebus*. The means of *Ateles* and *Cercopithecus* were significantly different from all taxa except each other, falling closer to the negative end. The remaining taxa (*Hylobates*, *Pan*, *Papio*, and *Procolobus*) also formed an exclusive group, with means different from other taxa but not each other. All of these ranges overlap substantially.

Differences among species of *Hylobates* evident on PC 3 were not manifest in CV 3. Differences between male and female *Ateles* specimens were similarly absent from this canonical axis. CV 3 did, however, completely separate male and female specimens of *Cebus*.

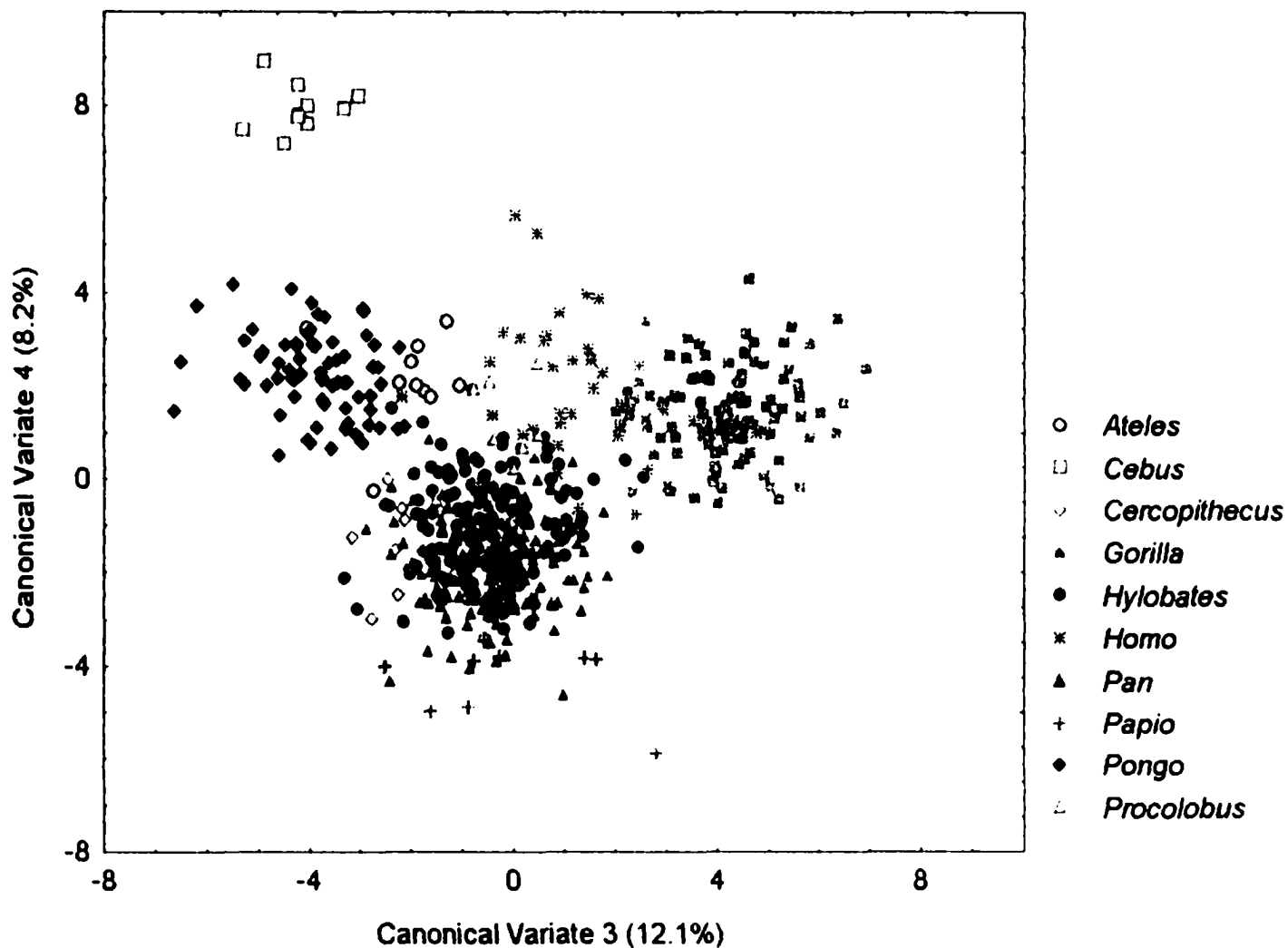


Figure 8-11 Plot of canonical variate scores for CV 3 and CV 4. CV 3 discriminates between *Cebus* and *Pongo* negatively and *Gorilla* at the positive extreme. CV 4 distinguishes *Cercopithecus*, *Hylobates*, *Pan*, and *Papio* from *Cebus*. *Ateles*, *Homo*, *Gorilla*, *Pongo*, and *Procolobus* fall between these.

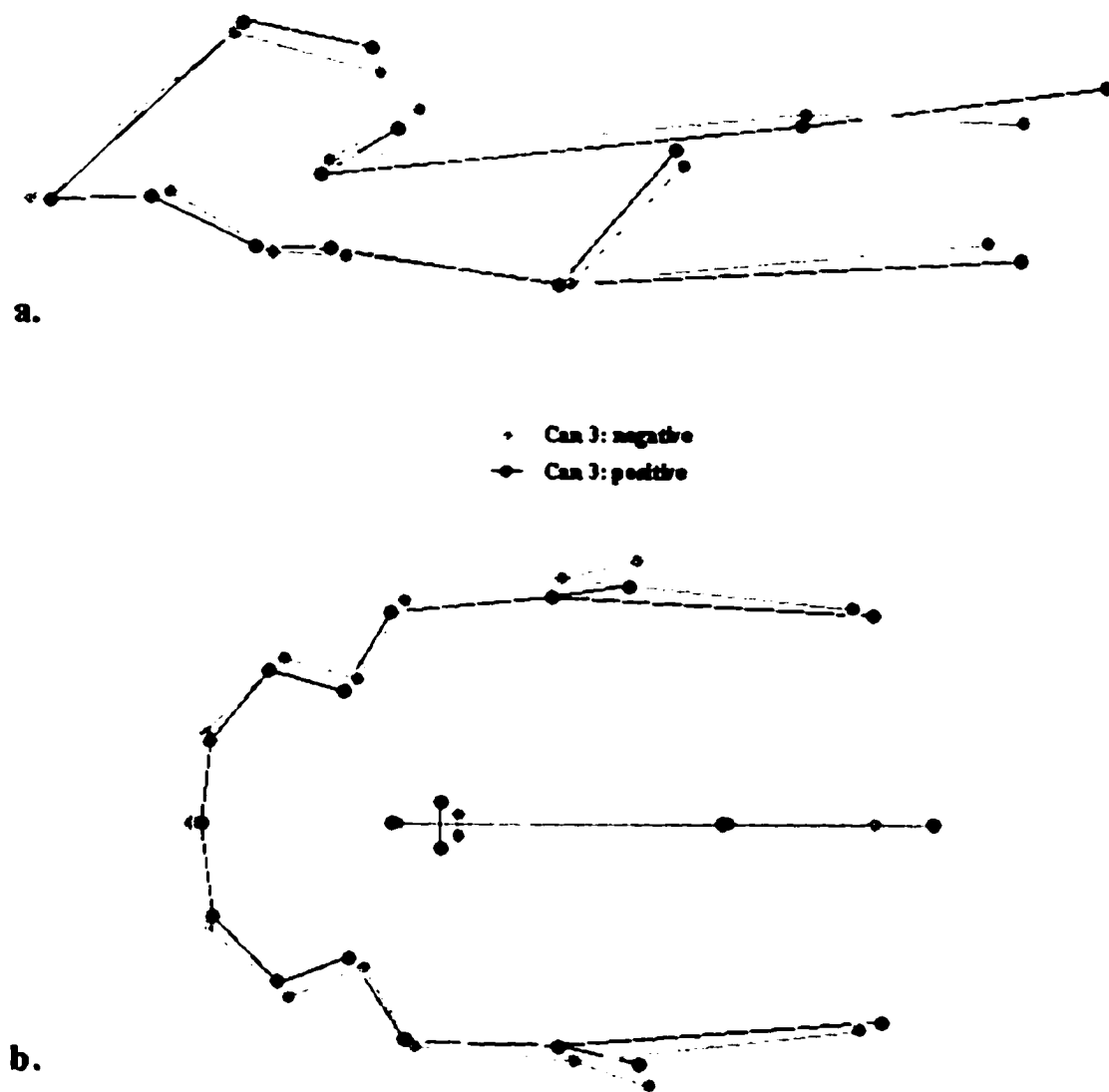


Figure 8-12 Shape change along CV 3. Black lines represent the positive loadings, gray lines show the negative loadings. (a) lateral view; (b) superior view. See Figure 8-1 for landmark references.

Figure 8-12 illustrates the differences in shape corresponding to the third canonical axis. The negative morphology (represented by *Cebus* and *Pongo*) is characterized by an anterior expansion of the subnasal clivus and broadening of the premaxillary morphology. This happens in conjunction with an inferior deflection of the nasal sill and superior displacement of **PIC** and **CLI**. Thus, the negative premaxillary morphology is somewhat more broad and protruding, with closer approximation between nasal sill and floor. The posterior incisive canal is also set more posteriorly at the negative pole, with **PIC** set closer to the midline; the positively loaded canals open more laterally. The post-canine dental arcade is also wider in the negative morphology, but shortened distally. The palatine process of the maxilla is generally similar at both extremes, but placed superiorly at the negative end. The horizontal palatine, however, shows considerable difference; in the negative morphology, **STA** is inferior (rather than superior) to **MAP**, with a relatively short distance between them. Combined with a superior deflection in the posterior dental arcade, the negative morphology would have a gradually shallower palate posteriorly.

Canonical variate 4

The fourth canonical axis represents 8% of the among-groups variation in the palates of these extant taxa. T-test results are listed in Table 8-7, while CV scores are plotted in Figure 8-11. CV 4 distinguished between *Papio* and the negative end and *Cebus* at the positive. T-tests found both taxa to be different from every other genus mean. *Cebus* was clearly distinct, overlapping no other taxa; *Papio*'s range overlapped *Cercopithecus*, *Hylobates*, and *Pan*. Among these latter, t-tests found both *Hylobates* and *Pan* to be different from every genus (including each other) except *Cercopithecus*—

whose mean was situated between theirs. *Ateles*, *Gorilla*, *Homo*, *Procolobus*, and *Pongo* ranged more positively, with substantial overlap among them. No additional effects related to taxonomy or sex were found on this axis.

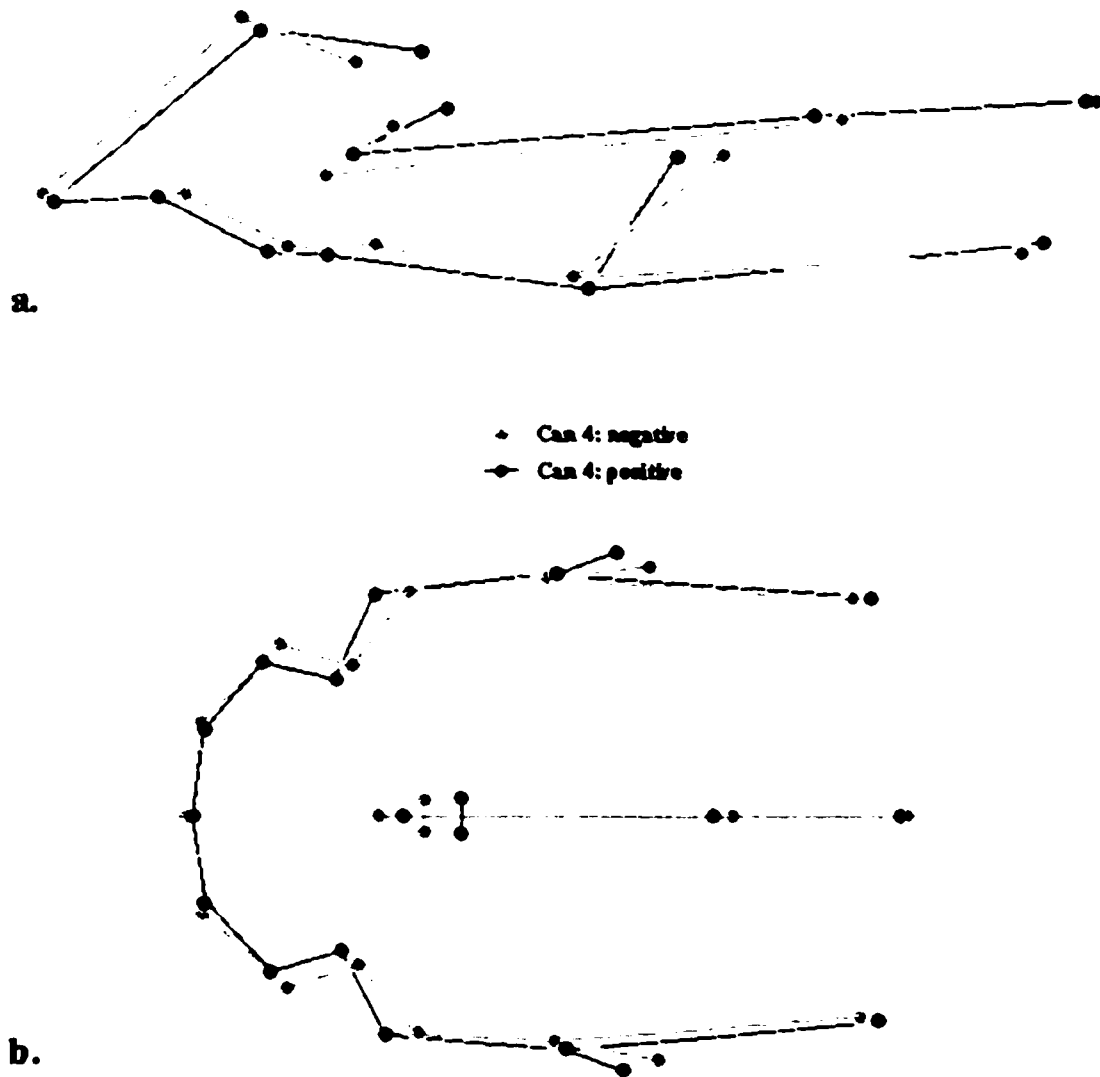


Figure 8-13 Shape change along CV 4. Black lines represent the positive loadings, gray lines show the negative loadings. (a) lateral view; (b) superior view. See Figure 8-1 for landmark references.

Figure 8-13 illustrates the shape changes associated with canonical variate 4. The anterior morphology at the negative extreme shows substantial differences. It is characterized by anterior expansion of all premaxillary landmarks, superior displacement of **ANS**, but inferior placement of **CLI**. This latter is correlated with the inferior deflection of **INC** and **PIC**, through inferior rotation of the anterior maxillary palatine processes. In contrast, the dental arcade is somewhat superiorly placed from alveolare through the canine and premolars, yielding a shallower anterior palate at the negative extreme. This morphology also demonstrates marked antero-posterior expansion of the maxillary palatine processes and mesio-distal expansion of the canine (**IPM—CPC**). Finally, the malar root origin of the negative morphology is substantially posterior and somewhat medial to that of the positive morphology.

Canonical variate 5

CV 5 comprises nearly 6% of the palatal variability among these genera. Pairwise differences are listed in the t-test results of Table 8-7. These differences are represented graphically in the plot of canonical variate scores shown in Figure 8-14. CV 5 clearly separates cercopithecoids from platyrrhines; hominoid taxa, however, overlap with most of these. Both platyrrhines are significantly different from all other taxa, scoring most negatively on this axis; *Papio* is also significantly different from all genera, placing at the positive extreme. *Cercopithecus* and *Procolobus* are indistinct from each other and from *Homo* and *Pongo*; means of these latter two are significantly different from each other, however. The mean of *Gorilla* is different from those of the other nine taxa; *Pan* and *Hylobates* are different from every genus except each other. Ranges of all hominoid genera, however, overlap substantially.

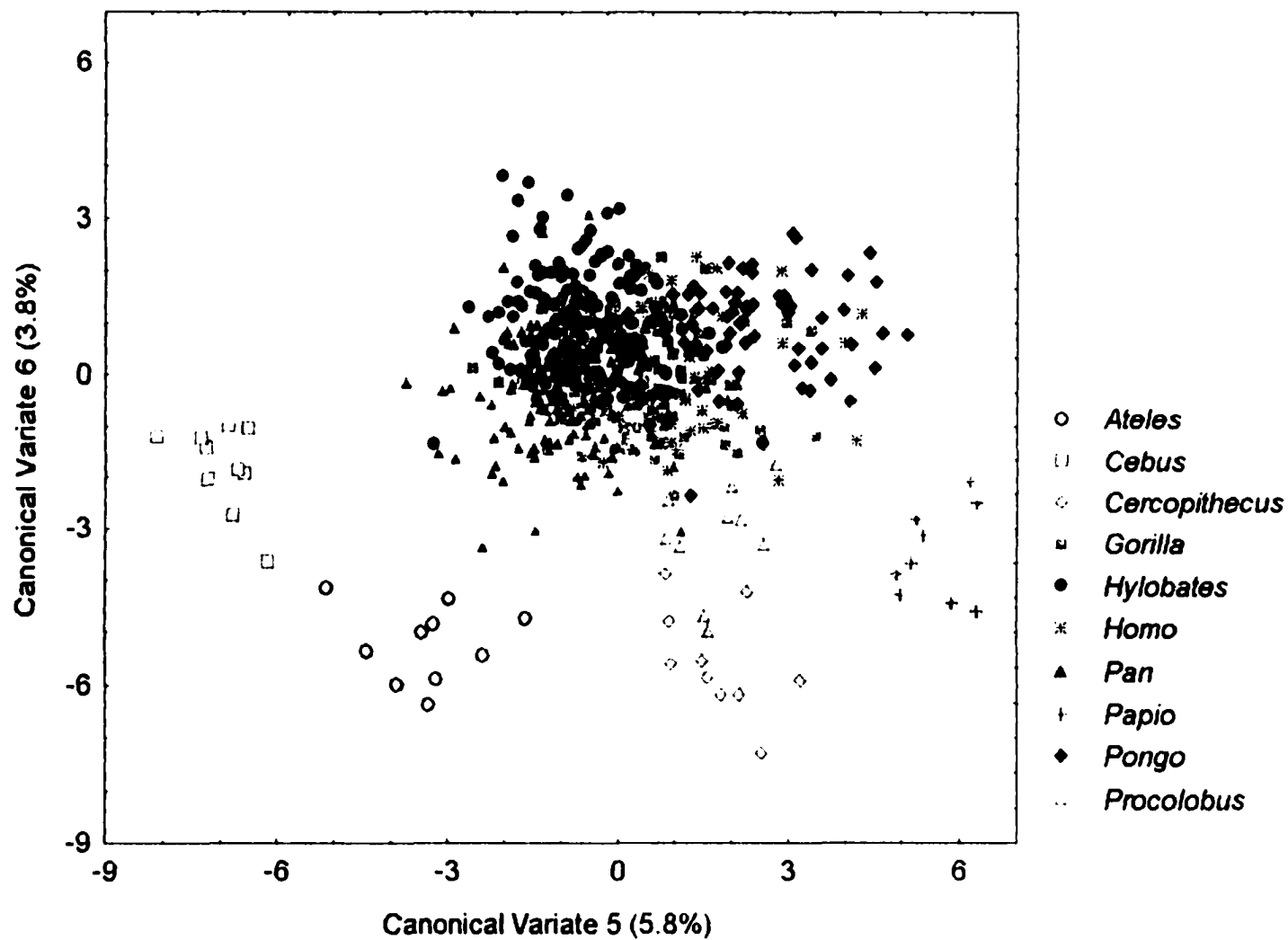


Figure 8-14 Plot of canonical variate scores for CV 5 and CV 6. CV 5 clearly discriminates between platyrrhines on the negative end and cercopithecoids on the positive end; hominoids generally fall between these, though *Pongo* specimens all score positively. CV 6 distinguishes hominoids from the other genera.

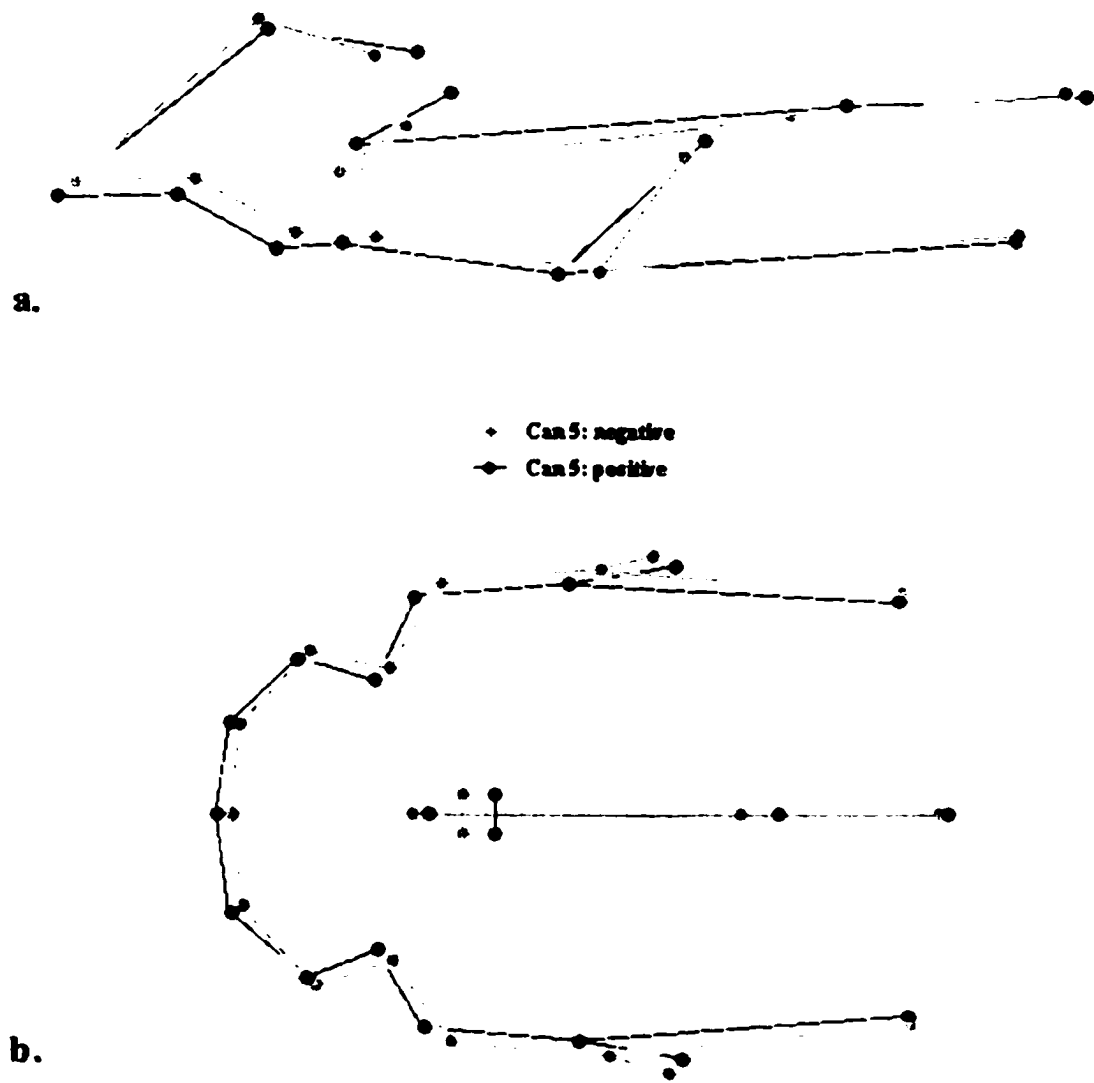


Figure 8-15 Shape change along CV 5. Black lines represent the positive loadings, gray lines show the negative loadings. (a) lateral view; (b) superior view. See Figure 8-1 for landmark references.

Shape change represented by CV 5 is illustrated in Figure 8-15. The negative morphology (represented by the platyrrhines) shows substantial superior deflection of the premaxillary features. This is particularly evident in the anterior dental arcade, where landmarks are also displaced posteriorly. The anterior nasal spine, on the other hand, is positioned superiorly and anteriorly relative to its positive counterpart. **CLI**, **PIC**, and **INC** are deflected inferiorly, the latter two more severely than the former. Along the dental arcade, landmarks of the negatively loaded morphology are shifted posteriorly (except **DM3**), while the midline palate is placed anteriorly; the arcade is also broader distal to **I12**. Finally, the malar root origin is placed antero-inferiorly relative to its positive counterpart, more closely approximating **PMC**.

Canonical variate 6

The sixth canonical variates axis summarizes about 4% of the among-genera variation in palate form. Differences on this axis are shown graphically in Figure 8-14, and between particular genus pairs in Table 8-7. This axis nicely separates the hominoid from non-hominoid genera. At the negative end, *Ateles* and *Cercopithecus* have means that are significantly different from all other taxa except each other; the same is true for *Papio* and *Proconsul*, who place slightly less negatively. The *Cebus* mean is different from all other taxon means. Among the hominoids there are two exclusive groups: hominines and non-hominines. Genera in these clusters have significantly different means from other genera, but not from each other. Hominoid ranges all overlap substantially. The range of *Cebus* overlaps with the lower end of all hominoid ranges and the upper end of *Papio* and *Procolobus*. Ranges of these latter two overlap all genera

except *Hylobates*. *Ateles* and *Cercopithecus* ranges only overlap those of *Papio* and *Procolobus*.

Differences in shape summarized by CV 6 are pictured in Figure 8-16. The negative (non-hominoid) morphology is greatly expanded anteriorly in the inferior premaxilla, with protruding midline subnasal clivus, but posteriorly placed **IPM**. This gives the mesial dental arcade a rounded appearance from the inferior perspective. Along with the anterior premaxillary expansion, the negative maxillary palatine processes are set somewhat posteriorly; thus, **CLI** and **PIC** are antero-posteriorly distant, while they are more proximate in the positive morphology. The posterior incisive canals are also relatively more distant at the negative end, being closer to the midline at the positive. The distance between lingual canine landmarks is reduced at the negative pole, supporting the hypothesis that hominoids have a wide anterior palate (Harrison, 1987; Rae, 1993, 1997; Harrison & Rook, 1997). In the post-canine dentition, the negative dental arcade extends more distally, with longer mesio-distal fields for both premolars and molars. This is contrasted in the palatine bone, however, which is greatly shortened in antero-posterior dimension. The malar root origin is set posteriorly at the negative pole, but its relationship to **PMC** is similar to the positive morphology.

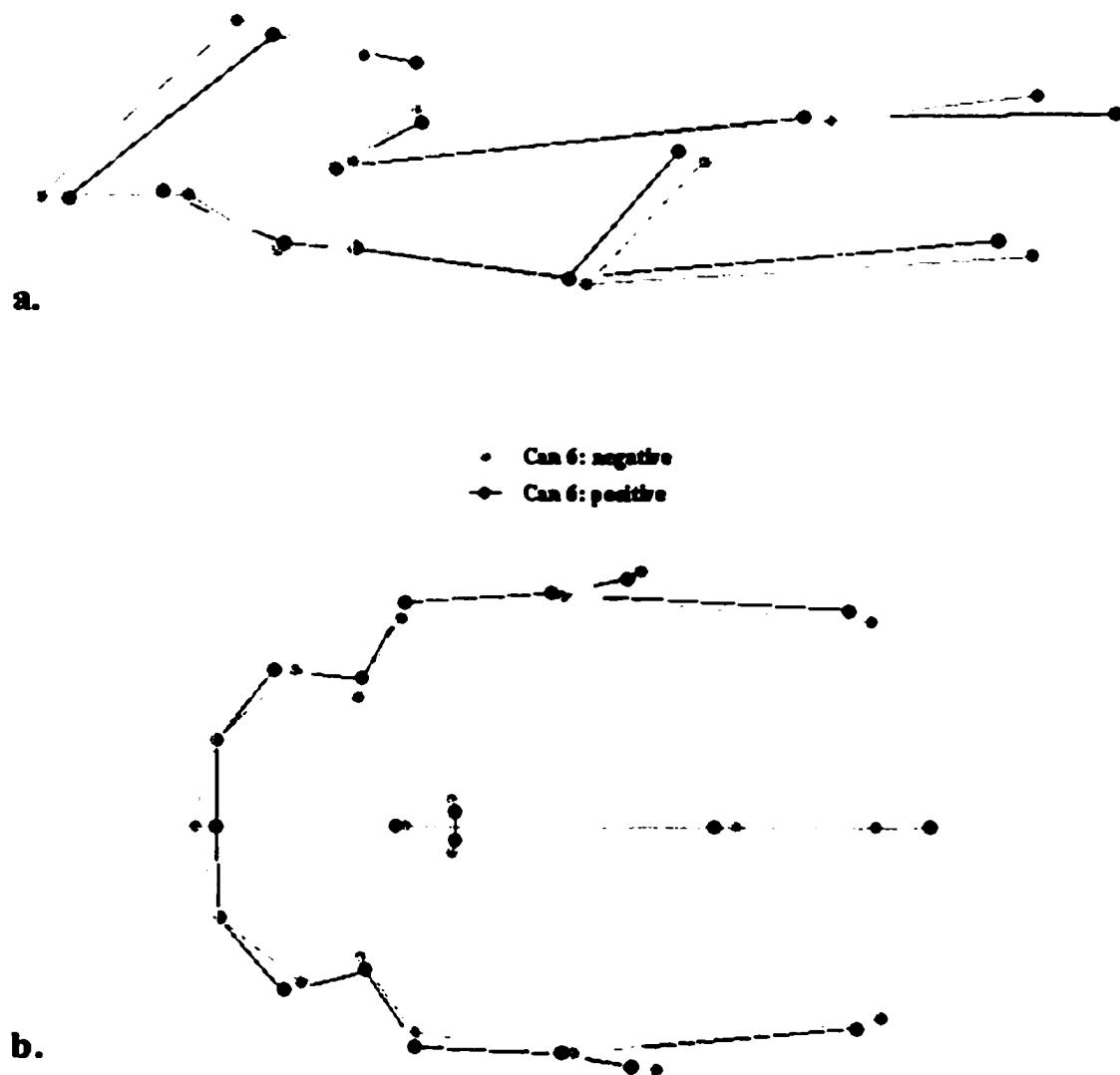


Figure 8-16 Shape change along CV 6. Black lines represent the positive loadings, gray lines show the negative loadings. (a) lateral view; (b) superior view. See Figure 8-1 for landmark references.

MAHALANOBIS DISTANCE

As part of the canonical variates analysis, unbiased Mahalanobis D^2 values were computed for the extant genera and used to compare them in canonical space. Hotelling's T^2 tests of pairwise comparisons found highly significant differences ($p < 0.0001$) between every genus pair. A randomization procedure was also used to examine the effect of unequal sample size in this analysis. As described in Chapter 5, Mahalanobis D^2 values were computed for 10,000 randomly chosen, equal sample groups. Table 8-8 lists the D^2 values for both the whole-sample (values in the lower triangle) and the mean values from the equal-sample (values in the upper triangle) analyses. While numbers from the whole-sample analysis are not directly comparable to those from the equal-sample, relative distances between taxon pairs can be compared. If sample size had no effect, then these relative distances should be the same.

Table 8-8 Matrix of unbiased Mahalanobis distance estimates between pairs of genera. Values in the lower triangle were computed from the whole sample; values in the upper triangle are mean distances computed from the randomization procedure. Values from upper and lower triangles are not directly comparable, but relative differences within each should be similar if unequal sample size was not a significant factor determining distances.

Genus	Atel	Cebu	Cerc	Gori	Homo	Hylo	Pan	Papi	Pcol	Pong
Atel		268.1	268.5	467.0	844.8	261.6	572.5	547.7	306.8	517.8
Cebu	116.4		555.6	591.8	954.0	430.0	696.8	949.7	457.4	580.6
Cerc	98.4	217.8		426.6	829.0	170.1	530.3	220.8	116.1	452.9
Gori	129.4	188.6	144.1		672.6	282.5	221.2	582.3	293.8	251.7
Homo	263.2	318.2	264.1	216.9		726.5	514.7	1118.5	796.2	754.7
Hylo	83.2	158.0	67.6	79.0	207.9		450.0	276.8	152.6	407.3
Pan	163.8	219.3	178.2	62.3	168.7	129.3		796.6	455.9	175.3
Papi	179.2	360.3	99.2	183.0	367.9	102.1	258.3		281.9	642.5
Pcol	105.0	170.7	47.4	81.5	226.3	51.7	133.3	113.6		369.0
Pong	146.1	167.3	154.8	74.3	227.1	115.3	51.0	222.3	108.1	

Distances between taxa remained largely the same in both analyses, with a few exceptions. In the equal-sample analysis, *Cebus* was relatively closer to *Ateles* and *Cercopithecus*, but more distant from *Pongo*. *Homo* moved closer to *Gorilla* than it was to *Hylobates*, while these latter two became more distant from each other. Perhaps the most significant difference was between *Papio* and *Procolobus*: among all comparisons involving *Procolobus*, *Papio* was only sixth closest in the whole-sample analysis, but third closest in the equal-sample.

To visualize these relationships, nearest neighbors were joined in a minimum spanning tree. Figure 8-17 illustrates the MST for the whole sample: tree topology does not change if values from the equal-sample analysis are used instead. As with the analysis of the entire cranium, three major anthropoid groups (platyrrhines, cercopithecoids, and hominoids) are readily distinguishable. *Hylobates* occupies the central location, having the lowest average D^2 value; the average for *Procolobus* is only slightly greater. *Cebus* is closest to *Ateles*, though fairly distinct from all taxa (see Table 8-8); *Ateles* is closest to *Hylobates*. The cercopithecoids are separate from the other taxa when only the closest neighbor is considered: both *Papio* and *Procolobus* are both closest to *Cercopithecus* which, in turn, is closest to the latter. The Old World monkey genera attach to the tree through the next smallest distance: *Procolobus*—*Hylobates*. The hominid genera attach to *Hylobates* as well, though it is only the third closest pairing of *Gorilla*. This reiterates (see Figures 8-2 and 8-8) the substantial degree of morphological differentiation between the great ape palate and those of other taxa. *Homo*, with the greatest average Mahalanobis D^2 values, has the most distinct palatal morphology. Nevertheless, it is most similar to *Pan*, followed by *Gorilla* (in the equal-sample analysis).

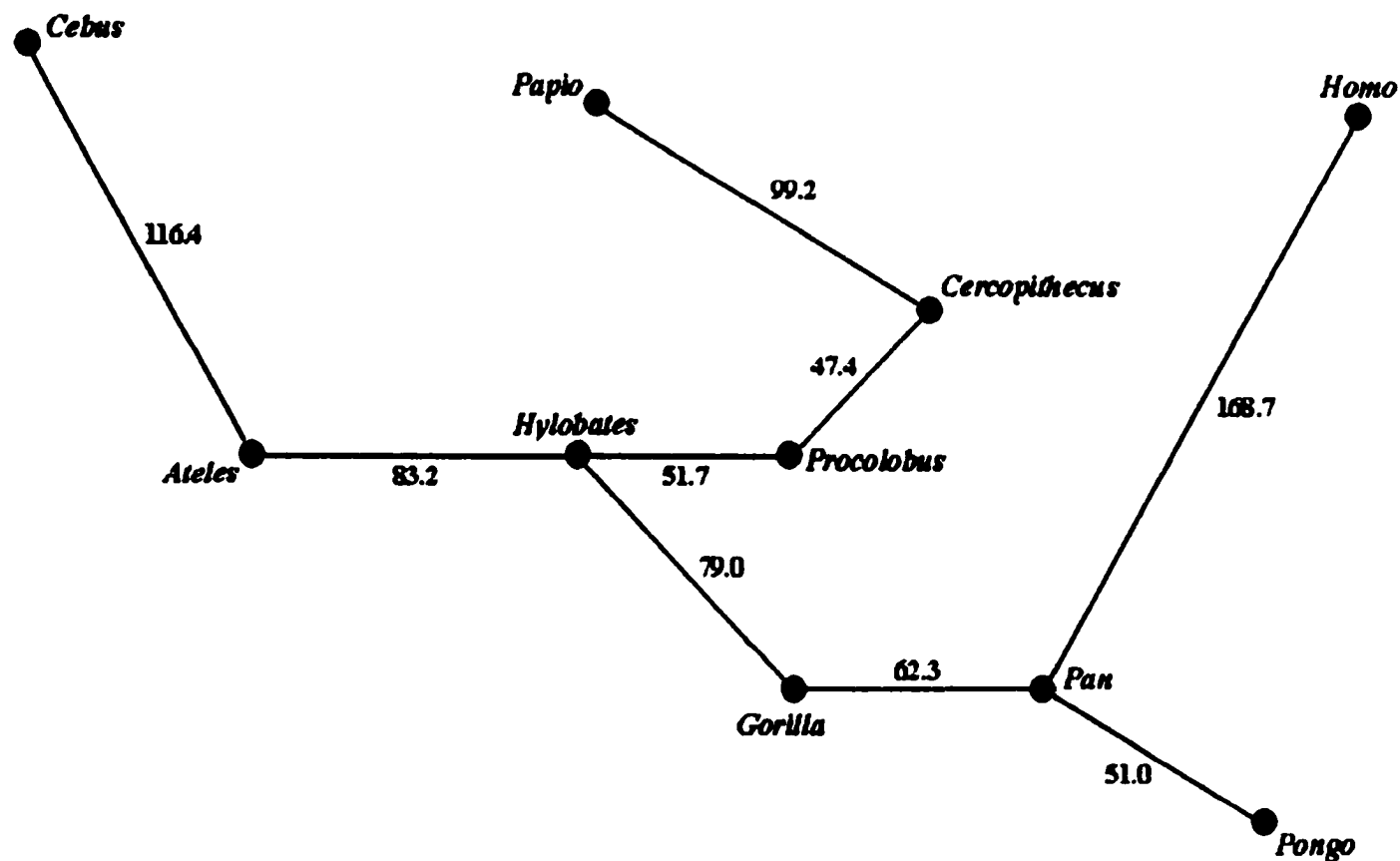


Figure 8-17 Minimum spanning tree showing the nearest-neighbor for each genus as measured by Mahalanobis D^2 values from the whole-sample analysis; using mean values from the equal-sample randomizations does not alter the tree topology. Relationships between connected taxa are drawn to scale; distances between un-joined genera are not to scale. Additional Mahalanobis distances are given in Table 8-8 for both whole-sample and equal-sample analyses (see text for discussion).

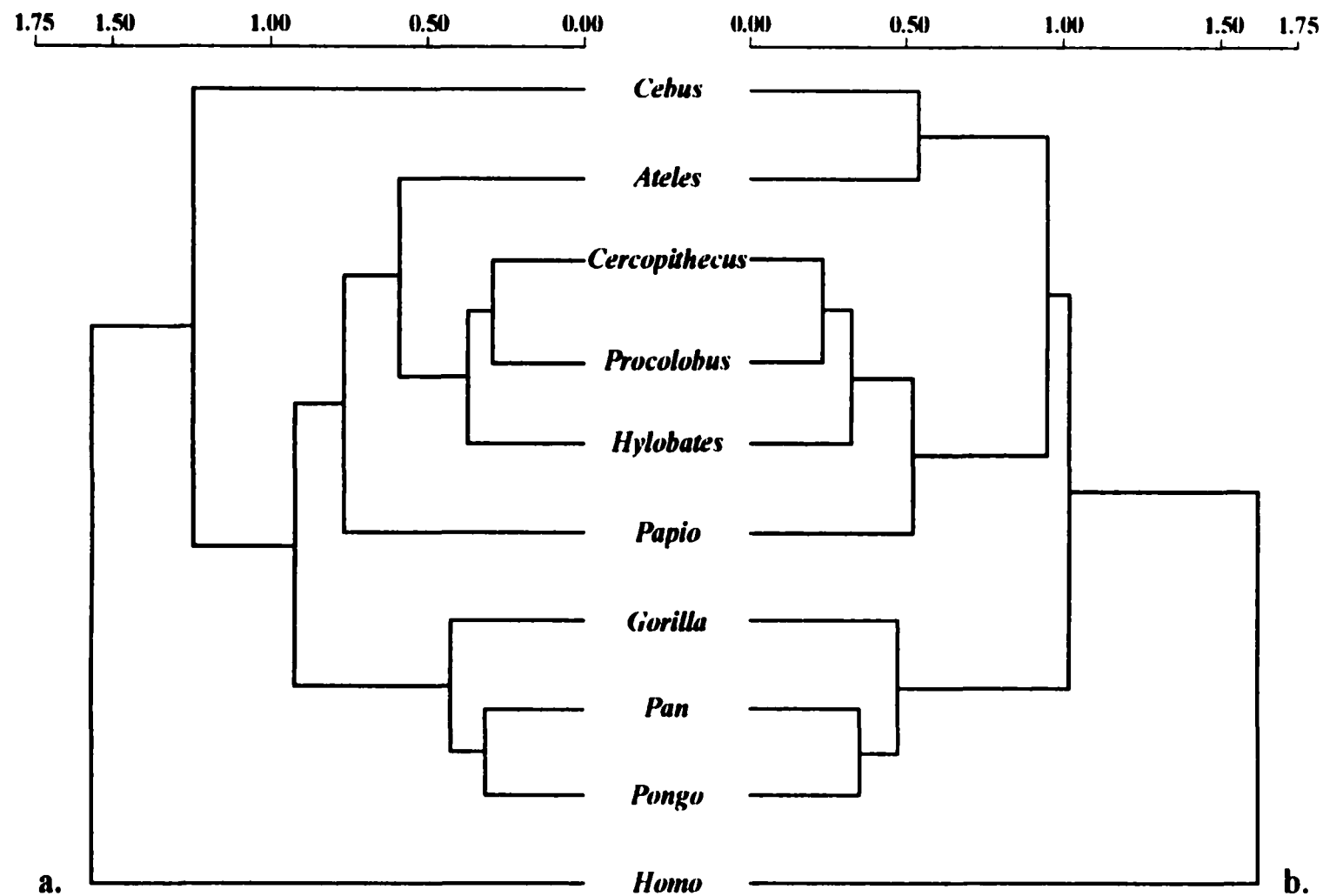


Figure 8-18 Results of UPGMA cluster analyses based on (a) Mahalanobis D^2 values from the whole sample, and (b) mean Mahalanobis D^2 values of equal-sample replicates ($n=10,000$). The distance matrices are given in Table 8-8.

Figure 8-18 illustrates the hierarchical relationships among these taxa through a UPGMA cluster diagram of Mahalanobis D^2 values. The tree on the left (Figure 8-18a) represents values from the whole-sample analysis; on the right side (Figure 8-18b) is a cluster of mean D^2 values from the randomized equal-sample analysis. Relationships among most of the genera are similar in both trees. The closest pairing is between *Cercopithecus* and *Procolobus*; they are joined by *Hylobates* in both trees, though the *Pan*—*Pongo* cluster is shorter in the whole-sample analysis. The greatest difference between trees occurs in the placement of *Cebus*. As noted above, *Cebus* moves relatively closer to *Ateles* in canonical space when sample size is controlled. Thus, in the equal-sample analysis, the platyrrhines cluster together. In conjunction with this, *Papio* more closely approximates the other cercopithecoids—especially *Procolobus*—when samples are held equal. Thus, Figure 8-18b shows three distinct clusters, all separated by nearly equal distances: platyrrhines, non-hominid catarrhines, and great apes. Among all of these, the morphology of *Homo* is quite unique; while most similar to the other African apes, the modern human palate is too distinct to cluster among them here.

All of these results largely corroborate previous studies done on the subnasal morphology of catarrhine primates (e.g. Ward & Kimbel, 1983; McCollum *et al.*, 1993; McCollum & Ward, 1997). Although this data subset included a number of landmarks outside of the subnasal region, the majority of variation among these taxa occurs in premaxillary morphology. Ward and Brown (1986) have hypothesized that hylobatids and cercopithecoids retain a subnasal pattern similar to that of the primitive catarrhine morphotype. Here, *Hylobates* approximated the centroid of the taxa being studied—being on average most similar to all other genera; *Procolobus* was only slightly less central.

Add to that the similarity of *Ateles* to both genera, and it seems reasonable to conclude that the hylobatids—along with cercopithecoids in general—share a subnasal and palatal morphology that is likely primitive for catarrhines (see Ward & Kimbel, 1983). Indeed, the proximity of *Ateles* to *Hylobates* may indicate that this subnasal pattern is generalized for anthropoids. The fairly unique morphology of *Cebus*, however, makes such a conclusion tentative. By far, the greatest distinction among these taxa is between hominids and the other genera. This division in particular is driven by differences in the subnasal morphology (see e.g., Figure 8-3), suggesting that rearrangement of the premaxilla likely played a key role in the evolutionary transformation of the hominid palate.

SHAPE DIFFERENCES BETWEEN CROWN CLADES

More than either of the previous analyses, the palatal morphology examined here is robust for distinguishing among groups. This is evidenced by the remarkable similarity between PCs 1-2 and CVs 1-2: the axes of greatest variation among specimens largely correspond to the canonical axes that separate genera. The greatest difference within this sample is between hominid and non-hominid genera. Somewhat less in magnitude is the difference of the modern human palate from and all of the others.

In order to examine differences that correspond to the morphologies of particular crown clades, a series of two-group discriminant analyses were used to test for differences at each node of a phylogenetic tree (see Figure 8-19). Details of this procedure are given in Chapter 6. ANOVAs were performed on the discriminant scores for each test. In every case, highly significant ($p < 0.0001$) differences were found. Cross-

validations were also computed to assess the robusticity of discriminant functions in separating the taxa. To visualize morphological differences at each node, canonical coefficients from each DA were applied to the consensus landmark configuration.

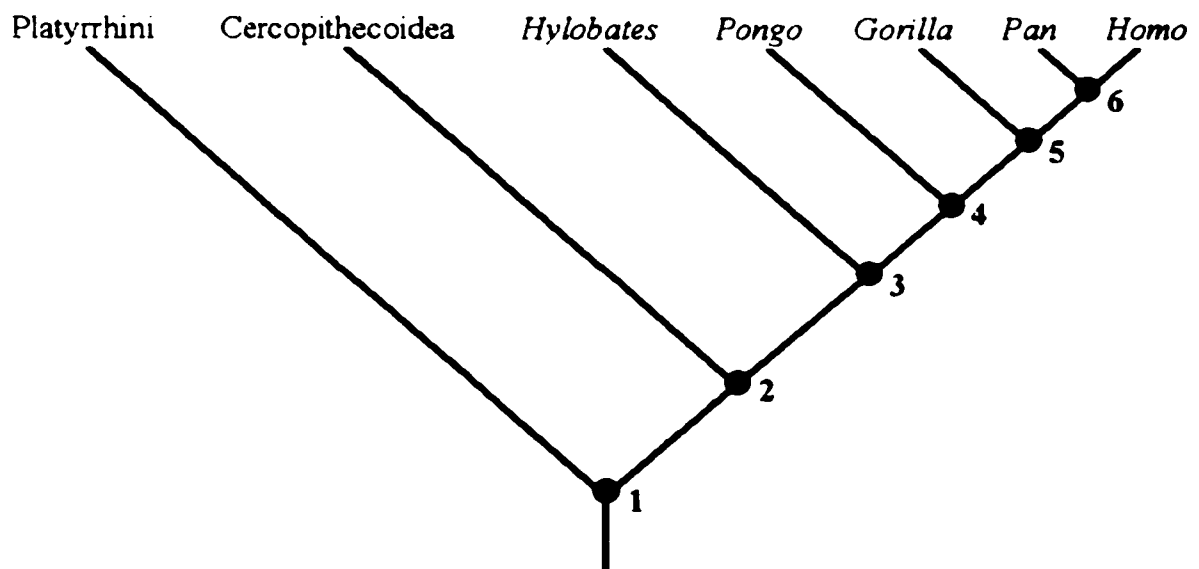


Figure 8-19 Consensus phylogeny of the relationships among extant apes and the main anthropoid clades. Nodes are referred to by number in the text.

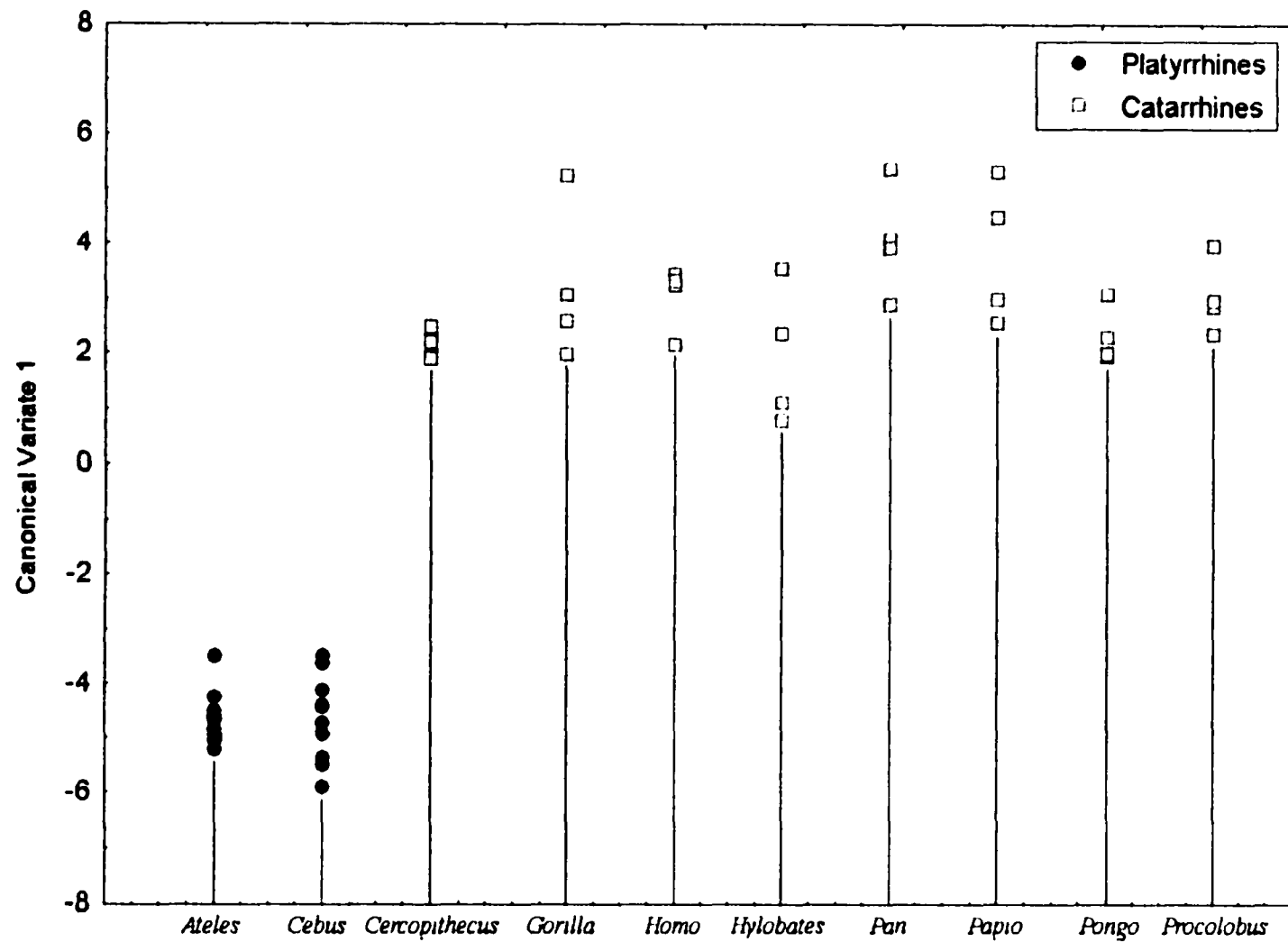


Figure 8-20 Plot of CV scores for the discriminant axis separating platyrrhines from catarrhines. Although only the two groups were used for class variables, these results are illustrated by genus to better depict the distribution of specimens on the axis.

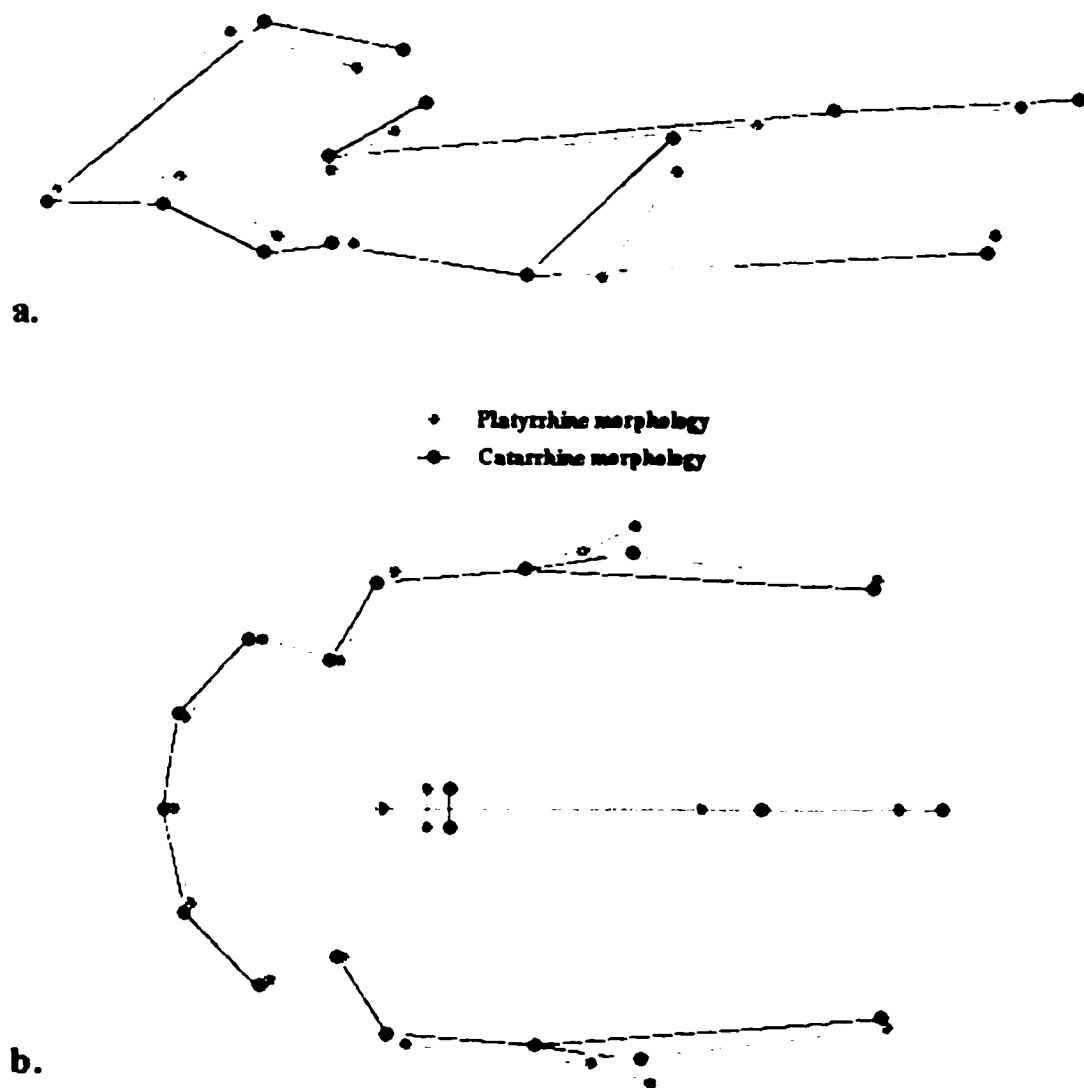


Figure 8-21 Shape change corresponding to the discrimination between platyrrhines (gray) and catarrhines (black) sampled for this analysis. (a) lateral view; (b) superior view. See Figure 8-1 for landmark references.

Node 1: Platyrrhines vs. Catarrhines

Node 1 in Figure 8-19 separates the platyrrhines from the catarrhines. While the sample of platyrrhines is only 20, thirty-two catarrhines were included so as to have 2 males and 2 females from each of the genera. Results of the cross-validation, shown in Table 8-9, indicate the robusticity of these landmarks in distinguishing between samples from these infraorders. This is corroborated by the plot of discriminant scores shown in Figure 8-20. There is no overlap between platyrrhine and catarrhine ranges; *Hylobates* occupies the lowest range among catarrhines, while *Pan* has the highest mean score.

Table 8-9 Cross-validation results for DA of palatal morphologies in catarrhines and platyrrhines. Each cell gives the number (n) and percent (%) of individuals from the taxa on the left assigned to the taxa across the top.

Taxon		Catarrhine	Platyrrhine
Catarrhine	N	32	
	%	100.00	
Platyrrhine	N		20
	%		100.00

Shape differences defining the samples of platyrrhine and catarrhine specimens are illustrated in Figure 8-21. Variation between these groups is evident at most of the landmarks. The premaxillary morphology in the platyrrhines is substantially reduced in height; the subnasal clivus is shortened and somewhat anteriorly placed in its superior aspect. Both **LCM** and especially **IPM** are displaced superiorly. **CLI** and **PIC** are antero-inferior to the catarrhine positions, in conjunction with an inferior deflection of the anterior maxillary palatine. Thus, the relationship between the nasal sill and floor are similar in both platyrrhines and catarrhines as groups; the catarrhines, however, have a

substantially thicker maxillary palatine. Posterior to the canines, the platyrrhine dental arcade is broader relative to the catarrhine. The premolar field in the platyrrhines extends far distally, perhaps owing to retention of P^2 ; this relationship is reversed in the molar field, however, so that both dental arcades are similar in antero-posterior dimension. The differences of greatest magnitude are in the antero-posterior dimension of the maxillary palatine. In catarrhines, the maxillo-palatine suture is substantially posterior to the platyrrhine. This, in turn, results in a posteriorly extending hard palate. The catarrhine palate midline is also superior to that of the platyrrhine, yielding a deeper palate arcade. Finally, the malar root origin is superiorly placed in catarrhines, towards the level of the palate midline; in platyrrhines the malar root sits well below the palate midline.

Node 2: Cercopithecoids vs. Hominoids

Differences between palatal morphologies of hominoids and the cercopithecoid sample are defined by node 2 (See Figure 8-19). Cross-validation (Table 8-10) correctly assigned all of the specimens in both samples. A plot of discriminant scores (Figure 8-22) confirms the robusticity of the function with a clear separation between cercopithecoid and hominoid scores.

Table 8-10 Cross-validation results for DA of cercopithecoid and hominoid palate morphologies. Each cell gives the number (n) and percent (%) of individuals from the taxa on the left assigned to the taxa across the top.

Taxon		Cercopithecoids	Hominoids
Cercopithecoids	n	30	
	%	100.00	
Hominoids	n		30
	%		100.00

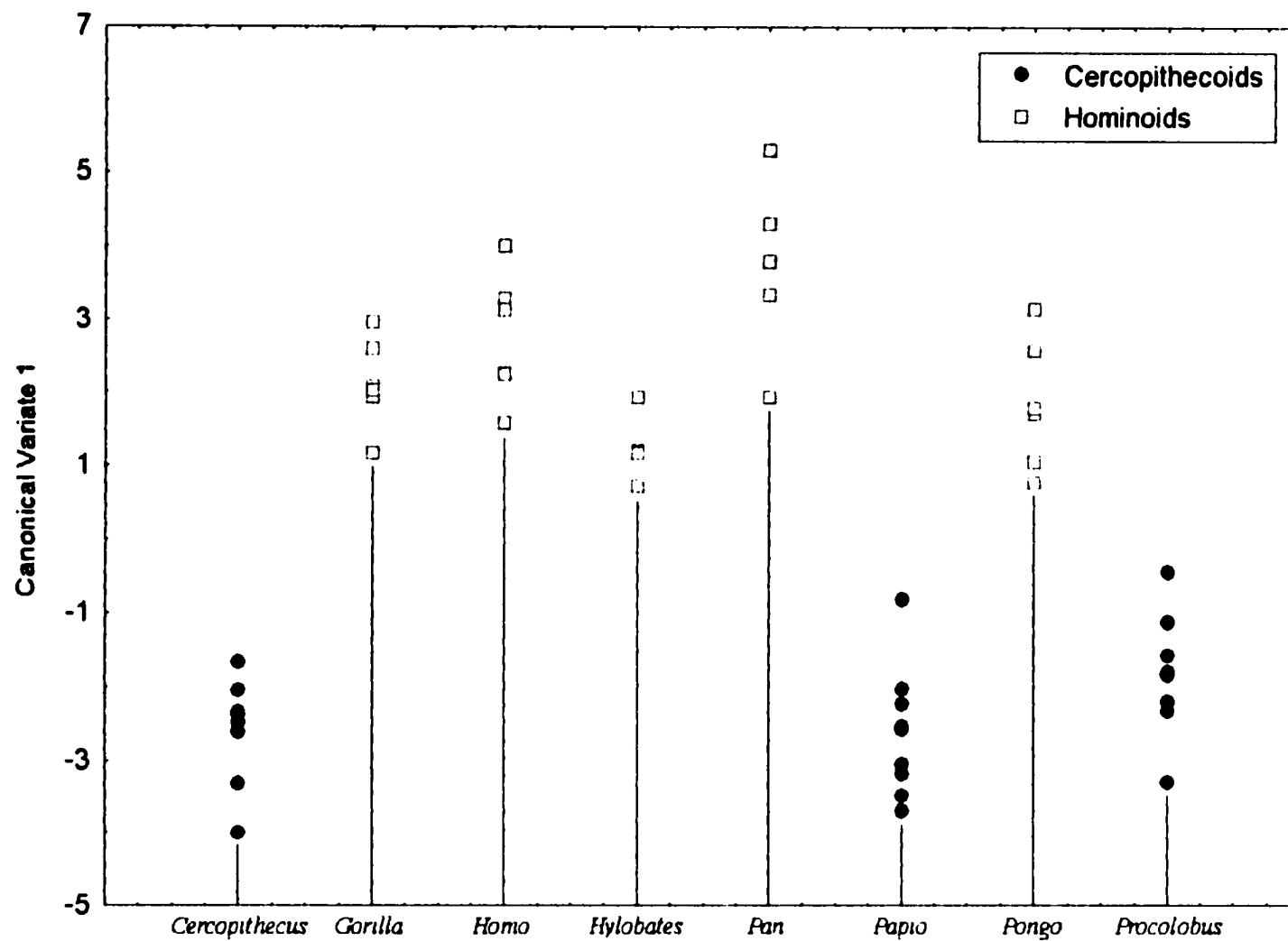


Figure 8-22 Plot of CV scores for the discriminant axis separating cercopithecoids from hominoids. Although only the two groups were used for class variables, these results are illustrated by genus to better depict the distribution of specimens on the axis.

Figure 8-23 illustrates the differences in morphology defined by these samples. The majority of variation occurs in the anterior aspects of the palate. The cercopithecoid nasoalveolar clivus is shorter and anteriorly placed relative to the hominoids. This is accomplished largely through a relative postero-superior displacement of the hominoid nasal sill. This result runs counter to the shape differences associated with canonical variate 6—which also tended to separate hominoids from non-hominoids. Yet, in distinguishing particularly between hominoid and cercopithecoid palatal morphologies, clivus height seems to be an important feature. The anterior maxillary palatine is inferiorly deflected in hominoids, yet the posterior (nasal) incisive canal is superior to its cercopithecoid counterpart. This is indicative of a relatively thicker hominoid palate. Fewer changes can be seen in the rest of the dental arcade. The inter-canine distance is somewhat reduced in cercopithecoids; in fact, a broader anterior palate has been cited as one of the few characteristics distinguishing hominoids from stem eucatarrhines (Harrison, 1987; Rae, 1993). Relative to cercopithecoids, the post-canine dental arcade is also broader among hominoids—though this is probably a primitive features (see below). The greatest difference in the posterior palate occurs at the malar root origin: **MRO** in cercopithecoids is set further back along the palate.

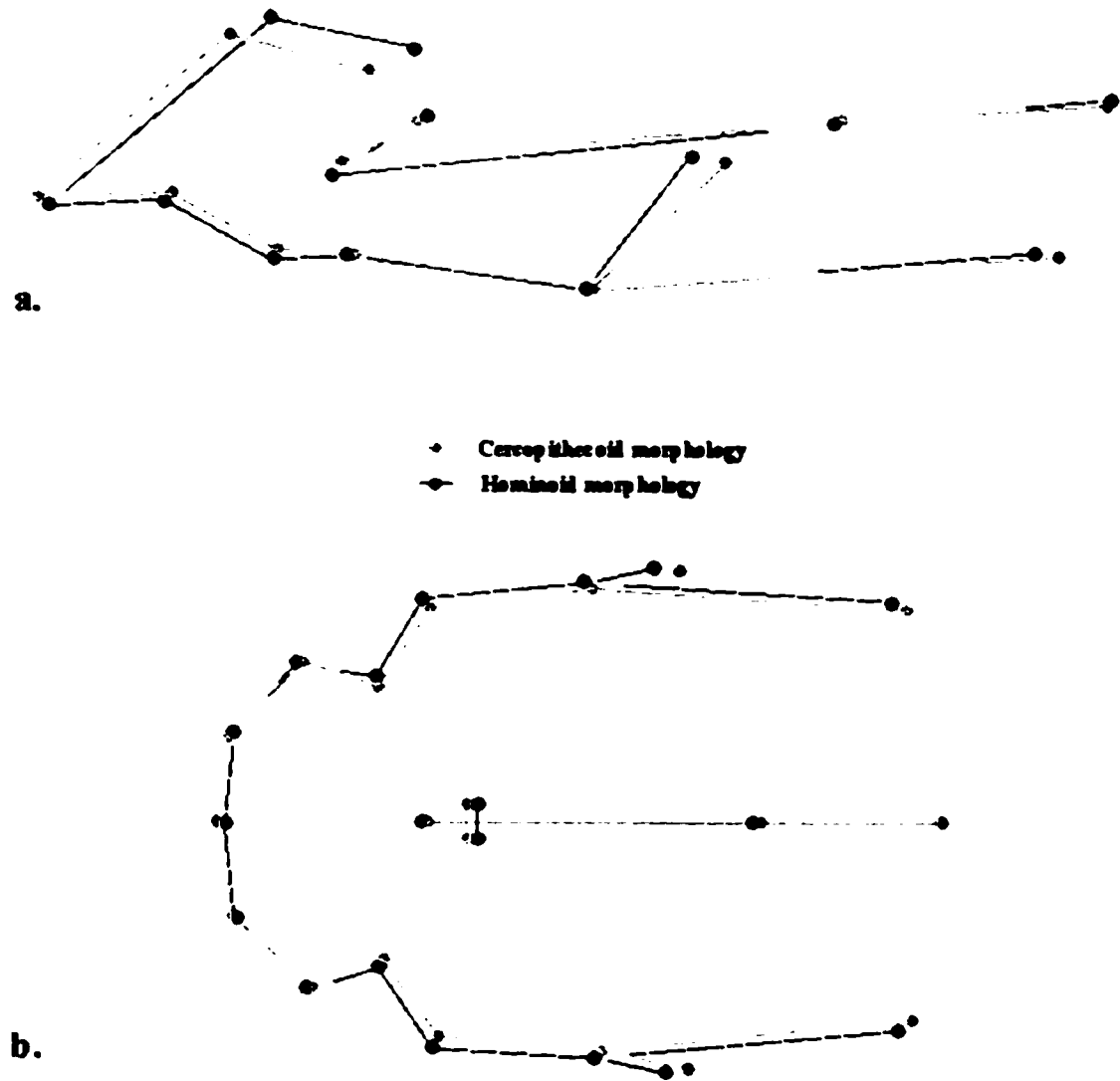


Figure 8-23 Shape change corresponding to the discrimination between cercopithecoid genera (gray) and the hominoids (black). (a) lateral view; (b) superior view. See Figure 8-1 for landmark references.

Node 3: Hylobatids vs. Hominids

The difference between hylobatid and hominid palatal supraorbital morphologies corresponds with the greatest axes of variation among specimens (PC 1) and genera (CV

1). It is not surprising, then, that discrimination at node 3 was highly successful. Cross-validation results (Table 8-11) demonstrate a perfect record for classifying specimens of both families. This difference is illustrated by the plot of discriminant scores in Figure 8-24. Shape differences corresponding to this discriminant axis are generally similar to those described for PC 1 (and CV 1). There are, however, some variations, and so shape differences are discussed below.

Table 8-11 Cross-validation results for DA of hylobatid and hominid palatal morphologies Each cell gives the number (n) and percent (%) of individuals from the taxa on the left assigned to the taxa across the top.

Taxon		Hylobatids	Hominids
Hylobatids	N	130	
	%	100.00	
Hominids	N		128
	%		100.00

Figure 8-25 shows the differences in palatal morphology that correspond to the axis discriminating hylobatids from hominids. Again, the majority of differences are concentrated in the anterior palate. The hominid nasopalveolar clivus is considerably longer than the hylobatid, through postero-inferior displacement of ANS and CLI. PIC is similarly displaced, preserving the relationship between nasal sill and floor in both. This results in thickening of the anterior palate and lengthening of the incisive foramen into a canal among hominoids. Such differences correspond to features cited by other authors (e.g., Ward & Kimbel, 1983) to distinguish between these groups. The other major difference can be seen in the anterior inter-dental landmarks. These are all superiorly placed in hylobatids, contributing to reduced height of the premaxilla. Finally, the malar root origin is set anteriorly and superiorly in the hominids, relative to the hylobatids.

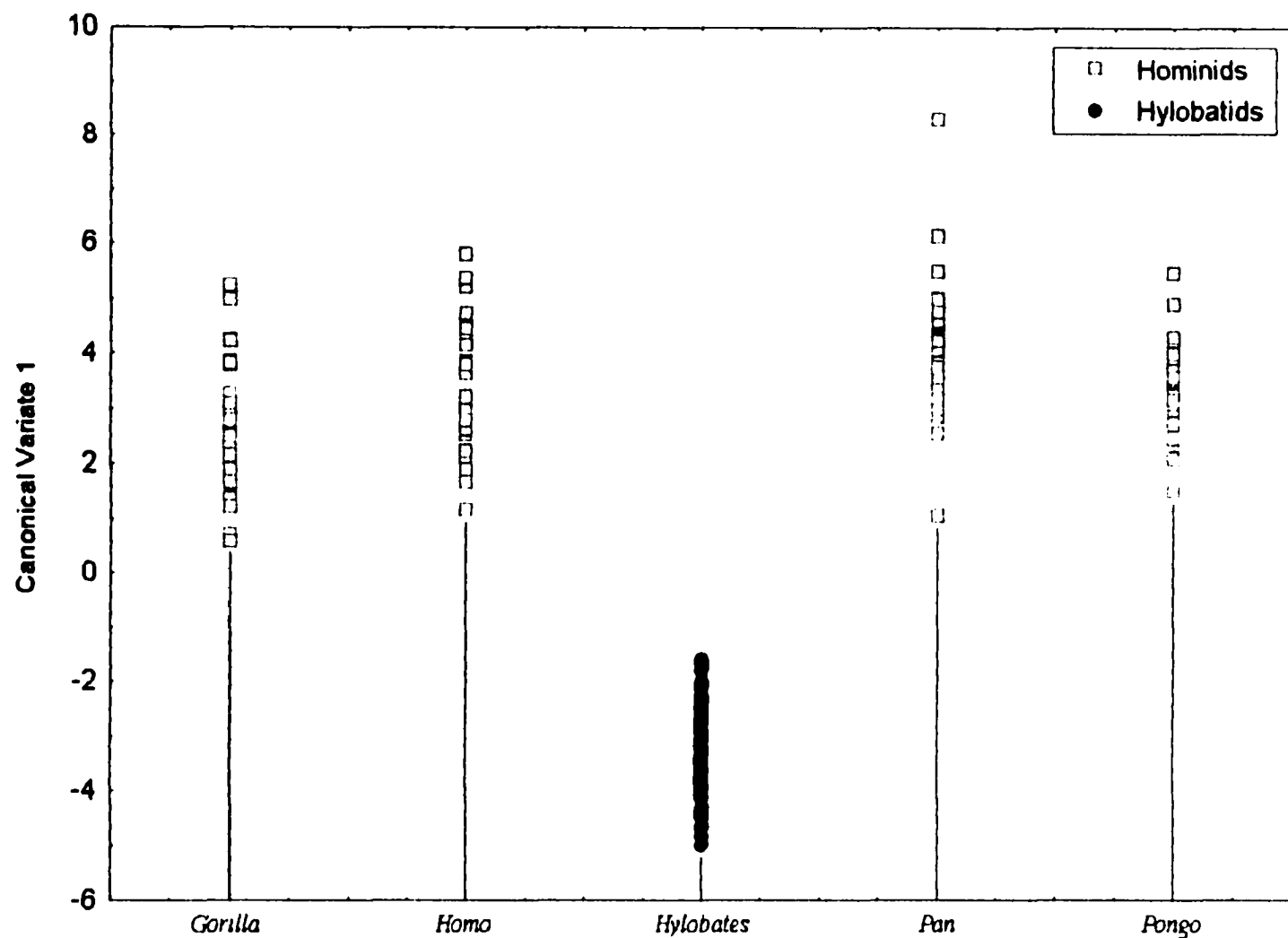


Figure 8-24 Plot of CV scores for the discriminant axis separating hylobatids from hominids. Although only the two groups were used for class variables, these results are illustrated by genus to better depict the distribution of specimens on the axis.

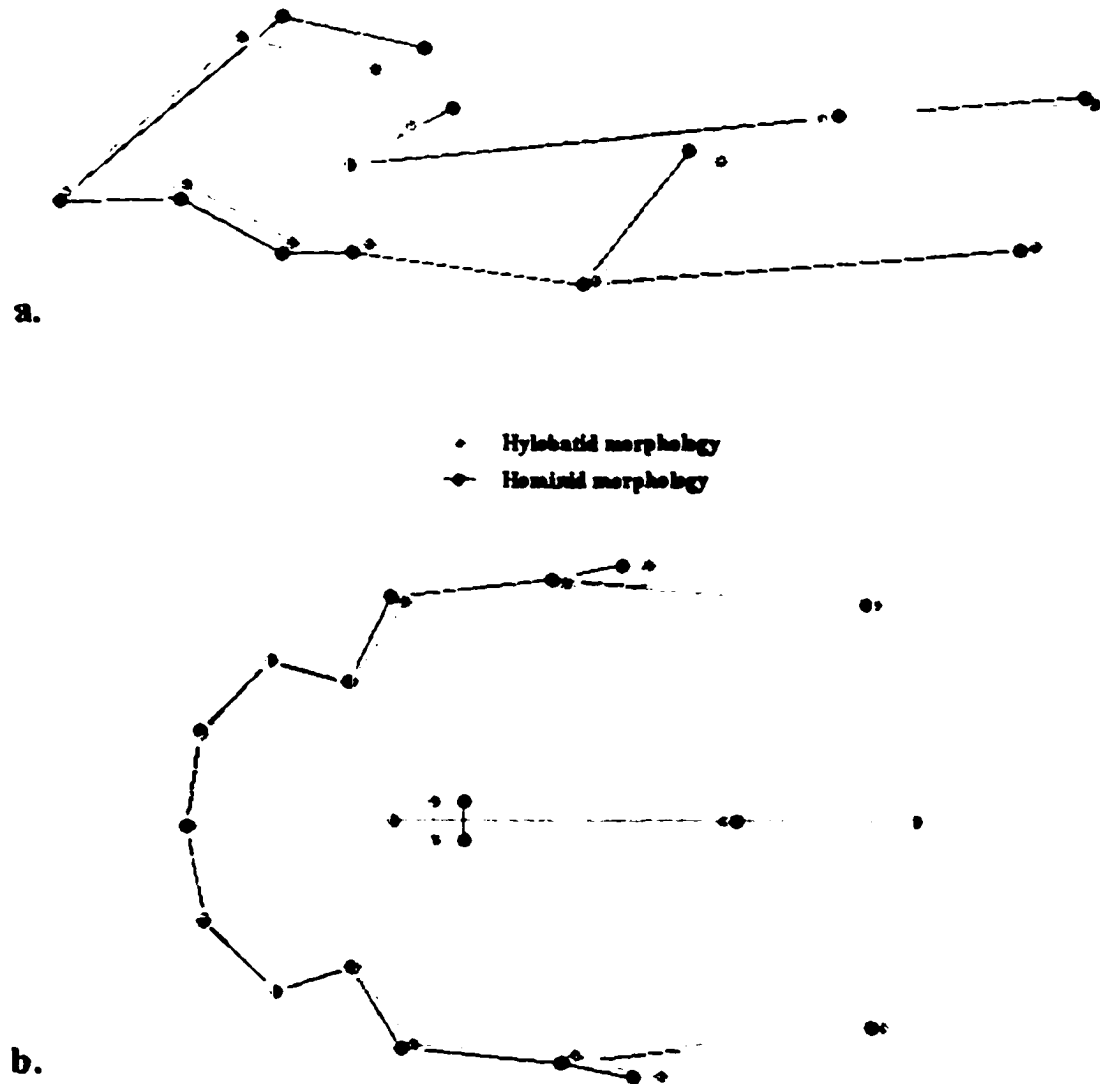


Figure 8-25 Shape change corresponding to the discrimination between hylobatids (gray) and hominids (black). (a) lateral view; (b) superior view. See Figure 8-1 for landmark references.

Node 4: Pongines vs. Hominines

Node 4 separates the orangutans from the African apes and humans. Cross-validation (Table 8-12) correctly assigned all of the specimens to their subfamilies. The plot of specimen scores in the discriminant axis (Figure 8-26) illustrates the substantial separation between pongine and hominine values.

Table 8-12 Cross-validation results for DA of pongine and hominine palatal morphologies. Each cell gives the number (n) and percent (%) of individuals from the taxa on the left assigned to the taxa across the top.

Taxon		Pongines	Hominines
Pongines	n	71	
	%	100.00	
Hominines	n		72
	%		100.00

Figure 8-27 depicts the morphological differences that correspond to this discriminant axis. The pongine morphology is characterized by a flatter subnasal clivus, through anterior placement of the premaxillary alveoli (**ALV**, **I12**, and **IPM**) and postero-inferior placement of both **ANS** and **PIC**. Thus, the orangutan premaxilla is expanded in the antero-posterior dimension, but diminished in height. The anterior maxillary palatine is deflected inferiorly in hominines relative to pongines. This, combined with differences in the nasal sill (**ANS** and **PIC**) contributes to the substantial relief between nasal sill and floor in the African apes and humans. In contrast, the pongine anterior maxillary palatine is deflected superiorly such that **PIC** approximates **CLI** in height; right and left **PIC** are also closer to the midline in *Pongo*. Again, such differences are similar to those observed by other workers (e.g., Ward & Kimbel, 1983; Ward & Brown, 1986; McCollum & Ward, 1997). Variation in posterior pongine morphology, though minor by comparison, includes posteriorly placed **PMC** and **MRO**, reduced antero-posterior dimension of the horizontal plate of the palatine, and a distal narrowing of the dental arcade.

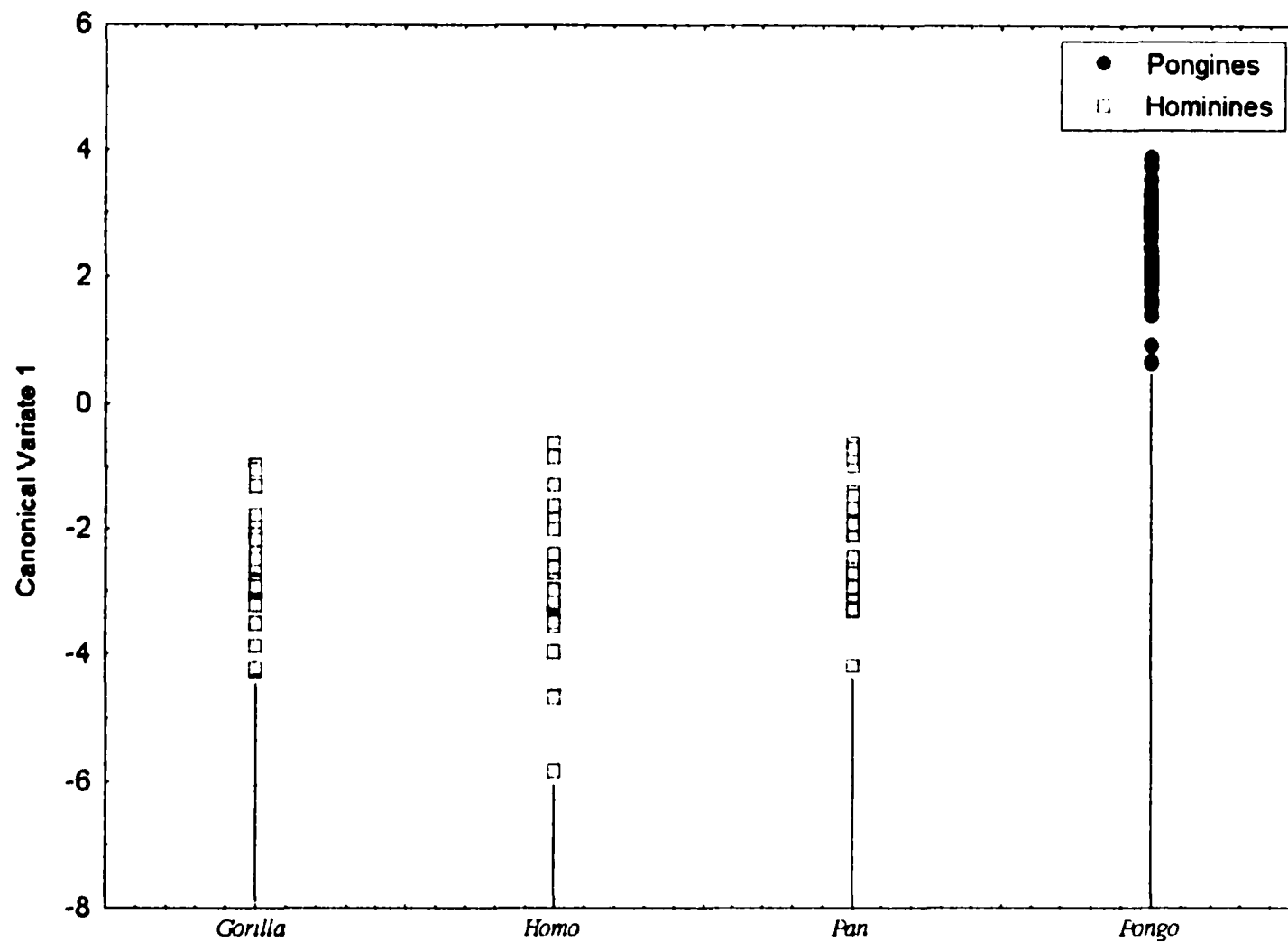


Figure 8-26 Plot of CV scores for the discriminant axis separating pongines from hominines. Although only the two groups were used for class variables, these results are illustrated by genus to better depict the distribution of specimens on the axis.

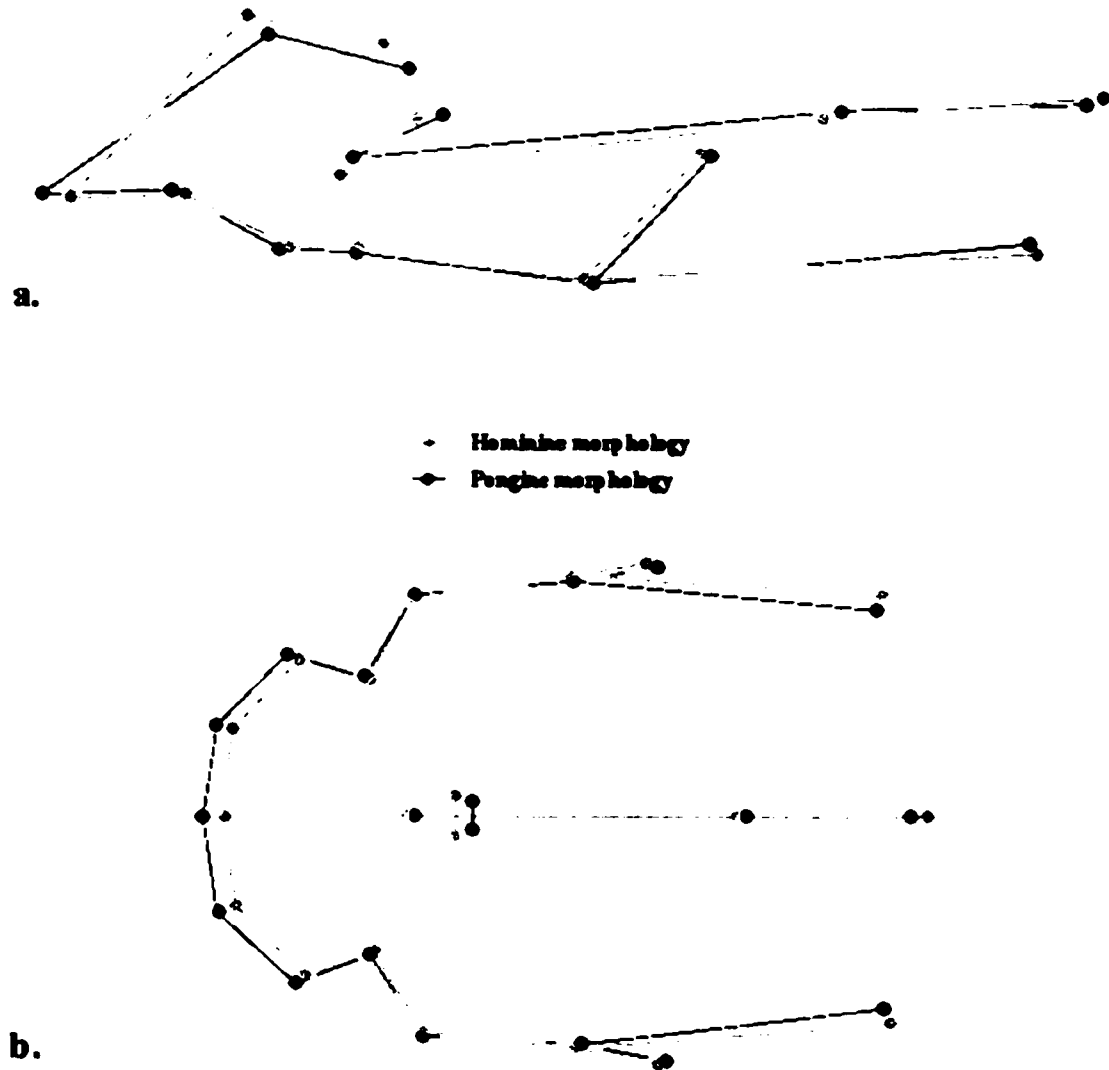


Figure 8-27 Shape change corresponding to the discrimination between hominines (gray) and pongines (black). (a) lateral view; (b) superior view. See Figure 8-1 for landmark references.

Node 5: *Gorilla* vs. *Pan-Homo*

Differences in morphology that correspond to node 5 are potentially the most difficult to detect. As evidenced in the analysis of all cranial landmarks, it may not always be possible to successfully discriminate between these clades with these methods. That is not the case here, however. Results from cross-validation (Table 8-13) indicate complete success in re-assigning the specimens based on the discriminant function. A plot of discriminant scores (Figure 8-28) shows the separation between these groups along this axis. It is clear, therefore, that while *Gorilla* and *Pan* share many features to the exclusion of *Homo*, humans and chimpanzees do share similarities in their palatal morphologies.

Table 8-13 Cross-validation results for DA of *Gorilla* and *Pan-Homo* morphologies. Each cell gives the number (n) and percent (%) of individuals from the taxa on the left assigned to the taxa across the top.

Taxon		<i>Gorilla</i>	<i>Pan-Homo</i>
<i>Gorilla</i>	n	78	
	%	100.00	
<i>Pan-Homo</i>	n		78
	%		100.00

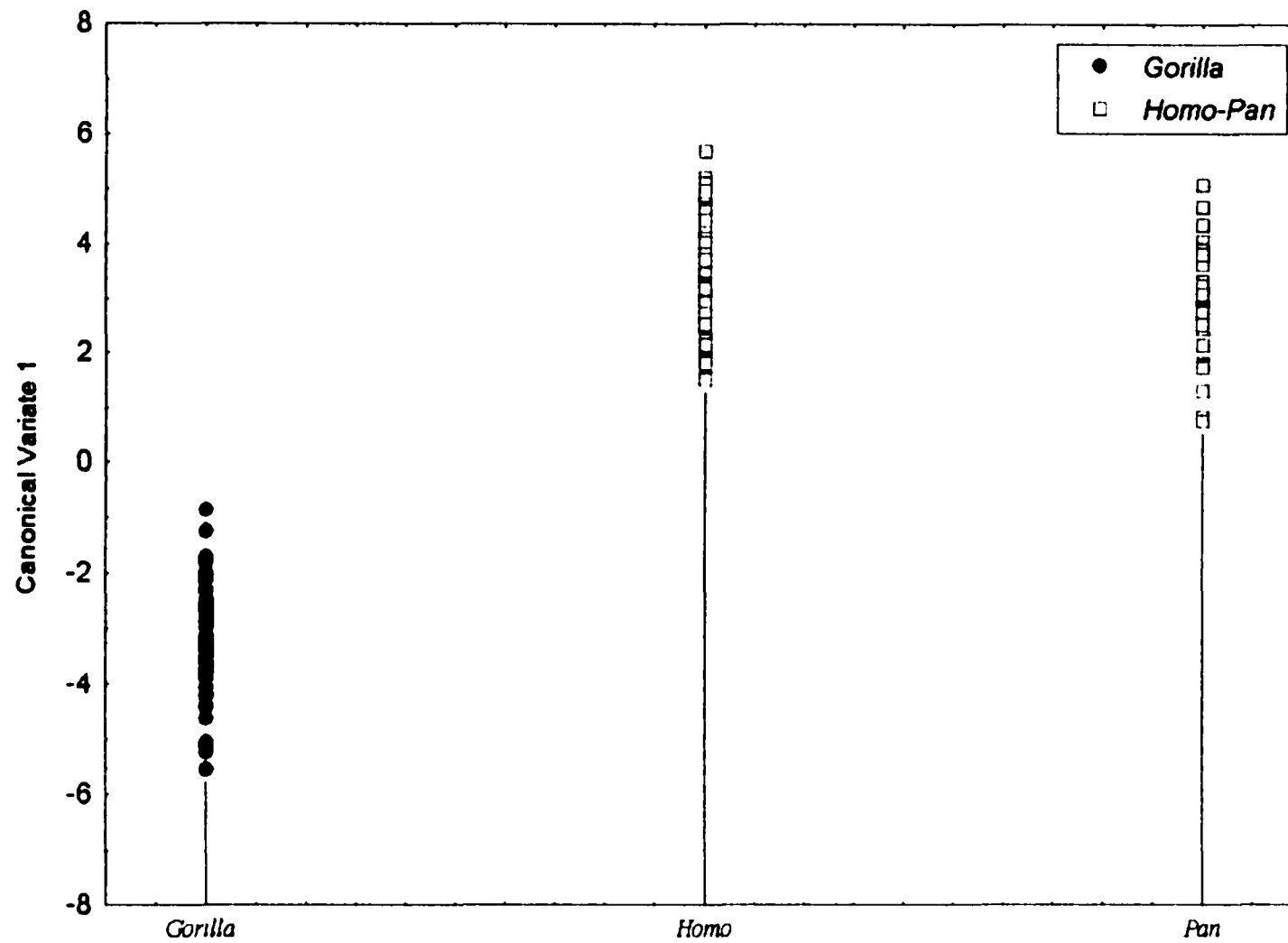


Figure 8-28 Plot of CV scores for the discriminant axis separating *Gorilla* from the *Pan-Homo* clade. Although only the two groups were used for class variables, these results are illustrated by genus to better depict the distribution of specimens on the axis.

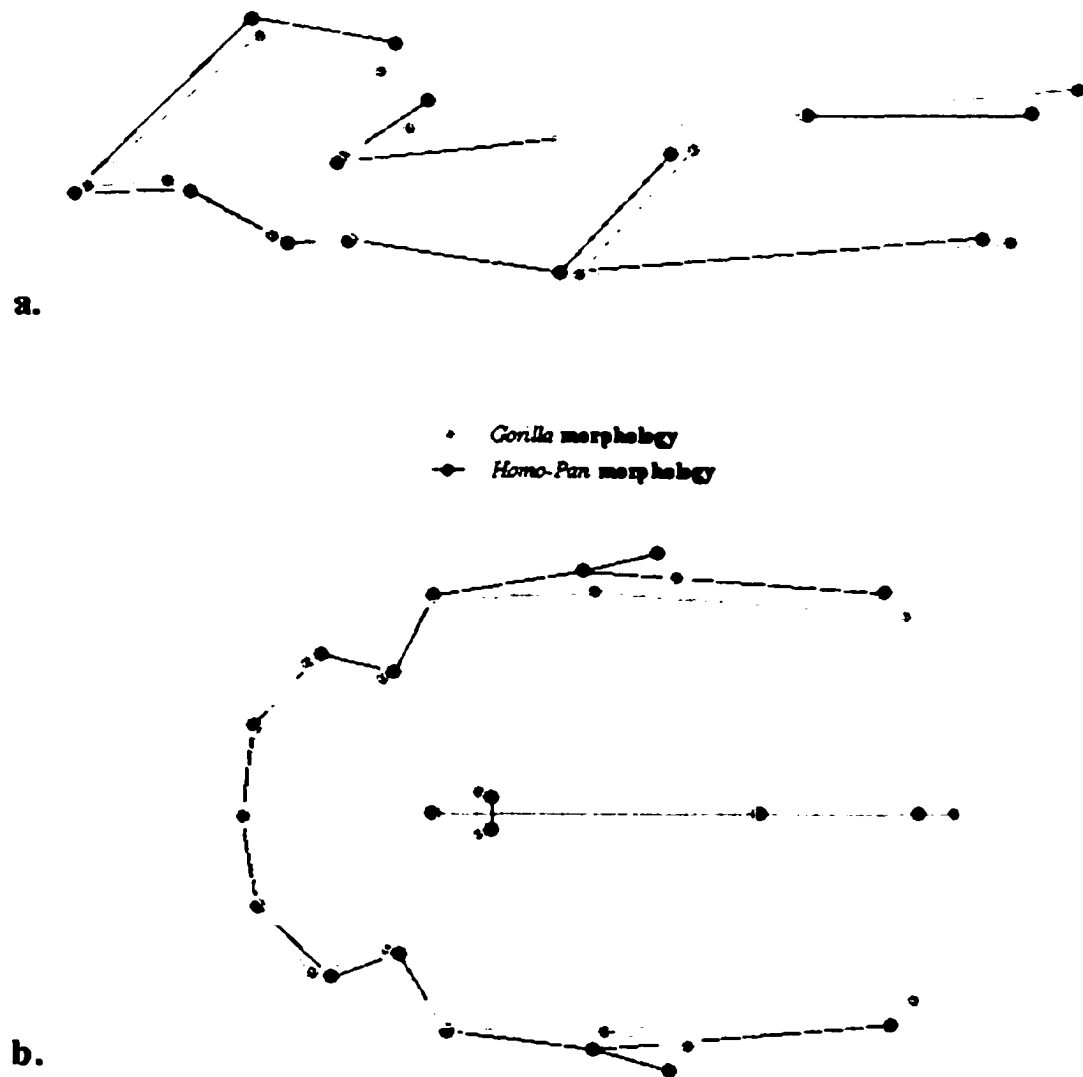


Figure 8-29 Shape change corresponding to the discrimination between *Gorilla* (gray) and *Homo-Pan* (black). (a) lateral view; (b) superior view. See Figure 8-1 for landmark references.

Morphological differences between *Gorilla* and a clade of *Pan* and *Homo* are depicted in Figure 8-29. The *Gorilla* nasoalveolar clivus is reduced supero-inferiorly and antero-posteriorly, with a particular dorsal deflection of the posterior clivus. This corresponds with a marked inferior displacement of **PIC**, yielding a thinner maxillary

palatine process and reduced incisive canals. The latter are set more laterally relative to those in the *Homo-Pan* group. Posterior to the canines, the palate of *Gorilla* is relatively longer in the tooth row and hard palate. The latter is accomplished through posterior extension of the horizontal plate of the palatine. The dental arcade is also considerably narrower in the gorilla posterior to the canine. The posterior palatal morphology in *Homo* and *Pan* is characterized by a dorsal deflection of the horizontal plate of the palatine and superior displacement of the distal arcade. This results in a somewhat shallower posterior hard palate, relative to *Gorilla*.

Node 6: *Pan* vs. *Homo*

The difference between palates of humans and chimpanzees was easily discernable in this analysis. Table 8-14 shows a perfect concordance in the cross-validation of both species. As corroboration, Figure 8-30 illustrates a wide separation between their discriminant scores. Differences between these genera largely correspond to those shown by PC 2 and CV 2, separating *Homo* from all other taxa. Nevertheless, they are discussed below.

Table 8-14 Cross-validation results for DA of *Pan* and *Homo* morphologies. Each cell gives the number (n) and percent (%) of individuals from the taxa on the left assigned to the taxa across the top.

Taxon		<i>Pan</i>	<i>Homo</i>
<i>Pan</i>	N	38	
	%	100.00	
<i>Homo</i>	N		38
	%		100.00

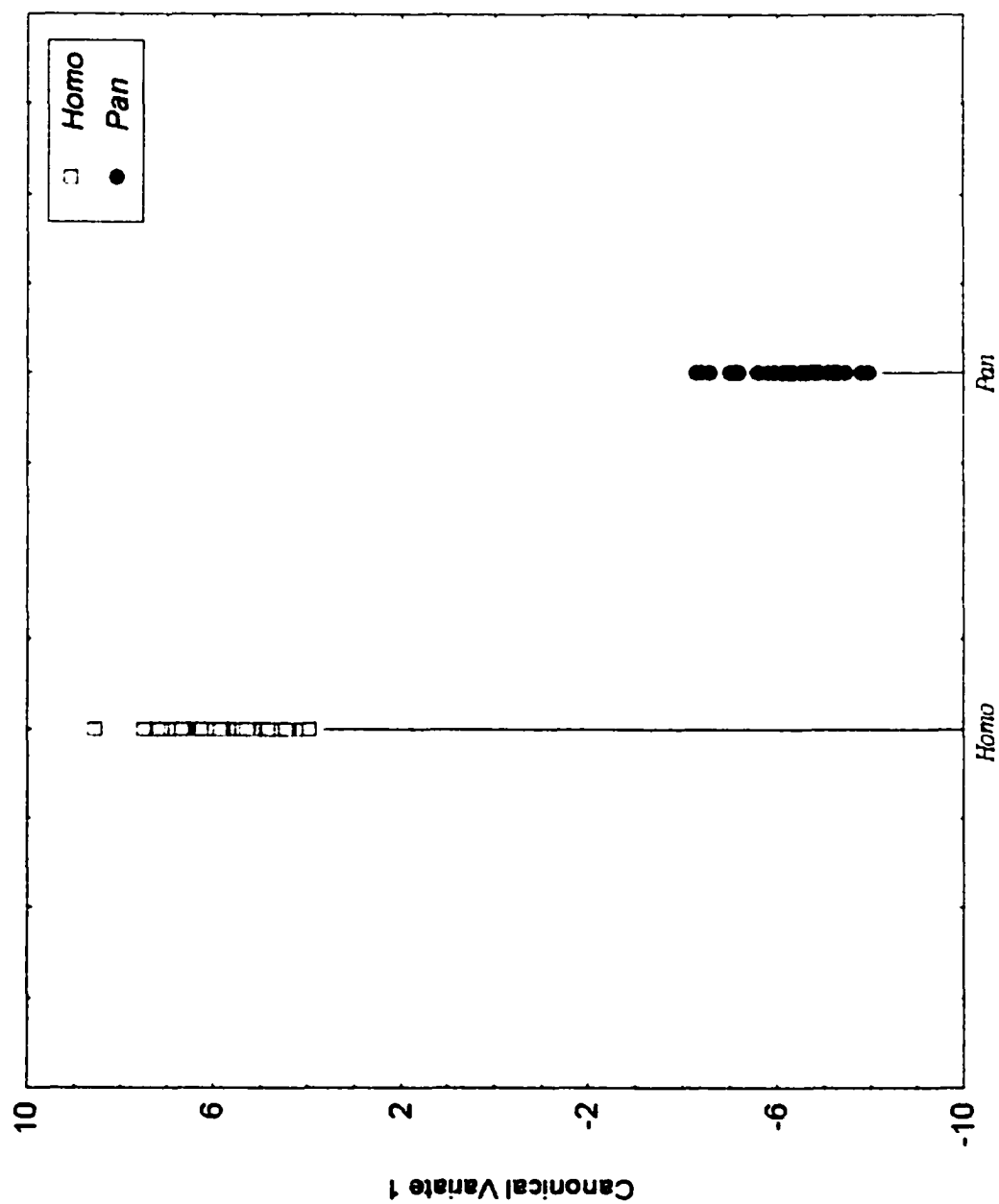


Figure 8-30 Plot of CV scores for the discriminant axis separating *Pan* and *Homo*.

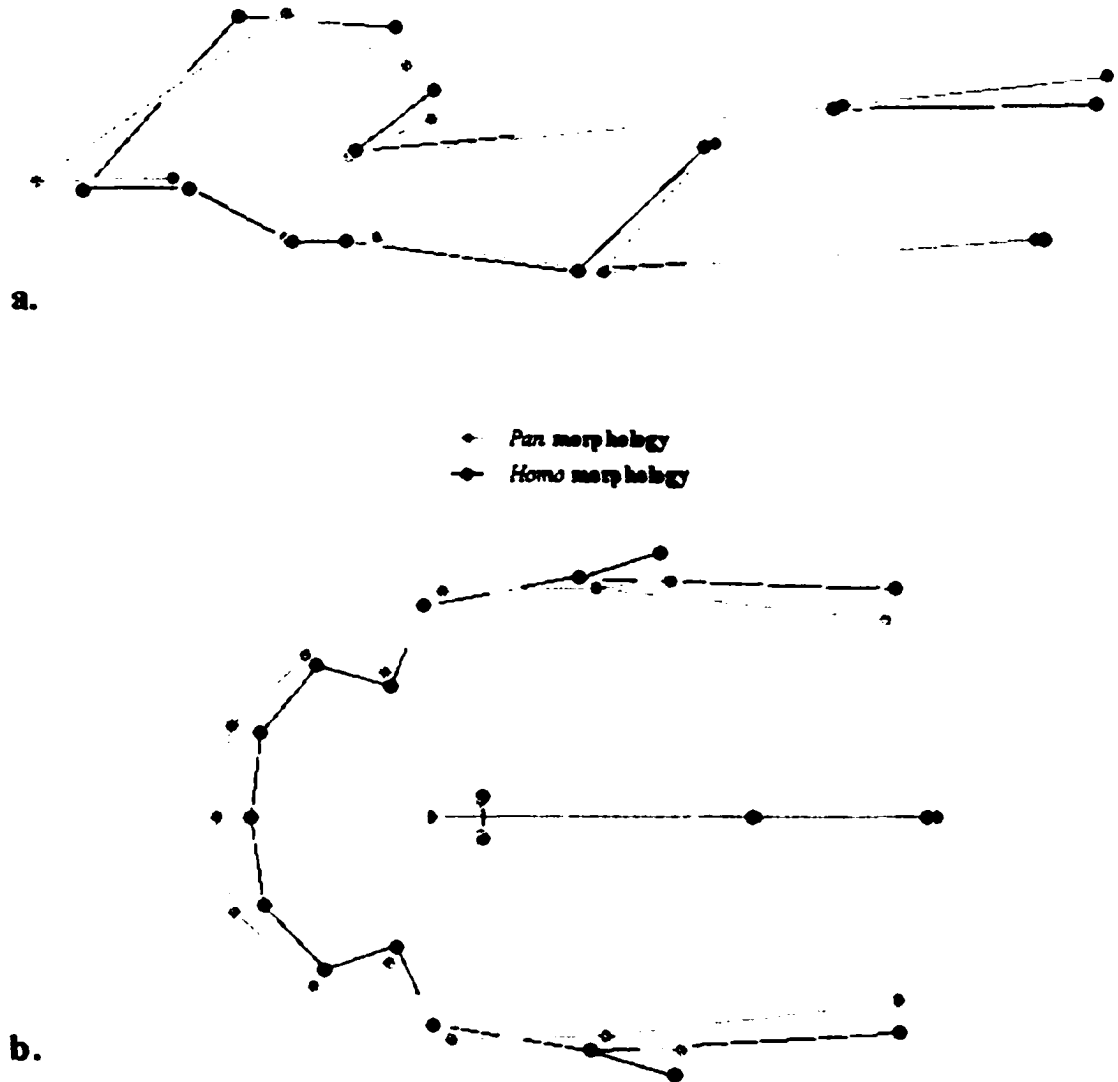


Figure 8-31 Shape change corresponding to the discrimination between *Pan* (gray) and *Homo* (black). (a) lateral view; (b) superior view. See Figure 8-1 for landmark references.

The differences between *Homo* and *Pan* were visible at most of the palatal landmarks, as illustrated by Figure 8-31. Relative to modern humans, the *Pan* premaxilla seems largely to be rotated dorsally. This is very evident in nasal sill (**ANS** and **CLI**) and nasal floor (**PIC**) landmarks; it is less so in the inferior premaxilla, where inter-dental landmarks are antero-superiorly displaced, but maintain their orientation with respect to the horizontal. In addition to this, the chimpanzee premaxilla is relatively wider than that of *Homo*, extending back to the premolars; this corresponds in part with a reduction in the mesio-distal dimension of the human canine. The superior placement of **CLI** in *Homo* corresponds with a proportionately displacement of **PIC**. Thus, the difference in height between nasal sill and floor is greater than in *Pan*, while the anterior hard palate is substantially thicker. In post-canine dentition, *Homo* displays anterior placement of **CPC** and **PMC**. As the posterior limit of the dental arcade is similar in both, however, this indicates relative expansion in the mesio-distal dimension of the molars. The arcade of *Homo* is also broader than in *Pan*, with the latter narrowing through the premolars and molars. Finally, the horizontal plate of the palatine shows a marked dorsal deflection in *Homo*, with **STA** inferior and anterior to its counterpart in *Pan*.

FOSSIL SPECIMENS

The sample size of the fossil genera prohibits their direct inclusion in canonical variates analysis; instead fossil specimens were treated as unknowns and placed into extant taxa by canonical discrimination. An initial discriminant analysis was computed at the genus level to demonstrate affinities between these fossils and extant genera; subsequently, 2-group discriminations were performed at each of the nodes in a

consensus phylogeny (Figure 8-19). As described in Chapter 5, both whole-sample and 1,000 equal-sample replicate analyses were computed for each discrimination class. Thus, a single assignment from the former and a distribution of assignments from the latter were generated for every fossil. A χ^2 test for equal proportions was used to determine whether assignment distributions were evenly divided among extant class groups. This served as a vehicle for testing whether a specimen is equally dissimilar to both groups, making its classification spurious. Three-group DAs were also employed to allow specimen assignments in a group comprising all taxa external to the node. These were useful in detecting spurious assignments in cases where a fossil was systematically grouped in one taxon only because of its dissimilarity to the other. Three-group analyses were not used at nodes 5 and 6, as analyses of nodes 4 and 5 represent, respectively, their likely sister taxa. See Chapter 5 for a complete discussion of this procedure.

Table 8-15 Assignment of fossils to modern genera from discriminant analysis. Boldface indicates the single genus assignment for each fossil specimen based on the whole-sample analysis. Numbers show additional assignments out of 1000 randomized DAs using equal sample sizes. The first row beneath genus names lists the mean percentage of extant specimens correctly re-assigned in the replicate cross-validations. A χ^2 test for equal proportions ($\phi = 0.1$) found highly significant ($p < 0.0001$) deviations in the frequency distribution for each fossil.

		Atel	Cebu	Cerc	Papi	Pcol	Hylo	Pong	Gori	Pan	Homo
Mean reclassified in correct genus (%)		100.00	100.00	98.17	99.84	100.00	97.36	99.46	100.00	99.98	99.65
Proplio	DPC 2803	22		5			973				
	DPC 3161	5		363			632				
Procon	RU 16000					2	998				
Moroto	UMP 62-11					51	748		201		
Rangwa	SO 700					228	227		545		
Siva	GSP 15000					11	87	703	198	1	
Graeco	RPI 128						43	2	955		
	XIR 1						73		927		

Table 8-16 Results of fossil assignments to modern groups defined by nodes 1-4 (see Figure 8-19). Two-group analyses forced fossils into one branch deriving from each node; three-group analyses allowed the additional option of assignment in a group comprised of taxa external to the node ("primitive"). Boldface indicates the single assignment for each fossil specimen based on the whole-sample DA. Numbers show additional assignments out of 1000 randomized equal-sample DAs. The first two rows beneath taxon names list the mean percentages of extant specimens correctly re-assigned in the replicate cross-validations. * indicates a *lack of significance* from a χ^2 test for equal proportions.

Mean Cross-Validation %		NODE 1			NODE 2		
		platyrrhine	catarrhine		cercopithecoid	hominoid	primitive
2-group		100.00	99.99		99.98	97.92	
3-group					99.98	97.45	100.00
DPC 2803	2grp	87	913		5	995	
	3grp				15	932	53
DPC 3161	2grp	167	833		178	822	
	3grp				181	807	12
RU 16000	2grp	0	1000		12	988	
	3grp				38	962	0
UMP 62-11	2grp	0	1000		287	713	
	3grp				259	741	0
SO 700	2grp	9	991		3	997	
	3grp				64	931	5
GSP 15000	2grp	0	1000		44	956	
	3grp				37	963	0
RPI 128	2grp	25	975		0	1000	
	3grp				1	998	1
XIR 1	2grp	0	1000		0	1000	
	3grp				1	999	0

Table 8-16 (cont.)

Mean Cross-Validation %		NODE 3			NODE 4		
		hylobatid	hominid	primitive	pongine	hominine	primitive
2-group		100.00	99.99		98.24	97.91	
3-group		96.57	99.84	95.03	98.44	97.24	99.99
DPC 2803	2grp	1000	0		108	892	
	3grp	1000	0	0	0	0	1000
DPC 3161	2grp	1000	0		997	3	
	3grp	658	0	342	0	0	1000
RU 16000	2grp	1000	0		86	914	
	3grp	1000	0	0	0	0	1000
UMP 62-11	2grp	1000	0		522*	478*	
	3grp	999	1	0	0	0	1000
SO 700	2grp	6	994		0	1000	
	3grp	51	943	6	0	333	667
GSP 15000	2grp	2	998		997	3	
	3grp	13	987	0	958	3	39
RPI 128	2grp	6	994		42	958	
	3grp	51	949	0	89	910	1
XIR 1	2grp	116	884		2	998	
	3grp	105	895	0	0	901	0

Five fossil specimens preserve the complete landmark configuration analyzed in this chapter: specimens of the basal catarrhine *Propliopithecus* (DPC 2083, DPC 3161), the Early Miocene putative hominoids *Proconsul* (RU 16000) and *Morotopithecus* (UMP 62-11), and the Late Miocene genus *Sivapithecus* (GSP 15000). The analysis of three additional fossil specimens was enabled by dropping the posterior incisive canal (PIC) and staphylion (STA) landmarks. This expanded sample includes specimens of *Rangwapithecus* (SO 700) and *Graecopithecus* (RPI 128, XIR 1). Results for analyses on both the complete and reduced configurations are shown in Table 8-15 (generic discrimination) and Table 8-16 (node 1-4 discrimination). Table 8-17 lists additional results for specimens of *Graecopithecus* from discrimination at nodes 5-6. Mean cross-

validation results listed in these tables are the lesser values from analyses of either the complete palate configuration or the reduced dataset.

Basal catarrhines

Propliopithecus

In generic discrimination, both palates of *Propliopithecus* were assigned to hylobatids. DPC 2803 placed there in more than 97% of the replicates, with minimal classifications in *Ateles* and *Cercopithecus*; DPC 3161 had weaker support at 63% in *Hylobates*, 36% in *Cercopithecus*, and 0.5% in *Ateles*. Results from nodes 1 and 2 placed both specimens within catarrhines and hominoids, respectively, deriving strong support from randomizations. In both cases, DPC 2803 achieved stronger results (> 90%), while DPC 3161 support was just over 80%. At node 3, both specimens were assigned to hylobatids over hominids. DPC 2803 grouped there in all of the replicates, from both 2- and 3-group analyses. DPC 3161 did the same in the 2-group tests, but grouped with hylobatids in only 66% of the 3-group—the balance of assignments was to the “primitive” group. Node 4 results placed DPC 2803 with hominines (89% support) and DPC 3161 with the pongines (99% support) in 2-group tests; when the “primitive” category was added, however, both placed there in every case.

The above results reiterate the polymorphic morphology of fossils placed within this taxon. As shown in previous chapters, specimens of *Propliopithecus* do not always perform similarly in these analyses. In this case, DPC 2803 had a strong affinity with *Hylobates*; this is evident from discrimination at the generic-level and at node 3. DPC 3161, while ultimately grouping with the same taxa, had a less biased distribution of replicate assignments. The greatest difference was demonstrated at node 4; although 3-

group results here show that neither fossil really groups with pongines or hominines, the vast difference in 2-group results suggests a real diversity in morphology.

The most important conclusion one can draw from these results is that the palatal morphology of *Propliopithecus*—as captured by these landmarks—bears a strong resemblance to that of *Hylobates*. Most researchers are reasonably convinced that *Propliopithecus* is a primitive catarrhine (Simons, 1967; Delson & Andrews, 1975; Kay *et al.*, 1981; Fleagle & Kay, 1983; Kay & Simons, 1980, 1983; Harrison, 1987; Simons, 1987; Benefit & McCrossin, 1993; Leakey *et al.*, 1991; Ross *et al.*, 1998). This affinity between hylobatids and *Propliopithecus* (and those of other Early Miocene African taxa: see below) suggests that palatal morphology may have remained largely conservative in the catarrhine lineage leading to the hominoids; put another way, the more primitive members of the Hominoidea—including *Hylobates*—may be indistinguishable from basal ancestral catarrhines in the features represented here (see Harrison, 1987). The fact that there is a clear distinction between catarrhines and platyrrhines (see Figures 8-19, 8-20) and between hominoids and cercopithecoids (see Figures 8-21, 8-22) suggests that the latter may have evolved somewhat from this ancestral pattern.

It should be noted that the methods used here could be similarly applied to distinguish hominoids from basal catarrhines: determining specific differences in morphology and placing the African Early Miocene fossils accordingly. Such an analysis, however, would require a reasonably sized sample of undoubted basal catarrhines. Indeed, without such a sample, any analysis—morphometric or otherwise—that tries to untangle this problem can only be regarded as tentative.

Early Miocene putative hominoids

Proconsul

The position of *Proconsul* among anthropoids is still largely debated within the literature (see Walker, 1997; Harrison, 2002). Traditionally linked to some or all of the extant apes, current arguments conform to three phylogenetic hypotheses: *Proconsul* is a basal hominid (e.g., Walker & Teaford, 1989; Rae, 1993, 1997; Begun, 1994), a basal hominoid (e.g., Szalay & Delson, 1979; Andrews, 1985; Martin, 1986; Andrews & Martin, 1987, 1991; Begun *et al.*, 1997; Rose, 1997; Ward, 1997; Begun, 2001), or a basal catarrhine (Harrison, 1982, 1987, 1993, 2002). Despite this disagreement, most workers regard the subnasal and palatal morphology of *Proconsul* to be generally shared with both hylobatids and Old World monkeys (e.g., Ward & Kimbel, 1983; Ward & Pilbeam, 1983; Ward & Brown, 1986; McCrossin & Benefit, 1994; Benefit & McCrossin, 1995; McCollum & Ward, 1997). Rae (1993; 1997), however, has cited a wide anterior palate among his characters linking *Proconsul* to extant hominids.

Results from discrimination among genera place *Proconsul* with *Hylobates* in both whole-sample analysis and more than 99% of the replicate tests; the two exceptions were assignments in *Procolobus*. At node 1, RU 16000 placed with the catarrhines in both the whole-sample and in all of the replicate tests. Node 2 results were similarly unambiguous, classifying it with hominoids in better than 96% of both 2- and 3-group analyses; in the latter, there were no placements in the “primitive” category. Results from node 3 classified this specimen with hylobatids unanimously. At node 4, 91% of the 2-group randomizations placed RU 16000 with the hominines, while 100% of the 3-group tests put it in the “primitive” category—whole-sample results were consistent with these.

Ward and colleagues (Ward & Kimbel, 1983; Ward & Pilbeam, 1983; Ward & Brown, 1986; McCollum & Ward, 1997) have suggested that hylobatids and African catarrhines from the Early Miocene share a primitive subnasal pattern with the cercopithecoids. This is certainly true in one sense, as the greatest axes of variation among specimens and groups segregate these taxa from the hominids. Yet, this work has demonstrated that there are clear differences between *Hylobates* and cercopithecoids (and indeed among the cercopithecoid genera). Were hylobatid and cercopithecoid morphologies equivalent, one might expect a more equal distribution of the *Proconsul* classifications among these genera. Table 8-15, however, shows nearly unanimous placement of RU 16000 with *Hylobates*; only 2 out of 1000 discriminations grouped it elsewhere (*Procolobus*). Analyses at nodes 1-4 corroborate this result. Thus, there is a clear distinction between the palatal morphologies of hylobatids and cercopithecoids—and *Proconsul* has clear affinities with the former.

That having been said, what phylogenetic conclusions can be drawn? If the primitive catarrhine palatal morphology is best represented by the platyrrhines (i.e., cercopithecoid and hominoid morphologies are separately derived from an ancestral anthropoid/catarrhine morphology), then results shown here would place *Proconsul* among the hominoids—as per the 3-group analysis at node 2. By the same reasoning, if the cercopithecoid palate were indicative of the primitive catarrhine morphology, then one could conclude that *Proconsul* shares derived features with the hominoids. If, however, the cercopithecoid palatal morphology were derived among catarrhines, while the hylobatid is primitive, RU 16000 would simply be another representative of this conservative morphology (e.g., Harrison, 1987, 1993, 2002; Harrison & Rook, 1997).

Results shown above for *Propliopithecus* indicate that the latter hypothesis is likely to be the case. The affinity between these basal catarrhine specimens and *Hylobates* suggests that the ancestral catarrhine palate may have looked very similar to that of extant hylobatids—and *not* cercopithecoids (see Harrison & Rook, 1997). That being the case, it is unlikely that the origin of the Hominoidea involved a significant rearrangement of the palate configuration. And thus, the hominoid status of *Proconsul* cannot be reliably determined from these data.

Morotopithecus

The Moroto palate (UMP 62-11) was originally referred to *Proconsul* by early workers (Allbrook & Bishop, 1963; Bishop, 1964; but see Leakey, 1963) and associated with *P. major* (Pilbeam, 1969). Later researchers (Kelley & Pilbeam, 1986; Andrews & Martin, 1987; Leakey *et al.*, 1988) noted its similarities to the subsequently discovered *Afropithecus turkanensis* and *A.* [= *Heliopithecus*] *leakeyi*. A combination of derived postcranial and primitive cranial morphology (e.g., Gebo *et al.*, 1997), as well as some unique features among Early Miocene catarrhines (e.g., Kelley & Pilbeam, 1986; Leakey & Leakey, 1986; Pickford *et al.*, 1999) rendered the taxonomic status of the Moroto fossils questionable (Walker, 1997). The discovery of additional postcranial materials, however, spurred Gebo and colleagues (1997) to assign these remains to a new genus and species: *Morotopithecus bishopi*. Despite sharing some postcranial features with living hominoids (e.g., Walker & Rose, 1968; Filler, 1981; C. Ward, 1993, 1997; Sanders & Bodenbender, 1994; Harrison, 2002), most workers have regarded the palatal morphology of Moroto as primitive among hominoids (e.g., Ward & Kimbel, 1983; Begun, 1994; McCrossin & Benefit, 1994; Leakey & Walker, 1997).

Among extant genera, UMP 62-11 was assigned to *Hylobates* in the whole-sample test, and in 75% of the replicates; remaining assignments were in *Gorilla* (20%) and *Procolobus* (5%). At node 1, there was unanimous support for assigning *Morotopithecus* to the catarrhines. Node 2 results were less strong, placing it with hominoids in just over 70% of 2- and 3-group analyses, but significant ($p < 0.0001$) in a χ^2 test for equal proportions. *Morotopithecus* grouped almost exclusively with hylobatids at node 3, scoring only a single hominid classification in the 3-group analysis and none in the 2-group. Results at node 4 were indeterminate in the 2-group analysis. Though classified with hominines in the whole-sample DA, this specimen placed equally ($\chi^2: p = 0.1641$) among pongines and hominines in the randomization—suggesting that *Morotopithecus* is not similar to either. This was confirmed in the 3-group analysis, where the specimen placed in the “primitive” group unanimously.

The results presented for *Morotopithecus* are broadly similar to those reported for *Proconsul* and support previous analyses of this specimen (e.g., Ward & Kimbel, 1983; Ward & Pilbeam, 1983; Begun, 1994). The Moroto palate was most similar to *Hylobates*; unlike *Proconsul*, however, it also displayed an affinity with *Gorilla*. As discussed above, the palatal morphology quantified here cannot reliably distinguish between ancestral catarrhine and basal hominoid. As such, the phylogenetic relationships of *Morotopithecus* are best determined by other aspects of its morphology.

Rangwapithecus

Originally assigned to the genus *Proconsul*, Andrews (1974) named a new subgenus and species *Dryopithecus (Rangwapithecus) gordonii* based on SO 700. The palatal morphology of this specimen is thought to represent another variant on the

primitive African Miocene pattern (e.g., Ward & Kimbel, 1983; Ward & Pilbeam, 1983; Kelley & Pilbeam, 1986)—similar to *Proconsul*. Yet, several authors (Ward & Kimbel, 1983; Kelley & Pilbeam, 1986; Benefit & McCrossin, 1995) have noted differences between *Proconsul* and *Rangwapithecus* palates, suggesting that SO 700 bears some similarities to *Gorilla*.

Generic-level discrimination placed SO 700 in *Hylobates*; this was belied, however, by the equal-sample replicate analyses, where 55% of its classifications were in *Gorilla* and the rest were evenly split between *Hylobates* and *Procolobus*. At node 1, this specimen was placed among catarrhines and received support from 99% of the replicates. Node 2 results placed it among the hominoids, with 99% and 93% support from 2- and 3-group analyses, respectively. Unlike the other early African Miocene fossils, SO 700 grouped with hominids at node 3; 99% of the 2-group replicates agreed with this, as did 94% of the 3-group—only 6 of 1,000 replicates placed it in the “primitive category.” Results from node 4 place *Rangwapithecus* with the hominines in the 2-group whole-sample analysis; all of the 2-group replicates confirm this. The 3-group results are somewhat different, however, classifying SO 700 in the “primitive” category, with support from 67% of the replicates; the other 33% were all among hominines.

These results are substantively different from those of the other Early Miocene putative hominoids. While demonstrating some affinity with hylobatids, SO 700 was more similar to *Gorilla*. Considering features that distinguish hylobatids from hominids (e.g., node 3), *Rangwapithecus* placed almost exclusively with the latter; this was true not just in the 2-group analysis, but also in the 3-group test, where it had the option of placing among all other taxa. As noted above, similarities between this palate and those

of African apes (especially *Gorilla*) have been noted by previous researchers (e.g., Ward & Kimbel, 1983; Benefit & McCrossin, 1995), and may have formed part of the rationale for its removal from the more primitive genus *Proconsul*. At node 4, SO 700 showed no affinity with orangutans. Yet, the 3-group results suggest that it is not strongly similar to the hominines. In light of these results, the *Rangwapithecus* palate seems best grouped with the hominid morphology. Among both specimens and extant genera, the greatest axes of variability (e.g., PC 1 and CV 1) segregate non-hominids from hominids; SO 700 clearly displays morphology similar to the latter—and distinct from the hylobatids.

Harrison's (2002) recent review of East African late Oligocene—Early Miocene catarrhines reiterated (e.g., Harrison, 1986; Kuniyatsu, 1992a, b, 1997) similarities shared among *Rangwapithecus*, *Nyanzapithecus*, and *Mabokopithecus*. Although too incomplete for inclusion in these analyses, it is worth noting that the premaxillary morphology of *Nyanzapithecus* also shares some of the same features which link SO 700 to extant great apes and humans (personal observation).

Late Miocene hominoids

Sivapithecus

The palate of the partial cranium GSP 15000 has been considered by most workers to share a number of unique features with *Pongo* (e.g., Ward & Kimbel, 1983; Ward & Pilbeam, 1983; Kelley & Pilbeam, 1986; Ward & Brown, 1986; Brown & Ward, 1988; Andrews & Martin, 1991; Moyà Solà & Köhler, 1995; Begun *et al.*, 1997; McCollum & Ward, 1997). While several authors have noted features of *Sivapithecus* that are primitive or unique among hominoids, these have been mid and upper facial (e.g., Ward & Kimbel, 1983; Ward & Brown, 1986; Ward, 1997), dental (e.g., Corruccini &

McHenry, 1980; Uchida, 1998), mandibular (Ward & Brown, 1986; Brown & Ward, 1988), or postcranial (Pilbeam *et al.*, 1990; Rose, 1997; C. Ward, 1997), rather than palatal (see S. Ward, 1997 for a broad review of this evidence). Thus, most workers would agree that—whether synapomorphous, symplesiomorphous, or homoplasious—the palates of *Sivapithecus* and *Pongo* are very similar.

Results from my analyses corroborate this. Generic discrimination classified GSP 15000 with *Pongo*, receiving support from 70% of the replicate analyses. About 20% of the classifications were in *Gorilla*, with 8% in *Hylobates*, 1% in *Procolobus*, and a single assignment to *Pan*. Results from all four nodes were very conclusive. This specimen was unanimously grouped with catarrhines at node 1. At node 2, it was placed with hominoids and received corroboration in better than 95% of the 2- and 3-group replicates. GSP 15000 placed among hominids at node 3, again with support from both replicate analyses. The node 4 results very clearly indicate the affinity between *Sivapithecus* and *Pongo* craniofacial morphologies. Both (2- and 3-group) whole-sample analyses placed GSP 15000 with the pongines; the 2-group replicates agreed in better than 99% of the trials, while the 3-group analyses did so in nearly 96% of them.

This analysis strongly supports assignment of GSP 15000 to *Pongo*. The configuration of its subnasal morphology seems to be a strong indication of its hominid status (e.g., Ward & Kimbel, 1983; see analyses above). In the features that specifically discriminate between extant hominine and pongine palates, that of *Sivapithecus* is clearly affine to the latter subfamily. If one accepts that *Hylobates* shares a primitive catarrhine (and therefore primitive hominoid) palatal morphology with cercopithecoids and *Propliopithecus*, there is no evidence here to indicate that the GSP 15000 palate is

primitive. Alternatively, one must also consider the possibility that these affinities arose convergently. McCollum (1999) has suggested that the many features shared between *P. boisei* and *P. robustus* may result from a single, shared morphogenetic scheme. Could convergent ontogenetic plans account for the high degree of similarity shown here? The presence of an incisive canal is unique among extant primates, found only in hominids; the specific palatal morphology of *Pongo* is similarly autapomorphic. Among all primates, only *Sivapithecus* shares this morphology (Ward & Pilbeam, 1983). Of the features used to distinguish *Sivapithecus* from *Pongo*, many are symplesiomorphic or autapomorphic and therefore of little value in determining phylogenetic relationships (see Richmond & Whelan, 2001). The balance of features may be found among other extant taxa to which *Sivapithecus* is unlikely to be closely related (e.g., cercopithecoids: see Pilbeam *et al.*, 1990). There is *evidence*, then, that such features can be convergently derived—thus far, no other primate displays palatal morphology convergent with *Sivapithecus* and *Pongo*. These arguments do not preclude the possibility that similarities between *Pongo* and *Sivapithecus* are convergent. Yet, lacking evidence to the contrary, these features seem most reliable for determining relationships (Richmond & Whelan, 2001).

Graecopithecus

Originally attributed to *Sivapithecus* based largely on palatal and dental remains (e.g., Szalay & Delson, 1979; Andrews & Tekkaya, 1980), the removal of matrix from its subnasal region revealed the *Graecopithecus* morphology to be similar to *Gorilla* (Bonis & Melentis, 1984). Consequently, most workers broadly identify the subnasal and palatal morphology of *Graecopithecus* with African apes (e.g., Bonis & Melentis, 1984, 1987;

Kelley & Pilbeam, 1986; Brown & Ward, 1988; Dean & Delson, 1992, as one option; Bonis & Koufos, 1993; Begun, 1994; Andrews *et al.*, 1996; Bonis & Koufos, 2001). This affinity corresponds largely to opinions regarding the phylogenetic relationships of this taxon. Alternatively, some workers have linked *Graecopithecus* to pongines (e.g., Moyà Solà & Köhler, 1993; Köhler *et al.*, 2001), *Gorilla* (Dean & Delson, 1992, as one option), or hominins (e.g., Bonis & Koufos, 1993, 1995, 1997, 2001)—albeit not based on palatal evidence.

Table 8-17 Results from discriminant analyses and assignments of *Graecopithecus* at phylogenetic nodes 4-6. Boldface indicates the assignment for each specimen based on DA of the entire extant sample. Numbers show additional assignments from 1000 randomized tests using equal sample sizes. The first row beneath each taxon name lists the mean percentage of extant specimens correctly reclassified in the replicate series. * indicates a *lack of significant difference* from χ^2 tests for equal proportions. See text for further discussion.

Mean Cross-validation Percentage (%):	NODE 4		NODE 5		NODE 6	
	pongine	hominine	<i>Gorilla</i>	<i>Homo-Pan</i>	<i>Pan</i>	<i>Homo</i>
	98.24	97.91	99.99	99.98	100.00	100.00
RPI 128	42	958	1000	0	1000	0
XIR 1	2	998	1000	0	1000	0

Generic-level discrimination places both specimens with *Gorilla*, receiving better than 92% support from replicate analyses; the remaining classifications are all in *Hylobates*, excepting two placements of RPI 128 in *Pongo*. Results from nodes 1-2 were unambiguous, classifying both specimens among catarrhines and hominoids (respectively) with better than 97% support. Node three results were similarly strong for RPI 128, placing it among hominids with 99% (2-group) and 95% (3-group) support from replicate tests. XIR 1 was similarly classified among hominids, with just over 88% support. Neither placed in the “primitive” category in any of the randomizations at node

3. At node 4, both specimens grouped with hominines, and received corroboration from more than 90% of the replicates. At node 5, both specimens unanimously placed within *Gorilla* instead of the *Homo-Pan* group; similarly, there was complete placement in *Pan*—rather than *Homo*—at node 6.

In considering the greatest differences among this extant sample, both RPI 128 and XIR 1 fall on the side of the hominids. Among great apes and humans, there is no evidence for an affinity between *Graecopithecus* and *Pongo*. In features that distinguish *Gorilla* from a *Homo-Pan* clade, both specimens are like the former; unsurprisingly, the *Graecopithecus* palates are more similar to those of chimpanzees than humans. Interpretation of these results depends heavily on the way this morphology is polarized. Begun (1992, 1994, 1995) has suggested that the subnasal morphology of *Gorilla* is primitive for the hominid lineage, based on its similarities to specimens of *Dryopithecus* and extant hylobatids. In this case, the palatal features of *Graecopithecus* would place it among great apes, but not within any particular lineage. McCollum & Ward (1997), however, have argued convincingly against this based on quantitative ontogenetic evidence. Rather than primitive, they see the subnasal morphology of *Gorilla* as highly derived among extant apes. In this case, the strong affinity (note particularly the lack of ambiguity in node 4 results) between the *Graecopithecus* and *Gorilla* palates might be indicative of a true phylogenetic relationship (Dean & Delson, 1992). This presumes, however, that the palatal morphology of *Gorilla* has evolved significantly from the condition of the ancestral hominine. Such an assumption can only be tentative, given the evidence currently available (McCollum & Ward, 1997).

DISCUSSION

The first half of this chapter undertook analyses guided purely by exploratory phenetics. The aim of these tests was to examine structures of palate variation manifest within the data. This included principal components analysis, canonical variates analysis, taxon clustering, and other considerations of Mahalanobis distances. Subsequent analyses, however, were mapped onto an assumed phylogeny of extant platyrrhines, cercopithecoids, and ape genera (see Figure 8-19). The goal in these was to examine variations in palatal morphology that correspond to specific differences between crown clades. Results from both sections are discussed below.

Data-driven analyses

The greatest difference found in this sample was between hominid and non-hominid taxa. Indeed, there was nearly complete separation between these clusters on PC 1—on CV 1 they are completely distinct. This result corroborates work done by Ward & Kimbel (1983), who noted several features of the subnasal region that set the great apes and humans apart from other catarrhines. Most of these features were prominent in the shape differences on both PC 1 and CV 1, including in hominids: a longer nasoalveolar clivus, an incisive canal, a thicker anterior hard palate, and vertical dissociation of nasal sill and floor.

The second principal component and canonical variate axes segregate *Homo* from the other specimens, with humans scoring negatively. Relative to the other taxa, the negative morphology displays a taller (supero-inferiorly) subnasal morphology, more vertical nasoalveolar clivus, thicker anterior palate, shorter horizontal plate of the palatine, and a more U-shaped dental arcade. Interestingly, PC 2 axis also sorts male and

females specimens of *Cercopithecus*, *Gorilla*, *Pan*, *Papio*, *Pongo*, and *Procolobus*, as well as separating gibbons from siamangs and bonobos from common chimpanzees. In these cases, females tended to score more negatively, as did gibbons (relative to siamangs) and bonobos (relative to common chimpanzees). Thus, many of the differences in shape between humans and their hominoid compatriots are associated with female members of most of these catarrhine genera.

The similarities between PC 1-2 and CV 1-2 were quite striking. The variability among specimens sorted out taxa very well. Moreover, the first two axes of variation corresponded strongly to those which elucidate differences among specified genera. This suggests that palatal morphology bears a great deal of taxonomic information.

Looking purely at generalized distance metrics, three palatal morphologies were manifest: platyrrhines, non-hominid catarrhines, and great apes. These clusters were fairly distinct, and nearly equidistant from, each other. The cluster of New World monkeys (Figure 8-18b) indicates that the platyrrhine palate may be derived somewhat differently relative to other extant anthropoids. On the other hand, while *Cebus* was in every case most similar to *Ateles*, *Ateles* was closer to *Hylobates* than to *Cebus* (Figures 8-17, 8-18a). An expanded study of extant platyrrhine palatal morphology would be important for substantiating a distinct New World anthropoid morphotype; indeed, detailed descriptive analyses of subnasal morphology (e.g., Ward & Kimble, 1983; Ward & Pilbeam, 1983; Ward & Brown, 1986; Brown & Ward, 1988) have not yet been expanded to include platyrrhine taxa. The cluster of non-hominid catarrhines groups *Cercopithecus* and *Procolobus*, followed successively by *Hylobates* and *Papio*. This is not unexpected given the autapomorphic morphology of the baboon snout (e.g.,

Freedman, 1957). Similarities between hylobatid and cercopithecoid palates support the supposition (e.g., Ward & Brown, 1986) that *Hylobates* shares a common palatal morphology with cercopithecoids—perhaps primitive for catarrhines. Note, however, that the analyses presented here also indicate unique aspects of the cercopithecoid palatal morphology. The great ape cluster corroborates work of McCollum & Ward (1997), showing that the palates of *Pan* and *Pongo* are somewhat more similar than either is to *Gorilla*. Humans did not fit in any cluster, having by far the most distinct palate (Figure 8-17). Nevertheless, the human morphology is most similar to those of the great apes, as shown in PC 1 and CV 1, as well as in Mahalanobis D^2 . Among hominids it is most similar to *Pan*.

Beyond relationships among taxa, it was evident from these analyses that the majority of variation in the inferior maxillary-premaxillary complex occurs in the premaxillary morphology. While the rest of the palate does exhibit shape variation, its degree is relatively minor compared to the nasoalveolar morphology.

Table 8-18 Summary of shape differences determined from discriminant analyses between crown clades in the extant phylogeny (Figure 8-19). For each discrimination, the characteristics listed describe differences between the taxon in boldface with respect to the taxon in parentheses.

Catarrhines (vs. platyrrhines)

nasoalveolar clivus expanded antero-posteriorly and supero-inferiorly
 lateral premaxillary border expanded inferiorly
 anterior maxillary palatine process thicker
 maxillary palate expanded antero-posteriorly
 post-canine dental arcade narrower
 premolar field reduced mesio-distally
 molar field expanded mesio-distally
 malar root origin placed superiorly

Hominoids (vs. cercopithecoids)

nasoalveolar clivus expanded antero-posteriorly and supero-inferiorly
 anterior maxillary palatine process thicker and deflected ventrally
 post-canine dental arcade broader
 malar root origin placed anteriorly

Hominids (vs. hylobatids)

nasoalveolar clivus expanded antero-posteriorly
 and supero-inferiorly
 anterior maxillary palatine process thicker
 incisive foramen elongated to form a canal
 malar root origin placed anteriorly and superiorly

Hominines (vs. pongines)

nasoalveolar clivus expanded supero-inferiorly, but reduced antero-posteriorly
 reduced subnasal prognathism
 midline hard palate deflected ventrally
 palate shallower
 nasal incisive fenestrae placed laterally
 palatine bone expanded antero-posteriorly
 dental arcade broader in the molar field

Table 8-18 (cont.)

***Homo-Pan* (vs. *Gorilla*)**

nasolabial clivus expanded antero-posteriorly and supero-inferiorly
 nasal sill more horizontal
 incisive canal longer
 anterior maxillary palatine process thicker
 post-canine dental arcade broader, but reduced mesio-distally
 horizontal palatine bone reduced antero-posteriorly and deflected dorsally

***Homo* (vs. *Pan*)**

nasolabial clivus rotated ventrally
 - subnasal prognathism reduced
 - nasal sill more horizontal
 canine reduced mesio-distally
 premaxillary palate narrower
 post-canine dental arcade broader
 molar field expanded mesio-distally
 horizontal palatine bone deflected dorsally

Phylogenetic node discrimination

Relationships among specimens and taxa are predicated in large part on a mixture of plesiomorphic and apomorphic features exhibited by each group. Thus, the initial analyses performed here were purely phenetic in nature. Alternatively, the second half of the chapter was driven by a phylogenetic hypothesis of relationships among the sample taxa (see Figure 8-19). Rather than elucidating the affinities of specimens and genera, later analyses were designed to detect differences between crown clades that have been previously established and corroborated in other cladistic analyses. If one accepts the consensus phylogeny, then differences at each node can be discerned through discriminant analysis. Three goals were pursued for these analyses. First, palatal morphology was tested using cross-validation for its robusticity in discriminating between crown clades; reclassification was perfect at every node, indicating that this

region of morphology is useful in delineating among clades. The second goal was to examine the shape differences that drive the discriminant function. As canonical discriminant analysis determines axes of maximum variation between groups relative to that within (Neff & Marcus, 1980), the corresponding shape differences are those features in which one clade differs from the other, but are similar among its constituents. Shape differences at each node were visualized by the method described in Chapter 5, and are summarized in Table 8-18. Finally, discriminant analysis was used to classify fossil specimens with extant genera and at each of the phylogenetic nodes. This was done both on the entire sample and in 1000 randomized replicates of equal sample size.

Results of node classifications for specimens of *Propliopithecus* argued strongly for its inclusion within the Catarrhini. Among catarrhines, it showed a strong affinity to *Hylobates*, both in genus and node discriminations; DPC 2803 was most similar to hylobatids, while classifications for DPC 3161 were somewhat more varied. This affinity between basal catarrhines and hylobatids supports the hypothesis (e.g., Ward & Brown, 1986) that the hylobatid subnasal morphology is primitive for catarrhines. More importantly, these results suggest that the palatal data used here are unlikely to distinguish basal catarrhines from basal hominoids (see Harrison, 1993). Accordingly, palates of *Proconsul* and *Morotopithecus*, which performed similarly to *Propliopithecus* in these analyses, cannot be grouped conclusively with hominoids based on these landmarks. The other Early Miocene specimen (SO 700), however, scored very differently. The palate of *Rangwapithecus* showed strongest affinities with *Gorilla* in genus-level discrimination. Moreover, this specimen grouped strongly with hominids rather than hylobatids at node 3. This corroborates observations made by other

researchers (e.g., Ward & Kimbel, 1983) and suggests that *Rangwapithecus* shares derived palatal features. Although too incomplete to include in these analyses, the closely allied *Nyanzapithecus* (e.g., Harrison 2002) also exhibits subnasal features reminiscent of hominid morphology (personal observation).

The implications of the SO 700 results are interesting. First, it demonstrates the diversity of morphologies present in the Early Miocene of East Africa: *Proconsul* exhibits largely primitive cranial (e.g., Harrison, 1987) and postcranial features (e.g., Rose, 1997; C. Ward 1997); *Morotopithecus* has a primitive palate and derived vertebrae (e.g., Gebo *et al.*, 1997); *Rangwapithecus* has some derived palatal features (e.g., Ward & Kimbel, 1983; Ward & Pilbeam, 1983; Ward & Brown, 1986; Benefit & McCrossin, 1995; see above), but a primitive postcranium (e.g., Rose 1997; Ward, C. 1997). If the derived similarities shared between *Rangwapithecus* and extant hominid palates are homologous, the implication would be convergent or parallel evolution of postcranial similarities among extant hominoids (see Larson, 1998). Alternatively, if the hominoid synapomorphies of the Moroto vertebrae are homologous, then either the hominid palatal features or the primitive postcranial similarities of *Rangwapithecus* were independently derived. Note that either supposition is based on the assumption that hylobatid palatal morphology is primitive among hominoids; yet, this seems reasonable in light of work by previous authors (e.g., Vogel, 1968; Andrews & Delson, 1975; Ward & Kimbel, 1983; Andrews, 1985; Ward & Brown, 1986; Harrison, 1987) and results from this project. Determining the better of these alternatives is not a trivial endeavor, particularly given the paucity of cranial or postcranial remains attributed to either *Rangwapithecus* or *Morotopithecus*; the reliability of associating such specimens simply exacerbates this

difficulty. The combination of derived palatal and more primitive postcranial morphologies is not unique among fossil taxa (e.g., *Sivapithecus*). Yet, this additional occurrence cannot inform this debate, as the phylogenetic significance of *Sivapithecus* features is still debated (see Ward, 1997; Pilbeam & Young, 2001). What can be said of these results is that they further illustrate the mosaic of evolutionary patterns represented by Early Miocene catarrhines from East Africa. Sorting among this montage of plesiomorphic, synapomorphic, and autapomorphic morphologies will likely remain an ongoing problem for years to come.

Results for the Late Miocene specimens of *Sivapithecus* and *Graecopithecus* were more straightforward. GSP 15000 had strong affinities with *Pongo* among genera and in node analyses. Both specimens of *Graecopithecus*, however, were strongly supported among *Gorilla*. This particular relationship has been suggested by Dean & Delson (1992) based largely on supraorbital features. While these results add some support to this hypothesis, it is possible that the *Gorilla* palate retains the primitive hominine morphology. There was no evidence to group the *Graecopithecus* palates with *Pongo*.

CHAPTER 9: CONCLUSIONS

This chapter brings together results from all previous sections into one discussion. The first part focuses on extant taxa, reviewing the conclusions drawn from each of the three analytical units (cranial, supraorbital, palatal). This is followed by a review of the shape differences that distinguish between extant members of anthropoid crown clades. Finally, the discussion concludes with a look at the results obtained from analyses of fossil genera.

ANALYTICAL UNITS OF MORPHOLOGY

This project endeavored to pursue three goals towards the better understanding of hominoid morphology and paleobiology. First, analyses were designed to quantitatively assess craniofacial shape variation among extant hominoid specimens and genera. Second, the degree of morphological separation between crown anthropoid clades was tested and the corresponding shape differences between them examined. And third, fossil specimens were tested according to these models both for their similarity to modern genera, and for their affinities to specific crown anthropoid clades. These goals were pursued using three-dimensional geometric morphometric methods, combined with a battery of multivariate statistical analyses. Like traditional approaches, these techniques offer the advantage of quantification and rigorous testing of morphological variation. Yet, landmark-based morphometrics capture substantially more anatomical detail than do traditional caliper measurements. Moreover, geometric morphometric data are analyzed within the biological and geometric framework of the original landmark configuration.

These methods, then, can approach the fineness of detail available through descriptive comparisons, while incorporating the rigor of statistical analysis.

The difficulty in applying any quantitative method to fossil specimens is the inevitability of missing data. The vagaries of fossil preservation and recovery ensure that even the most complete fossil specimens still have missing anatomy. Therefore, this project was designed to specifically accommodate the biases in fossil preservation. One method to accomplish this was to include in the dataset landmarks that would quantify known fossil specimens. More importantly, however, separate analyses were performed on three different analytical units: cranial, supraorbital, and palatal. The cranial analyses included the entire set of landmarks, except type III or semi-landmarks. This unit was employed to examine the overall morphology of and phenetic relationships among hominoid crania. Several fairly complete fossils were also examined here through a reduced set of cranial landmarks.

Supraorbital analyses used only those landmarks demarcating the supraorbital region as well as nine semi-landmarks defining the ridge curve across the superior border of this morphology. The preservation of a number of fossil supraorbital specimens means that phylogenetic hypotheses for these taxa are at least moderately (and sometimes strongly) influenced by conclusions drawn from this region. This analytical unit explored the variation in supraorbital morphologies and the distinction between the morphologies of crown anthropoid clades. Twenty fossil supraorbital morphologies were examined here. Analyses of the palate incorporated those landmarks defining the inferior maxillary-premaxillary complex. Study of this region is important both due to its frequency of preservation in the fossil record and because of the taxonomic and phylogenetic value

many researchers attribute to it. Geometric morphometric analyses were used both to test the differences described by previous researchers and to find additional relationships beyond those already proposed. This study was able to examine the affinities of eight fossil palates.

Analysis of cranial morphology

The first analysis applied to the cranial dataset was employed to determine the usefulness of applying a size adjustment to these data. It was demonstrated in Chapter 5 that Procrustes-aligned data were still highly correlated with centroid size. This is often likely to be the case when a body-size dichotomy is superimposed on a phylogenetic dichotomy (e.g., great apes vs. lesser apes). When variation correlated with taxonomic (i.e., genus membership) and sex differences was removed from the sample, however, there were still demonstrable size effects within the data. Creel (1986) demonstrated that cranial allometry in hominoids can greatly obscure phylogenetically relevant shape information in quantitative analysis of continuous data. As size was shown to be an important factor contributing to the cranial variation in this sample—beyond differences due to taxonomy or sex—residuals from a regression of aligned coordinates on log of centroid size were used in analyses of the cranial dataset.

Initial analyses of the cranium (PCA, CVA, Mahalanobis distance analyses) supported the overall distinction of platyrrhine, cercopithecoid, and hominoid morphologies. Among these anthropoids, cercopithecoid and hominoid crania were closer phenetically than either group was to the platyrrhines. In fact, a cluster diagram of Mahalanobis distances was remarkably similar to the consensus phylogeny for these genera, with one exception: *Gorilla* and *Hylobates* were found to have a strong affinity.

In fact, the relationships among both African ape genera and the hylobatids were shown to be very close in these analyses. This result can be attributed to one of three explanations: the similarity is due to shared primitive morphology, shared derived morphology, or a convergently acquired morphology. It was argued here that the first explanation is most likely. A close phylogenetic relationship between *Hylobates* and the African apes can be discounted based on morphological (e.g. Pilgrim, 1927; Simpson, 1945, 1949, 1953; Weidenreich, 1946; Delson & Andrews, 1975; Greenfield, 1979, 1980; Andrews, 1985; Harrison, 1987, 1993, 2002; Begun, 1992; 1994; Moyà Solà & Köhler, 1995; Andrews *et al.*, 1996; Begun, *et al.*, 1997; Rose, 1997; C. Ward, 1997; Singleton, 2000) and molecular (Goodman, 1963; Sarich & Wilson, 1967; Sarich, 1971; Caccone & Powell, 1989; Ruvolo, 1994, 1997; Goodman *et al.*, 1998) evidence. The argument for convergence is more difficult to dispute. A dietary explanation for this similarity, however, is not convincing given the highly folivorous nature of gorillas; *Hylobates* has a more frugivorous diet, though there is substantial interspecific variation (Kay & Ungar, 1997). A postural explanation is similarly discounted due to the substantial differences in the locomotor and postural behaviors of hylobatids and gorillas.

Therefore, the similarity between *Hylobates* and the African apes (especially *Gorilla*) seems best explained as symplesiomorphic. A number of authors (Vogel, 1968; Delson, 1975, 1977; Delson & Andrews, 1975; Ward & Kimbel, 1983; Andrews, 1985; Harrison, 1987; Strasser & Delson, 1987) have proposed a hylobatid model for some or all aspects of ancestral catarrhine or hominoid cranial morphology. Alternative models of the ancestral catarrhine morphotype (e.g., Simons, 1987; Benefit & McCrossin, 1993, 1995) do not exclude—and in some features imply—a hylobatid-like morphology for the

ancestral hominoid. If gibbons and siamangs are cranially conservative among hominoids, then the most parsimonious explanation for their similarity to the African apes is one of shared, primitive retention.

This has important implications for conducting phylogenetic analyses on hominoids. The overall degree of similarity between *Hylobates* and *Gorilla* suggests that the latter exhibits a very conservative cranium. Even if this similarity were due to convergence (and not conservatism), one would expect other analyses of hominoid crania to record similar findings. Yet, this has not been the case. In two recently published large cladistic matrices (Begun *et al.*, 1997; Collard & Wood, 2001), more than half of the cranial characters were given the same code in the two African apes but a different one in hylobatids; a similar observation was made for smaller published matrices (e.g., Rae, 1999; Moyà Solà & Köhler, 1995). The fact that this similarity has been overlooked might be indicative of a more fundamental problem at the level of character coding. The substantial difference in body size between hylobatids and gorillas makes it difficult to reconcile affinities between their morphologies; allometric scaling would further obscure any such similarities. The product of this confounding factor would be inflated levels of polymorphism recognized in hominoid crania: gibbon and gorilla characters would be coded differently for features that are (allometrically or isometrically scaled) size variations of the same shape. Unfortunately, the conjunction of size differences (lesser apes vs. great apes) with phylogenetic differences (hylobatids vs. hominids) in the sample of extant hominoids increases the chance that such errors will go unnoticed. A phylogenetic analysis using characters that were largely miscoded in this manner might still yield the “correct” phylogeny. Since the sister taxon of the hominids is of

substantially smaller mass, *incorrectly* assigning character states to *Hylobates* that were different from those assigned the African apes would still tend to place hylobatids as the sister taxon to great apes and humans.

This is not to suggest that all, or even a majority, of the features coded differently in hylobatids and African apes must be incorrect. Yet, the degree of similarity between them, as demonstrated here, indicates that some error in this regard is likely. For phylogenies of extant taxa, the implications of this are probably negligible; they are greatly magnified, however, for analyses of fossil specimens. The nature of the fossil record guarantees that the majority of specimens recovered will be largely incomplete. Phylogenetic hypotheses concerning such specimens are based, by necessity, on a limited character set. Any errors in character coding could tremendously impact the forthcoming conclusions. Note, for example, the phylogenetic inference drawn by Simons (1987) from an analysis (Andrews & Martin, 1987) of “*Heliopithecus*.” He concludes that *Propithecus* [= *Aegyptopithecus*], because of its affinity to *Afropithecus* (and thereby “*Heliopithecus*”), “stands confirmed as ancestral or closely related to what has been ranked as the earliest hominoid” (Simons, 1987: 286). While the characters in question are not at all disputed here, this example illustrates the potential impact that one fragmentary specimen can have on hypotheses of evolutionary history. The miscoding of even a few characters, therefore, can be potentially quite harmful to phylogeny reconstruction among fossils.

In addition to the initial phenetic analyses discussed above, a series of discriminant analyses was undertaken based on groups defined by a consensus phylogeny. While still phenetic in origin, this approach focuses on those differences that

vary minimally within clades but greatly between them. The aims of these analyses were to test for differences between these clades, examine the shape differences that distinguish them, and test fossil specimens for their affinities on such axes of variation. The last two goals will be addressed in other sections below. In terms of testing for differences, node discrimination was highly successful in distinguishing between extant clades at every node except node 5. The discriminant function separating *Gorilla* from a *Homo-Pan* group correctly reclassified specimens at a rate only marginally better than chance. While somewhat disappointing, this result was hardly a surprise given the autapomorphic nature of modern human crania and the strong phenetic affinity between African ape crania.

Analysis of supraorbital morphology

As with the previous unit, an initial determination was made of the role that size plays in determining supraorbital form. A regression analysis found that size was an important factor contributing to variation on several PC axes. Yet, when taxonomic and sex effects were sequestered from the data, none of the subsequent PC axes was significantly correlated with size. This does not mean that allometry is irrelevant to the morphogenesis of anthropoid supraorbital morphology. Rather, it suggests that the role of allometry cannot be partitioned from the effects of phylogeny. Therefore, Procrustes-aligned coordinates were used in all analyses without any additional size adjustment.

Results from initial phenetic analyses support a system of three character states for extant hominoid supraorbital morphologies. The hominines were all shown to be quite similar, particularly when sample sizes were equalized. *Hylobates*, on the other hand, was markedly more similar to *Ateles* than to any other genus. *Pongo*, though also most similar

to *Ateles* (but dissimilar to *Hylobates*), was shown to have the most autapomorphic features among these genera. It is interesting to note the strong similarity between *Pan* and *Homo*, suggesting that the configuration of supraorbital landmarks in modern humans is largely unchanged from the hominine condition. Such results argue against the recognition of a fourth character state for human brow morphology. Similarly, collapsing the morphologies of *Pongo* and *Hylobates* into a single character state is not justified by these data. Köhler *et al.* (2001) argue elegantly that the lack of a strict definition for “torus” renders its diagnosis meaningless. The same must be said, however, for supraorbital “rims” or “costae.” Diagnosing supraorbital variation only in terms of a torus, whether treated as a binary (e.g., Moyà Solà & Köhler, 1995) or polymorphic (e.g., Begun *et al.*, 1997) character, discounts any variability among taxa that lack a torus. And, as demonstrated here, this variability is quite significant. Thus, the results from this analysis indicate that there are three distinct supraorbital morphotypes among extant apes.

This project does not offer better definitions or labels for these character states, but rather suggests that such terms are probably not useful in a broad sense. Among this sample of extant anthropoids were taxa displaying supraorbital tori (*Gorilla*, *Pan*, *Papio*), costae (*Pongo*), and rims (*Ateles*, *Cebus*, *Cercopithecus*, *Hylobates*, *Procolobus*), as well as superciliary arches (*Homo*). Yet, when analyzed, these “character states” did not cluster together here. Thus, the utility of these terms, as applied to this sample of taxa, seems dubious. The close grouping of *Papio* and *Cercopithecus*, with a slightly more distant *Procolobus*, cut across such traditional descriptive typologies. In terms of character states, then, it must be concluded that this—admittedly small—sample of cercopithecoid taxa would be assigned to a single distinctive character state.

Phylogenetic node discrimination was highly successful at distinguishing between morphologies at all of the nodes in the consensus phylogeny. This includes a clear distinction between the morphologies of *Gorilla* and a *Homo-Pan* group. Results from analyses of fossil taxa are discussed individually below. However, it is worth commenting here on Benefit & McCrossin's (1993, 1995) ancestral catarrhine morphotype as it pertains to supraorbital morphology. They have argued that the characteristic costae of *Victoriapithecus* are representative of the stem eucatarrhine morphology, based on its strong affinities to *Propliopithecus*, *Afropithecus*, *Dryopithecus*, *Sivapithecus*, and *Pongo*. While *Victoriapithecus* was not analyzed here, the relationships of these other taxa were all examined. There was no evidence in this research to support an affinity between *Propliopithecus*, *Afropithecus*, or *Dryopithecus* and *Pongo*. Some similarities were noted in the performance of *Propliopithecus*, *Afropithecus*, and one specimen of *Dryopithecus* (CLI 18000) during phylogenetic node discriminations. There was also a strong phenetic resemblance demonstrated between *Sivapithecus* and *Pongo*. Based on the data analyzed here, however, the strength of Benefit & McCrossin's (1993) ancestral catarrhine morphotype is substantially weakened with regard to supraorbital features.

Analysis of palatal morphology

An initial test for size-correlated effects in the dataset found several PC axes to be correlated with the log of centroid size. As with supraorbital morphology, however, allometric effects could not be decoupled from differences due to taxonomy or sex. Therefore, a size correction was not employed and Procrustes-aligned coordinates were the variables used in statistical analyses.

Results from PCA, CVA, and Mahalanobis distance computations strongly supported the work of Ward & colleagues (Ward & Kimbel, 1983; Ward & Pilbeam, 1983; Ward & Brown, 1986; Brown & Ward, 1988; McCollum *et al.*, 1993; McCollum & Ward, 1997) on subnasal morphology. The greatest axis of variation among specimens (i.e., PC 1) almost completely sorted great apes and humans from all other taxa. This separation was driven primarily from variability in the anterior palate and nasoalveolar morphology, corresponding to shape differences discussed by the above authors. The second PC axis largely separated modern humans from the other taxa through a ventrally rotated nasoalveolar clivus and more parabolic dental arcade. Interestingly, this axis also corresponded to sex differences in all catarrhines except humans and hylobatids, and to differences between gibbons and siamangs and chimpanzees and bonobos. The first two canonical variate axes were nearly identical to these principal component axes, indicating that a substantial portion of the variability among specimens corresponds to the structure of variability among genera. Put another way, much of the variation in these specimens occurs along taxonomic lines.

Not surprisingly, Mahalanobis distances and cluster analysis recovered a distinct great ape clade; *Homo* was closest in similarity to *Pan* and the *Gorilla*, but too autapomorphic to cluster with the other hominids. The similarity between *Pongo* and *Pan*, as noted by McCollum & Ward (1997), was also seen here as the two genera grouped fairly closely. The cercopithecoids and *Hylobates* also formed a distinct cluster apart from both platyrrhines and hominids. Based on this result and analyses of fossil specimens (see below), the author concurred with Ward & Kimbel (1983) specifically, and other authors (Vogel, 1968; Delson, 1975, 1977; Delson & Andrews, 1975; Ward &

Kimbel, 1983; Andrews, 1985; Harrison, 1987; Strasser & Delson, 1987) more generally, that hylobatid palatal morphology likely retains the primitive hominoid and catarrhine condition. Alternatively, the two platyrrhine genera displayed a distinct morphology from these others, though phenetically they were closer to the cercopithecoid-*Hylobates* cluster than either was to the great apes.

Shape differences between crown clades are discussed in detail below. Despite initial expectations of this study, the majority of variation in the palatal complex was confined to the subnasal region. On almost every multivariate axis, features of the nasoalveolar clivus and incisive canal had the heaviest loadings. The malar root origin displayed a moderate level of variation, while differences in dental arcade shape were minor. Discriminant analyses at every node in the consensus phylogeny were unanimously successful in reclassifying extant specimens through cross-validation. This, combined with observations noted above in PCA and CVA, indicates that palatal morphology should be useful in determining some phylogenetic relationships. On the other hand, the concordance between *Hylobates* and the projected ancestral catarrhine and hominoid morphologies suggests that it will be of little use in separating stem catarrhines from basal hominoids. This might not be the case, however, if there were a better sample of (undisputed) stem catarrhines (e.g., *Propliopithecus*, *Pliopithecus*). For example, the phylogenetic node discriminations described here would provide a useful method for determining the differences between a sample of stem catarrhines and hominoids. Such a study will have to await the discovery of additional fossil material.

DISTINGUISHING FEATURES BETWEEN CROWN CLADES

A series of discriminant analyses was also undertaken in order to study specific differences between the morphologies of crown clades. This approach was based upon an assumed phylogeny of anthropoid taxa (see, e.g., Figure 5-1). For these tests, each branch deriving from a node in the phylogeny was treated as a single group. Thus, each node represents a 2-group discriminant analysis between the derived clades that it joins. Like canonical variates analysis, the discriminant analysis separates taxa based on traits that are shared within a group but differ between groups. Thus, a series of node discriminations was used to determine those features which specifically distinguish between extant crown clades. Shape differences were visualized by deforming the consensus landmark configuration according to the discriminant vector. Note that this approach is not a method for reconstructing ancestral morphotypes at each of these nodes. Rather, it is a method to visualize the shape differences between clades that resulted from the cladogenetic event.

Traits distinguishing catarrhines from platyrrhines

The differences between catarrhines and platyrrhines are illustrated elsewhere in the text (Cranial: Figure 6-20; Supraorbital: Figure 7-21; Palatal: Figure 8-21), but summarized here. Most of the features distinguishing these clades are concentrated in the neurocranium and the lower face. The catarrhine neurocranium is more globular overall—both taller and wider, but relatively shorter antero-posteriorly. The basi-occiput is greatly reduced in length, and less flexed relative to the palate. Zygomatic arches are placed more superiorly on the cranium, contributing to their vertical dissociation from the tooth row. The upper face in catarrhines is dorsally rotated on the neurocranium, with the

lateral supraorbital morphology set even further posteriorly. This contributes to a more acute angling across the front of the catarrhine face. The upper face is broader in catarrhines, with a thick orbital pillar and the inferiorly set fronto-malar suture. The angling in the upper face is contrasted somewhat by reduced angling in the midface, as the lateral zygoma is set further anteriorly and also inferiorly. The greatest differences occur in the maxillary-premaxillary complex. The entire lower face is supero-inferiorly expanded; this is exaggerated in the nasoalveolar region which is also inflated antero-posteriorly. The catarrhine palate is lengthened antero-posteriorly largely through expansion in the maxillary palatine process. In the tooth row, the catarrhine premolar field is reduced (due to fewer premolars), but the molar field is expanded mesio-distally.

Traits distinguishing hominoids from cercopithecoids

The features that distinguish extant hominoids from this sample of cercopithecoids are all shown in Figures 6-22, 7-23, and 8-23. One of the greatest differences is expansion of the neurocranium at all relevant landmarks. This corresponds to a ventral rotation of the upper face and somewhat less flexion in the cranial base. The hominoid upper face is flatter across the front with a slightly depressed medial superior supraorbital margin. The nasal bones are substantially shorter relative to those in cercopithecoids and more vertically oriented. This contributes to a fairly orthognathic upper face, with increased prognathism through the nasal region and inferiorly. The hominoid nasal aperture is shorter and broader than the cercopithecoid, and placed relatively superiorly on the face. The lower face is substantially more airorhynch. The nasoalveolar clivus is expanded both antero-posteriorly and supero-inferiorly, and the anterior maxillary palatine is thicker and deflected slightly ventrally relative to the

horizontal process of the palatine bone. The dental arcade is relatively broader in the post-canine dentition of hominoids, while the malar root is set superiorly.

Traits distinguishing hominids from hylobatids

The morphologies that distinguish these two extant clades are illustrated in Figures 6-24, 7-25, and 8-25. The hominid neurocranium is expanded substantially supero-inferiorly and slightly antero-posteriorly, with an anterior shift in the foramen magnum. The upper face is flatter across the front and rotated dorsally on the neurocranium. The hominid brow is expanded laterally, with a thicker lateral orbital pillar and an inferiorly placed fronto-malar suture, especially postero-laterally. The medial morphology of the upper face is shifted markedly superiorly. This is particularly true of nasion, which is also situated somewhat posteriorly. In contrast, the glabellar region is expanded anteriorly. The hominid orbits are relatively smaller and set somewhat closer together. The nasal bones are longer in correlation with a lower set nasal aperture. The zygomatic arches are set substantially superiorly on the hominid cranium, while the lateral zygoma is placed more anteriorly. In the lower face, the nasoalveolar clivus is greatly expanded in both antero-posterior and supero-inferior dimensions. This corresponds with a thicker palate and an elongated incisive canal.

Traits distinguishing hominines from pongines

Illustrations of these shape differences are shown in Figures 6-26, 7-27, and 8-27. The hominine neurocranium is expanded relative to the pongine, particularly in antero-posterior and supero-inferior dimensions. This latter feature corresponds with an anteriorly placed foramen magnum, lengthened occipital squama, and substantially flexed basi-occipital, relative to the palate. The upper faces of African apes and humans are

broader and more angled across the front, and rotated ventrally on the neurocranium. Laterally, the supraorbital margins are more "squared," with a narrower lateral orbital pillar relative to that of the pongines. Medially, the upper face is expanded superiorly, with a substantially broader interorbital region. In profile, the hominine face is more vertical, owing to both the ventral rotation of the upper face and reduced subnasal prognathism. The nasoalveolar clivus is markedly reduced antero-posteriorly, with a more horizontal nasal sill that is dissociated from the nasal floor. The incisive canal is relatively shorter and more vertical, with the nasal incisive fenestrae set more laterally. The hard palate is deflected ventrally, although the dental arcade is not. This results in a shallower palate anteriorly. The horizontal plates of the palatine bone are expanded antero-posteriorly in hominines, while the dental arcade is somewhat broader towards the distal margin.

Traits distinguishing *Homo* and *Pan* from *Gorilla*

The discriminant analysis between cranial morphologies of *Gorilla* and a *Homo-Pan* clade could not sufficiently distinguish between them. Therefore, no discriminating characteristics were taken from the cranial analyses. Features from the supraorbital and palatal analyses, however, are illustrated in Figures 7-29 and 8-29. Differences in the upper face include a reduction in the lateral extension of the brow, increased distance between glabella and nasion, reduction in the toral thickness, and a broader interorbital region. In the lower face, the nasoalveolar clivus is expanded both antero-posteriorly and supero-inferiorly. The nasal sill is more horizontal, while the incisive canal is shorter and more vertically oriented. The dental arcade is relatively broader distally but narrower in

the anterior face. Finally, the horizontal plate of the palatine is reduced antero-posteriorly and deflected dorsally.

Traits distinguishing *Homo* from *Pan*

Traits distinguishing *Homo* from *Pan* are illustrated in Figures 6-29, 7-31, and 8-31. The brain of *Homo* is substantially larger in all dimensions. The squamous occipital is longer, whereas the basi-occipital is much shorter, correlated with an anterior shift in the foramen magnum. The upper face is rotated ventrally on the neurocranium, with no post-toral sulcus. The supraorbital margins in humans are reduced in lateral dimension, with a narrower lateral orbital pillar. Midline landmarks are anteriorly placed, with glabella also superiorly situated, and the interorbital breadth is expanded. The human profile is more orthognathic than the chimpanzee, although the nasal bones are short and protruding. In the lower face, the nasoalveolar clivus is rotated ventrally in correlation with reduced subnasal prognathism, and a horizontally oriented nasal sill. The dental arcade is more parabolic in shape with the hard palate (and particularly the palatine bone) deflected dorsally. In dental dimensions, the human canine is reduced, while the molar field is expanded mesio-distally.

ANALYSES OF FOSSIL SPECIMENS

Analyzing fossil specimens through a statistically based study is always an indirect proposition. The inadequate “sampling” methods of fossilization and discovery typically preclude any reasonable assessment of group variability; even when a decent sample is available, the paucity of biological information available from bony morphology makes group membership uncertain. Hence, this project used models of

variation in extant taxa in order to draw some conclusion about the affinities of fossil specimens. In cases where fossils preserve all of the landmarks used in an analysis, these specimens were included in a PCA with extant taxa. Canonical variates analysis, which requires a computation of within-group variability, cannot be legitimately undertaken for the fossil samples used here. The related canonical method of discriminant analysis (DA), however, can be used to classify specimens based on discriminant functions derived from extant groups. It is according to this method that the majority of fossil analyses were conducted.

Two sets of discriminant analyses were undertaken. The first was a discrimination at the genus level. In these, each fossil was placed into a modern taxon according to the discriminant functions that separate extant genera. This was computed both for the entire sample and for 1000 randomized equal-sample replicates. The second set of DAs were based on groups defined by the consensus extant phylogeny. For these, each node on the cladogram defined two test groups based on the branches deriving from that node. Samples from these groups were analyzed using DAs, again both on the whole sample and on 1000 equal-sample replicates. Three-group analyses were also computed separately by creating a group from all taxa external to the node being studied. This combination of generic and node discriminations provided a useful tool in analyzing the morphological affinities of these fossil specimens.

Basal catarrhines

Propliopithecus

Three specimens of *Propliopithecus zeuxis* were analyzed in this project: DPC 2803, DPC 3161, CGM 42842. The latter specimen was not included in analyses of the

palate due to missing data. It should be noted that the third molars of DPC 3161 are not in full occlusion, although both canines are, indicating that this individual was just reaching adulthood (Simons, 1987). The extant sample used in this project was chosen to analyze definite and putative fossil hominoids from Miocene-Recent times. As such, this project was not intended to provide a comprehensive analysis of catarrhine primates from the Fayum. Specimens of *Propliopithecus* were included here as examples of basal catarrhine morphology—the analogue of a cladistic outgroup. Harrison (1987, 1988, 1993, 2002; Harrison & Rook, 1997) has argued convincingly that stem eucatarrhine morphology was probably similar to that of basal hominoids. Given that most researchers (e.g., Simons, 1967; Delson & Andrews, 1975; Kay *et al.*, 1981; Fleagle & Kay, 1983; Kay & Simons, 1980, 1983; Harrison, 1987; Simons, 1987; Benefit & McCrossin, 1993; Leakey *et al.*, 1991; Ross *et al.*, 1998) regard *Propliopithecus* as a stem catarrhine, it was used here as a benchmark for recognizing other stem catarrhines. Note, however, that this genus is not a basal eucatarrhine and might be expected to differ from these (Harrison, 1987; but see Simons, 1987).

Considering the overall cranium, these specimens were demonstrably different from hominoids. In fact, genus classifications were very broadly distributed, indicating the lack of a strong affinity to any extant taxon. This is not altogether unexpected in a catarrhine of primitive aspect. Unlike its congeners, DPC 3161 showed a fairly strong affinity to cercopithecoid crania, both at the generic level and in analyses of node 2. Results from supraorbital analyses yielded very similar results. DPC 2803 and CGM 42842 had widely diverse genus classifications. In features distinguishing hominoids from cercopithecoids, they grouped with the former, but showed no affinity to either

hylobatid or hominid morphologies. DPC 3161 performed markedly differently. Its brow morphology grouped with *Procolobus* in more than 99% of the genus classifications; in features distinguishing hominoids from cercopithecoids, it strongly favored the latter. Palatal analyses demonstrated more concordance between the two specimens studied. Based on strong similarities to the hylobatids, it was concluded that these methods are unlikely to differentiate among stem catarrhines, eucatarrhines, and hominoids based on the palatal morphology of presently known specimens. Though showing a strong affinity to *Hylobates*, it was noted that DPC 3161 had a moderate (36%) frequency of classification in *Cercopithecus*.

Despite its ancillary use here as a surrogate for eucatarrhine morphology, two salient conclusions can be drawn from this project. First, there is no evidence here linking the morphologies of *Propliopithecus* and *Pongo* (or *Sivapithecus*, by extension of results shown herein). Benefit & McCrossin's (1993, 1995) model for the ancestral catarrhine morphotype draws its strength from broad similarities they attributed to basal catarrhines, cercopithecoids, putative hominoids, and hominoids. This project demonstrates, however, that there is little support among supraorbital, palatal, or overall cranial features for including *Pongo* or *Sivapithecus* in this typology (see also below). While this does not invalidate their model, it lessens the strength of their supporting evidence.

The other conclusion drawn here is that there are two distinct morphologies comprising this sample of *Propliopithecus*. DPC 2803 and CGM 42842 performed with remarkable concordance in these analyses. DPC 3161, however, achieved radically different results. In both cranial and supraorbital analyses, this specimen was strongly affine to cercopithecoids; in the palatal analysis, it was most similar to *Hylobates* (argued

to be primitive for catarrhines) but still placed moderately with *Cercopithecus*. It seems unlikely that these differences are due to the lack of complete maturity of DPC 3161, as it arguably would not have changed radically in its next several years of life (the hypothesized age difference between this and CGM 42842; Simons, 1987). Results from this study imply that this specimen probably warrants a separate taxonomic designation, although the level of separation is not yet clear.

Early Miocene Putative Hominoids

Afropithecus

The single, well-preserved craniofacial fossil of *Afropithecus* (WK 16999) was analyzed in cranial and supraorbital studies; its matrix-filled nasal aperture prevented its inclusion in the palatal analyses. In cranial analyses, this specimen was determined to probably group with hominoids, receiving some support as a hominid. The first conclusion was reached based on comparisons with *Propliopithecus* specimens. Unlike these, *Afropithecus* demonstrated a fairly strong affinity to apes (especially *Pan*) in genus discrimination. Moreover, node 2 results placed *Afropithecus* strongly with the hominoids, rather than ambiguously splitting among groups (DPC 2803), grouping in the “primitive” category (CGM 42842), or placing with cercopithecoids (DPC 3161). Its support as a hominid (vs. hylobatid) was less strong, placing there in 63% of the replicates. Supraorbital analyses corroborate its affinity to hominoids, albeit very weakly. In fact, the performance of WK 16999 in these tests was fairly similar to two specimens of *Propliopithecus*. The main difference, and thus the only supraorbital evidence supporting a hominoid allocation, was a strong affinity to *Hylobates* in genus discriminations; *Propliopithecus* specimens were broadly distributed. Thus, the overall

cranial morphology supports the hominoid (and perhaps hominid) affinities of *Afropithecus*, while the supraorbital morphology only weakly supports this; there is some evidence (cf. node 3 results), however, to suggest that the supraorbital morphology of this specimen may be fairly autapomorphic among this sample.

There was no evidence from these analyses supporting the affinity of *Afropithecus* to *Pongo* (or *Sivapithecus*). Some similarities were noted between the results of *Afropithecus* and *Propliopithecus* in the supraorbital analyses, but these do not constitute strong evidence of their affinity. In both cases, no similarities supporting Benefit & McCrossin's (1993) ancestral catarrhine morphotype were found.

Morotopithecus

A single, reasonably complete facial specimen of this genus was examined in the palatal analyses. Results demonstrated convincingly that the palatal morphology of UMP 62-11 is very similar to that of *Hylobates*, concurring with descriptive analyses done by previous workers (e.g., Ward & Kimbel, 1983; Ward & Pilbeam, 1983; Begun, 1994). As noted above, the gibbon palatal morphology is argued to be ancestral for catarrhines based on its strong similarities to *Propliopithecus*. Therefore, the taxonomic affinities of *Morotopithecus* cannot be resolved from the palatal morphology analyzed here.

Proconsul

RU 16000 was the only undistorted specimen of *Proconsul* complete enough to include in this project. As primarily an inferior facial specimen, it was studied only through palatal analyses. Results for this specimen were nearly identical to those of UMP 62-11, suggesting that it shares a primitive catarrhine palatal configuration (Ward & Kimbel, 1983; Ward & Pilbeam, 1983; Ward & Brown, 1986; McCollum & Ward, 1997).

Note that while its hominoid status could not be supported or rejected here, there is no palatal evidence to support its allocation to the hominids.

Rangwapithecus

The type specimen of *Rangwapithecus gordonii* (SO 700) was also included in analyses of the palate. Unlike its East African penecontemporaries, this specimen demonstrated fairly strong affinities to the hominids. In genus discrimination, it placed with *Gorilla* in 55% of the replicates, and split the remaining classifications between *Procolobus* and *Hylobates*. More importantly, at node 3 (hominid vs. hylobatid) it was strongly grouped with great apes and humans—unlike *Propliopithecus*, *Proconsul*, and *Morotopithecus*. This corroborates observations made (but not conclusions reached) by other workers (Ward & Kimbel, 1983; Kelley & Pilbeam, 1986; Benefit & McCrossin, 1995). Bearing in mind that the greatest axis of variation among extant specimens and genera separates hominids from the other taxa, these results are taken as evidence of the hominid affinities of *Rangwapithecus*. Knowing that postcranial remains attributed to this genus reflect primitive catarrhine morphology, one could argue that this subnasal morphology (and that reported for *Afropithecus*; Leakey & Walker, 1997) evolved independently of the hominid lineage. On the other hand, it seems less parsimonious at this point to postulate the convergent evolution of the hominid subnasal pattern as opposed to the primitive retention of catarrhine postcranial features. It was also noted that specimens of the closely allied *Nyanzapithecus* (e.g., Harrison, 2002), although too fragmentary to include here, were observed by the author to bear some resemblance to the hominid subnasal morphology.

Turkanapithecus

The single, well-preserved cranium of *Turkanapithecus* (WK 16950) was examined in both cranial and supraorbital analyses. Results from the whole cranium generally support the affinities of this specimen to hominoids, based on comparisons with *Propliopithecus* specimens. In genus classifications, *Turkanapithecus* placed almost exclusively among ape genera, rather than more broadly among the sample. It also performed markedly different from *Propliopithecus* specimens in discriminations between hominoids and cercopithecoids. The ambiguous results at node 3, however, urge caution with any conclusion reached. Cranially, WK 16950 does not bear a strong affinity to hylobatids, hominids, cercopithecoids, or platyrrhines, yet seems to have some general hominoid affinities. This is a pattern one might expect in a basal catarrhine of modern aspect (Harrison, 1987, 1988, 2002). In supraorbital analyses, *Turkanapithecus* was shown to be strongly affine with *Hylobates* both in genus discrimination and at node 3. These results were substantially different from those seen in *Propliopithecus*. Therefore, while the balance of evidence from these analyses supports allying *Turkanapithecus* with the hominoids, the sum of this evidence is not convincing. This morphology of WK 16950 does not seem to fit well into any of the alternatives, which may be indicative of an overall primitive *Bauplan*.

Late Miocene Hominoids

Dryopithecus

Three specimens of *Dryopithecus* were analyzed in this project: RUD 77, RUD 200, and CLI 18000. RUD 200 was the only specimen complete enough to include in the cranial analyses; all three were studied in supraorbital analyses, but none could be

included in an analysis of the palate. Cranially, RUD 200 was best grouped with the hominids. Although evidence to the contrary was fairly weak, it was somewhat greater than might be expected: at node 2, it grouped among cercopithecoids in 25% of the replicates; at node 3, it placed in the “primitive” category with similar frequency. There was little evidence to support the hominine affinities of RUD 200. In supraorbital morphology, all three specimens placed strongly among hominoids; RUD 200 also grouped strongly with hominids, while RUD 77 placed there with moderate support. CLI 18000 results were markedly different. Most similar to *Hylobates* at the genus level, this specimen was statistically ambivalent in discriminations between hylobatids and hominids. In fact, the performance of CLI 18000 was remarkably similar to that of *Afropithecus* supraorbital morphology. Therefore, there is no evidence linking the Spanish *Dryopithecus* specimen with hominids.

There is also no evidence here to support the pongine affinities of any *Dryopithecus* specimens (*contra* Moyà Solà & Köhler, 1993, 1995; Pickford *et al.*, 1997; Köhler *et al.*, 2001). Despite the variety of affinities demonstrated among these fossils, none of them showed similarities to the orangutan.

Graecopithecus

Two specimens of *Graecopithecus* were included in this project: RPI 128 and XIR 1. Despite the fact that XIR 1 preserves most of the facial morphology, at least unilaterally, this specimen was not analyzed in the cranial unit due to distortion that spans both sides of the sagittal plane (Köhler *et al.*, 2001). Rather, the supraorbital torus and palate were analyzed separately; RPI 128 was examined through analyses of the palate. Results of the supraorbital analyses confidently linked *Graecopithecus* with the

hominines. Within this clade, there was moderate support for placing it with the *Gorilla* lineage: 81% placement in generic discrimination, 67% placement at node 5 discrimination. In palatal analyses, both specimens of *Graecopithecus* scored similarly and were likewise grouped with the hominines. Node 5 results placed them unanimously in *Gorilla*. This concurs with better than 92% placement there in generic discrimination. Thus, both supraorbital and palatal analyses place *Graecopithecus* with the lineage of hominines, and more specifically with *Gorilla*—a hypothesis put forth by Dean & Delson (1992). One should, however, bear in mind the possibility that both *Gorilla* and *Graecopithecus* exhibit primitive hominine morphology and are therefore not phyletically related. Such a proposal is not testable given the analyses pursued here.

There was no evidence supporting an affinity between *Graecopithecus* and *Pongo* (*contra* Köhler *et al.*, 2001). Secondary affinities (after *Gorilla*) were with *Pan* for the supraorbital region and *Hylobates* for the palate. Support for even these similarities, though, was negligible. There was also no evidence from these data demonstrating a link between *Graecopithecus* and *Homo* (*contra*, e.g., Bonis & Koufos, 2001). Not once in all of the replicates for supraorbital or palatal genus discriminations did these specimens place in *Homo*. At node 6, 20% of the supraorbital classification were in *Homo*, but this was not taken as conclusive evidence; none of the palatal discriminations at node 6 resulted in a classification in *Homo*.

Sivapithecus

The partial cranium of GSP 15000 was examined in both supraorbital and palatal analyses. In brow morphology, these tests generally confirmed the much discussed (e.g., Pilbeam, 1982; Ward & Brown, 1986; Brown & Ward, 1988; Pilbeam, 1997; S. Ward,

1997; Pilbeam & Young, 2001; Pilbeam, 2002) similarity between *Sivapithecus* and *Pongo*. The evidence was not unequivocal, however. Support from genus classification was generally strong (80%), with a secondary affinity (16%) to *Ateles*. At node 3, *Sivapithecus* placed with hylobatids in 63% of the 2-group replicates; it grouped with hominids in 41% of the 3-group replicates. At node 4, however, it was strongly supported (> 93%) as a pongine. Such results are difficult to interpret. While GSP 15000 has a clear affinity to *Pongo*, it is moderately more like *Hylobates* in features that distinguish hominids from hylobatids. One explanation might be that the brow of *Sivapithecus* still retains some aspects of a more conservative morphology. Alternatively, the lack of a clear affinity to the hominid clade might suggest that the pongine costae of *Sivapithecus* are derived independently from *Pongo*. Such an explanation would be supported by the distinctly primitive postcranial bones reported for this genus (e.g., Pilbeam *et al.*, 1990; Pilbeam, 1996, 1997, 2002; but see Richmond & Whelan, 2001).

Analyses of the palate were clearer in their support of *Sivapithecus* having a close affinity to *Pongo*. Seventy percent of the genus classifications were in *Pongo*, with another 20% in *Gorilla*. Node 3 results were almost unanimous in placing GSP 15000 among hominids. Node 4 results were nearly as strong in linking it to *Pongo*. Thus, in both supraorbital and palatal morphologies, *Sivapithecus* bears a strong resemblance to *Pongo*. The interesting result here is the lack of hominid affinities in those supraorbital features that separate great apes and humans from gibbons and siamangs.

Plio-Pleistocene hominins

Australopithecus

A single specimen of *Australopithecus africanus* (Sts 5) was tested in cranial and supraorbital analyses. Cranially, this specimen was most similar to modern *Homo* in genus discrimination, with a secondary affinity to *Pan*. Node 6 discrimination, however, placed it unanimously with the chimpanzee. In supraorbital morphology Sts 5 grouped with *Pan* (52%) most frequently, followed by *Homo* (32%). At node 6, *Australopithecus* classified nearly evenly in both, with more (57%) replicates in *Pan*, but the whole-sample classification in *Homo*. One must be cautious about interpreting equal classification distribution as a transitional morphology between two groups. However, the distributions were not equal for cranial data: *Australopithecus* was clearly linked to *Homo* in genus discrimination, and *Pan* in node 6 classification. Rather than ambiguity, this suggests similarities to *Homo* and *Pan* based on different sets of characteristics. The supraorbital morphology, on the other hand, is fairly ambiguous in both generic and node 6 classifications. Thus, while it bears clear affinities to hominines, the Sts 5 brow is not demonstrably similar to either *Pan* or *Homo*.

Paranthropus

Four specimens of *Paranthropus* were examined through both cranial (ER 406, WT 17000) and supraorbital (ER 406, ER 732, ER 13750, WT 17000) analyses. Cranial results were nearly identical to those of *Australopithecus*: strongly placed in *Homo* during genus discriminations and unanimously grouped with *Pan* at node 6. As noted above, this suggests a clear affinity with *Homo*, but a greater similarity to *Pan* in those features which discriminate between chimpanzees and modern humans. In supraorbital

morphology, all four specimens placed most frequently in the genus *Gorilla*; ER 406 did so with great frequency (74%), while the others had substantial showings in *Pan* and *Homo*. This is belied, however, by the lack of support for *Gorilla* features at node 5. Thus, in specific features that distinguish between *Gorilla* and a *Homo-Pan* clade, all specimens placed strongly in the latter. Node 6 results were mixed. WT 17000 placed most frequently in *Pan*, but only with 66% support. ER 406 and ER 732 placed in *Homo* with moderate (81% and 74%, respectively) support. ER 13750 placed evenly in both *Pan* and *Homo*. It is interesting that in a broader phenetic sense, *Paranthropus* supraorbital morphology is most like *Gorilla*; yet, these specimens do not share the features that separate *Gorilla* from the other clade of hominines. Similarly, when the overall cranium is considered, *Paranthropus* most resembles *Homo* in genus discrimination. But, in those features distinguishing the cranium of *Homo* from that of *Pan*, these specimens are strongly affine with the chimpanzee. Note, there is no support here for equating the *Paranthropus* supraorbital morphology with that of *Pongo* (*contra* Clarke, 1977).

Early *Homo*

Five specimens of early *Homo* were examined in analyses of the cranium (ER 1813, ER 3733) and supraorbital region (ER 1470, ER 1813, ER 3732, ER 3733, ER 3883). Cranially, both specimens of *Homo* were strongly grouped with modern humans in genus classification. Only ER 3733, however, could be placed in *Homo* at node 6, while ER 1813 results were equivocal. In supraorbital features, all five specimens grouped most frequently in the genus *Homo*; support was only fair (68%), however, for ER 3733, and very weak for ER 3732 (46%). In differences between chimpanzee and modern human

supraorbital morphologies, ER 1470, ER 3733, and ER 3883 all grouped strongly with *Homo*. ER 1813 and ER 3732, however, placed in *Pan* with relatively weak support (53% and 60%, respectively). Considered overall, these results can only support allocation of three specimens to the *Homo* group: ER 1470, ER 3733, and ER 3883. ER 1813 is equally distant from (not necessarily equally close to) both *Pan* and modern *Homo*. ER 3732 has demonstrable affinities with *Pan*. In fact, the distribution of classifications for this specimen more closely resembles those of *Paranthropus* and *Australopithecus* than any of these early *Homo* specimens.

SUMMARY

Three-dimensional geometric morphometrics, though increasingly popular in the physical anthropology literature, have not previously been applied to cranial analyses incorporating all extant hominoids. Yet, results from this project demonstrate the importance of taking this broader perspective. At the most basic level, this study provided a detailed, quantitative assessment of the craniofacial morphologies in hominoids and their closest allies. Unlike traditional approaches, landmark-based morphometrics analyze data from within a geometric framework that is consistent with the morphologies of the original specimens. Utilizing such methods, this project analyzed the similarities and differences manifest among extant specimens and groups. The results provided additional support for (as well as some evidence against) many of the morphological affinities noted by previous workers. More importantly, however, geometric morphometrics proved to be a powerful tool in detecting subtle differences in shape. Thus, I was able to discern additional morphological affinities, previously un-remarked upon by most authors.

Beyond quantification of extant morphologies, this project outlined an approach for delineating, testing, and visualizing differences in morphology between crown anthropoid clades. Combining discriminant analyses with morphometric techniques, this project was able to illustrate the specific regions of the cranium that vary most between extant groups in a given phylogeny. The discriminant analyses also provided a means for testing the degree of overlap between these morphologies. By isolating and testing the structures most affected by cladogenetic events, the approach used here can greatly enhance the practice of phylogeny reconstruction, as well as inform studies of function, ontogeny, and character integration. Finally, this project outlined a new statistical approach for testing the affinities of fossil specimens within an assumed phylogenetic tree. Successive discriminant analyses were used to assign fossil specimens to extant clades at each node of the phylogeny based on those features which distinguish between clades. In this case, however, a randomization technique was used to generate an assignment distribution for each fossil. Though not a cladistic approach, *per se*, this method tests the phenetic affinities of fossil specimens based only on features shared within, but differing between, extant clades. As such, this method was used to test alternative hypotheses, as well as generate new ones, regarding the affinities of fossil specimens.

Thus, the work undertaken here provides a new perspective on the craniofacial morphology of hominoids and their close relatives. Building on this project, there are a number of areas which could serve as the focus of new research. First, detailed studies of additional aspects of cranial morphology would complement this work. In particular, a geometric morphometric analysis of structural integration would greatly enhance our

knowledge of cranial morphology. Expanding this project to include more cercopithecoids and platyrrhines might prove helpful in addressing questions regarding the morphology of stem hominoids. Perhaps of greatest interest would be a broad morphometric study of cranial ontogeny, which included all of the extant apes. Given the cranial affinities demonstrated in this work, a developmental assessment of these similarities would be singularly informative. Finally, geometric morphometric methods would be useful in exploring the functional aspects of cranial morphogenesis, though few researchers have as yet used them for such.

It is cliché for paleontologists to hypothesize that additional fossils will help to answer the many remaining questions. Nevertheless, the discovery of new and diverse fossil apes can only increase our knowledge of hominoid paleobiology, all the while raising new questions and instigating more debates. What is more important, however, is that new techniques—those developed here and in many other projects—provide better tools for understanding these fossils as they are uncovered. In this manner, hominoid paleontology can move towards achieving the degree of consensus that now marks the study of extant apes.

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