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ORIGINS.

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RAMAPITHECUS, AND EARLY HOMINID ORIGINS

by

Leonard Owen Greenfield

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
(Anthropology)
in The University of Michigan
1977

Doctoral Committee:

Associate Professor Milford H. Wolpoff, Chairman
Professor C. Loring Brace
Professor Frank B. Livingstone
Professor R. Glenn Northcutt

DEDICATION

This work is dedicated to the memory of my late father,

Louis Greenfield

ACKNOWLEDGMENTS

I would like to thank and express my deep appreciation to the members of my doctoral dissertation committee: Dr. M. H. Wolpoff, chairman, Dr. C. L. Brace, Dr. F. B. Livingstone, and Dr. R. G. Northcutt. I owe an especially large debt of gratitude to Dr. Milford H. Wolpoff who has been instrumental in my training and professional development and has supported and encouraged me to undertake the present work. I also thank Dr. W. L. Jungers for support and critical review, and Dr. D. R. Pilbeam for helpful discussions and information on the immediate topic.

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Dr. Wolpoff also provided a complete set of australopithecine dental measurements, morphological observations he obtained from the original materials in South and East

Africa, and measurements and observations on the Rudabanya hominoids.

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CHAPTER I

INTRODUCTION

Accumulating discoveries and diverse interpretations of the genus Ramapithecus have made it desirable to reassess this taxon, discussing the included specimens, and systematically comparing them to contemporary and extant pongids, and early hominids. This thesis is an attempt to determine the horizontal and vertical relations of the taxon based upon specimens available through 1976. The goals are threefold: determination of the particular specimens which actually comprise the taxon and analysis of their morphology in an adaptive framework, comparison of the taxon with contemporary hominoids with the purpose of determining Miocene phylogenetic relationships and their evolution, and comparison of the taxon with early undoubted hominids (especially the new and earlier material from the Afar and Laetoli) to critically examine the alleged ancestor-descendant relationship, which is commonly proposed.

A review of the history of Ramapithecus discoveries and interpretations is critical to this analysis; the influence of a relatively few workers underlies many of the continuing controversies, and the evolution of interpretations can best be understood through the treatment of the various discoveries in a historical context. Unfortunately, most of the early discoveries were fragmentary, and many of the important aspects of Ramapithecus

have only recently been established with relatively complete gnathic and dental material.

Following this discussion, is a brief description of the Ramapithecus specimens mentioned throughout the analysis. Virtually all of these were examined by the author. The review of geological and paleoecological reconstructions for the Ramapithecus bearing deposits suggests important constraints on the adaptive interpretations of the taxon. Further, the reconstructions and zoogeographic information establishes a temporal and geographic context necessary to determine evolutionary trends and a phylogeny.

Because of the controversy regarding which specimens should be included in the taxon, the author has decided to utilize two sample sets, labeled R1 and R2. Both are systematically compared in the feature by feature analysis with all relevant hominoids. This in depth analysis of each of the known features was considered a prerequisite to a determination and comparison of the adaptive pattern of Ramapithecus.

The reconstructed adaptive pattern of Ramapithecus was subsequently compared to adaptive patterns of (Proconsul), (Sivapithecus), australopithecines, and extant pongids in order to assess trends in hominoid evolution, to determine whether taxonomic revisions of Ramapithecus and contemporary dryopithecines were necessary, and to reconstruct a phylogeny.

Ultimately, several phylogenetic schemes were presented. These schemes were constrained by the information gleaned from the comparisons of adaptive patterns, geology, paleoecology, zoogeography, and phenetic analysis of the relations between the living great apes and man.

CHAPTER II

HISTORICAL BACKGROUND

Interest in hominid origins was greatly accelerated by the discovery of a fossil pongid jaw from the Miocene of France (later made the type of D. fontani) because its describer (Lartet 1856) believed it represented an animal which was phylogenetically closer to humans than to extant pongids. This, and subsequent finds in Europe, stimulated interest in other parts of the old world. By 1879, Lydekker had described the first fossil ape jaw from India (GSI D.1), but it was not until after the turn of the century that workers first proposed, and debated, the possibility that any of the Siwalik hominoids were in, or near, the ancestry of hominids.

Beginning with the earliest discoveries of the 20th century, Pilgrim was the first to suggest that one of his described Siwalik hominoids (Sivapithecus indicus) represented an ancestral hominid (1910, 1916). Pilgrim, however, did not recognize a generic distinction for the material (GSI D.118/119 and GSI D.185) later assigned to Ramapithecus punjabicus. Instead, he placed these specimens within Dryopithecus (D. punjabicus) in his first publication (1910). He felt D. punjabicus was more closely related to extant pongids, while Sivapithecus indicus was in, or near, the ancestry of hominids (a conclusion reached primarily on the basis of a comparison with Plitdown). However, in a later publication (1927) he

modified his position, although retaining Sivapithecus as the most likely hominid ancestor. This phyletic association was based upon two shared characteristics: deep palate, and nearly vertical mandibular symphysis.

In the next decade, the works of W. K. Gregory (1922, 1926) further strengthened the position that a hominid ancestor could be found among the dryopithecines. Gregory stressed basic similarities in the molar morphology of Dryopithecus and human fossils, although he did not consider any of the Ramapithecus specimens human-like. Rather, he supported "some form of Dryopithecus, possibly related to D. rhenanus" as a human ancestor. D. rhenanus, a European taxon erected by Schlosser (1901), was based upon several isolated molars. In addition to his theoretical contributions, Gregory was also partly responsible for the recovery and description of three new mandibles from the Siwaliks (AMNH 19411, AMNH 19412, and AMNH 19413, the types of D. pilgrimi, D. cautlevi, and D. frickae, respectively), and material recovered in the 1935 expedition to India (specimens GSI D. 298, GSI D.299/300, GSI D.301-8, YPM 13828, YPM 13831 (see Brown, Gregory, and Hellman 1924 and Gregory, Hellman, and Lewis 1938). Gregory's influential monographs, remain, to this day, vital sources of information.

Discoveries of the 1932 Yale Expedition to North India were described by Lewis (1934). This included specimens YPM 13799, YPM 13806, and YPM 13814, all

currently accepted Ramapithecus specimens. Lewis made YPM 13799 the type of R. brevirostris, a taxon he considered to be a possible member of Hominidae (1934). This possible phyletic association between R. brevirostris (which originally included only the type specimen YPM 13799) and hominids, was supported by a number of supposedly shared features. These included a parabolic dental arcade, slight premaxillary prognathism, absence of a functional diastema, and small canines. The other two specimens, mandibles YPM 13806 and YPM 13814, were assigned by Lewis as types of Dryopithecus sivalensis and Bramapithecus thorpei, respectively. In 1937, Lewis, in his unpublished Ph.D. dissertation, formally included Ramapithecus in the Hominidae.

However, Lewis' position on Ramapithecus did not go unopposed. Hrdlička (1935) published a critical note on Lewis' 1934 paper, and challenged the idea that Ramapithecus was a hominid. More specifically, Hrdlička noted that it was not possible to reconstruct the dental arcades for the maxillary fragment (YPM 13799), and that the subnasal prognathism was marked. In addition, he sexed YPM 13799 as female, and concluded that the canine socket was not particularly small relative to the cheek teeth when compared to female pongids. Further, the extreme cusp heteromorphy of P^3 also convinced Hrdlička that Ramapithecus was a pongid. However, he did conclude that it was more hominid-like than any other dryopithecine.

Lewis never responded to Hrdlička's critical note.

In 1938, Gregory, Hellman, and Lewis published a descriptive monograph on new material collected in 1935 by the Yale-Cambridge Expedition to India. Four genera of Siwalik hominoids were recognized: Sivapithecus, Bramapithecus, Sugrivapithecus, and Ramapithecus. This represented a reduction in the number of prior taxa. Association of maxillary and mandibular specimens, previously assigned to different taxa, promoted this lumping (also see Lewis 1937a). R. brevirostris was considered a pongid, but "almost at the human threshold."

The controversy over the hominid status of Ramapithecus was not reopened until the early sixties. At this time, paleoanthropologists, who had studied a majority of relevant original specimens, again seriously considered Ramapithecus as the hominid ancestor.

Two important papers on Ramapithecus appeared in 1961 (Leakey 1961; Simons 1961). In one of these, Leakey described a new genus of hominoid from the Lower Pliocene of East Africa (Fort Ternan): Kenyapithecus wickeri (now dated to the Middle Miocene because of the redating of the Miocene/Pliocene boundary). In later publications, Leakey maintained a generic distinction between Kenyapithecus and Ramapithecus, as represented in India (1963, 1967, 1968), but continued to support both as early members of Hominidae. He supported a generic distinction between them for two reasons. He thought that Kenyapithecus had a deep

mandibular corpus while Ramapithecus had a shallow corpus; and that Kenyapithecus had relatively large incisors, whereas Simons and Pilbeam (1965) had reported relatively small incisors for Ramapithecus (it is now known that the mandible fragment which led Leakey to believe Kenyapithecus had a deep corpus is a (Proconsul) specimen). In addition, a mandible fragment (FT 45), which was only recently recognized as a Kenyapithecus specimen (Andrews 1971), has a very shallow mandibular corpus. It is also now known that the incisor Leakey associated with the original Kenyapithecus maxilla (FT 46/47) is too large to fit the reconstructed dental arcades (Walker and Andrews 1973). Thus the two features Leakey used to separate Kenyapithecus from Ramapithecus no longer distinguish the two.

A few years later, Leakey erected Early Miocene Kenyapithecus africanus (1967, 1968) as a species ancestral to K. wickeri. However, most of the specimens included in this proposed ancestral taxon have been shown to be referable to (Proconsul) (Pilbeam 1969a; Zwell 1973; Greenfield 1973). Originally, three of the specimens included in K. africanus had been called Sivapithecus africanus (Le Gros Clark and Leakey 1951): BMNH 16649, MB 107, and RU 1692. These specimens may not belong within (Proconsul), and will be discussed later.

In the other important 1961 publication, Simons defended Lewis' position on the maxilla of R. brevirostris, but excluded a mandible placed in that taxon by Gregory,

Hellman, and Lewis in 1938 (GSI D.298). Further, he reiterated the criteria Lewis used to support a phyletic relationship between Ramapithecus and hominids. Later, in 1964, he assigned mandibular fragments to Ramapithecus; YPM 13814, YPM 13806, GSI D.118/119, YPM 13833, previously assigned to Bramapithecus thorpei, Bramapithecus sivalensis, D. punjabicus, B. punjabicus, respectively, and BMNH 13264, no previous attribution. He also included Leakey's K. wickeri maxilla in R. punjabicus. Taxonomically, the 1964 publication made R. brevirostris a subjective synonym of D. punjabicus; hence the taxon R. punjabicus was erected. This work also established the existence of additional features supposedly shared by Ramapithecus and hominids; low crowned molars, maxillary molars with open occlusal foveas, and short rostrum.

In the following year, Simons and Pilbeam published a major work on all dryopithecines in an attempt to eliminate unnecessary taxa. They demonstrated that the proliferation of taxa did not reflect a major adaptive radiation, but rather poor taxonomic practices. Consequently, only three species were recognized for all Indian hominoid specimens, D. indicus, D. sivalensis, and R. punjabicus, and D. indicus and D. sivalensis were placed within (Sivapithecus), a subgenus of Dryopithecus. (Proconsul) and (Dryopithecus) were erected as subgenera for African and European dryopithecines, respectively.

In subsequent publications (Simons 1968, 1972; Simons

and Pilbeam 1972; Pilbeam 1969a, 1970, 1972), the list of criteria supporting Ramapithecus as a hominid increased, and now includes more than thirty features. As of 1975, the Asian specimens included in R. punjabicus are YPM 13799, YPM 13806, YPM 13814, YPM 13833, BMNH 15423, GSI D.185, GSI D.199, GSI No.18064, GSI No.18068, AN 612, a molar from the Swabian Jura, and the type GSI D.118/119 (Conroy and Pilbeam 1973; Simons 1968).

In 1971, Andrews associated a mandibular fragment (FT 45) with the 1961 maxilla found at Fort Ternan. This mandible fragment includes sockets for all the incisors, one half of the right C_1 socket, the entire socket for the left C_1 , P_3 and P_4 crowns, and one half of the roots of the left M_1 . Later, Walker and Andrews (1973) used the associated maxillary and mandibular fragments (FT 45/46/47) to reconstruct the dental arcades and face. Contrary to prior claims (Simons 1961; Simons and Pilbeam 1965), Walker and Andrews reported the tooth rows were straight and elongated, anteriorly convergent and posteriorly divergent, not parabolic.

This resulted in a reassessment of the relations between African and Asian materials. Recent publications (Pilbeam 1972; Andrews 1971; Walker and Andrews 1973; Conroy and Pilbeam 1973) have suggested that the probably earlier, geographically distant African specimens should be included in another species, R. wickeri. This assessment was made on the premise that the Fort Ternan material

showed more "primitive" features. The specimens included in R. wickeri are FT 45/46/47, FT 7, FT 3318, and FT 48. Additional African specimens, BMNH 16649, MB 107, and RU 1692, may also be referable to this ancestral taxon.

Currently, there is disagreement about which specimens should be included in R. punjabicus. In particular, there has been debate over the Domeli (Pilbeam 1969; Leakey 1969; Greenfield 1974) and Calcutta mandibles (Simons and Pilbeam 1972; Greenfield 1974).

Finally, several new possibly related discoveries from Southcentral Europe and Southwest Asia have been described in the past few years. One is a poorly preserved mandible (an old adult) from Greece (von Koenigswald 1972) referred to a new genus and species, Graecopithecus freyburgi. Additionally, three mandibles from Turkey have been described (De Bonis, et. al. 1974, 1975), and are fairly complete. All of the above are similar to Indian dryopithecines and Ramapithecus. De Bonis has referred his material to Dryopithecus macedoniensis. A much smaller, but also complete mandible, from Turkey, has been referred by Tekkaya (1974) to (Sivapithecus). And most recently, Kretzoi (1975) has described a number of Hungarian mandibles and maxillae, preserving canines and incisors. He considers them similar to Kenyapithecus and Ramapithecus, but even more hominid-like. Thus a new taxon was erected, Rudapithecus hungaricus. This, and another Hungarian taxon, Bodvapithecus, will be considered in the conclusions.

CHAPTER III

MATERIALS

This study is largely based upon direct observation and measurement by the author of original fossil materials at Yale Peabody Museum, the Geological Survey of India in Calcutta, and the Kenya National Museums in Nairobi. This includes all specimens described prior to 1975 and attributed to Ramapithecus. The Afar australopithecines were examined at the Cleveland Museum of Natural History. In addition, (Sivapithecus) materials at Yale Peabody Museum (including the new Pakistan specimens), and (Proconsul), and other Early Miocene hominoids at the Kenya National Museums were also examined.

Dental measurements for Ramapithecus and (Sivapithecus) specimens are listed in the appendix. Specimens in the appendix are listed within taxa recognized in the species and genus level revisions below. However, currently accepted nomina are used in the feature by feature analysis and adaptive pattern comparisons which precede the taxonomic revisions. Thus, (Sivapithecus), in the analysis, is considered a subgenus of Dryopithecus.

The definitions of mesiodistal and buccolingual, given by Mahler (1973), were followed. The mesiodistal length was defined as the maximum mesiodistal length along the midline of the tooth. The buccolingual measurement was taken as the maximum dimension perpendicular to the

mesiodistal length. The irregular shapes of particular teeth made measuring consistency more difficult. The P_3 , in all cases, was measured by taking the maximum length along the long axis of the tooth as the mesiodistal length, then taking the maximum perpendicular dimension as the buccolingual breadth. There were some unavoidable inconsistencies in the measurements of canines compiled from different sources. However, the errors introduced were kept to a minimum because the single measurements were never dealt with in this thesis. Rather, cross sectional areas were used and the different source took canine measurements that he thought would best represent, when multiplied, the cross sectional area of the tooth. I consistently measured the long axis of the canines, and took the maximum buccolingual breadth perpendicular to the long axis.

Numerous pictures, measurements (see appendix), and descriptions, of new Hungarian ramapithecines (Kretzoi 1975) and the entire pre-1975 australopithecine sample were provided by M.H. Wolpoff. Two Hungarian canines were measured by this author from photographs taken by Wolpoff. This was a consequence of our different measuring techniques for canines which were discussed above. I believed that the measurements taken by Wolpoff were not comparable to those I had taken on specimens that were similar to the Hungarian ramapithecines. Measurements of most British Museum (Proconsul) specimens were taken from

the literature.

Dental measurements of extant pongids were derived from two sources: Mahler (1973) (Pan troglodytes, Gorilla gorilla, and Pongo pygmaeus), and Dr. D.C. Johanson (unpublished data for Pan paniscus). All other gnathic or facial measurements of extant pongids, in addition to morphological observations, were taken by the author at the following museums: American Museum of Natural History, Chicago Field Museum, Cleveland Museum of Natural History, the Smithsonian, and Yale Peabody Museum.

Summary dental data for Papio were derived from the literature (Lauer 1975), however, all other morphological or metric observations were taken by the author.

It should also be noted, that a number of indices used in the present work could not be corrected for the effects of interproximal wear. Indices were not calculated for those specimens that displayed extensive interproximal wear. However, indices or ratios including interproximally worn teeth in the denominator should be considered slight overestimates. This is especially true in the section on molar shape which was metrically expressed by dividing the buccolingual breadth (not affected by interproximal wear) by the mesiodistal length. More complete discussions of this problem are presented in the analysis.

The following table of abbreviations is presented in order to provide an efficient reference sytem.

TABLE 1
ABBREVIATIONS

AMNH	American Museum of Natural History
BMNH	British Museum of Natural History
CMNH	Cleveland Museum of Natural History
GSI	Geological Survey of India, Calcutta
GSP	Geological Survey of Pakistan
KNM	Kenya National Museums
UMP	Uganda Museum of Paleontology
YPM	Yale Peabody Museum

Specimen Abbreviations

AL	Afar Locality (Ethiopia)
D. or No.	GSI specimen
ER	East Rudolph
FT	Fort Ternan
LH	Laetoli Hominid
MB	Maboko
OH	Olduvai Hominid
RU	Rusinga Island
RUD	Rudabanya (Hungary)
SO	Songhor

Statistical abbreviations: $\bar{x}$ (mean), SD (Standard Deviation), OR (Observed Range), N (sample size), CV (Coefficient of Variation).

CHAPTER IV

GEOLOGY AND PALEOECOLOGY

The purpose of this section is to present geological and paleoecological information of hominoid bearing deposits which will be relevant to reconstructing possible phylogenetic relationships and ecological settings for Ramapithecus and related fossil forms. It is not intended to be an in-depth analysis of work done in this area.

Early Miocene - East Africa

Early Miocene (defined here as 22.5-16 mya following Andrews and Van Couvering 1975) hominoids are presently known only from East Africa (Andrews and Van Couvering 1975). Materials recovered since the early 1930s, from deposits in Kenya and Uganda, document an adaptive radiation of (Proconsul) species that in all likelihood represents the stock which ultimately gave rise to later pongids and hominids. Contemporary faunas in Eurasia have failed to yield a single hominoid prior to faunal interchange with Africa. Additionally, more than one (Proconsul) (and (Rangwapithecus)) species appear at many of the African sites, and are clearly contemporaneous, if not sympatric (sympatry is not necessarily indicated by the presence of two or more fossil forms in one faunal assemblage). There are, however, certain fossil species that are never found at the same sites. In particular, D. nyanzae and D. major have never been found together. This may reflect different habitat preferences, sampling error, or in-

correct taxonomy (the specimens assigned to these taxa may belong to one taxon). However, at sites like Rusinga Is. D. africanus, D. nyanzae, D. gordani, D. vancouveringi and Limnopithecus species have been reported, and at Songhor, D. major, D. africanus, D. gordani, and D. vancouveringi. Thus, the contemporaneity of multiple hominoid taxa can be documented in the Early Miocene of East Africa (Van Couvering and Van Couvering 1976).

Two of the (Proconsul) species (D. nyanzae and D. africanus) have also been reported from Middle Miocene deposits (following Andrews and Van Couvering, 16-10.5 mya at Fort Ternan (Andrews and Walker 1976), in addition to D. legetet. However, these specimens are very incomplete, and little can be deduced about their adaptive and morphological patterns. It is possible that this later material, associated with what has been called a Fort Ternan Type fauna (Andrews and Van Couvering 1975), could be different from earlier (Proconsul) species. However, at present, this later material is only significant in that it extends the known temporal range for the subgenus and is contemporary with Ramapithecus.

During most of the Early Miocene, Africa was an isolated land mass separated from Europe and Asia by a large body of water, The Tethys. However, sometime after 18 mya, continental connections between Africa and Europe via Gibraltar (Bergren and Phillips 1971; Bergren 1969), and between Africa and Asia via the Arabian Peninsula

(Dewey and Bird 1970) were established. Probably the most significant factors directly influencing the appearance of African faunas in Eurasia, and vice versa, were the shrinking of The Tethys, and the development of a continuous forest corridor (Van Couvering and Van Couvering 1976). Subsequent to Tethys' recession, and the development of forest corridors, faunal exchange occurred, and hominoids entered new available niches all throughout Eurasia. A consequence of faunal interchange was the derivation of the characteristic Fort Ternan type fauna in East Africa and Middle Miocene faunas of Eurasia (Savage 1967).

With respect to the paleoecology of the Early Miocene East African hominoids, Andrews and Van Couvering (1975) tentatively suggested (primarily on the basis of in situ excavations at Rusinga Island) that the fauna associated with D. major and D. gordani indicates they were forest dwelling. On the other hand, they proposed that it was possible, based also upon Rusinga excavations, that D. nyanzae and D. africanus lived outside the forest because of an absence of associated forest forms, and presence of faunal elements "of uncertain status or possible non-forest affinities." Certainly, additional taphonomic studies of the East African faunas are required before more definitive conclusions can be reached.

Middle Miocene - East Africa

The Middle Miocene of East Africa (defined here as

16-10.5 mya) was characterized in part by faunal interchange with Eurasia which changed Rusinga type faunas to Fort Ternan type faunas (Andrews and Van Couvering 1975; Van Couvering and Van Couvering 1976; Andrews and Walker 1976). This change in faunas probably does not reflect local changes in environment, but rather a simple introduction of new faunal elements (Van Couvering and Van Couvering 1976). Hominoid material recovered at the best Middle Miocene site, Fort Ternan, has been assigned to R. wickeri, D. africanus, D. nyanzae, and D. legetet.

The sediments at Fort Ternan from which these hominoids were derived have been dated radiometrically between 12.5 and 14.0 mya (Bishop, Fitch, and Miller 1969). The R. wickeri material is perhaps closer to the 14 mya date (see Andrews and Walker 1976 for pro and con arguments). Synchrony of (Proconsul) and Ramapithecus established at this site is significant because it demonstrates that there are two major distinct lineages of hominoids represented in the Middle Miocene of East Africa.

Major questions about the paleoecology of R. wickeri still remain open. On both geological and faunal evidence, Andrews and Walker suggest the possible presence of three different ecological zones around Fort Ternan; evergreen forest on the slopes of Tinderet, stream or lake shore, and possibly an open woodland to scrub habitat on the phonolite plateau. Unfortunately, neither (Proconsul), nor Ramapithecus, can be certainly associated with any of the

three zones. However, on the basis of the quality of preservation and the overwhelming numbers of open country forms in the total fauna (bovids for example), Walker and Andrews favor consideration of R. wickeri as an open country form.

Middle Miocene - Eurasia

Absence of hominoids in Early Miocene deposits in Eurasia indicate that the early history of this group was confined to Africa (Van Couvering and Van Couvering 1976). In this light, faunal interchange was an important zoogeographic event which led to expansion and radiation in new available niches in Western Europe, and throughout the forested regions of Asia.

In addition to invasion by African hominoids and fauna, the Vindobonian of Europe was marked by increasing replacement of tropical/subtropical flora and fauna with deciduous vegetation preferring cooler and dryer conditions (Klotz 1955). This shift proceeded north to south, with tropics retreating toward the equator. Similar drying trends are indicated in Nagri deposits in India (see below).

The early Valesian (12-10.5 mya, Campbell and Bernor 1976) of Southern Europe continued to be characterized by predominantly warm moist forests, while contemporary deposits in India show an increasing number of open country forms that ultimately dominate the total faunal assemblage in the Dhok Pathan.

Middle Miocene - Southern Eurasia

Middle Miocene hominoids in Southern Eurasia relevant to the present work have been found at a number of sites.

Recently, Kretzoi (1975) reported numerous hominoid finds from Hungary (Rudabanya). Among these were several small specimens which Kretzoi has suggested are ramapithecines. Measurements of these specimens, taken by M. H. Wolpoff, are listed in the Appendix. Although there are no radiometric dates available for Rudabanya, faunal evidence appears to suggest a date of about 12 mya. More specifically, an early form of Hipparion is present like the one found in the Siwaliks at the Chinji/Nagri boundary (see below). Hipparion first appears in North America at 12 mya (Evernden, et. al. 1964).

With respect to the paleoecology, Kretzoi states that the "flora indicates Mediterranean - Subtropical climatic conditions with traces of zonation from aquatic through wet forest to grassland...". Certainly, more detailed analyses of the flora and fauna will be published. However, tentatively, this author considers the Hungarian ramapithecines contemporary with hominoids derived from Nagri deposits in Pakistan and India and living in broadly similar environments (the Hungarian site is probably slightly cooler).

India/Pakistan - Middle Miocene

Most of the pre-1975 Eurasian material has been derived from the Siwalik Hills of India, and more recently from the Potwar Plateau of Pakistan. Hominoids have been assigned by most workers to R. punjabicus, D. sivalensis, D. indicus, D. giganteus and G. bilaspurensis. The first three appear commonly at localities in the Chinji and Nagri, while the latter two seem to be restricted to the Nagri and Dhok Pathan. Although radiometric dates are not presently available for the Siwalik series (newly discovered volcanic materials are now being used to derive dates), faunal remains can be used to correlate these faunas with those at radiometrically dated sites. Recent studies of Chinji suids, bovids and rodents (associated with hominoid material), show that these faunal elements are similar to 13 million year old counterparts in Europe and North Africa (Pilbeam, personal communication). In addition, after careful recent collecting, it has been generally concluded that Hipparion appears at the base of the Nagri, and therefore the Chinji/Nagri boundary is around 12 mya (Hussain 1969; Simons, Pilbeam, and Baker 1971; Pilbeam, personal communication). On the basis of faunal comparisons, the Nagri/Dhok Pathan boundary should be placed around 9 mya (Pilbeam, personal communication).

Pilbeam's, as yet unpublished, recent field work in Pakistan has demonstrated the synchronous existence in the Nagri of R. punjabicus, D. sivalensis, and D. indicus.

It also now seems likely that G. bilaspurensis (or a D. giganteus-sized creature) is contemporary with these smaller species. Two G. bilaspurensis (or D. giganteus) sized molars have been recovered by Pilbeam in Pakistan in Nagri deposits (field no. 7144 at Locality 311 is one). In addition, all small species (R. punjabicus, D. sivalensis and D. indicus) have been found at Haritalyangar, and are associated with very late Nagri fauna which are indistinguishable from Dhok Pathan fauna, associated with the well known G. bilaspurensis mandible (Simons and Chopra 1969). Thus, it appears that there was a Middle Miocene adaptive radiation of hominoids in Eurasia following faunal interchange; R. punjabicus, D. sivalensis and D. indicus are reported from the Chinji.

During the Chinji and major portion of the Nagri, tropical evergreen forest conditions prevailed. This has been supported by lithological (Krynine 1937), faunal (Tattersall 1969a, b), and floral (Prasad 1971) analyses. Krynine's sedimentological analysis indicated flat country with high seasonal rainfall, occasional flooding, and humid tropical forest. However, by late Nagri times he recognized a transition to open prairie conditions (and later arid conditions). Faunal analysis by Tattersall has shown a plethora of forest forms also present throughout the Chinji and most of the Nagri. He wrote, "that of many thousands of fossils which have come from numerous sites at many levels within the Nagri formation, very few belong to

animals related in any way to characteristically savannah adapted forms." Lastly, Prasad's analysis of the flora show the presence of dicotyledenous woods. These species exist in warm, moist, evergreen forests with heavy rainfall. Thus, it appears likely that for the Chinji, and most of the Nagri, hominoids were living in warm, moist, tropical (or subtropical) rainforests. However, by late Nagri times, this situation changed, and forests were replaced by open prairies (with open country type faunas). Therefore, it is possible that in late Nagri times the hominoids were changing their niches, or were reduced in number as their favored niches were becoming more restricted. The latter seems more likely to this author because of the far fewer hominoid finds in the Dhok Pathan which contains a large savannah fauna.

Late Miocene

The last part of the Miocene (10-5.5mya) included "dramatic geological, climatological, and paleontological changes throughout Eurasia" (Campbell and Bernor 1976). The Mediterranean basin became arid and dessicated (Hsu 1972; Delson 1973), and in the middle latitudes of Eurasia there was a general deforestation. Late Miocene faunas of Eurasia show a disappearance of forest forms and replacement by savannah elements like hypsodont bovids, giraffes, and hyaenids (Campbell and Bernor 1976). One site in Africa, reported by Bishop and Chapman (1970), also contains open country fauna.

The faunal relations between Africa and Eurasia in the Late Miocene remain unclear at present. Cooke (1972) takes the position that the two forested migration routes of the Middle Miocene were broken (after 12 mya), and faunal exchange was eliminated until about $2\frac{1}{2}$ mya.

Similar work done on Late Miocene faunas from Eurasia and Africa (Coryndon and Savage 1973) shows that many mammalian families are represented in both areas. However, many of the genera, included in these shared families, are unique to Africa. The shared families may represent groups that were established in both regions during faunal interchange in the Middle Miocene. If isolation ensued, as Cooke states, one would expect divergence and differentiation at lower taxonomic levels; hence, fewer shared genera. Certainly, a species level investigation is nece-

ssary to clear up questions of faunal isolation during the Late Miocene. Campbell and Bernor (1976) also concluded that it would be "important to investigate faunal migration between the land masses to determine the major periods during which gene flow ceased."

Thus, it is very possible that after hominoids like Ramapithecus established themselves in Africa and Eurasia in the Middle Miocene, genetic isolation ensued and this ultimately led to speciation.

With respect to australopithecine origins, these early undoubted hominids are known only from Africa during the later part of the interval from 12 to $2\frac{1}{2}$ mya. In fact, the earliest undoubted hominid materials outside Africa are not demonstrably different from early H. erectus. Thus, on the basis of circumstantial evidence alone, it would appear that australopithecines evolved in Africa, and later migrated to Eurasia. Contemporary ($2\frac{1}{2}$ to 5 mya) faunas from Eurasia have failed to yield a single recognizable australopithecine fossil.

Thus, the probability of physical or ecological barriers to population movement and migration during the Late Miocene, the possibility of speciation for a Ramapithecus-like hominoid during this interval, and the known distribution of australopithecines, lend support to the idea that the earliest undoubted hominids originated in Africa (assuming that the unique australopithecine adaptations could not have arisen independently in a

Eurasian hominoid). This point will be discussed in greater detail below.

CHAPTER V

DESCRIPTIONS OF R1/R2 SPECIMENS

One result of discussions over the past 10 years is that two different sets of specimens allocated to Ramapithecus have emerged. This is mainly the result of current disagreements about particular specimens to be included in this taxon. I will use the set R1 to refer to all those specimens which have been included in previous publications on Ramapithecus (Conroy and Pilbeam 1973). R2 is the smaller set of R1 specimens which I suggest represents the Eurasian taxon. African R1 specimens are treated separately in the section on taxonomy. The R2 set is partially included within the R1 set, but includes the following additional specimens: YPM 13830, GSI D.186, GSI D.187, GSI D.298, YPM 13809, and Hungarian specimens RUD 1, RUD 2, RUD 12, RUD 15, and RUD 17.

R1 includes the following (*italicized specimens are also in R2*): GSI D.118/119, GSI D.185, GSI D.199, YPM 13799, YPM 13806, YPM 13814, YPM 13833, AN 612, KNM FT 45/46/47, BMNH 13264, GSI No.18064, GSI No.18068, Swabian Jura molar, and BMNH 15423.

Justification for R2 will be given after all criteria have been tested for taxonomic relevance. Measurements for each specimen are listed in Appendix I. Specimens are listed and described below, according to the chronology of their publication. R1 and R1/R2 specimens are listed first.

- 1) GSI D.118/119 is composed of right and left

mandibular fragments with M3 and M2 preserved, in situ, respectively (Pilgrim 1910). The fragments were reported found at Chinji Village, India in Chinji deposits. Pilgrim assigned these fragments to D. punjabicus, however, later they were made the type of R. punjabicus (Simons and Pilbeam 1965). The crowns are well preserved, and M2 is moderately worn on its occlusal surface while M3 is slightly worn. On both teeth, buccal cusps are worn more than lingual cusps (more so on M2 than on M3), and there is very little interproximal attrition. The outer bone table is well preserved but the ascending rami are broken at their bases, and the gonial angles are not present. GSI D.118/119 is not included in R. and will be formally transferred to Sivapithecus sivalensis.

2) GSI D.185, a right maxilla first reported by Pilgrim (1910) from Nagri deposits at Haritalyangar, preserves four good crowns, P4-M2, and half of the C1 socket. Pilgrim originally assigned this specimens to D. punjabicus, but subsequently Simons and Pilbeam formally transferred it to R. punjabicus. A small interproximal wear facet on the distal plane of M2 indicates that M3 had erupted. This is the youngest and least worn R1/R2 specimen. The greatest occlusal wear occurs on M1, and lingual cusps on all the teeth are worn more heavily than buccal cusps. On the maxilla itself, the zygomatic process originates between M1 and M2, and inserts high above the teeth, flaring laterally for a great distance. The tooth

row is straight, not curved. It is included in R2.

3) GSI D.199 was described by Pilgrim (1927), and placed within Paleopithecus sylvaticus. It was found in Nagri deposits at Haritalyangar, India. In 1965, it was transferred by Simons and Pilbeam to D. sivalensis, but was later removed (1972) and assigned to R. punjabicus.

Another more recent analysis of the specimen (Greenfield 1974) supported Simons and Pilbeam's original assignment, and favored reassignment to D. sivalensis. Four heavily worn crowns, P4-M3, in a badly damaged left mandibular corpus are present. M1 is broken lingually, and there is extensive enamel perforation on this tooth, and moderate perforations on P4 and M2. M3 lacks major perforations, but is worn almost flat. All buccal cusps show greater wear than lingual cusps, and interproximal wear is moderate to heavy between P4 and M1, and between M1 and M2, but there are only very small contacts between M2 and M3, and P3 and P4. Additionally, the tooth row angles outward, relative to the corpus as one moves anteriorly from M3 to P4, rather than curving towards the midline. The inferior portion of the ramus has been eroded away, and very little external bone surface remains, making it impossible to determine the total depth and thickness of the corpus. Relative to other R1 specimens, GSI D.199 has the largest dentition, and based upon metric criteria it should probably not be included in R2 but rather transferred to S. sivalensis, perhaps as a male of that taxon.

4) YPM 13799, a right maxilla with P3-M2, was discovered at Haritalyangar (Nagri) and assigned to R. brevirostris (Lewis 1934). Later, it was transferred by Simons and Pilbeam (1965) to R. punjabicus. In addition to the four crowns, the socket for C1 (slightly damaged) is also present, as well as the root of I2, and half of the I1 socket. On the maxilla, the inferior portion of the nasal aperture is preserved, and there is a canine fossa; however, the bone in this region has been broken inwards giving it a deeper appearance. There is a diastema (2.1 mm) between the small canine socket and the root of I2 and the tooth row is straight, not curved. There is moderate occlusal wear on all teeth, and broad interproximal wear facets between M1 and M2, and M1 and P4. Additionally, lingual cusps on all teeth are worn more than buccal cusps, as on all maxillae in R1. YPM 13799 is also included in R2.

5) YPM 13806, a right mandibular fragment with M3 and M2, was recovered from Haritalyangar and assigned to D. sivalensis (Lewis 1934), but was transferred later by Simons and Pilbeam (1965) to R. punjabicus. Both teeth have slight to moderate occlusal wear and buccal cusps are worn more than lingual cusps. There is only slight interproximal wear. The external bone table is well preserved and one can readily observe that the corpus is very thick relative to its depth, however, both ascending ramus and gonial angle are gone. YPM 13806 is included in R2.

6) YPM 13814, a left mandibular fragment with M2 and M3 and roots of M1 was found at Hasnot, Chinji, and described by Lewis (1934) who made it the type of Bramapithecus thorpei. However, Simons and Pilbeam (1965) more recently placed it in R. punjabicus. There is moderate to heavy occlusal wear on M2, but only slight wear on M3. Again, buccal cusps show greater wear. There is considerable interproximal attrition between M2 and M3 and a deep facet on the mesial side of M2 resulting from contact with M1. Extensive interproximal attrition makes M2 and M3 appear broad. If one estimates the position of M1 from the preserved roots, then it is clear that the tooth row is straight and angles outwards as one moves anteriorly. However, it is important to note that as the tooth row angles out, the mandibular corpus is curving towards the midline. This is like D.199, but YPM 13814 has much smaller teeth. Further, the corpus of YPM 13814 is thick underneath the M3. This specimen is included in R2.

7) YPM 13833, a right mandibular fragment with M3 was found at Kanatti, Chinji, and described by Gregory, Hellman, and Lewis (1938). They originally assigned it to Bramapithecus punjabicus, a taxon lumped by Simons and Pilbeam (1965) into R. punjabicus. Only a tiny fragment of the lingual side of the corpus remains. The tooth shows slight occlusal wear on its buccal cusps, almost no wear on the lingual side and there is a small interproximal facet. The tooth narrows distally and is relatively slender.

Compared to other R1 M3s it is very large, and for this reason it is excluded from R2 and included in S. sivalensis.

8) AN 612, five lower cheek teeth, two P4s, two M2s, and one M3, all from the same individual, were found at Keiyuan, Yunnan Province, China, and described by Woo (1958) who assigned this material to a new species, D. keiyuanensis. It was later suggested (Simons and Pilbeam 1965) that this specimen should be included in R. punjabicus. Both M2 and M3 are slightly worn with most of the wear occurring on the buccal sides of these teeth. Small interproximal wear facets are also present. M2 and M3 are very narrow, and metrically these teeth are much larger than most of the specimens assigned to R2, and therefore they are excluded from R2 and considered S. sivalensis specimens.

9) KNM FT 46/47, right and left maxillary fragments containing M1 and M2 and C1, P4-M2, respectively, were described by Leakey (1961) and assigned to Kenyapithecus wickeri. A mandibular fragment, FT 45, from the same individual was described by Andrews (1971). It contains P3 and P4 crowns, and root sockets for the left C1, all four incisors, part of the right C1 socket, and half of the root of the left M1. This material was recovered from Fort Ternan, Kenya. Tuffaceous deposits immediately below the specimen were dated at approximately 14 mya (Bishop, Fitch, and Miller 1969) and a date of 12.5 mya was obtained from tuffs 70 feet above the stratum which yielded the

specimen. Thus the material is from 12.5-14.0 million years old (Middle Miocene). The maxillary crowns are well preserved, P4, M1, and M2 have slight to moderate occlusal wear with lingual cusps being more heavily worn than buccal cusps. The canine has honing wear on both mesial and distal edges, and morphological features of this tooth suggest it was a female as Leakey originally observed (1961). The tooth row is slightly (?) curved. On the maxilla, a deep canine fossa is present, and the zygomatic process originates between M1 and M2 in a lower position than the zygomatic of D.185. The mandibular P3 is a sectorial tooth (discussed in detail later), and a pongid-like C1/P3 hone complex is present. Moreover, reconstruction of the dental arcades (Walker and Andrews 1973) indicates nearly straight elongated rows and a narrow palate.

With respect to the taxonomy of the specimen, Simons suggested (1963) that K. wickeri was a junior synonym of R. punjabicus, but Leakey (1963) continued to support the generic distinction between Kenyapithecus and Ramapithecus. More recently, workers have placed the Fort Ternan material within R. wickeri (Andrews 1971; Conroy and Pilbeam 1973; Tattersall 1975) an earlier species of Ramapithecus. In addition to this specimen, there are several recently described (Andrews and Walker 1976) specimens from Kenya which probably represent the same taxon as the maxilla. These newly described specimens are FT 7, a right mandible

fragment with P_4 and M_1 , FT 48, an isolated M_2 , and two isolated canines, FT 8 (still in its crypt), and FT 3318. Three additional specimens, previously assigned to Sivapithecus africanus (Le Gros Clark and Leakey 1951), may also belong to this African taxon (BMNH 16649, MB 106, and RU 1692). All of the above will be discussed in detail later, and none are included in R2.

10) BMNH 13264, a right mandibular fragment from Attock (upper Chinji), India was described and placed within R. punjabicus by Simons (1964). It preserves an almost unworn M_3 crown, however, a small interproximal wear facet is present. The corpus is somewhat thick but not deep. The tooth is large relative to other R1 specimens, and for this reason it is not included in R2.

11) GSI No.18064, a right maxillary fragment with M_1 - M_3 , was recovered from Haritalyangar (Nagri) and reported by Prasad (1964). He suggested placement in Sivapithecus sivalensis, however, by 1969, he changed his opinion and placed it in R. brevirostris (along with YPM 13799, the type). Since Simons sunk R. brevirostris, he included No.18064 in R. punjabicus (1972). The molars display a moderate molar wear gradient, and lingual cusps are worn more heavily than buccal cusps. The interproximal wear facet between M_1 and M_2 is moderate, and between M_2 and M_3 , very slight. Unfortunately, both M_1 and M_2 were damaged and it is difficult to obtain an accurate set of measurements. However, the positions of the three

teeth indicate a straight tooth row. Because the molars are very large relative to other R1 specimens, No.18064 is not included in R2.

12) GSI No.18068, an isolated maxillary left M3 was found at Haritalyangar (Nagri) and described by Prasad (1964) who originally included it in D. punjabicus, but later (1969) reassigned it to R. punjabicus. This specimen has only very slight occlusal wear and a tiny interproximal wear facet. It is included in R2.

13) One isolated molar from the Swabian Jura was included in R. punjabicus by Simons and Pilbeam (1965). Given the extensive morphological overlap among molars of different hominoid taxa, it is equally likely that this very worn tooth belongs to one of the European dryopithecine species. Therefore, it is not included in R2.

14) BMNH 15423, a left mandibular corpus with broken crowns for P3-M3 was found at Domeli, Pakistan. It was described in detail by Pilbeam (1969a), and placed in R. punjabicus. Most of the teeth are broken and/or heavily worn. Specifically, the P3 crown is broken off at its base; two roots are present, angled to the tooth row, and their general outline suggests an elongated tooth (sectorial premolar). Both P4 and M2 are broken lingually, M1 is broken on both buccal and lingual sides, and the entire surface of M3 is gone; all that remains is the outline of a long narrow tooth. Additionally, all crowns display

extensive enamel perforations, and a slight molar wear gradient exists between M1 and M2. The mandibular corpus reaches near the midline and a distinct shelf is present (Greenfield 1974). Unlike most other R1 specimens, the mandibular corpus is slender. This and the relatively small teeth suggest that this specimen represents a female, a conclusion which Conroy and Pilbeam (1973) also suggested. There has been much debate over the placement of this specimen (Pilbeam 1969a; Leakey 1969; Greenfield 1974), however, it is included here in R2.

The following are descriptions of R2 specimens not in R1. In addition to GSI D.185, YPM 13799, YPM 13806, YPM 13814, No.18068, and BMNH 15423, the following specimens are included in R2: GSI D.186, GSI D.187, YPM 13809, YPM 13830, GSI D.298, RUD 1, RUD 2, RUD 12, RUD 15, and RUD 17.

1) GSI D.186, an isolated left maxillary M3 crown reported found at Chinji (Chinji), was placed in D. punjabicus by Pilgrim (1915) and later transferred to D. sivalensis (Simons and Pilbeam 1965). The crown is almost unworn and has no interproximal wear facet. It has a relatively closed occlusal fovea and angled sides (discussed later).

2) GSI D.187, an isolated left maxillary M2 was also recovered at Chinji (Chinji) and assigned to D. punjabicus (Pilgrim 1915). It was later transferred to D. sivalensis by Simons and Pilbeam (1965). It has only slight occlusal wear and a very small interproximal facet. Its occlusal

fovea is somewhat constricted.

3) YPM 13809, a small isolated left maxillary C1, was recovered at Kundal Nala, India (Chinji) and referred to Dryopithecus sp. (Lewis 1934). Simons and Pilbeam later transferred it to D. sivalensis (1965). Of the two canine morphotypes found among Indian dryopithecines, this specimen clearly follows the male pattern. It is a long tooth and has honing wear on its mesial border. The distal border is unworn. The pattern of wear indicates that this tooth was honing against the mandibular C1 but not the sectorial P3. This condition is not unusual for Indian hominoids, and in fact occurs on the majority of canines. Further, the crown is compressed somewhat buccolingually. Since it has male morphology (contrasting strongly with female canines like those of GSI D.299/300 for example), and is as small as the only known female D. sivalensis C1 (and much smaller than the known male C1 of that taxon), it is included in R2 as a male (this inclusion will be discussed, in detail, later).

4) YPM 13830, a mandibular left P4, was recovered at Haritalyangar (Nagri) and described by Gregory, Hellman, and Lewis (1938) and placed in D. sivalensis by Simons and Pilbeam (1965). It is a heavily worn tooth with large interproximal wear facets. Like all R1/R2 mandibular P4s, it is worn more heavily on the buccal side. Placement in R2 is based upon its small size.

5) GSI D.298 was recovered at Chinji (Chinji), and

described by Gregory, Hellman, and Lewis (1938) and assigned to R. brevirostris. More recently, after much deliberation, Simons and Pilbeam (1965) favored placement in a European dryopithecine species, D. laietanus. The mandibular corpus is well preserved and it reaches the midline; P3-M2 are preserved, and root sockets for C1 and I1 and I2 are also present. All teeth are well worn occlusally and there is extensive interproximal wear. Further, a moderate molar wear gradient is indicated, and the cheek teeth are aligned in a straight row. The small C1 socket, small posterior teeth, and gracile mandibular corpus (like BMNH 15423) suggest this specimen probably represents a female. P3 is sectorial, and the wear on this tooth indicates pongid-like hone and interlock with the maxillary C1 existed. One unusual feature is the relatively equal amounts of occlusal wear on buccal and lingual cusps.

New Discoveries

Systematic analysis of new Greek and Turkish materials is not possible or appropriate in the present work, given their brief published descriptions. However, short discussions of the more complete specimens from Hungary assigned to Rudapithecus (Kretzoi 1975) are presented and will be included in the systematic analysis. Slides, pictures, measurements, and observations of the originals were graciously provided by M.H. Wolpoff. These new Hungarian specimens are included in R2. There will be a

general discussion of the Greek, Turkish, and remaining (Bodvapihhecus) Hungarian materials in the final chapter on phylogenetic conclusions. With the possible exception of the Candir mandible (Tekkaya 1974), none of these materials are considered R2 specimens.

Hungarian Specimens Included in R2

A small sample of Hungarian ramapithecines was partially described in Nature (Kretzoi 1975). The information from this article and slides, measurements, and observations of the originals by M. H. Wolpoff have been used by this author in order to present the following short specimen descriptions (tooth measurements are listed in the Appendix).

1) RUD 1, the type of Rudapithecus hungaricus, is a weathered, left mandibular fragment preserving damaged P4-M3 crowns.

2) RUD 2 consists of damaged (crushed) right and left mandibular corpora, with ascending rami, and intact gonial angles. The right corpus fragment contains, in situ, P3-M3 and a broken C1, and left fragment M1-M3. A fragmented left C1 is also preserved. Measurements listed for C1 in the appendix are based upon both right and left damaged C1s, and are therefore estimates. An unattached right mandibular condyle is also preserved.

3) RUD 12 is a left maxillary fragment preserving bone along the palatal midline. The intermaxillary suture is well preserved. Undamaged crowns, I1, C1-M1 are in

situ, and an isolated unerupted M3 is believed to be associated. A tiny root socket for I2 is also present. The external bone surface is in excellent condition and crushing is absent. The C1 measurements listed in the Appendix were taken by this author from a photograph because Wolpoff's measurements of C¹ are not homologous to those used in the present work. This is also discussed in the section on measurements.

4) RUD 15, another maxilla, preserves both right and left sides, however, the outer bone table is imperfect. The right fragment (very little bone) contains P3-M2. Additionally, there are two isolated right incisor crowns associated. The left maxillary fragment, preserving part of the intermaxillary suture includes, in situ, I2-M2 and isolated I1. The same problem of homology between Wolpoff's measurements of C1 and mine necessitated taking a set of measurements off a photograph. These photograph measurements are listed in the Appendix.

5) RUD 17 preserves right mandibular corpus from C1-M3, and left corpus fragment with P3-M2, also in situ. The depth of the C1 root is particularly interesting because it almost extends to the mandibular base.

Turkish Specimen from Candir

Recently, Tekkaya (1974) described a V-shaped mandible with P3-M3 crowns and anterior tooth sockets. The published dental measurements (Tekkaya and Andrews 1976) correspond closely to Indian and Hungarian R2 specimens.

However, I have no further information on the specimen other than the published descriptions, and therefore will not deal with this specimen in the systematic analysis. It will be mentioned in the concluding chapter on phylogeny.

CHAPTER VI

ANALYSIS OF FEATURES

This work employs a systematic comparative method as the tool of analysis. Ramapithecus is compared with earlier (Proconsul), contemporary (Sivapithecus), and extant pongids (Pan paniscus, Pan troglodytes, Pongo pygmaeus, and Gorilla gorilla), and with australopithecines. Comparisons with these taxa are considered essential if the vertical and horizontal phylogenetic relationships and adaptive pattern of Ramapithecus are to be determined.

Two types of comparisons will be made: a comparison of taxa by individual features, and a comparison of their adaptive patterns. Final phylogenetic conclusions will be based upon the latter set of comparisons. While it is recognized that these conclusions about Ramapithecus must ultimately be based upon a comparison of adaptive patterns, it is particularly important to proceed from a feature by feature analysis, testing and quantifying both the adaptive significance, and inter and intra species distributions of each feature. This is deemed necessary because of the confusion concerning which features actually characterize Ramapithecus generated by the usual "trait list" approach. An additional historical (phylogenetic) perspective will be provided for each characteristic, completing a total framework in which Ramapithecus can be considered.

In this analysis, Ramapithecus is compared to australopithecines and not to anatomically modern Homo sapiens.

Comparisons between Ramapithecus and Homo sapiens may be misleading, since if Ramapithecus is a hominid, it did not directly evolve into Homo sapiens. Moreover, if 5-10 million year old hominids are found, they will provide a more germane comparison with Ramapithecus than the australopithecine sample available at this time.

In the comparisons which follow, (Sivapithecus), when compared to Ramapithecus, does not include any of the R1 specimens. Further, the term R1/R2 refers to both sets and can be thought of as R1 and R2.

Certain restrictions on the comparative method exist, and are recognized in this analysis. Le Gros Clark (1964) outlined a number of rules which will be applied in order to insure the comparison of equivalent measures. Two important fallacies in comparative method are worth noting here; comparing individuals or samples of different age or sex. Clearly, when such factors significantly affect the phenotypic expression of a feature, samples or individuals of like sex or age should be compared. Sex differences in canine size, and morphology, or age changes due to interproximal wear, for example, must be controlled in interspecific comparisons. It is important to note that few published works on Ramapithecus have considered the effects of sexual dimorphism on phenotypic variation, despite a large literature on the subject for closely related extant forms. Thus, many studies comparing Ramapithecus were not controlled and may be invalid because equivalents were not

compared. Thus, in this analysis, features affected by these complicating factors (in addition to those just mentioned) will be specified, and an attempt made to control for them.

In past analyses, many features have been used to distinguish Ramapithecus from dryopithecines and extant pongids and to support a phyletic relationship between Ramapithecus and hominids. They are the foci of the initial portion of this analysis. These include 1) slight premaxillary prognathism, 2) more vertically implanted incisors, 3) relatively smaller incisors, 4) roots (and inferentially crowns) of the central and lateral incisors equal in size, 5) a reduced canine, 6) a non-projecting canine, 7) no diastema, 8) semi-sectorial lower third premolar, 9) loss of projecting P^3 paracone, 10) markedly bicuspid maxillary premolars, 11) absence of a shearing wear facet on the anterior slope of the paracone of P^3 , 12) relatively broad molars, 13) broad P_4 , 14) marked interstitial wear (more correctly referred to as interproximal attrition), 15) tightly packed tooth rows, 16) thick molar enamel caps, 17) flat wear on molars, 18) bunodont molar cusps, 19) cusps on maxillary molars widely spaced with subsequently large central occlusal foveas, 20) molars with vertical buccal and lingual sides, 21) all molars approximately equal in size, 22) differential molar wear gradient, 23) deep palate, 24) parabolic dental arcade, 25) palate short and broad, 26) short thick

mandibles, 27) mandibular ramus which deepens anteriorly, 28) internal morphology of the mandibular symphysis, 29) high insertion of the zygomatic, 30) deep face, 31) anterior zygomatic, 32) vertical ascending ramus, and 33) more anterior coronoid process. This list is not exhaustive and therefore additional features which may shed light on the relationships of Ramapithecus will be analyzed below.

The feature by feature analysis that follows immediately will, in most cases, conform to a pattern. First, there will be a reiteration of prior statements about Ramapithecus (R1) with respect to that feature, and then a discussion of its possible adaptive significance. Inter- and intraspecific variation of extant pongids will be documented and this data will then be used to test the proposed functional model. Subsequently, Early Miocene (Proconsul) will be examined to determine a probable ancestral state for the feature, and a comparison with extant forms will suggest trends in pongid evolution. The (Proconsul) data will also be used to test the functional significance of the feature. Next, australopithecines will be examined, followed by a comparison with (Proconsul) to determine possible trends in the hominid lineage. Finally, comparisons with all living pongids will be used to further test the adaptive model. At this point, a functional and historical framework will be established into which R1/R2 and (Sivapithecus) can be placed. This will establish whatever differences exist between R1 and R2

and (Sivapithecus), and suggest any relationships with pongids or hominids.

(1) Slight Premaxillary Prognathism

Lewis (1934) was the first to cite slight premaxillary prognathism as a hominid-like feature of R1. In more recent publications (Simons 1961,1968; Simons and Pilbeam 1965; Conroy 1972; Tattersall 1975) Lewis' original observation has been supported.

A reasonable functional model can be proposed to explain the adaptive significance of interspecific variation in this region. According to this model, hominoids with hypertrophied incisors, especially Pan and Pongo, have, in addition, hypertrophied anterior tooth roots which require considerable length of bone for their support. Hence, one would predict greater subnasal prognathism (or premaxillary prognathism) in these taxa. On the other hand, relatively and absolutely smaller hominid incisor crowns and roots predictably do not require this expanded region of bone.

All arguments concerning reduction of the forefacial region in R1 center around YPM 13799, which preserves the lower margin of the nasal aperture and the alveolus of the lateral incisor. Lewis (1934) noted that the distance from the nasal margin to the alveoli of the incisors was short and therefore unlike extant pongids. Later, an index was devised (using YPM 13799) to quantify Lewis' contention (Simons 1961). The distance from the most inferior point on the right border of the nasal aperture to the alveolus of the lateral incisor was measured. This distance was divided

by the length of P^3-M^2 and the result multiplied by 100. P^3-M^2 length was used because these crowns are preserved on the specimen, and, therefore, under the circumstances, P^3-M^2 length is the only quantifiable estimate of the total length of the face.

In order to establish a picture of interspecific variation in this index, identical sets of measurements were taken on extant and fossil pongids and hominids (Table 2).

Among extant pongids, the index is highly variable both within and between taxa. Moreover, Pan and Pongo show considerably higher indices than Gorilla. This supports the functional model since they both have hypertrophied incisors while Gorilla does not.

In contrast to extant pongids, there is greater index homogeneity between fossil pongid taxa. This is expected since none of the Early Miocene species (or Oligocene Aegyptopithecus) possessed hypertrophied incisors, and thus all predictably show little subnasal prognathism. Among extant taxa, Gorilla is more similar to ancestral pongids than either Pan or Pongo. The functional model is supported by the fact that pongid taxa with small incisors show little subnasal prognathism and the converse is also true.

The australopithecine data, however, appear to be contradictory. They have small incisors, yet their forefacial regions are larger than those of all pongids except Pan. To explain this contradiction, one might suggest that perhaps australopithecine incisor roots are long relative to

TABLE 2
FOREFACIAL SHORTENING INDEX*

	N	$\bar{x}$	OR	SD
R1/R2 (YPM 13799)	1	44.0	--	--
(<u>Sivapithecus</u>)	2	51.0	47-55	--
<u>Aegyptopithecus</u>	1	32.0	--	--
<u>D. africanus</u>	2	39.0	33-45	--
<u>D. gordani</u>	1	43.0	--	--
<u>D. major</u>	1	43.0	--	--
<u>Pan</u>	20	84.0	69-111	12.6
<u>Pongo</u>	18	51.0	34-65	7.3
<u>Gorilla</u>	20	41.0	27-54	7.0
australopithecines	8	58.0	49-63	6.5

*see text for a definition of the index.

the size of their crowns. Alternately, a more complicated explanation might be that the stress related necessities of the long posterior tooth roots has selectively increased the volume of bone necessary for their support (high maxillary sinuses demonstrate this). Consequently, to maintain the anterior teeth in the same plane, a lengthening of bone in the forefacial region was necessary. It is unlikely that the high australopithecine indices are the result of short P^3-M^2 , because their posterior teeth are expanded relative to body size, and this expansion probably occurred in both mesiodistal and buccolingual directions. Given this expansion, it is more likely that their calculated indices are underestimates rather than overestimates of subnasal prognathism. A measure of relative root length may be useful in testing these suggested alternatives.

But, in general, among pongids, subnasal prognathism appears to be related to relative incisor size. Historically, incisor hypertrophy occurred in two pongid lineages with a predictably great enlargement of the premaxillary region. Thus, while more recent taxa show generally higher indices (including early hominids) than earlier forms, the extent and timing of these increases probably varied among lineages.

This interspecific and historical perspective of premaxillary prognathism provides a framework in which $R1/R2$ and (Sivapithecus) may be considered. Since the data (Table 2) show that both possess slightly larger premaxillary regions than those of earlier pongid taxa it may be concluded

that extant pongids, australopithecines, R1/R2, and (Sivapithecus) exhibit similar trends; they are all increasing their subnasal prognathism.

Given that R1/R2 and (Sivapithecus) fall within the ranges of Pongo and Gorilla, the differences between them are probably not significant. That the premaxillary region in R1/R2 is abbreviated, cannot be denied. However, the index aligns it with (Sivapithecus), and differentiates it from australopithecines, and some, but not all, living pongids. Further, the index supports the observation that R1/R2 incisors were relatively small. However, this too indicates a phylogenetic association with fossil pongids and not necessarily, or uniquely, with hominids. Since small incisors appear to be the pongid ancestral condition, R1/R2 has maintained this condition like (Sivapithecus). Therefore, on the basis of this criterion, R1/R2 cannot be separated from contemporary pongids, and is evolving in a direction taken by all other hominoids considered.

In conclusion, the functional model relating incisor size to subnasal prognathism can be supported in pongids. Incisor hypertrophy, which characterizes only Pan and Pongo among all fossil and extant pongids, is associated with higher indices. Moreover, the ancestral pongids with small incisors, had small premaxillary regions. However, australopithecines, an exception to the general functional model, have small incisors and expanded subnasal regions. One can further conclude that R1/R2 and (Sivapithecus) do not differ

significantly from each other, they follow the same trends, and R1/R2 falls below the australopithecine range. The index clearly aligns R1/R2 with contemporary dryopithecines.

(2,3,4) Vertically Implanted Incisors, Relatively
Small Incisors, Metric Equality of Lateral
and Central Incisors

Lewis (1934) discussed three features of R1 incisors he considered hominid-like. He concluded that unlike extant pongids, the incisors of R1 were more vertically implanted, relatively smaller, and homomorphic, i.e., the crowns of the lateral and central incisors were metrically equal. Many workers have supported Lewis' observations (Simons 1961; Simons and Pilbeam 1965; Conroy 1972; Tattersall 1975). However, of the three features, only relative incisor size has been investigated quantitatively (Pilbeam 1969; Yulish 1970; Conroy 1972).

Vertically Implanted Incisors

One of the major differences in the anterior dentitions of pongids and hominids is in the angle of incisor implantation. Extant pongid maxillary incisors project outwards (are procumbent), while hominid incisors are directed inferiorly. These differences are presumably related to dietary factors. Pongids use their anterior teeth to peel (strip) fruits, and husk vegetation. The australopithecines probably used their anterior teeth in a variety of ways (slicing and gripping); however, the forces exerted on these teeth were perhaps more vertical, which selected for increased incisor verticality.

Again, to establish a picture of interspecific variation and trends, maxillary central incisor angles were obtained

for extant pongids, African fossil pongids, australopithecines (casts were used), (Sivapithecus), and R1/R2. Figure 1 shows schematically how the angles were obtained relative to the occlusal plane of the posterior teeth. The inferior two thirds of the central incisor was used (including the crown and most of the root), while the posterior segment of the root (which in many individuals curves at a more acute angle with the occlusal plane) was ignored.

Although no African or Indian R1/R2 or (Sivapithecus) specimens preserves I¹ in situ, some specimens preserve I¹ root sockets. For these specimens (YPM 13799, GSI D.1, and GSI D.196), the angles listed in the table below are estimates (based on sockets). The angles for YPM 13799 and GSI D.1 were easily obtained because their I¹ root sockets are exposed cross-sectionally. To obtain an angle for GSI D.196, a cast was made and its I¹ root socket was cross-sectioned and measured.

Marked age changes in this angle were found among extant pongids. Their incisors, surprisingly, become more nearly vertical with age. In some individuals, these changes are so dramatic that a number of older specimens have their incisors implanted almost 90 degrees to the occlusal plane (see Figure 2, 2 Pongo males are pictured). In general, older individuals in all extant pongid species, having more nearly vertical incisors, are not the exceptions, but rather the rule. A rough estimate of the magnitude of this change can be found by comparing the two (different age classes)

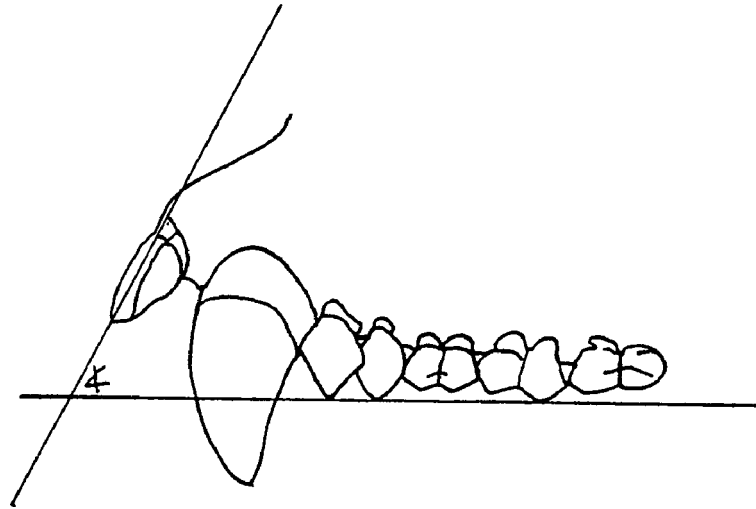


Figure 1 Central incisor angle measurement.



Figure 2 Male Orang (young adult) with procumbent incisors.

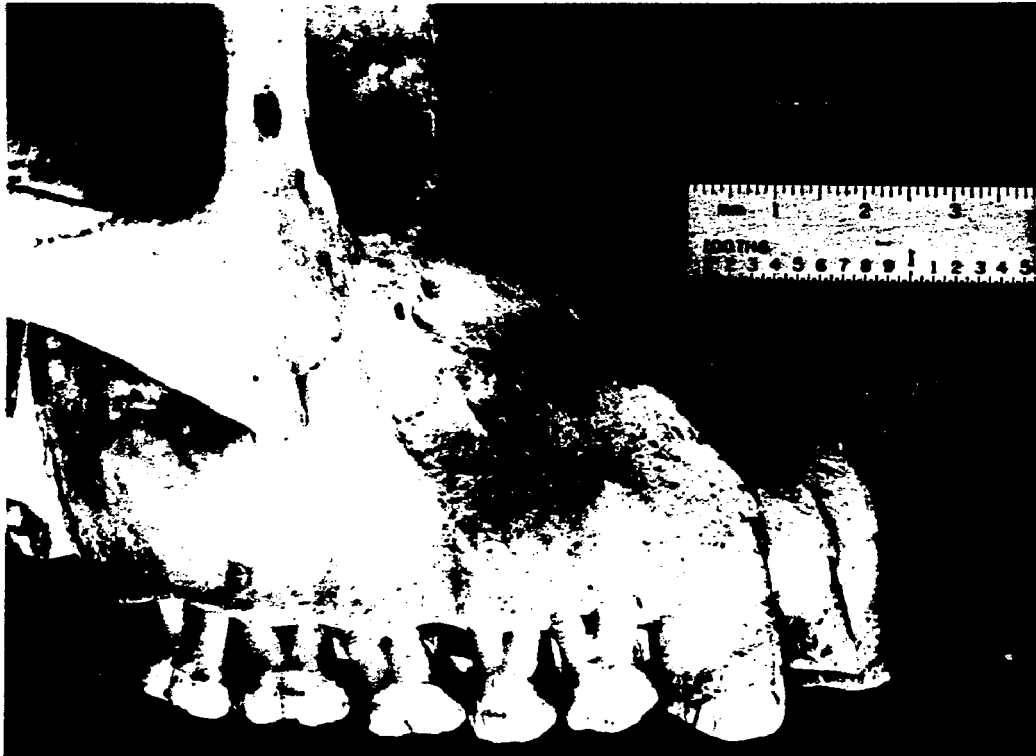


Figure 2 Male Orang (old) with nearly vertical incisors.

Pan samples listed below (Table 3). Whether or not the angle increased in fossil pongids or R1/R2, cannot be determined from the small samples of associated incisors. One should, however, be aware of this possibility.

Turning now to the comparisons, the extant pongid incisor angle means (Table 3) indicate very little difference between these taxa. However, the range within each taxon is considerable. Consistent with age changes noted above, virtually all of the higher values in these taxa were found on dentally older individuals.

A comparison between the Early Miocene pongids and extant pongids shows that the fossil forms had more procumbent incisors. The difference is probably not related to the ages of the specimens included in both sets. The D. major specimen (UMP 62-11) is a fairly old individual, and one of the three D. africanus specimens is also old. Unfortunately, the small fossil samples preclude any in-depth analysis of age related changes in incisor procumbency. However, the D. africanus sample (N=3), despite its small size, suggests a wide range also probably characterized these fossil pongids. In sum, the data show that there has been a trend towards slightly more vertical I^1 in pongids, and that a more procumbent condition characterizes fossil pongids of the Early Miocene.

Relative to extant pongids, australopithecines show a more substantial increase in the angle, if derived from the same Early Miocene pongids. However, one cannot say that

TABLE 3
INCISOR ANGLES*

	N	$\bar{x}$	OR	SD
<u>D. africanus</u>	(3)	41.0°	30-50	--
<u>D. major</u>	(1)	42.0°	---	--
<u>D. vancouveringi</u>	(1)	38.0°	---	--
R1/R2 (Indian)	(1)	55.0°	---	--
R2 (Hungarian)	(1)	60.0°	---	--
(<u>Sivapithecus</u>)	(2)	58.5°	58-59	--
<u>Pongo</u>	(20)	58.0°	38-72	7.0
<u>Pan</u>	(30)	57.0°	39-72	7.2
<u>Gorilla</u>	(30)	58.0°	48-70	6.3
australopithecines	(4)	72.0°	69-77	--
<u>Pan</u> (old)	(14)	76.0°	65-87	6.6

*measurement defined in Figure 1.

australopithecine central incisors are perpendicular to the occlusal plane. Thus, in both pongids and hominids, similar trends have occurred since the Early Miocene. Moreover, their ranges overlap considerably if one excludes old individuals from the pongid samples, and completely when old individuals are included. Consequently, the major difference between extant pongids and hominids is that in hominids the trend towards verticality has been more dramatic.

Age changes in pongid incisors can be tentatively explained. According to Epker and Frost (1965,1966), loaded bone responds to stress by deforming in a direction which opposes the load. In this instance, extant pongid incisors and sockets are subjected to anteriorly directed loading, which acts to bend the anterior premaxilla outwards causing decreasing convexity of the anterior surface. Predictably, the result is more nearly vertical incisors, supported in sockets which have become oriented inferiorly and posteriorly (Figure 2).

As articulated previously, the angles calculated for R1/R2 and (Sivapithecus) were based upon specimens that do not preserve central incisor crowns, but which retain only the root sockets for this tooth. These angle estimates show that (Sivapithecus) has slightly more vertical central incisors than R1/R2. However, the difference is probably not significant. Moreover, because the R1/R2 specimen (YPM 13799) is dentally older than the contemporary

(Sivapithecus) specimens, age cannot explain the difference. Compared to Early Miocene pongids, both R1/R2 and (Sivapithecus) exhibit a trend (like later pongids and hominids) towards verticality. However, R1/R2 incisors cannot be considered vertical or differentiable from those of contemporary dryopithecines.

In addition to Indian R1/R2, Andrews (1971), and Walker and Andrews (1973), have also noted that the Fort Ternan R1 specimen (FT 45/46/47) should be reconstructed with procumbent incisors. More recently, Kretzoi (1975) reported and pictured a new hungarian ramapithecine that preserves its premaxilla and an in situ I^1 (RUD 12). The angle for this specimen is about 60 degrees, comparable to the angles obtained for Indian (Sivapithecus). This new information further supports the conclusions presented above.

In sum, similar trends can be seen in virtually all pongid and hominid lineages since the Early Miocene. All evolved more vertically implanted I^1 , although the magnitude of change was greater in hominids. Further, R1/R2 and contemporary (Sivapithecus) are very similar, and the known maxillary central incisors of R1/R2 were clearly placed in a more procumbent position than the known australopithecine maxillary incisors.

Relative Incisor Size

Recent comparative works (Yulish 1970; Pilbeam 1969b; Conroy 1972) have clarified in detail the metric trends and intraspecific variation in relative incisor size

since the Early Miocene. Consequently, it is now widely recognized that only two pongids developed hypertrophied incisors, Pan and Pongo. All known fossil pongids and Gorilla do not exhibit incisor hypertrophy.

Functionally, incisor hypertrophy has been related to fruit eating habits. Hylander (1975) has demonstrated an association between feeding on large food objects (large fruits), which require more extensive incisal preparation, and large incisors.

Pilbeam (1969b) was the first to point out that Early and Middle Miocene pongids had relatively small incisors; this appears to be the ancestral condition. Only Pan and Pongo have significantly deviated from this condition, and both are highly frugivorous. Using Pilbeam's index,

$$\left(\frac{I^1 \text{ area}}{M^1 + M^2 \text{ area}} \right) \times 100$$

it is interesting to note that the range of index values in a small (N=30) Gorilla sample (a herbivore) includes all of the indices for Early and Middle Miocene pongids (19-36 for Gorilla, 21.4-32.0 for all Early and Middle Miocene forms).

In contrast, the index range obtained for australopithecines was 12.5-21.0. Thus, if derived from (Proconsul) like ancestors, there has been some relative reduction in incisor size in hominids. Since smaller australopithecines tended to have relatively, but not absolutely, larger incisors

(and canines) than larger specimens (Wolpoff 1971, 1974), variation in this index appears to be the result of variation in posterior tooth size, not anterior tooth size. Thus, the relationship between posterior teeth, not anterior teeth, and body size and diet may be significant.

Recent discoveries of very early australopithecine materials from the Afar and Laetolil (Johanson and Taieb 1976; Leakey, et. al. 1976; White 1977) fall at the high end of the listed australopithecine range, and one specimen (Al 200-1a) is within the range for Early and Middle Miocene dryopithecines. This is important because it supports the possibility that an australopithecine ancestor would have had larger incisors, relative to the posterior teeth, than those seen in the later australopithecine sample. It may also suggest that many of the australopithecine dental adaptations (seen in the geologically younger sample) arose fairly late in the course of early hominid evolution. Along with the incisors, the Afar and Laetolil canines are very large, and this too points to the conclusion that much of the anterior tooth reduction in hominids is a relatively recent (post-Miocene) development.

Unfortunately, no R1/R2 or (Sivapithecus) specimens from India or Africa preserve incisors in situ. In both, however, diminutive, dryopithecine-sized incisors are indicated by the small maxillary and mandibular root sockets for these teeth, the short forefacial regions (discussed

above), and the narrow anterior snouts. Thus, R1/R2 and (Sivapithecus) are, at present, indistinguishable from each other, and from other fossil pongids. The fact that their incisors were not hypertrophied functionally suggests they were not eating large fruits.

While precise quantifications for Indian and African R1/R2 and (Sivapithecus) specimens are not yet obtainable, two Hungarian R2 specimens preserve I^1 . One of them, RUD 15, also retains M^1-M^2 , and using Pilbeam's index, a value of 32 was calculated. This value falls at the high end of the dryopithecine range. The other specimen, RUD 12, preserves an absolutely smaller I^1 than RUD 15, but slightly larger M^1 (M^2 is not preserved), and therefore its I^1 was probably relatively smaller than RUD 15's. How much smaller is difficult to estimate, but perhaps it would fall near the lower end of the dryopithecine range. Taken together, they compare favorably with dryopithecines (not Pan or Pongo or the later australopithecines) and some of the australopithecines from the Afar and Laetolil.

In sum, fossil pongids and Gorilla (a herbivore) have relatively small incisors, unlike Pan and Pongo (both large fruit eating forms). Considerable incisor reduction is found in the later australopithecine sample. However, the earliest australopithecine materials from the Afar and Laetolil approach more dryopithecine-like proportions. Although precise metric comparisons between R1, (Sivapithecus), and other taxa are not yet available, both

do not appear to differ significantly from the ancestral condition, or from each other. The Hungarian R2 specimens support this conclusion. Lastly, according to Hylander's model (1975), it is unlikely that either R1/R2 or (Sivapithecus) were large fruit eaters, or that the dietary items they ingested required extensive incisal preparation.

Metric Equality of Lateral and Central Maxillary Incisors

Lewis (1934) and others (Simons 1961; Conroy 1972) have suggested that incisor crown homomorphy characterizes hominids and R1, while pongids are supposed to possess extremely heteromorphic lateral and central maxillary incisors. In R1, one specimen, YPM 13799, preserves this region, however, only the root socket is preserved for I^1 , and half of the root for I^2 . Thus, statements about incisor crown homomorphy in R1 have been based upon inferences drawn from root sockets and roots.

To test these contentions, interspecific and temporal variation is documented for extant pongids, fossil pongids, and australopithecines below (Table 4). To quantify heteromorphy, two indices are used: $100 \times I^2 \text{ length}/I^1 \text{ length}$ and $100 \times I^2 \text{ breadth}/I^1 \text{ breadth}$. Lower values indicate greater crown heteromorphy. Incisor areas were not used because they do not reflect the morphology or function of these teeth. Areas were used above in the section on relative incisor size simply because prior work on the subject utilized areas.

Among extant pongids there are considerable differences

TABLE 4 INCISOR HETEROMORPHY

	$100 \times I^2_L/I^1_L$				$100 \times I^2_B/I^1_B$			
	$\bar{x}$	N	OR	SD	$\bar{x}$	N	OR	SD
<u>Gorilla</u>	72.3	(30)	64.8-81.2	5.2	91.5	(30)	81.6-104.0	7.0
<u>Pongo</u>	63.2	(30)	55.0-74.7	4.9	71.4	(30)	62.7-81.8	4.6
<u>Pan</u>	76.8	(30)	69.1-87.4	5.4	93.4	(30)	84.0-113.0	5.8
<u>D. major</u>	81.9	(1)	--	--	112.0	(1)	--	--
<u>D. africanus</u>	84.3	(1)	--	--	--	-	--	--
australopithecines	69.1	(7)	64.9-74.3	3.5	82.8	(6)	70.7-93.9	8.6
R2 (Hungarian)	60.0	(1)	--	--	86.3	(1)	--	--

between means, although the ranges overlap extensively. Pongo exhibits the greatest crown heteromorphy for both indices, followed by Gorilla and Pan. Compared to Early Miocene pongids, extant forms display greater heteromorphy, but the magnitudes of change since the Early Miocene differ considerably among pongids. It is interesting to note that in Pan both maxillary incisors have become hypertrophied, whereas, in Pongo, only the central maxillary incisor appears to have been enlarged.

Similarly, australopithecines exhibit greater crown heteromorphy when compared to earlier taxa. All of the recent finds from the Afar and Laetolil fall within (but at the high end) the range of values for the later australopithecines. Among extant pongids, only Pongo exhibits greater incisor crown heteromorphy than the earliest undoubted hominids. Therefore, contrary to prior contentions, homomorphy is not a characteristic of early hominids. In fact, clearly the opposite is true. Perhaps more significant is the observation that no hominoid taxon displays homomorphy.

In sum, the data demonstrate similar trends in pongid and hominid lineages: both show increasing maxillary incisor heteromorphy. Among the hominoids examined, only Pongo has more heteromorphic maxillary incisors than the australopithecines.

Although no in situ incisor crowns are preserved for (Sivapithecus), root sockets (GSI D.1, GSI D.196, and new

Pakistan specimens) clearly indicate considerable heteromorphy (precise quantification is not yet possible).

Similarly, Indian R1/R2 specimen YPM 13799 preserves no crowns, only I^2 root and half of the I^1 root socket. Since it is very difficult to interpret such fragmentary material, any conclusions must be very tentative. However, both RUD 12 and RUD 15 (Hungarian R2 specimens) clearly show (from crowns and root sockets) extreme heteromorphy. For RUD 15, the listed indices (Table 3) fall either within the range for Pongo (I^2L/I^1L), or the australopithecines (I^2B/I^1B). Additionally, RUD 12, which only preserves I^1 , has a very tiny socket preserved for I^2 . Together, the crown and socket suggest extreme heteromorphy. Thus, while Indian R1/R2 is difficult to interpret, Hungarian specimens (R2) clearly show extreme heteromorphy.

In sum, the data suggests that in all hominoid lineages since the Early Miocene, maxillary incisor crown heteromorphy has increased. Extreme heteromorphy is neither typically a pongid or hominid characteristic. Thus, the extreme heteromorphy indicated for (Sivapithecus) and R2 does not suggest any special affinities with either extant pongids or australopithecines.

(5,6,7,8) The C/P₃ Complex

Lewis (1934) was the first to suggest that the canines of R1 were relatively small, like those of hominids, and unlike the large tusklike canines of extant pongids. This interpretation has received much support and has been elaborated upon (Simons 1961; Leakey 1961; Simons and Pilbeam 1965; Pilbeam 1969b; Conroy 1972; Tattersall 1975). It has further been suggested that the canines of R1 were not only relatively small, but also incisiform and non-projecting, and that the P₃ was "semi-sectorial" and incipiently molarized. However, recently (Freyer 1976) it was noted that the evidence for a non-dryopithecine canine is lacking, and that the P₃ was sectorial.

Some of the most significant dental differences between pongids and early undoubted hominids can be found in the canines and entire C/P₃ complex. These differences in relative size and function, reflect important dietary and behavioral divergences between pongids and hominids. To explain why hominids evolved relatively diminutive and functionally different canines and P₃, several models have been proposed. These models can be divided into two sorts: dietary and tool. The models are not necessarily mutually exclusive, i.e., they can be used together without one contradicting the other.

Jolly (1970) has been the major proponent of the dietary model which draws upon an analogy with gelada baboons. Briefly summarized, Jolly's seed eater hypothesis

suggests that an australopithecine's tough savannah diet required an expansion of posterior teeth and a concomitant reduction in the anterior teeth. Further, these dental changes occurred in conjunction with changes in the architecture and musculature of the skull. According to the model, canines were part of the anterior dentition and presumably they reduced along with the incisors. Their reduction can either be perceived as a passive change, or one might posit some positive selection for reduction (or selection against larger canines). Functionally, long projecting canines might be considered selectively disadvantageous to an animal which requires free movement of the mandible. In support of this possibility, there is some evidence from studies of Gorilla (St. Hoyme 1971) and extant cercopithecoids (Smith 1969; Butler and Bernstein 1974) that large canines restrict mandibular movement. In addition to canine reduction, Jolly's model also attempts to explain the loss of honing function on P_3 . This tooth (P_3) was incorporated into the grinding and crushing complex of the expanded posterior teeth, extra cusps were added, and they became lower and more bulbous. These changes presumably helped satisfy the increased need for posterior tooth grinding and crushing surface.

Another model, first proposed by Darwin (1871), is a behavioral model. According to this theory, tools replaced the canines as defensive weapons. The result was

a reduction in canine size and loss of honing function. According to this model, canine reduction can either be viewed as the probable response to the accumulation of neutral mutations, or possibly the result of a new function for the canines favoring reduction, or some disadvantage for large canines.

More recently, Holloway (1967) suggested that canine reduction in hominids was associated with hormonal factors. He proposed that a general reduction in hormonal dimorphism which was a consequence of greater cooperation and reduced intragroup aggression, reduced the dimorphism in canines.

In any event, these changes in relative size, function, and dimorphism characterize the australopithecine C/P₃ complex, and pongid-like shearing, puncturing, and aggressive functions were lost. Perhaps australopithecine canines were used to grip or manipulate food and extra-dietary items. Further, P₃, especially in large individuals, was incorporated into the crushing and grinding posterior tooth complex. One might readily expect such changes to characterize earlier hominids.

Clearly then, with respect to Ramapithecus, it is necessary to consider not only relative canine size, but also canine morphology and the function of the entire C/P₃ complex. Therefore, in this section, the following will be discussed: a) relative canine size in hominoids, b) comparative morphology of the C/P₃ complex, and c) specimens in R1/R2 which preserve all or part of this

region of the dentition.

Relative Canine Size

Sexual dimorphism greatly influences the intraspecies variation in relative canine size. Consequently, controls must be incorporated into any interspecific comparisons; it is necessary to compare individuals or samples of like sex.

Extant pongid samples exhibit two canine morphotypes, each corresponding to a sex. This sexual pattern reflects underlying, biological differences in male and female behaviors; and different selective forces are operating to maintain these two morphotypes. Phenotypically, all dimensions of a female pongid's canine, relative to her posterior teeth, are much smaller than a male's relative to his. Consequently, the distribution of relative canine size in pongids is bimodal with each mode representing a sex. While there may be some overlap in the ranges, the magnitude of this overlap is very small; thus relative canine size is a good sexing criterion. Different species (Tables 5 and 6) do not have precisely similar numerical ranges but the distributional patterns are comparable.

Since there are two morphotypes, it is possible to discriminate all males from females using morphology alone. Female canines are small and do not project far beyond the occlusal plane; they may or may not shear or hone against the sectorial P_3 . The crown is not high and it is usually buccolingually compressed. In sharp

TABLE 5
MANDIBULAR C/M1 INDICES

	MALE				FEMALE			
	N	$\bar{X}$	OR	SD	N	$\bar{X}$	OR	SD
<u>D. africanus</u>	(4)	140.3	130.2-154.1	10.7	(4)	95.2	85.6-110.6	10.4
R2	(2)	82.9	72.8-93.0	---	--	---	---	---
(<u>Sivapithecus</u>)	(2)	99.1	87.2-111.1	---	(1)	50.0	---	---
<u>Pongo</u>	(30)	126.2	98.0-165.4	18.1	(30)	79.5	54.7-115.5	10.9
<u>Pan troglodytes</u>	(30)	137.2	101.7-186.4	21.6	(30)	96.2	73.6-117.2	9.5
<u>Pan paniscus</u>	(21)	93.9	73.0-118.6	12.7	(20)	65.1	49.7-76.2	8.9
<u>Gorilla</u>	(30)	125.5	92.0-185.9	19.4	(30)	72.3	54.3-92.1	7.8
australopithecines*	(22)	41.5	23.8-63.3	10.6	--	---	---	---
<u>G. bilaspurensis</u>	--	---	---	---	(1)	55.0	---	---
<u>G. blacki</u>	(1)	56.0	---	---	(1)	59.0	---	---

*Male and female samples pooled and presented here under male.

TABLE 6
MAXILLARY C/M1 INDICES

	N	$\bar{X}$	OR	SD	N	$\bar{X}$	OR	SD
<u>D. africanus</u>	(3)	138.7	132.0-145.0	6.5	(3)	104.3	100.0-108.0	4.2
R1	--	---	---	---	(1)	76.0	---	---
R2	(1)	81.0	---	---	(1)	57.0	---	---
<u>(Sivapithecus)</u>	(3)	119.7	111.0-120.0	6.4	(1)	71.5+	---	---
<u>Pongo</u>	(30)	132.2	97.2-177.0	20.5	(30)	87.1	56.1-104.5	10.9
<u>Pan troglodytes</u>	(30)	145.7	97.3-209.6	26.7	(30)	92.2	73.4-108.6	10.1
<u>Pan paniscus</u>	(20)	113.5	87.5-146.4	18.2	(23)	71.3	38.3-83.7	10.4
<u>Gorilla</u>	(30)	152.2	118.9-182.6	20.2	(30)	79.3	66.4-97.3	9.0
australopithecines*	(14)	48.2	33.0-73.4	12.6	--	---	---	---

*Male and female samples are pooled and presented here under male.
+average of right and left sides (67 and 76).

contrast, the male canines are large tusk-like teeth and when newly erupted, the tall crown projects far beyond the occlusal plane almost always honing against the sectorial P_3 . Lastly, buccolingual compression is not as pronounced.

In addition to the C/P_3 complex, other aspects of the pongid dentition and face are sexually dimorphic. In males, the remaining teeth are generally larger and their mandibles are either taller, thicker, or both, and the male's tooth rows may be less convergent, or more divergent anteriorly. This last feature is probably the result of the outward angulation of large male canines.

That these patterns are found in all extant pongid taxa, is significant in studies of fossil hominoids. Presumably similar, but not necessarily identical, patterns of sexual variation can be found in fossil samples, and models can be derived to sex fossil materials, which can then be compared interspecifically. Clearly, the best criterion for establishing a model of sexual variation in fossil hominoids is the existence of two distinct canine morphotypes. Using this, and other criteria (mentioned above), sex variation in D. africanus has been documented (Greenfield 1972). In this taxon, the specimens sexed as males have larger and morphologically distinct canines, generally larger posterior teeth, and larger mandibles. Similar, consistent sexual patterns can be seen in the Indian hominoids. However, in Chinese G. blacki, the

pattern is slightly different. The specimen (G1) with absolutely smaller canines, much smaller posterior teeth, and a more gracile mandible has larger canines relative to its posterior teeth. Probably the major contributing factor to this is the fact that the female (G1) had much smaller posterior teeth than the male (G3). In G. blacki and australopithecines, the anterior teeth had reduced and the posterior teeth expanded. This changed the pattern of the distribution in relative canine size. Consequently, in these taxa, male and female ranges overlap extensively for this index. For example, among australopithecines, OH 5, which is considered by most to be a male, has the lowest relative canine size index (33). It appears that large and small australopithecines have absolutely similar sized anterior teeth, but in the former, the posterior teeth are much larger and, consequently, the ranges of relative canine size overlap.

Using the sexing criteria derived from extant pongids, fossil pongids and R1/R2 were sexed in order to permit controlled interspecific comparisons of relative canine size. The sex of the Fort Ternan specimen is critical in the comparisons below because all prior statements about canines in R1 were based upon this specimen which preserves C^1 , M^1 , and P_3 . A morphological comparison of the FT 46 canine to those of closely related (Proconsul) sp. and (Sivapithecus) is considered most relevant in determining the sex of the specimen. In (Proconsul) (and all

hominoids from the Early-Middle Miocene of East Africa) and (Sivapithecus), two distinctive canine morphotypes are present. The Fort Ternan C¹ morphologically conforms closely to the female morphotype found in these Early and Middle Miocene forms. Basic similarities can be noted in Figure 3. Female canines pictured possess buccolingually compressed crowns, and the mesiodistal length and crown height are approximately equal (squat appearance). Note that this is in contrast to the male canines in which the height of the crown greatly exceeds the length. The female canines also exhibit well developed lingual cingula that terminate anteriorly in a small tubercle on the mesial side. The cingula on male canines are either poorly developed or absent and there are no anterior tubercles. Thus, the total pattern of the FT 46 C¹ is female-like.

In addition to these interspecific comparisons, one can also compare FT 45/46/47 to other R1 specimens from Africa. FT 7 preserves P₄ and it is larger than its homologue on FT 45. Since posterior tooth dimorphism probably characterized these hominoids, small teeth (on FT 45/46/47) make a female sex assignment more likely. Another specimen, BMNH 16649, generally not recognized as an R1 specimen (inclusion with Fort Ternan R1 is discussed in a later section) preserves the posterior portion of the C¹ socket and P³-M¹ crowns. The posterior teeth of this similarly short faced specimen (zygomatic begins over P⁴),

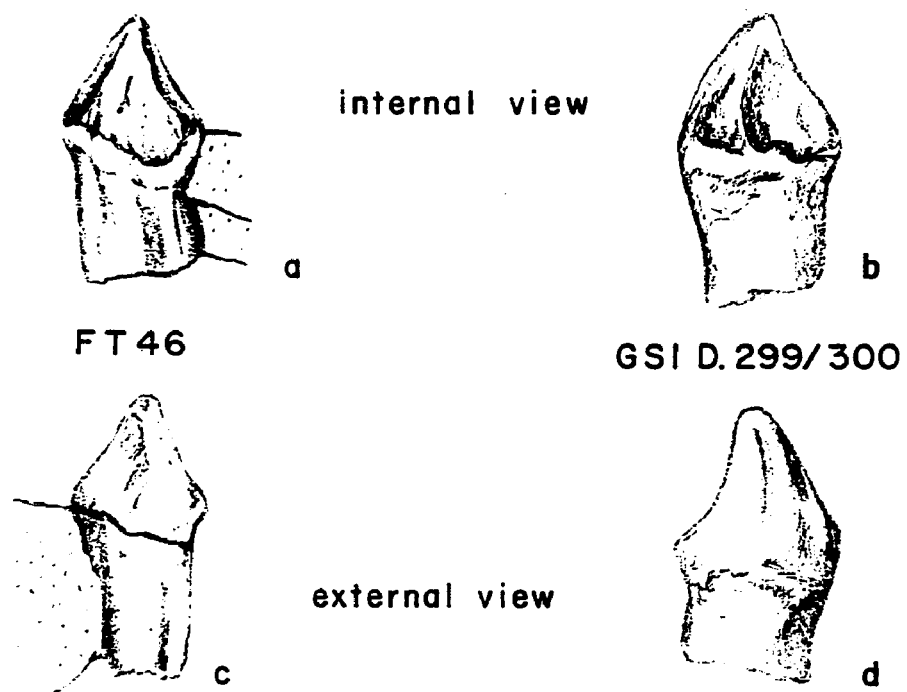


Figure 3 Female Canines

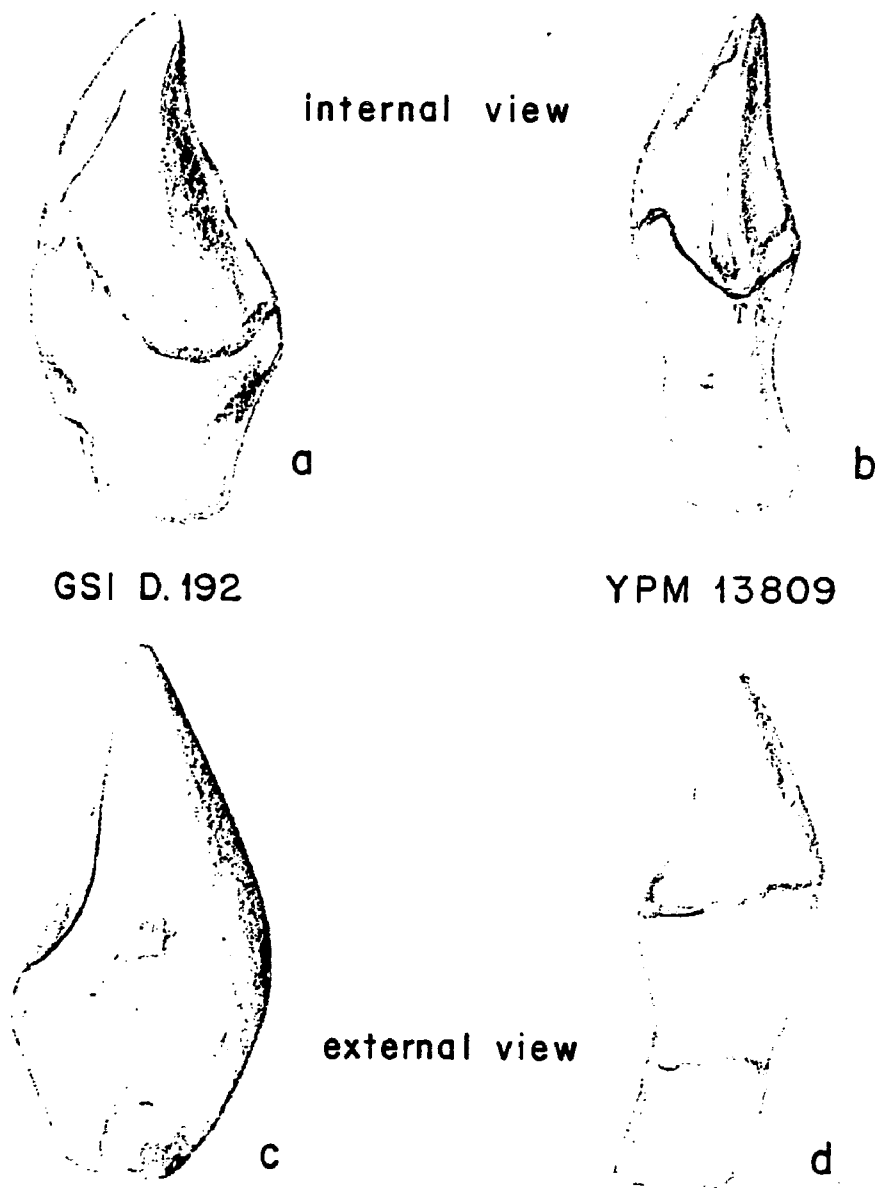


Figure 3 Male Canines

are slightly larger than those on FT 46/47. However, the preserved portion of the C¹ socket indicates a much larger tooth than the FT 46 canine. Thus, if this specimen is included in the sample, it most probably represents a male and FT 45/46/47 a female. Together (with FT 7) they indicate a pattern of sexual variation consistent with the models derived from extant pongids and similar to patterns found for all Early and Middle Miocene hominoids. For all of the above reasons, FT 46/47 is considered a female in the comparisons which follow.

To document patterns of relative canine size variation, and indicate trends, a relative canine size index was used (Tables 5 and 6), and is calculated by the following formula:

$$I = \frac{\text{canine area (MD X BL)}}{\text{first molar area (MD X BL)}} \times 100$$

An index, rather than absolute dimensions, was used to eliminate the problems inherent in comparing taxa of different overall size, and to provide an estimate of the importance of the canine relative to posterior teeth. The first molar was chosen to represent posterior tooth size for two reasons. First, it is the least variable posterior tooth and therefore will provide the least ambiguous indices. Second, it is the most common molar present in the fossils (the specimens with canines as well) and thus maximizes the number of specimens to compare. Additionally, this index is bimodally distributed in all

extant pongid species, and presumably reflects the underlying important behavioral differences between the sexes. The absence of clear bimodality in australopithecines and Gigantopithecus is a consequence of two factors: posterior tooth expansion (or anterior tooth reduction), and a change in the function of the C/P₃ complex.

Among extant pongids (Tables 5 and 6) there is considerable index variation within each sex, between sexes, and between taxa. Sexual dimorphism is marked. The data indicate so much variation within a taxon, that for the maxilla, the smallest female usually has an index which is as little as one third that of the largest male and in Pan paniscus as little as one fourth (this is not to say that it has the greatest sexual dimorphism). In the mandible, the lowest female index could be anywhere from two fifths (Pan troglodytes) to less than one third that of the largest male (Gorilla). Among extant forms, the pigmy chimpanzee consistently has the lowest indices; however, there is no general relationship between the index and body size.

Further, the data show that Early Miocene D. africanus also has a bimodal distribution for the index. Although the mandibular sample is small (N=8), there is still a considerable range between the smallest female and the largest male. Clearly, if extant pongids are derived from an animal like D. africanus, there has been considerable reduction in female indices (mandibular indices

for Pan troglodytes an exception). Also, in males, relative reduction has occurred in all taxa in the mandible although only for Pongo and Pan paniscus in the maxilla. However, if one considers Gorilla to be derived from D. major, as Pilbeam suggested (1969b), there is relative reduction in the maxillary canines of this extant pongid as well. This conclusion is based upon D. major specimen UMP 62-11 (the Moroto Palate). Sexed as male, its relative C^1 index is 196.0, well above the Gorilla mean, and range. This is significant even though UMP 62-11 is the only maxillary specimen in D. major from which the index could be obtained. In general, the data indicate relative canine size reduction in pongids since the Early Miocene.

In contrast, the sexing criteria which apply to fossil and extant pongid canines do not apply as well to hominid canines. Here, two australopithecine canine morphotypes are not clearly separable, although a bimodal distribution of canine breadths has been reported (Wolpoff 1976). No attempt is made by this author to sex australopithecine canines. However, regardless of sex, relative to their posterior teeth, australopithecine canines are very small. The data also show small relative canine size and absence of clear bimodality is characteristic of Gigantopithecus. As mentioned previously, the female G. blacki specimen (G1) has a relatively larger canine than the male (G3), probably a consequence of

marked sexual dimorphism in posterior tooth size and a shift in the function of the C/P₃ complex. If a similar degree of sexual dimorphism characterizes australopithecine posterior teeth, then extensive overlap of male and female ranges for the index is predicted. The likelihood of this distributional pattern is supported by the observation that the lowest maxillary index (33.0) and the lowest mandibular index (23.8) belong to probable males, respectively OH 5 and OMO L7-125. In sum, whatever the precise male and female ranges may be, there has been much greater reduction in hominid canines since the Early Miocene than in pongid canines, and a loss of clearcut bimodality in the index.

The new and earlier australopithecines from the Afar and Laetoli indicate that greater anterior tooth reduction (or posterior tooth expansion) characterizes later australopithecines. In the maxilla, most of these earlier specimens fall at the high end, or above the listed range (Table 6) for later australopithecines (this earlier material is not included in the ranges in Tables 5 and 6). Afar specimens AL 200-1a and AL 199-1 have maxillary C/M1 indices of 67 and 66, respectively, and Laetoli specimens LH 3 and LH 6 have indices of 77.0 and 60.6 respectively. In the mandible, an index of 68.3 was calculated for LH 3. All of these indices are much greater than the mean for later australopithecines, and they fall either at the extreme high end or outside of the later range.

Considering the canines and incisors of these earlier australopithecines together, it is clear that their anterior teeth are larger relative to posteriors than the later australopithecines, and consequently they fall in or closer to the dryopithecine ranges.

Given this interspecific and temporal framework, it is now appropriate to consider R1/R2 and (Sivapithecus). The data in Tables 5 and 6 show that if R1/R2 and (Sivapithecus) are derived from (Proconsul)-like ancestors they both have undergone relative canine size reduction. In R1, the Fort Ternan specimen is the only specimen which preserves both C^1 and M^1 . It is considered a female for reasons discussed above. The canine is a short squat tooth, exhibits buccolingual compression, has a well developed lingual cingulum, and relative to males, is much less projecting (projection of this canine will be discussed later). Leakey (1961), who described this specimen, presumed that it was a female, and I concur that all features suggest this specimen represents a female. In this light, the index value of 76 obtained for this specimen is not unusual for any extant female pongid. However, it would be unusually high for an australopithecine. Even when compared to (Sivapithecus), the Fort Ternan canine is slightly relatively larger, controlling sex. One must conclude therefore, that if the Fort Ternan specimen is a female, then its canine, relative to its posterior teeth, is not distinguishable from extant pongid

female canines.

In R2, several specimens can be sexed. In the maxilla, male RUD 15 has a large C^1 crown and root which extends high up into the maxilla, larger functional diastema (than that reconstructed for RUD 12), and a dental arcade that is divergent anteriorly (see section on sex variation in dental arcade shape and tooth row curvature). In addition, the C^1 crown extends far below the occlusal plane of the posterior teeth despite the fact that the tip is gone. Female RUD 12 has a smaller C^1 crown and root, smaller (reconstructed) diastema, and tooth row that converges anteriorly. There is very little C^1 projection beyond the occlusal plane. However, a considerable part of the original crown had been worn away, so it is difficult to determine how far it projected when unworn.

Together, these maxillary specimens exhibit, like (Sivapithecus), index dimorphism, however, both (more so for R2) have relatively reduced canines if derived from a (Proconsul)-like ancestor (Tables 5 and 6).

In the mandible, two R2 males with canines were recognized. RUD 17 has a projecting C_1 crown (although the tip of this tooth has been lost), and a C_1 that extends almost to the base of the corpus, in contrast to D.298 (probable female), which has a canine root that extends inferiorly only to the middle of the corpus (determined from the root socket). The second male, RUD 2 has reconstructed C_1 measurements that are larger than those for

RUD 17 (Wolpoff, who took the measurements feels that the C_1 estimates may not be reliable). As in the maxilla, the two R2 specimens have indices that would be considered low for most pongid males including (Sivapithecus), although one (Sivapithecus) male (AMNH 19412) has an index lower than that of RUD 2. Both have relatively reduced mandibular canines if derived from a (Proconsul)-like ancestor.

The differences between R2 and (Sivapithecus), with respect to the index, do not appear to be as great as those between two closely related extant pongids, Pan troglodytes and Pan paniscus, even though both are anterior tooth loaders and have incisor hypertrophy. Further, a general survey of the listed indices for all pongid taxa (except Gigantopithecus) shows a considerable range despite the fact that all have C/P_3 complexes designed for broadly similar functions. The new Turkish dryopithecine mandibles with pongid-like C/P_3 function would even further extend the lower range of indices for pongids because one specimen (RPI 54), a female, has an index of 48, and one male (RPI 55) an index of 68. What these observations suggest is that while relative canine size measures are important in evaluating R1/R2, C/P_3 function is perhaps more significant from the standpoint of phylogenetic and adaptive pattern reconstruction.

In sum, there has been relative canine size reduction in almost all hominoids since the Early Miocene, but australopithecine (and Gigantopithecus) canines have

undergone the greatest relative reduction and have lost clear index bimodality. R1, like (Sivapithecus), has reduced canines if derived from (Proconsul). Controlling sex, the canines of R1 are about the same size, relative to the cheek teeth, as those of any contemporary or extant (except Pan troglodytes) pongid female. However, R2 has relatively smaller canines than most pongids, but there appears to be index dimorphism.

Comparative Morphology of the C/P₃ Complex

There are many differences between pongid (fossil and extant) and hominid C/P₃ complexes. The high crowned, pointed cusped pongid complex is designed for puncturing, shearing, and aggressive display functions. However, a notable exception to this general pongid morphology is Gigantopithecus, which, as noted above, lost clear relative canine size dimorphism. Gigantopithecus' premolars, and perhaps female canines, were incorporated into the crushing and grinding posterior tooth complex. Like Gigantopithecus, and in contrast to the typical pongid condition, is the australopithecine complex which is designed for gripping, crushing, and freer movement of the mandible (due to loss of C/P₃ interlock).

Important dietary and behavioral changes were probably responsible for the divergence of the hominid (and to some extent Gigantopithecus) C/P₃ complex from the ancestral pongid condition. It seems plausible that both australopithecine and Gigantopithecus bunodont dentitions

probably evolved in response to diets which consisted partly of small, tough food objects (Jolly 1970; Wolpoff 1973; Simons and Ettel 1970). This kind of dietary item places a selective premium on flatter occlusal planes, articulating like millstones.

An added feature of this complex seems to have been an expansion of tooth surface area relative to body size (this known only for australopithecines). This expansion involved both simple metric increases in crushing tooth surface and morphological modifications. For example, in both taxa, P_3 was often molarized, a modification which included an increase in the number of cusps and closer size correspondence of buccal and lingual cusps. Generally, larger australopithecines exhibit more extreme molarization of P_3 than smaller individuals, perhaps an expression of a functional relationship between diet, tooth surface area, and body size. Presumably, larger individuals, with greater caloric requirements, may have needed both larger posterior teeth and greater surface for crushing and grinding than small individuals.

Additionally, Gigantopithecus and australopithecine canines were rapidly worn to the posterior tooth occlusal plane, wear blunting the tip of this tooth. Further, the canines' anterior and posterior edges did not shear. Similarly, P_3 cusps were blunted, and also lack shearing wear. Presumably, the typically non-hominid intraspecific agonistic display function of C^1 might have been replaced

by an increase in body size dimorphism, or by weapons (in australopithecines), or by combination of both. Alternately, only slight behavioral modifications may have been necessary to replace the reduced canine's aggressive function. Alexander and Hughes (1971) have shown that in a group of macaques, that removal of canines had little effect on the status of adult males. Thus, their study tends to play down the importance of large projecting canines in maintaining an adult male's status.

In sum, the hominid (and in part Gigantopithecus) C/P₃ complex includes reduced canines (loss of two distinct morphotypes and relative canine size dimorphism) which exhibit blunting wear, bunodont P₃ cusps, which also wear to a more flat occlusal plane, loss of shearing or puncturing functions, and an increase in the number, and change in proportions, of cusps on P₃.

In contrast, the typical pongid complex retains large, morphologically dimorphic canines which hone against a unicuspid P₃ (on the mesiobuccal plane). Puncturing and shearing functions are maintained. Further, as wear proceeds, P₃ is generally not incorporated into the grinding and crushing molar complex. (Proconsul) and extant pongid dentitions are, in general, also less bunodont (higher and more pointed cusped). Additionally, the buccal side of P₃ tends to be oriented more anteriorly in pongids; the homologue of the buccal side of the hominid P₃ is in a more mesial position in pongids. However, this

is a highly variable complex. In fact, the buccal side of a number of australopithecine P_3 s are oriented in a more anterior direction and overlap with pongids in this respect (KNM ER 1483, MLD 40, LH 4).

There are variations in the pongid pattern: relative size of C^1 , honing wear, accessory metaconids on P_3 . However, the general functional pattern is consistently present in extant and fossil forms.

In sum, the pongid and hominid C/P_3 complexes contrast functionally and morphologically, and given this comparative framework, $R1/R2$ and (Sivapithecus) complexes can be examined.

Both (Sivapithecus) and $R1/R2$ C/P_3 complexes clearly retain general pongid-like morphology and function. In $R1$, only FT 45/46, a female, preserves the entire complex. The maxillary canine displays wear characteristic of honing pongid canines (Leakey 1961), and there is a well developed shear facet on its posterior cutting edge. There is even a shearing wear facet on the anterior cutting edge, resulting from occlusion with the mandibular canine. Additionally, there is no indication of hominid-like blunting facets or flat wear on the tip of this tooth (a tiny fragment, probably post-mortem chippage, of the tip is gone). It was clearly designed and used as a pointed cutting tool. In the commonly accepted reconstruction of the position of the canine, the crown does not project well beyond the occlusal plane. It can be shown, however, that

this reconstruction is probably incorrect (a conclusion also presented by Frayer 1976, although for different reasons). When I occluded the originals in Nairobi, I found that the present reconstruction did not allow the entire length of shear facet on the posterior cutting edge (of C^1) to occlude with the anterior face of P_3 . Only by making the canine more projecting does this allow the entire cutting edge to touch P_3 . It would have been physically impossible for this individual to have produced the entire length of cutting edge with the present reconstruction (pictured in Andrews 1971). Therefore, it is likely that the canine did project beyond the occlusal plane, and when placed into this new configuration it projects by at least $4\frac{1}{2}$ millimeters. This is a minimum estimate because even though the entire length of cutting facet touches P_3 with the new reconstruction, it is not necessarily true that the facet was produced at the highest point on P_3 . It may have been the result of contact at some lower point on this tooth. If so, this would require even further projection of the canine. This minimum estimate also suggests the likelihood that the canine was interlocking and could have interfered with movement of the mandible.

With respect to the morphology of the $R1 P_3$, a number of workers have supported the idea that it was "semi sectorial" (Leakey 1961; Andrews 1971; Conroy 1972), and that incipient molarization is indicated. The presence of



AMNH 19412

FT 45

D. fontani

Figure 4 P₃ Morphology Comparison
(Casts)

a small accessory metaconid has been noted as evidence for this incipient molarization (Andrews 1971). To the contrary, the accessory metaconid on sectorial premolars is not an indication of incipient molarization (Fruyer 1976; Greenfield 1974). It occurs commonly in fossil and extant pongids, and in this case (FT 45) does not appear to suggest a new function for this tooth (Figure 4). The function of the sectorial P_3 in FT 45 is probably the same as it is in extant pongids (except Gigantopithecus); it sharpens the maxillary canine. No other functions are indicated. There is no flat grinding wear facet on the tip of the large pointed protoconid of this tooth. Rather, there is honing wear on the (mesiobuccal) anterior slope, the entire crown is angled to the tooth row, its roots bifurcate near the root-crown junction (as in pongids and almost never in hominids), and it is an elongated tooth. There is no evidence to suggest the R1 P_3 was incorporated into the grinding complex of the molars, a conclusion that applies equally to (Sivapithecus), which also displays all of the pongid-like features in its C/ P_3 complex.

In R2, the new Rudabanyan specimens confirm a completely pongid-like C/ P_3 complex. Every canine in occlusion shows honing wear, the P_3 s are sectorial honing surfaces for the maxillary canines, and there are large functional diastemata. In fact, one specimen (RUD 15) has honing wear on I^2 and C^1 created by occlusion with C_1 .

The entire C/P₃ complex in R2 is designed to provide shear and no other functions, with respect to diet, are indicated.

Thus, in no respects can the R1 C/P₃ complex be shown to differ from the typical pongid condition. In R2, canines appear to be relatively smaller than in most pongids, however, this is the only demonstrable difference.

Other Specimens in R1/R2

There are few specimens in R1/R2 besides the Fort Ternan and Hungarian specimens that preserve significant portions of the C/P₃ complex. One specimen, BMNH 15423, preserves the broken base of what probably was a pongid-like sectorial P₃. It was an elongate tooth, angled to the tooth row, and had two roots at the root-crown junction. Pilbeam (1969) had suggested that the canine (by inference from the roots) was reduced, however, no portion of the crown, root, or socket was visible in X-rays observed by Leakey (1970), and thus there appears to be no evidence for a non-dryopithecine canine. It was suggested (Greenfield 1974) that this specimen be temporarily removed from R1/R2. At that time, I assumed that there were hominid-like features in the C/P₃ complex of R1. Since more recently published evidence no longer supports this, I now believe that the hominid-like reconstruction of the C/P₃ complex cannot be used as a reason to exclude BMNH 15423 from R1 or R2. Aside from the C/P₃ complex, BMNH 15423 was excluded because it also possesses a slender mandibular corpus relative to other R1 specimens, but now

this difference can be explained in terms of a model of sexual variation for R2 (discussed in a later section). Therefore, BMNH 15423 is now included in R2 for reasons discussed by Pilbeam, and because there is no evidence that the C/P₃ complex in R1/R2 was different from that of contemporary pongids. Analysis of the specimen's morphology remains unchanged; it is the concept of R1/R2 that is different.

Another R1 specimen, D.199, also exhibits the indirect evidence for sectorial P₃. The interproximal wear facet between a sectorial P₃ and P₄ is often small and typically situated on the internal portion of the mesial plane of P₄. It is small because only a small part of the sectorial P₃ touches the P₄, and it is internally situated because of the angle the sectorial P₃ makes with the tooth row. In most australopithecines, this wear facet is on the central part of the mesial plane of P₄; it is a much broader facet and it becomes increasingly broad in older individuals. Specimen D.199, an old individual, has a small, internally situated facet on the mesial plane of its P₄, in spite of its age, suggesting it too had a sectorial P₃.

Since there is no evidence to the contrary among Indian R1, and because the Hungarian and Fort Ternan specimens have a pongid-like C/P₃ complex, D.298 is included in R2. Its well preserved P₃ crown follows the same pongid pattern found in other R1/R2 specimens, except

this individual is dentally older. The canine was very small, judging from the socket for this tooth. The sectorial P_3 is elongate, has an anterior shearing facet, and there is no evidence of molarization. Further, the specimen occludes very well with R1/R2 specimen YPM 13799. D.298 will also be included in the discussion on sex variation in R2.

Tentatively assigned to R2 is YPM 13809, an isolated C^1 with male morphology. It was previously placed in D. sivalensis (Simons and Pilbeam 1965), but is probably too small to be included in that taxon. Metrically, it is smaller than the right C^1 of D.299/300, a female D. sivalensis specimen, and contrasts strongly in morphology (see Figure 3); it is morphologically identical to known male Indian dryopithecine canines (D.196, D.192). YPM 13809 has shear on its anterior cutting edge, it is high crowned and probably projecting. Crown height exceeds its length. Further, a poorly developed internal cingulum is present (like the one on D.192) and an anterior tubercle is absent. However, other male canines assigned to D. sivalensis are much larger than the one female canine known (compare D.1 for example with D.299/300). Thus, YPM 13809 is the smallest Siwalik canine, yet it has male morphology. Presumably, then, it may belong to a smaller taxon, like R2. Given the above analysis of the R1/R2 C/P_3 complex, there are no morphological reasons why this canine cannot be an R2 canine.

In sum, all characteristics of the C/P₃ complex in R1/R2 are pongid-like. Some relative canine size reduction has occurred in R1/R2 if derived from (Proconsul), but some relative reduction also characterizes most pongids since the Early Miocene. All landmarks of a sexually dimorphic honing complex are present, and therefore there is no indication in R1/R2 of significant dietary or behavioral innovations in this portion of the dentition.

(9,10,11) Loss of Projecting P^3 Paracone, Absence of P^3
 Paracone Shear, Marked Bicuspidation of P^3

Three features of the R1 P^3 have been cited as evidence for a shift in the function of that tooth. These include loss of projecting paracones (buccal cusp), absence of shearing wear facets on the anterior faces of the paracones, and the development of two large subequal sized cusps separated by well defined antero-postero sulci (Conroy 1972; Tattersall 1975; Lewis 1934). All three characteristics are supposed to show the elimination of pongid-like puncturing and shearing function, and replacement by crushing and grinding in R1 (as in hominids).

To investigate whether or not R1/R2 P^3 s exhibit one pattern or the other, it is necessary to examine closely the precise differences in the pongid and australopithecine P^3 .

Clearly, morphological and occlusal wear differences between australopithecine and pongid P^3 s exist, and indicate an important functional divergence. Pongid (extant and fossil) P^3 s are characterized by two very heteromorphic cusps, this heteromorphy being greater in earlier forms like (Proconsul). The larger (and usually non-projecting in extant pongids) buccal cusp (paracone) normally occludes against the distal slope of the protoconid of P_3 . This articulation regularly produces a set of shear facets (one on P_3) which sharpens the paracone. Additionally, the shearing extends upwards and sometimes produces a pointed tip (perhaps for puncturing) which is maintained throughout

most of the animal's lifetime. Thus, dentally old individuals may retain pointed P^3 s. The smaller, lingual cusp also usually exhibits anterior shear, however, there may also be wear which blunts the tip of this cusp. This latter type of wear is also seen on the lingual cusps of the molars.

Thus, pongid P^3 s usually have two types of wear and presumably two functions. Initially, the unworn crowns possess heteromorphic cusps. Because the lingual and buccal cusps are worn differently, cusp height heteromorphy increases with age. Blunting wear reduces the height of the lingual cusp faster than shearing wear reduces the buccal cusp's height.

In contrast to this morphological and functional pattern, the australopithecine P^3 initially has more nearly homomorphic cusps, which both ultimately exhibit blunting wear. Shearing against P_3 is absent in almost all specimens. Because blunting wear proceeds more equally on buccal and lingual cusps, cusp height heteromorphy is minimized until one of the cusps becomes perforated and the softer exposed dentin is worn more rapidly. Thus, early hominid P^3 s usually have only a single type of wear (blunting), and it appears that the entire tooth is involved in crushing and grinding. Thus, dual function has been lost; shearing surface has been eliminated. Given this framework of variation, form, and function, (Sivapithecus) and R1/R2 can be compared.

Paracone Projection and Cusp Heteromorphy

Paracone projection estimates can only be obtained from unworn or slightly worn P^3 s in situ. Paracone projection cannot be determined from isolated P^3 s since it is measured in relation to the occlusal plane. Early Miocene (Proconsul) P^3 s display the greatest degree of paracone projection when compared to other hominoids. However, among fossil pongids the degree of paracone projection appears to be sexually dimorphic. Males tend to have more projecting paracones than females. In contrast to (Proconsul), extreme projection was not found on either extant pongids or australopithecines. Thus, in both lineages there has been a trend away from the condition in (Proconsul).

Within R1/R2, two Indian specimens retain P^3 in situ: GSI D.185 and YPM 13799. The former is almost unworn, the latter moderately worn. Unlike (Proconsul), the paracone of the P^3 of D.185 projects only very slightly, the paracone of the P^3 of YPM 13799 does not project at all. However, since both specimens probably represent females, it remains to be seen how much an unworn male P^3 might project (the Hungarian male specimen RUD 15 is moderately worn). Within (Sivapithecus), specimens GSI D.299/300 and YPM 13837 both preserve unworn P^3 crowns; however, both teeth are isolated. The P^3 of GSI D.196, although broken lingually, is the sole unworn (Sivapithecus) P^3 in situ, and it too has a non-projecting paracone. Thus, at present,

R1/R2 and (Sivapithecus) cannot be shown to differ. Both appear to be evolving in a direction typical of all later tertiary pongids and hominids.

Cusp Heteromorphy

With respect to cusp heteromorphy, R1/R2 and (Sivapithecus) clearly follow a pongid pattern; the buccal cusp is much larger in all dimensions and heteromorphy is increased with dental age because of blunting wear on the smaller lingual cusp. The unworn P^3 crown of R1/R2 specimen GSI D.185 possesses two pointed cusps. The larger buccal cusp has shearing wear (discussed below), and its greater mesiodistal length gives the entire tooth a more triangular appearance. R1/R2 specimen YPM 13799, dentally older, exhibits lingual cusp blunting, considerable cusp heteromorphy (as Hrdlicka noted, 1935), and a prominent paracone. A similar degree of heteromorphy characterizes the known P^3 s of (Sivapithecus).

Shearing Wear

P^3 shearing wear facets can be directly or indirectly observed on a majority of R1/R2 specimens (GSI D.185, FT 46/47, RUD 15). However, it is absent on one specimen, YPM 13799. This distribution is not unlike pongids previously discussed, or (Sivapithecus); all but GSI D.299/300 and GSI D.196 exhibit anterior shear.

There has been some support for the idea that the missing P^3 crown of FT 46/47 was hominid-like (Simons and Pilbeam 1965) in that it lacked shearing wear. To the

contrary, pongid-like shear can also be demonstrated for this specimen, but only indirectly. Since the shear facet on the P^3 in pongids is the result of occlusion with the posterior face of the protoconid of P_3 , the presence of a shear facet on the back of the protoconid of P_3 can be taken as indirect proof of the existence of a facet on the anterior plane of the paracone of P^3 .

While examining FT 45/46/47 in Nairobi, I removed a thin layer of shellac covering the posterior face of the P_3 protoconid. A shear facet was revealed, indication of pongid-like shear with P^3 . Additionally, australopithecine-like blunting wear was absent on the large protoconid. Similar observations were noted for other mandibles of R1/R2 like GSI D.298 and RUD 17 and for the vast majority of (Sivapithecus) mandibles.

Thus, R1/R2 and (Sivapithecus), like pongids in general, have dual function P^3 , unlike australopithecines who have lost shearing action between P^3 and P_3 and replaced it with blunting wear.

Markedly Bicuspid Maxillary Premolars

The last feature, marked bicuspidation and well defined antero-postero sulci on maxillary premolars of R1 merely indicates that it was a hominoid. All hominoids have two well defined cusps on their maxillary premolars. Perhaps, in (Proconsul), some specimens possess a ridge of enamel which transverses the antero-postero sulcus (BMNH 16647 for example). However, in all later fossil and

extant pongids and hominids, this transverse ridge is almost never present, or never as well developed. Small ridges may be present in some pongids, but these can also be seen in R1/R2 specimen GSI D.185.

(12,13) Relatively Broad Molars, Relatively Broad P⁴

It has been observed that R1 is characterized by relatively broad molars in both jaws, and that this feature supports its inclusion in the hominids (Conroy 1972; Simons 1972; Simons and Pilbeam 1972; Conroy and Pilbeam 1973; Tattersall 1975). The suggested functional model underlying this proposition is that taxa exerting powerful forces in chewing, such as australopithecines and Gigantopithecus can be expected to have broad posterior teeth in order to increase area for mastication, while maintaining a short face. Expansion in the buccolingual direction would mean a greater percentage of crushing and grinding surface available, posterior to the origin of m. masseter, a muscle that provides powerful vertical and lateral forces. The combination of short snout and large posterior teeth brings a large proportion of m. masseter force through the mid portion of the tooth row, in both vertical and lateral movements. In contrast, fruit and leaf eating pongids are supposed to have smaller posterior tooth areas, longer snouts, and narrower posterior teeth (the result is less tooth area in a longer palate).

These expectations were tested in living taxa of known diet, as well as in fossil hominoid samples, by use of a simple breadth/length index:

$$I = 100 \times \frac{\text{buccolingual breadth}}{\text{mesiodistal length}}$$

This index certainly includes the effects of inter-

proximal wear. Ideally, only unworn molars should be compared interspecifically. However, if interproximally worn molars are eliminated in the comparisons, the fossil samples would be drastically reduced or completely emptied. Consequently, all specimens, regardless of dental age, were included. Each sample contains a range of interstitially worn teeth. However, in the extant pongid samples, specimens with very heavy interproximal attrition were excluded. At the same time, it should also be noted that a number of specimens were included in R1 because they exhibited heavy interproximal wear. These were included in the R1 sample listed in Tables 7 and 8. Thus, the index means, for all taxa listed in tables 7 and 8 should be considered over-estimates, and conclusions derived from these comparisons are tentative.

Because molar shape has been used as a sorting criterion between (Sivapithecus) and R1, an additional set of comparisons, including only interproximally unworn or slightly worn specimens, were made to determine whether or not this criterion can be used to distinguish them.

Data for the three maxillary and mandibular molars (dental age not controlled) are presented in Tables 7 and 8. I have previously published some data concerning this question (Greenfield 1975) using measurements provided by D.R. Pilbeam. The results given here differ only slightly, but are based on a larger sample of measurements which this author recorded from the original specimens.

TABLE 7
MAXILLARY MOLAR BREADTH/LENGTH INDICES

TAXON	M ¹			M ²			M ³		
	$\bar{X}(N)$	OR	SD	$\bar{X}(N)$	OR	SD	$\bar{X}(N)$	OR	SD
<u>(Proconsul)</u>	118(19)	108-128	6.0	116(18)	107-125	5.6	126(9)	116-138	7.2
australop.	113(73)	94-136	9.9	115(48)	101-131	7.5	115(46)	98-133	8.6
<u>Gorilla</u>	105(350)	94-127	5.6	104(350)	95-119	5.1	104(350)	92-124	6.1
<u>Pongo</u>	109(137)	90-126	5.6	115(134)	101-132	6.9	116(111)	99-134	6.8
<u>Pan L.</u>	106(310)	85-127	7.7	107(330)	91-124	7.0	111(285)	92-131	6.8
<u>Pan P.</u>	112(53)	100-126	5.2	115(54)	100-137	7.0	120(32)	105-133	7.4
R1	110(4)	104-117	5.5	108(3)	106-111	---	110(3)	105-113	---
R2	113(5)	103-122	7.1	110(3)	105-115	---	113(3)	111-116	---
<u>(Sivapithecus)</u>	112(11)	104-118	4.2	111(7)	106-121	5.6	109(7)	105-115	4.3
<u>G. blacki</u>	105(118)	86-122	6.9	105(118)*	86-122	6.9	107(91)	88-134	8.8

*M¹ and M² not sorted.

TABLE 8
MANDIBULAR MOLAR BREADTH/LENGTH INDICES

TAXON	M ₁			M ₂			M ₃		
	$\bar{X}(N)$	OR	SD	$\bar{X}(N)$	OR	SD	$\bar{X}(N)$	OR	SD
(<u>Proconsul</u>)	87(29)	75-97	4.7	87(19)	82-94	3.3	79(21)	68-88	5.7
australop.	97(60)	82-123	8.3	94(56)	83-114	5.9	89(29)	74-105	6.5
<u>Gorilla</u>	87(370)	81-100	3.9	87(370)	79-102	4.3	88(335)	79-102	4.6
<u>Pongo</u>	91(125)	81-97	3.5	93(133)	75-106	5.3	89(110)	80-102	5.1
<u>Pan t.</u>	90(231)	78-100	5.6	94(237)	80-102	5.2	93(218)	77-130	6.0
<u>Pan p.</u>	92(48)	80-106	5.3	91(50)	78-104	5.1	94(37)	82-109	6.7
R1	---	---	---	89(5)	84-92	4.8	85(7)	83-92	3.1
R2	90(4)	88-96	---	92(6)	84-99	5.3	84(5)	77-92	4.1
(<u>Sivapithecus</u>)	87(16)	80-95	4.4	89(14)	75-94	5.0	83(16)	76-90	4.0
<u>G. blacki</u>	85(110)	75-96	4.1	*85(110)	75-96	4.1	83(65)	77-93	3.6

*M₁ and M₂ not sorted.

In the maxilla (Table 7), the living pongid taxa vary from Gorilla gorilla with the narrowest molars to Pan paniscus with the broadest. That this is not simply an allometric relation based upon body size, is indicated by the fact that Pongo, the second largest taxon, has molars almost as broad as those of the pigmy chimpanzee. On the other hand, the contrast between the two Pan species suggests that relative molar breadth is not directly related to diet, at least within the dietary range of the pongids represented.

With the exception of the (Proconsul) sample, all of the fossil taxa fall completely, or almost completely, within the living pongid ranges. Gigantopithecus blacki has molars almost as narrow as Gorilla while at the other extreme, the australopithecines closely resemble Pan paniscus in relative breadth. The (Proconsul) sample has the relatively broadest maxillary molars. If this is assumed to be the ancestral condition, it appears that relative breadth reduction characterizes both hominid and pongid lineages. In this context, R1/R2 could not be placed on either lineage on the basis of relative molar breadth. One might argue for pongid status because the molars are relatively narrower than the australopithecine sample, but on the other hand, the range of variation in living pongids shows that a substantial amount of variation can be expected in contemporary species. It is also

apparent that there are no significant differences between interproximally worn R1/R2 and contemporary (Sivapithecus) samples.

In mandibular relative molar breadths (Table 8), similar relations are apparent although the trends are almost exactly opposite. In this comparison, Gorilla has the narrowest molars, while the broadest are found in one or the other Pan species. If, again, (Proconsul) is taken as the ancestral condition, it is apparent that both extant pongids and fossil hominids are characterized by relative mandibular molar broadening. In contrast to the maxilla, the trend has proceeded further in australopithecines than in extant pongids: australopithecine M1s are the broadest of any hominoid. Alternately, the australopithecine M1 sample includes a number of specimens with very heavy interproximal wear, and therefore the difference with pongids may be a consequence of this. Interestingly, Gigantopithecus alone follows the opposite trend. The mandibular molars become relatively narrower, paralleling the maxillary teeth.

In this context, (Sivapithecus) molars are narrow, approaching, but not exceeding, the (Proconsul) condition. The few R1/R2 molars are not significantly different from contemporary (Sivapithecus) teeth. Since relatively narrow molars represent the ancestral condition in both pongid and hominid lineages, the relative narrowness of R1/R2 molars cannot be used to place the sample on either

lineage, and as in the maxillary, the index does not separate R1/R2 from (Sivapithecus). This is clearly true for the interproximally worn teeth listed above, and for the interproximally unworn (or slightly worn) specimens listed below (Table 9). The data show that relative molar breadth does not distinguish the two and therefore it cannot be used as a sorting criterion.

In sum, three points are raised by this analysis. First, the relation of relative molar breadth to diet does not seem obvious. In spite of the restricted dietary range, the living pongid range of maxillary relative molar breadths encompasses all of the fossils except (Proconsul). The two megadont fossil forms (australopithecines and Gigantopithecus) fall at opposite ends of the range. Second, if (Proconsul) represents the ancestral condition, there has been relative narrowing of the maxillary molars and a lesser degree of relative broadening of the mandibular molars in both the pongid and hominid lineages. In the maxilla, R1/R2 falls fully within the pongid range, and likely also within the expected hominid range. In the mandible, R1/R2 closely resembles the ancestral condition for both. Therefore in both jaws, relative molar breadth cannot be used to place R1/R2 on either lineage. Third, there is no significant difference between R1/R2 and the contemporary (Sivapithecus) sample.

TABLE 9
MOLAR LENGTH/BREADTH INDICES*

	M^1		M^2		M^3	
	$\bar{X}(N)$	OR	$\bar{X}$	OR	$\bar{X}$	OR
R1/R2	103(2)	102-104	107(3)	106-116	112(3)	105-116
(<u>Siva-</u> <u>pithecus</u>)	110(4)	104-114	112(3)	110-117	109(4)	106-115

	M_1		M_2		M_3	
	$\bar{X}(N)$	OR	$\bar{X}(N)$	OR	$\bar{X}$	OR
R1/R2	---	---	83(2)	83-83	85(4)	81-90
(<u>Siva-</u> <u>pithecus</u>)	84(4)	82-87	84(3)	75-91	84(6)	76-90

*Interproximally unworn or slightly worn specimens.

Relatively Broad P₄

There has been support for the idea that R1 and australopithecines are characterized by relatively broad P₄s (Pilbeam 1969a), and presumably this phenomenon was part of the general broadening for the molars. Given the same problem of control over interproximal attrition, the data (Table 10) show tentatively that this conclusion is not supported. All hominoid ranges overlap extensively, and further, R1/R2 P₄s could be characterized as narrow. Early Miocene (Proconsul) has relatively narrow P₄s and R1 R1/R2, if derived from (Proconsul), exhibits some relative broadening. However, (Sivapithecus) is relatively more broadened than R1/R2. Among extant pongids, only Pongo has narrower P₄s than australopithecines. Moreover, G. blacki, for which australopithecine-like diet and dental adaptations (including posterior tooth broadening) have been proposed, has the narrowest P₄s. In sum, the data tentatively do not support previous observations about R1, nor is there any corroboration of prior functional hypotheses.

TABLE 10
RELATIVE P_4 BREADTH/LENGTH INDICES

TAXON	N	$\bar{X}$	OR	SD
(<u>Proconsul</u>)	19	107	83-117	8.4
australopithecines	42	115	88-161	11.8
<u>Gorilla</u>	30	118	96-133	8.4
<u>Pongo</u>	30	111	98-125	6.3
<u>Pan troglodytes</u>	30	114	96-127	6.1
<u>Pan paniscus</u>	49	114	86-149	13.8
R1	3	112	102-125	---
R2	6	110	102-120	6.9
(<u>Sivapithecus</u>)	10	115	101-136	11.1
<u>G. blacki</u>	78	104	94-121	5.3

(14,15) Interproximal Wear, Tooth Crowding

Interproximal wear refers to the attrition between adjacent teeth. An adaptive model has been proposed relating the rate of interproximal attrition to diet. It has been suggested (Simons 1968, 1970; Conroy 1972; Tattersall 1975) that rapid and extensive interproximal wear is associated with savannah diet and that it is a diagnostic hominid feature. Further, it was supposed that this criterion presumably could be used to distinguish an early hominid from contemporary pongid species.

Interproximal wear is a function of dental age and rate of wear. Presumably, hominid rates should be greater than those found among extant pongids. To test this expectation, interspecific interproximal wear rates have been calculated for two groups relevant here: Pan, and the australopithecines (Wolpoff 1971). Wolpoff's data show that the average chimpanzee wears his teeth interproximally faster than the average australopithecine. Depending upon the tooth, the interproximal wear rates in Pan were $1\frac{1}{2}$ to 3 times greater than in australopithecines. Since Pan is primarily a frugivorous forest floor dweller, the functional model as it now stands, must be rejected. However, using another model (Wolpoff, personal communication) and additional data, the observed interproximal rates may be explained. Perhaps the higher rates in Pan reflect greater mesial force directed posteriorly when C^1 and the anteriorly directed P_3 occlude.

Absence of this occlusal relationship in australopithecines would diminish the mesial force and, subsequently, lower interproximal rates would be expected. Additional interproximal wear data for Krapina hominids show that the australopithecine rates are 3 to 12 times faster. So perhaps, the original dietary model does work with groups of taxa with similar C/P_3 relationships.

Although the rates are unknown, the dentitions of all fossil (and extant) pongids display extensive interproximal attrition. Among these taxa, in many instances, this wear is so great that the entire mesial and distal enamel tooth planes have been removed and there is dentin-dentin contact between adjacent teeth. Extensive interproximal wear is not typically hominid.

Among (Sivapithecus) and R1, the samples are too small and the rates of maturation unknown. It is impossible to estimate interproximal wear rates; however, one can observe that occlusally well worn teeth in (Sivapithecus) (No.18039, D.191, D.180, D.181, D.178, YPM 13807, and D.306) have well developed interproximal wear facets just like those found on heavily worn R1 teeth (YPM 13799, D.199). Similarly, slightly worn (Sivapithecus) specimens (for example YPM 13811, AMNH 19412, D.196, D.299/300) may show little or no interproximal wear; however, one can make identical observations on slightly worn R1 (D.185 No.18068, D.118/119, BMNH 13264) and R2 (D.185, D.186, D.187, No.18068) specimens.

Tooth crowding can also be found on old (Sivapithecus) (for example No.18039) and R1/R2 specimens (BMNH 15423), but it can be found in all pongid taxa and hominids (Wolpoff 1971) as well. Again, if one is to make inter-specific comparisons, dental age must be controlled. When this is done, it is clear that older individuals, regardless of familial association, will display great interproximal wear, and perhaps tooth crowding. At present, therefore, assessments of interproximal wear have little value in an analysis of R1/R2.

(16,17) Thick Molar Enamel, Flat Wear

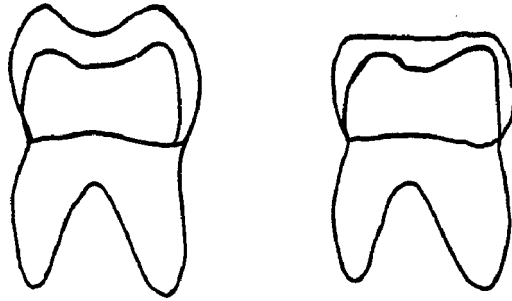
It has been suggested that R1 and australopithecine molars are characterized by thick enamel and flat wear (Simons 1972; Simons and Pilbeam 1972; Conroy 1972; Tattersall 1975; Pilbeam 1969b). Further, these features are supposed to be related to a rapid attrition diet which favored crushing and grinding and free mandibular movement. Roots, grass, seeds, rhizomes, and grit are some of the items included in this reconstructed diet.

Thick Molar Enamel

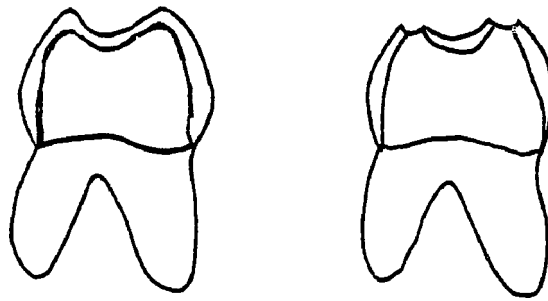
Until very recently, there were only rough techniques available for interspecific comparisons of molar enamel thickness. It is therefore necessary to emphasize the very tentative nature of the analysis below, which is based upon rough qualitative observations. Entirely different conclusions could be found when the more precise techniques are applied to the same specimens.

In the present work, a method of thick molar enamel detection, proposed by Simons and Pilbeam (1972), is used (with slight modifications). Basically, the nature of occlusal wear underlies the method. If cusps wear down considerably (even to a flat plane) without enamel perforation, then the enamel cap is thick. Conversely, if slight occlusal wear results in enamel perforation, then the enamel cap is thin. This relationship, between occlusal wear and enamel thickness, is shown schematically

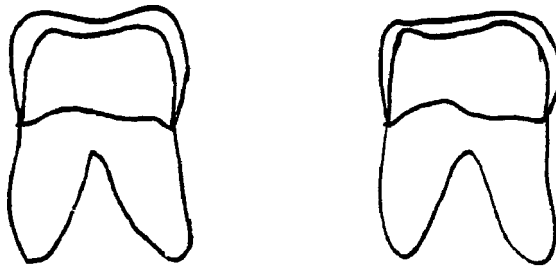
Figure 5 Molar Enamel Thickness and Occlusal Wear



a. Thick enamel and flat wear



b. Thin enamel and cupped wear



c. Thin enamel and flat wear

(Figure 5 a-b). An exception, however, can be noted. Molars with low unworn cusps can wear flat without enamel perforation despite the fact that their enamel may be thin (Figure 5c). This is so because the unworn crown is nearly flat (low crowned) prior to the onset of occlusal wear. Among hominoids, Pongo molars have this configuration (also Pan to some extent), a fact overlooked in a previous publication (Greenfield 1974). Thus, this method by itself cannot be used to demonstrate the presence of thick enamel with certainty. However, if used in conjunction with tooth morphology (of unworn molars), and broken specimens (where enamel thickness can be directly observed), perhaps a general (but not precise) picture of enamel thickness can be obtained for the relevant hominoids.

That enamel thickness and diet are related seems intuitively plausible. One could hypothesize that the diet of savannah or terrestrial forms, like australopithecines, including small hard foods (seeds), grasses (which contain silica), rhizomes, roots, and grit (Jolly 1970; Wolpoff 1971; Pilbeam 1972; Simons 1972) promotes rapid occlusal attrition. Thus, perhaps to delay the disadvantageous effects of attrition, thick molar enamel would be selectively advantageous. Interspecific observations are presented below to evaluate this possible functional relationship.

Among extant pongids there is considerable variation

in enamel thickness and cusp height, especially between taxa. Gorilla, a forest herbivore, has very high molar cusps which perforate after slight occlusal wear. This combination of high cusps and rapid perforation is probably an adaptation to leaf eating. On the other hand, Pan and Pongo molars have lower cusps than Gorilla and it appears to take longer (more wear) for enamel perforations to start. Thus according to the qualitative method, their enamel is thicker.

Like Pan and Pongo , Early Miocene (Proconsul) molars are lower crowned than Gorilla and appear to require greater wear (than Gorilla) to perforate. Thus the enamel caps of this Early Miocene form are perhaps as thick as those of Pan and Pongo, and thicker than Gorilla.

Compared to pongids, most australopithecine molars wear considerably prior to enamel perforation. Most occlusal details, ridges, cusps, groove patterns, etc. are worn away completely, or nearly so, prior to perforation. Broken specimens confirm the presence of very thick enamel (for example OH 30). Molnar and Gantt's (1977) recent quantitative investigations of enamel thickness have shown quantitatively that modern human molars possess thick enamel compared to macaques and pongids.

These interspecific comparisons, if accurate, support the hypothesized relationship between a diet which includes hard, tough, and gritty foods and thick

molar enamel. However, this association is based upon a reconstructed australopithecine diet. Perhaps, molar enamel of extant savannah cercopithecoids can be compared to closely related forest dwelling forms to confirm this relationship.

Compared to (Proconsul) and extant pongids, R1/R2 and (Sivapithecus) seem to possess thicker molar enamel caps. This is deduced from patterns of occlusal wear and broken specimens. First, no R1/R2 or (Sivapithecus) specimens are perforated after slight occlusal wear as in Gorilla. In R1, specimens D.199, YPM 13814, and YPM 13799 all possess at least one tooth with considerable occlusal wear and no perforations. (Sivapithecus) specimens D.1, D.179, D.180, and No.18070 demonstrate the same phenomenon. In addition, broken (Sivapithecus) specimen YPM 13842, slightly worn, has a very thick enamel cap, and No.18070, although worn nearly flat without extensive perforation, still has some enamel cap left (this was observed at its broken portion).

The cusps of R1/R2 and (Sivapithecus) molars are more bulbous and less pointed than in (Proconsul), but are more or less equal in height. Since it seems that greater occlusal wear was required to perforate enamel in R1/R2 and (Sivapithecus), they possess thicker molar enamel than (Proconsul). A similar trend, but of greater magnitude, is indicated for australopithecines. Presumably, similar dietary selection was operating in these taxa.

In sum, conclusions about interspecific variation in molar enamel thickness and its adaptive significance can only be very tentative in the present work. Precise quantification of large samples is required. This kind of investigation is currently being done by Molnar and Gantt. However, according to a proposed method which gives rough estimates (hopefully somewhat accurate) of enamel thickness, extant pongids and (Proconsul) seem to possess thinner enamel than R1/R2, (Sivapithecus), and australopithecines. It was further hypothesized that thicker enamel may be associated with harder and tougher foods and that the posterior teeth of R1/R2 and (Sivapithecus) were evolving in that direction.

Flat Wear on Posterior Teeth

Flat wear is a consequence of approximately equal rates of wear on buccal and lingual cusps. Eventually, prior to enamel perforation, a flat occlusal plane is produced.

An adaptive model can be proposed to explain the relationship between flat occlusal planes produced by blunting wear, and diet. With flatter occlusal morphology, slicing, shearing, and puncturing functions are de-emphasized while grinding and crushing are favored. Presumably, a diet including small, hard, or tough foods requires powerful crushing and grinding and selects for flatter occlusal morphology. Additionally, flat wear, as

defined above, indicates that the entire surface of each posterior tooth is used for this purpose and displays blunting wear on all cusps. Perhaps the reduction of cusps by blunting wear promotes the loss of inter-locking cusps and thus permits greater mandibular mobility in both antero-postero and bucco-lingual directions.

Flat chewing posterior tooth planes are rarely observed among extant and Early Miocene pongids. Rather, a different pattern of posterior tooth wear is observed, for most individuals. In these taxa, mandibular molars and premolars display much greater buccal, rather than lingual, cusp wear and premolars possess shearing planes. Conversely, on maxillary posterior teeth, greater wear occurs on lingual cusps. Given the unequal rates of wear, as the animal ages, the wear differential between buccal and lingual cusps increases. Thus on any one individual, M1 almost always has the greatest wear differential (because it is the first permanent posterior tooth to erupt) and wear differentials decrease posteriorly (M1-M3). Blunting (from crushing and grinding) wear is greater on one side of each posterior tooth in pongids. The other side is used for shear (premolars) or exhibits less blunting wear. This is probably a consequence of the more broadly set maxillary tooth rows.

One can compare the pongid pattern with the flatter and generally more even wear pattern frequently observed

on unperforated australopithecine posterior teeth. While many australopithecine posterior teeth show cusp wear asymmetry they are blunted by wear and shearing is absent. Presumably, this flatter wear from blunting indicates the dietary selection operating. The effects of this selection are a maximization of crushing and grinding tooth surface and free movement of the mandible. Perhaps the more flat wear reflects more equally spaced maxillary and mandibular dental arches in australopithecines.

The pongid pattern also characterizes R1/R2 and (Sivapithecus) posterior teeth. A few specimens (GSI D.199, No.18070, and D.298) may have flat occlusal planes (on one or more teeth) but the majority, like pongids, show differential buccal and lingual cusp wear (lingual wear on maxillary molars and premolars is greater, buccal wear on mandibular molars and premolars is greater). In addition, R1/R2 and (Sivapithecus) premolars possess shear. One can also observe that wear differentials decrease posteriorly. Thus, crushing and grinding surface was not maximized and not all posterior tooth cusps wear worn down by blunting.

In sum, pongids, R1/R2, and (Sivapithecus) share a pattern of asymmetric cusp wear on posterior teeth and also exhibit shear on premolars. In comparison, some australopithecines have flat wear but most appear to have blunting wear on all posterior tooth cusps.

(18) Bunodont Cusps

Another aspect of the crushing and grinding complex supposedly shared by R1 and australopithecines is bunodontia. Bunodont molars possess low and rounded cusps and occlude like mortar and pestle; they are designed for crushing and grinding. In contrast, pointed cusps, or molars with elaborate enamel crests are designed for puncturing and shearing functions, respectively.

Compared to other primates, hominoid molars are, in general, bunodont. However, among hominoid taxa, there is considerable variation. Among extant pongids, Gorilla has the highest cusps, however, these do not remain pointed. Rather, they are perforated quickly by slight occlusal wear and subsequently become cupped. These cups, surrounded by much harder enamel, may be analogous to the ridged occlusal patterns of other mammalian herbivores. Shearing is related to this configuration. It is also noteworthy that perforations first develop on the lingual cusps of the maxillary molars and buccal cusps of the mandibular molars. In contrast, Pan and Pongo, frugivores, have much lower cusps and greater surfaces for grinding. For example, talonid basins are relatively much larger. These taxa, especially Pongo, also have very detailed enamel wrinkling and unworn cusps can be pointed and connected by sharp ridges. However, none of these configurations appear to be specifically designed (when first erupted) for mortar and pestle action.

Unworn Early Miocene (Proconsul) molars have low cusps like Pan and Pongo; however, they are usually more pointed and many sharp crests connect these cusps. Talonid basins are not nearly as open as they are in Pan and Pongo. A few (Proconsul) specimens display flat occlusal wear (RU 2061, RU 1674, UCMP 52112), but the majority become perforated and cupped after moderate occlusal wear.

Compared to these taxa, australopithecine cusps are generally lower and more rounded. On many specimens, occlusal wear continues to blunt them, eventually, in many specimens, to a flat plane. Crowns appear bulbous and uncomplicated, especially after slight occlusal wear.

Both R1/R2 and (Sivapithecus), like australopithecines, possess uncomplicated tooth crowns. Cusps are low and rounded, and are blunted by occlusal wear. However, this blunting wear occurs predominantly on lingual cusps of maxillary molars, and buccal cusps of mandibular molars. In most respects, however, their molars can be called bunodont. This is not true for the premolars, which are more pointed and worn down in large part by shearing action.

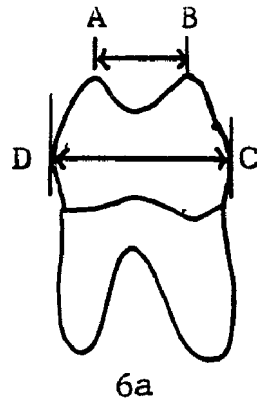
(19,20) Maxillary Molars with Large Open Occlusal
Foveas, Maxillary Molars with Vertical Buccal
and Lingual Sides.

There has been much support for the idea that the maxillary molars of R1 and australopithecines are characterized by open occlusal foveas, and more nearly vertical and shorter buccal and lingual slopes, while the maxillary molars of dryopithecines contemporary with R1 exhibit more closed occlusal foveas, and longer, angled buccal and lingual slopes (Pilbeam 1968, 1969b; Simons 1971, 1972; Conroy 1972; Tattersall 1975).

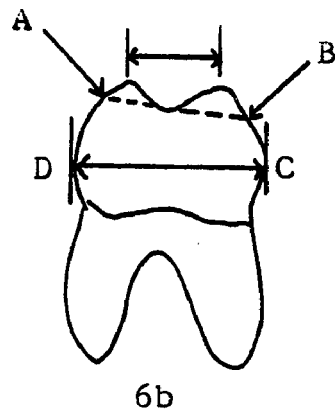
Maxillary Molars with Large Open Occlusal Foveas

One can suggest, if open foveas uniquely characterize australopithecines, an adaptive model explaining the selective advantage of this feature. In hominids, a savannah based diet, including many small, hard foods, selected for expansion of posterior tooth surface. It is known that relative to body size, australopithecines possessed very large posterior teeth when compared to pongids. However, it could also be true that posterior tooth surface expansion in hominids may have included, not only an increase in size, but also an increase in the percentage of grinding surface.

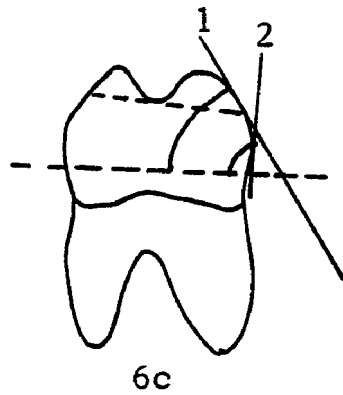
A quantification of this feature is based upon the distance between the apices of the protocone and paracone, relative to the maximum buccolingual breadth taken across these two cusps. An index (Pilbeam 1969b) "of minimum to



$$\frac{AB}{CD} \times 100 = \text{index}$$



AB increases with wear
and $\frac{AB}{CD}$ increases



molar slope angle
increases with wear

Figure 6 Occlusal Fovea Index and Age Changes in the Index.

maximum buccolingual breadth accross the protocone and paracone" has been used in prior publications. Figure 6 illustrates the measurements taken and calculation of the index which is also used in this study.

However, before interspecific data were collected, this author investigated the possibility of age related changes in the index. It was found, in all relevant taxa, that as maxillary posterior tooth wear proceeds, the apices of the lingual cusps migrate lingually as they reduce in height. Similarly, although to a lesser degree (much less in pongids), the apices of the buccal cusps migrate buccally as they are worn. Further, these "migrations" begin after only slight occlusal wear. These age changes are illustrated in Figure 6. In 6b, the minimum buccolingual breadth (AB) has been increased by the "migration" of the highest point on each cusp. Clearly, the index is directly increased. Figure 6c further shows how a long, angled slope can be reduced to a shorter and more nearly vertical condition. This evidence indicates that there must be a control on age related changes in interspecific comparisons. This can be accomplished by excluding all worn specimens. Thus, comparisons which follow are made between samples of unworn specimens. This is the only way morphological equivalents can be compared.

Given the above restrictions, data from unworn extant and fossil pongid and australopithecine maxillary posterior teeth (P^4 - M^3) were collected. Contrary to prior ex-

pectations, the results (Table 11) do not support the proposed functional model because relative to all other taxa, extant pongids have generally wider occlusal foveas. In fact, there has been considerable increases in both Pan and Gorilla if derived from a (Proconsul)-like ancestor. Similarly there has been some increase in the index in australopithecines also, however the magnitude of change was greater in extant pongids. Clearly, the data show wide occlusal foveas are not associated with savannah based diets, and both a frugivorous form (Pan), and an herbivorous form (Gorilla), exhibit wide open foveas. Thus, the functional significance of this feature remains obscure.

The small (Sivapithecus) and R2 samples of unworn specimens suggest that they are very similar to each other and to (Proconsul) and australopithecines. Both R2 teeth fall within the ranges of variation for the corresponding teeth in (Sivapithecus). This criterion does not separate R2 from contemporary pongids, and shows that both are like australopithecines.

In sum, the extant pongids have diverged more from the ancestral condition (represented by (Proconsul)) than other listed taxa. A more closed condition characterizes the maxillary posterior teeth of (Proconsul), (Sivapithecus), R2, and australopithecines, and the proposed functional model relating open occlusal foveas to a savannah based diet has been rejected.

TABLE 11
OCCLUSAL FOVEA INDICES (UNWORN TEETH)

	P ⁴			M ¹			M ²			M ³		
	(N) $\bar{X}$	OR	SD	(N) $\bar{X}$	OR	SD	(N) $\bar{X}$	OR	SD	(N) $\bar{X}$	OR	SD
<u>Gorilla</u>	(11)61	53-70	5.0	(13)60	54-68	7.0	(11)60	52-66	4.5	(10)65	59-74	5.5
<u>Pan t.</u>	(12)59	49-70	6.7	(15)61	53-75	8.0	(11)60	50-68	6.1	(9)66	58-74	5.7
<u>(Proconsul)</u>	(3)46	45-47	---	(3)49	40-54	---	(6)46	34-53	---	(3)50	43-55	---
<u>australopith.</u>	(3)47	43-51	---	(3)55	52-59	---	(5)48	43-54	---	(6)57	48-64	6.0
<u>(Sivapithecus)</u>	(1)44	---	---	(1)52	---	---	(3)47	44-52	---	(4)50	37-54	---
R2*	---	---	---	---	---	---	(1)51	---	---	(1)47	---	---

*There are no unworn P⁴-M³ in R1, and data for the Rudabanyan specimens were unavailable.

Maxillary Molars with Vertical Buccal and Lingual Sides

With respect to angled slopes, it was further observed that all unworn R2, (Sivapithecus), and australopithecine maxillary molars are characterized by long, angled slopes which become more nearly vertical as occlusal wear increases. Prior statements about this feature were based upon worn R1 specimens. Unworn R2, (Sivapithecus), and australopithecine maxillary molars are morphologically very similar and in most respects indistinguishable from each other.

(21) Subequal Sized Molars

In a recent publication (Simons 1972) a number of observations about molar size progressions in R1, australopithecines, and fossil, and extant pongids were presented. It was concluded that the molar size progression in R1 and australopithecines was typically $M1 \ M2=M3$, and in Dryopithecus, $M1 \ M2 \ M3$ (from here on, molar size progressions will be specified without the use of =, , or ; from left to right the smallest to largest molar will be listed). Thus, in hominids, it has been suggested that molars are more or less equal in size, whereas, in pongids, molars typically increase in size posteriorly.

A functional model explaining the proposed difference can be hypothesized. Perhaps the powerful chewing mechanism in australopithecines, combined with snout shortening comes to include the use of the anterior portion of the posterior teeth, selecting for larger P_3^3 , P_4^4 , and M_1^1 . If the ancestral (Proconsul) sequence was $M1M2M3$, then more dramatic increases in the size of $P3$, $P4$, and $M1$ might alter the sequence. In other words, powerful chewing would be shared more equally by all of the posterior teeth. The presence of molarized premolars and the anterior origin of masseter supports the idea that some of the powerful crushing and grinding occurred more anteriorly in australopithecines than in pongids.

Tables 12 and 13 list data to test prior statements about pongids and hominids, and the proposed functional

TABLE 12
MOLAR SIZE PROGRESSION
MAXILLARY MOLARS

SEQUENCE	<u>Gorilla</u>		<u>Pongo</u>		<u>Pan troglodytes</u>		<u>Pan paniscus</u>		<u>australopithecines</u>	
	N	%	N	%	N	%	N	%	N	%
M1 M2 M3	(7)	2.8	(9)	16.9	(2)	3.0	(0)	0	(12)	54.5
M2 M1 M3	(0)	0	(2)	3.7	(2)	3.0	(0)	0	(1)	4.5
M3 M1 M2	(125)	50.8	(20)	37.0	(30)	46.1	(18)	58.0	(1)	4.5
M1 M3 M2	(109)	44.3	(14)	26.4	(13)	20.0	(3)	9.6	(7)	31.8
M3 M2 M1	(3)	1.2	(7)	13.2	(16)	24.6	(9)	29.0	(1)	4.5
M2 M3 M1	(2)	1.8	(1)	1.8	(2)	3.0	(1)	3.2	(0)	0
Total N	(246)		(53)		(65)		(32)		(22)	

TABLE 13
MOLAR SIZE PROGRESSION
MANDIBULAR MOLARS

SEQUENCE	<u>Gorilla</u>		<u>Pongo</u>		<u>Pan troglodytes</u>		<u>Pan paniscus</u>		<u>australopithecines</u>	
	N	%	N	%	N	%	N	%	N	%
M1 M2 M3	(77)	34.5	(16)	26.6	(6)	5.1	(0)	0	(23)	79.3
M2 M1 M3	(0)	0	(0)	0	(3)	2.5	(1)	2.9	(0)	0
M3 M1 M2	(9)	4.0	(12)	20.0	(43)	36.7	(22)	64.7	(1)	3.4
M1 M3 M2	(137)	61.4	(32)	53.3	(34)	29.0	(4)	11.7	(5)	17.2
M3 M2 M1	(0)	0	(0)	0	(30)	25.6	(6)	17.6	(0)	0
M2 M3 M1	(0)	0	(0)	0	(1)	.8	(1)	2.9	(0)	0
Total N	(223)		(40)		(117)		(34)		(29)	

model. These data are based upon tooth areas, buccolingual breadth X mesiodistal length.

The data show that extant pongids display a great deal of variation within and between taxa. In the maxilla, only Pongo shows frequent presence of M1M2M3 (16.9%). All other extant pongid taxa, contrary to prior contentions, show very low frequencies of this sequence. In Pan, Pongo and Gorilla, M3M1M2 and M1M3M2 are the most frequently encountered sequences. Further, in both species of Pan there are considerable frequencies of M3M2M1 (24.6% and 29.0% for Pan troglodytes and Pan paniscus, respectively). Thus, in general, M2 is the largest tooth among extant pongids, while among australopithecine maxillary dentitions, M1M2M3 is the most frequently encountered sequence (54.5%) with M1M3M2 next most frequent (31.8%).

One can reach similar conclusions based upon the sequences for mandibular dentitions. Among extant pongids, M2 is generally the largest tooth. Further, australopithecine mandibular dentitions show that by far M1M2M3 is the most common sequence (79.3%).

In addition, average cross sectional areas for each molar were calculated (Table 14), and essentially support the data just presented. Most extant pongids have large M2s while australopithecines possess molars that increase in size posteriorly. The suggested functional model is clearly not supported by the data, nor are the prior

TABLE 14
CROSS-SECTIONAL AREAS FOR MAXILLA AND MANDIBLE

Maxilla

TAXON	M1		M2		M3		Sequence*
<u>Gorilla</u>	224.1	(409)	256.9	(409)	223.3	(363)	M3M1M2
<u>Pan t.</u>	115.5	(313)	109.9	(334)	91.2	(229)	M3M2M1
<u>Pan p.</u>	87.6	(52)	88.9	(54)	79.2	(33)	M3M1M2
<u>Pongo</u>	161.3	(138)	170.4	(134)	154.4	(112)	M3M1M2
aust.	187.6	(72)	223.9	(48)	231.3	(47)	M1M2M3

Mandible

TAXON	M1		M2		M3		Sequence*
<u>Gorilla</u>	208.7	(374)	262.3	(370)	252.5	(335)	M1M3M2
<u>Pan t.</u>	107.8	(231)	114.7	(231)	99.1	(218)	M3M1M2
<u>Pan p.</u>	85.2	(48)	90.2	(51)	76.9	(37)	M3M1M2
<u>Pongo</u>	154.1	(129)	176.6	(133)	170.0	(110)	M1M3M2
aust.	191.4	(59)	229.5	(59)	242.2	(59)	M1M2M3

*Sequence of average cross-sectional areas.

general statements about pongid and hominid variation.

Unfortunately, the small fossil pongid and R1/R2 samples do not permit detailed comparisons of frequency distributions. However, on the basis of the few specimens that do retain all three molars, patterns are suggested. Among Early Miocene (Proconsul), M1 is by far the smallest molar. Generally, M2 is smaller than M3, but there are a few individuals that show the opposite. Thus compared to extant pongids and australopithecines, it appears that australopithecines are more similar to the ancestral condition. Further, the specimens of R1/R2 and (Sivapithecus) that retain three molars show that they are also more similar to the ancestral condition, and australopithecines, than they are to extant pongids. In (Sivapithecus) and R1/R2, M1 is always smaller than M3 or M2. In some specimens, M2 is larger than M3, but in the majority of instances, M3 is larger than M2 (similar to (Proconsul)).

Perhaps, in all these taxa, the largest molar simply indicates the preferred chewing site. Some of the data on molar wear gradients, presented below, support this functional hypothesis.

In sum, molar progressions in (Proconsul), R1/R2, (Sivapithecus), Gorilla, and australopithecines are usually M1M2M3, with a smaller percentage M1M3M2. Pan and Pongo differ in that M2, more often than M3, is the largest in the sequence, and frequently M1 is largest.

(22) Differential Molar Wear Gradient

Adaptive interpretations of R1 and australopithecines have included a consideration of differential molar wear patterns. The term, molar wear gradient, has been used and it refers to differences in occlusal wear between adjacent molars (Simons and Pilbeam 1972; Simons 1972). It has been claimed that steep molar wear gradients are absent in pongids, while they occur commonly in R1 and australopithecines.

Referring to australopithecines, Le Gros Clark (1967) originally suggested that great differences between M1 and M3 occlusal wear (steep gradient) directly reflected temporally well spaced gingival eruptions, and indirectly a prolonged maturation, more like modern humans than extant pongids. More recently, Mann (1968, 1976), from X-rays of original materials, disclosed a modern human-type pattern of tooth eruption times in australopithecines, thus supporting Le Gros Clark's original conclusion. However, Mann's evidence, by no means, demonstrates the significance of molar wear gradient information in supporting that conclusion. In fact, Mann points out that it is independent of eruption spacing.

Others (Simons and Pilbeam 1972; Conroy 1972) have utilized this feature in interpretations of R1, concluding it to demonstrated delayed maturation (especially see Todd and Blumenberg 1974), and/or rapid occlusal attrition. However, two works (Mann 1968; Wolpoff 1971)

cast severe doubt on the usefulness of this feature as an indicator of delayed maturation.

It is important, before presenting interspecific data, to define exactly what is meant by steep, moderate, and slight molar wear gradients. Note these categories refer to differences in occlusal wear (this refers only to lingual cusp wear on maxillary molars and buccal cusp wear on mandibular molars) between M1 and M3 and not simply to heavily worn teeth.

Gradients were determined from combinations of varying stages of wear on the molars. The stages were defined as follows:

1. Stage 0: crown has no occlusal wear.
2. Stage 1: cusps show some wear, perhaps with slight perforations, but they remain fairly high and well defined. All original major grooves between cusps are present.
3. Stage 2: cusps exhibit more extensive enamel perforations, are worn nearly flat and are poorly defined. Perforations may be beginning to connect.
4. Stage 3: tooth worn heavily, cusps worn flat with extensive enamel perforation. Individual cusp perforations have united to form a much larger single perforation. Grooves and cusp patterns are obliterated.

Using these stages of wear, gradients were determined

as follows:

1. absent -- no difference in stages of wear on M1 and M3;
2. slight -- a difference of one stage between M1 and M3 (M1 with a higher stage);
3. moderate -- a difference between M1 and M3 of two stages (M1 with a higher stage);
4. steep -- a difference of three stages between M1 and M3 (M1 with a higher stage).

A few specimens had even greater (Stage 4) wear on M1 than defined under Stage 3. A combination of this extreme wear on M1 and Stage 1 wear on M3 was considered a steep gradient.

The Hamann/Todd collections in Cleveland provided sufficiently large samples of extant pongids to estimate frequencies of steep, moderate, and slight gradients. Pathological individuals with missing teeth were not included. Casts of R1 specimens GSI D.199 (mandibular) and GSI No.18064 (a maxilla) were compared to each extant pongid. These fossils preserve all three molars and have the greatest gradients in R1. In Pongo (N=8), 12.5% were steep, 25% moderate, 62.5% slight. In Pan (N=66), 6% were steep, 20% were moderate, 69% slight, and 5% absent. In Gorilla (N=100), 2% were steep, 24% moderate, 67% slight, and 7% absent. Since No.18064 has a moderate gradient and D.199 a slight to moderate gradient, 25% or more of each extant pongid sample had gradients as steep or steeper than

the two R1 specimens that are maximum for their sample. Clearly, moderate and steep gradients occur commonly in extant pongids. Further, hominid-like delayed maturation cannot be used to explain this variation.

For australopithecines, the following frequencies were obtained: steep -- 28%; moderate -- 50%; slight -- 21%; absent -- 0%. Thus, while frequencies of steep and moderate gradients are high in australopithecines, there is extensive overlap with extant pongids. Clearly, there has been an overestimation of the taxonomic relevance of this feature.

These data do not necessarily support rejection of the delayed maturation model. However, data on Papio, an extant savannah cercopithecoid, clearly do. Very high frequencies of steep (and moderate) molar wear gradients have been reported for that taxon (Mann 1968). Gradient frequencies obtained by this author for Papio (N=55) were: steep -- 11%; moderate-- 52%; slight -- 37%; absent -- 0%. These frequencies are much more like those obtained for australopithecines than for extant pongids. Further, since the duration of Papio dental maturation is roughly one half that of extant pongids, the delayed maturation model, as it now stands, can be rejected. If delayed maturation is a factor, it cannot, by itself, explain the observed interspecies frequencies of steep and moderate gradients. Consequently, a number of alternate explanations were sought.

One likely factor is the rate of occlusal attrition.

The delayed maturation model assumed that rates of attrition were constant between taxa, and only the length of the intervals between eruptions was significant. This notion can readily be rejected because higher rates of attrition can be associated with certain diets. Highly abrasive grit (and grass with silica), and tough, hard foods certainly wear down teeth more rapidly than frugivorous or herbivorous foods obtained in a forest environment (given a constant body size/tooth size relationship).

Since Papio's diet includes much more abrasive substances than extant pongid diets, subsequently higher rates of occlusal attrition could explain the observed high frequencies of steep and moderate gradients (63%) in this savannah adapted cercopithecoid. However, the much lower occlusal attrition rates predicted for extant pongids do not entirely explain the molar wear gradient frequencies obtained, and therefore alternate explanations were sought. The simple possibility that extant pongids prefer to chew in the anterior portion of the molar series was investigated. One method of testing this possibility is to observe age changes in frequencies of steep, moderate, and slight gradients. If all three molars are used equally after they have erupted, then dental age should have no effect on the frequencies. If M1 and M2 are used more so than M3, then frequencies of steep and moderate gradients should increase with dental age. The opposite is expected if M3 is used more than M2 or M1. Since it is difficult

to quantify dental age, only two age classes were used; class 1 -- M3 just coming into occlusion and unworn; class 2 -- all other adults with M3 already in occlusion. Gradient frequencies were calculated for both classes and then compared.

In extant pongids, less than 5% of class 1 individuals had steep or moderate gradients, while class 2 frequencies of steep and moderate gradients were increased over the total sample's frequencies (listed above). Thus, preferential M1 and M2 chewing may explain the observed frequencies in the total adult sample. Additionally, in extant pongids, M2 (and sometimes M1) is the largest molar (see section on molar size progression). This may also be indicative of preferred chewing site and it supports the preference chewing hypothesis generated to explain the molar wear gradient frequency changes.

The Papio sample was also tested for effects of preferential tooth use. For class 1 individuals there were 0% absent, 14.3% slight, 66.7% moderate, and 19% steep gradients (total sample was 0, 37%, 52%, and 11%). For class 2 individuals, the following frequencies were obtained: 0% absent, 47.8% slight, 45.5% moderate, and 6.6% steep. Thus the opposite occurs here. High attrition rates (probably) produce great numbers of steep and moderate gradients in class 1 individuals. However, at later dental ages, preferential chewing on M3 decreases the the numbers of steep and moderate gradients. Additionally,

data published by Lauer (1975) show that M3 is by far the largest molar (almost twice the size of M1 in the mandible, and one and one half times larger in the maxilla) in Papio, and therefore may underscore the relatively greater importance of this tooth. Further, it is likely that rapid destruction of the M1 crown would lead to preferred chewing at a more posterior site. Similarly, australopithecine M3s are the largest molars and perhaps a Papio-like pattern could be demonstrated (small sample size prohibits testing at present).

One could hypothesize that other variables may directly or indirectly affect the distributional pattern of molar wear gradients. For example, baboons and australopithecines have expanded tooth surface (relative to body size), and therefore there is less attrition per unit tooth area than in pongids. This high tooth area/body size ratio in hominids would naturally tend to decrease gradients, and may therefore be a significant factor. In addition, there are undoubtedly interspecific differences in enamel hardness. Even slight differences could result in very different rates of attrition and change the distributional pattern of gradients. Unfortunately, at present, little information is available on interspecific differences and consequently it cannot be investigated further. Lastly, flatter and more even wear on many australopithecine molars indicates more total tooth surface utilization, while in pongids (and R1/R2), greater cusp wear asymmetry

indicates less than total tooth surface utilization. Thus, if one could control all other factors, australopithecines probably further reduced attrition per unit tooth surface by simply using a greater percentage of the available surface of each molar. The effect upon gradient distributional patterns is obvious.

Clearly, no simple explanations for the observed interspecies distributions of gradients is supportable. The original delayed maturation model can be rejected because both rapidly maturing baboons and slowly maturing australopithecines exhibit comparably high frequencies of moderate and steep molar wear gradients. Alternate explanations, including varying rates of attrition and preferential tooth use, are supported by most of the data, although other factors like enamel hardness, the percentage of utilized tooth surface, and enamel thickness are undoubtedly significant. Certainly, dental age must be controlled in any interspecific comparisons. In fact, the only way of limiting the effects of preferential tooth use on the distribution of gradients is to compare class 1 individuals, i.e., those specimens that have erupting M3s. Thus, with respect to R1, the only specimens which one can be sure are not affected by preferential tooth use are the youngest adult specimens.

It can be further concluded from the above that the only evidence acceptable as proof for delayed maturation in R1 should be patterns of dental eruption taken from

X-rays of subadult and juvenile specimens as did Mann (1968, 1975) for the australopithecines. This is a more reliable method of estimating relative rates of maturation in hominoid fossils. Unfortunately, no juvenile R1/R2 exist, and therefore the rate of maturation is unknown.

Under the constraints discussed above, R1/R2 and (Sivapithecus) can be compared. However, because interspecific differences can only be understood (if at all) in the distributions of larger samples, it is difficult, at present, to evaluate R1/R2 and (Sivapithecus). Further, since age factors greatly influenced the distributional patterns of extant taxa examined, it is appropriate to consider only the very youngest adults in the R1/R2 and (Sivapithecus) samples to eliminate potential changes in gradient frequencies which are a consequence of preferential chewing. At a very young adult age, it is more likely that the observed gradients reflect attrition rates and/or maturation rates. At older adult ages, one almost certainly adds in a factor which cannot be controlled.

The youngest adult specimens in R1/R2 are D.185, BMNH 16649, and D.118/119. D.185 has M^1 and M^2 erupted, and in occlusion and on the distal side of M^2 there is a small interproximal wear facet indicating that M^3 was probably in occlusion as well. M^1 has only stage 1 wear. Thus, if M^3 was unworn, this specimen would have a slight gradient. Similarly, BMNH 16649, which is generally not

accepted as an African R1 specimen, also probably had a slight gradient. Present is a very slightly worn M^1 crown and the broken roots for a fully erupted M^2 . The preserved portion of the C^1 socket shows that it was large at the alveolar margin, suggesting that a considerable part of this tooth had erupted. If true, it is usually the last tooth in the sequence to erupt in male pongids, and therefore it is possible that M^3 was in occlusion as well. If M^3 was unworn and in occlusion the gradient was very slight. If the M^3 had not yet erupted through the gingiva, the molar wear gradient might have been slight had the animal lived until the M^3 was in occlusion. Finally, the type specimen of R1, D.118/119, has an M_3 with very slight occlusal wear and M_2 with stage 1 wear. If M_1 had stage 2 wear, the gradient would have been slight, or slight to moderate.

Similarly, most young adult (Sivapithecus) specimens (YPM 13811, YPM 13825, D.196, D.299/300) have only slight gradients. However, one specimen, AMNH 19412, exhibits a nearly moderate gradient. Thus, the molar wear gradient evidence for rapid attrition and/or delayed maturation in R1/R2 or (Sivapithecus) can be considered negative or inconclusive at best (if one considers the molar wear gradient information useless). Since the majority of young adult specimens in R1/R2 and (Sivapithecus) have slight gradients like pongids, it is likely that steeper gradients found on dentally older specimens are a conse-

quence of preferential chewing. Thus, given the fact that the most significant difference between the distributions of gradients of forest dwelling pongids and savannah forms like Papio (and australopithecines) revolves around the young adult specimens, R1/R2 and (Sivapithecus) clearly follow a more pongid-like pattern.

It is interesting to note that two young adult mandibles from Turkey (De Bonis et. al. 1974, 1975), similar in size to D. indicus, have moderate gradients, unlike R1/R2 and (Sivapithecus).

(23,24,25) Deep Palate, Parabolic Dental Arcade, Palate
Short and Broad

Deep Palate

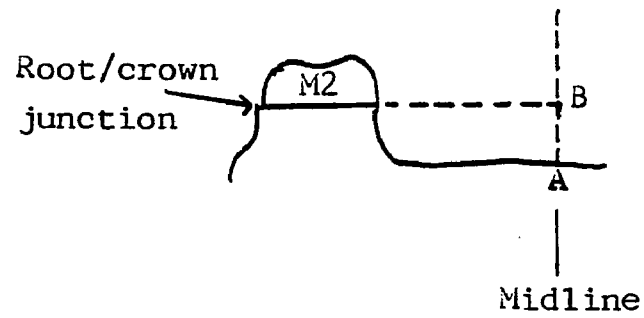
A deep palate has been reconstructed for R1 and is supposedly a feature shared with australopithecines, while pongid palates are typically shallow (Conroy 1972; Tattersall 1975).

Jolly (1970) suggested a functional relationship between diet and palate depth. He said:

... a possible functional explanation involves the tongue. Experiments with grain chewing in Homo sapiens suggest that objects not crushed by one masticatory stroke tend to be pushed by the rolling action into the oral cavity, whence they are guided back to the teeth by the tongue. This demands much more constant, agile, lingual motion than is needed in masticating a fibrous bolus of fruit (or turf). Thus a chewing apparatus of the hominid type might be expected to include a thick, muscular, mobile tongue, accommodated in a large oral cavity. The highly arched palate, capacious interramal space, and absence of a simian shelf may all be interpreted as elements of the large oral cavity....

This functional model may also be used to explain the adaptive significance of the widely spaced dental arches in australopithecines.

To test the functional model, comparative data (measurements defined in Figure 7) are presented below (Table 15). These data show extant pongids, contrary to prior claims and expectations, possess deep palates. Within this extant group, much larger and herbivorous Gorilla does not have an appreciably deeper palate than Pan and Pongo. Further, females of all three taxa have



$\overline{AB}$ = palate depth at M^2

Figure 7 Measurement of Palate Depth at M^2

TABLE 15
PALATE DEPTH AT M²*

	$\bar{x}$	OR	SD
<u>Gorilla</u> male (25)	19.3	16.6-22.2	1.4
female (25)	18.9	15.6-22.1	1.9
<u>Pongo</u> male (10)	18.5	14.7-21.0	2.6
female (10)	17.4	15.9-20.4	1.8
<u>Pan</u> male (25)	15.3	11.4-18.4	1.9
female (25)	14.4	12.0-17.4	1.5
australopith- combined (9) ecines sexes	15.3	9.5-22.5	2.8
<u>D. nyanzae</u> male (1)	10.0	---	---
<u>D. major</u> male (1)	10.5	---	---
R1+ female (2)	9.0	7.0-9.0	---
R2 female (1)	11.0	---	---
(<u>Sivapithecus</u>) male (3)	13.5	12.5-14.0	---

*Defined in Figure 7.

slightly shallower palates than males.

One can contrast the extant pongids with Early Miocene (Proconsul). The D. major palate from Moroto (UMP 62-11) is 10.5mm deep at M2, a value which falls below the ranges for Pan and Pongo, yet its teeth are metrically similar. In addition, other (Proconsul) specimens (1948, 50, BMNH 16647), Aegyptopithecus, and (Rangwapithecus) (KNM SO 700) support the conclusion that the earliest pongids all have shallow palates. Thus from the above, three conclusions can be drawn: there is considerable variation among pongids (blanket statements are not supportable), extant forms have evolved much deeper palates than their ancestors, and the functional model proposed by Jolly is not supportable.

Like extant pongids, the data show australopithecines possess deep palates relative to early Miocene (Proconsul), and thus a similar trend characterizes both lineages. However, one significant difference between extant pongid and australopithecine samples is the great range of variation found only within the latter. It is of further interest to point out that the new Afar specimens reported by Johanson and Taieb (1976) have shallow palates compared to the later australopithecine sample and fall at the low end of the total range.

A comparison with all of the above taxa shows R1 palates (FT 46 and YPM 13799) cannot be considered particularly deep. The R1/R2 values listed (Table 15) are

estimates, however, at the points they were taken (near the palatal midline) the palate arches were leveling off and therefore they probably are fairly accurate. FT 46, dentally larger than YPM 13799, has a much shallower palate. This may reflect its greater antiquity, i.e., it is more like ancestral (Proconsul) specimens. Contrary to prior contentions, contemporary (Sivapithecus) palates are deeper; however, this may be related to their greater overall size. But, in general, Indian R1/R2 and (Sivapithecus) palates are deeper than those in (Proconsul) and thus are evolving in the same direction as extant pongids and hominids.

In sum, extant pongids, australopithecines, R1/R2, and (Sivapithecus) evolved deeper palates, regardless of dietary preference. Thus, the suggested functional model is not supportable. Further, R1/R2 palates cannot be considered deep when compared to (Sivapithecus).

Parabolic Dental Arcades. Palate Short and Broad

Reconstruction of the dental arcades and palate shape in R1 has been the focus of a number of recent publications (Simons 1961; Vogel 1973; Walker and Andrews 1973; Frayer 1976; Petit-Maire 1974). Originally it was believed that the dental arcades of the Indian R1 specimens (YPM 13799) indicated a hominid-like (parabolic) condition distinguishable from the U-shaped arcades of extant pongids (Lewis 1934). Later it was further suggested that not only Indian R1 specimens, but African R1 specimens too,

had parabolic dental arcades (Simons and Pilbeam 1965). Unfortunately, all of these early reconstructions were based upon specimens that were not complete past the midline. This led to variable splaying of the tooth rows posteriorly, and consequently different reconstructions. However, more recently (Andrews 1971), a mandible fragment (FT 45) which preserves sockets from the left C1 to the medial portion of the socket for the right C1, has been associated with the Fort Ternan maxilla (FT 46/47). This association permitted a more reliable reconstruction of the dental arcades, at least for African R1. After orienting the mandible fragment in the correct position, Walker and Andrews (1973) occluded the maxillary fragments. The result was "posteriorly diverging and nearly straight tooth rows, rather than widely spaced and curved tooth rows such as are found in modern man. The palate is narrow and tooth rows are relatively very elongated."

Vogel (1973) and Frayer (1976) have questioned the reconstruction of parabolic arcades for Indian R1. They suggested that one could justify a reconstruction with straight, more nearly parallel tooth rows.

Recently, new and more complete R2 specimens have been described by Kretzoi (1975). One specimen, RUD 12, a female, is virtually identical to the Fort Ternan specimen as reconstructed by Walker and Andrews (1973). RUD 12, a maxilla (preserving considerable bone along the midline) has a straight tooth row, which gently converges

anteriorly. Another specimen, RUD 15, a male, has an almost anteriorly divergent tooth row like D. indicus male GSI D.196. An additional mandible from Candir, Turkey (Tekkaya 1974) is more strongly V-shaped with long straight tooth rows.

A functional model relating parabolic dental arches and broad, short palates to powerful vertical masticating strokes can be proposed. It has been noted that an orthognathic face contributes to powerful chewing by placing greater posterior tooth surface posteriorly, and permitting more vertical arrangements for m. masseter and m. temporalis. However, in powerful masticators, like australopithecines, orthognathy was accompanied by great enlargement of posterior tooth surface relative to body size. Without additional modifications, this expansion might have lead to greater prognathism. Perhaps, in order to maintain orthognathism despite the presence of large posterior teeth, tooth rows became curved anteriorly, posteriorly divergent, and more widely spaced. In addition, an equally useful alteration is disproportionate tooth broadening (see section on relative molar broadening). That M1, in australopithecines, the center of the posterior tooth row, was significantly broader than in any other taxon, supports this possibility. Together, the net effect of these modifications is a reduction or maintenance of the straight distance from M3 to C1 despite tooth expansion. These structural modifications

would maintain orthognathy unlike straight parallel tooth rows in a long, narrow palatal arrangement. Alternately, more broadly spaced tooth rows may reflect a general cranial base broadening and increasing cranial capacities in hominids. Mandibular condyles would be set further apart, in turn affecting the spacing of the tooth rows.

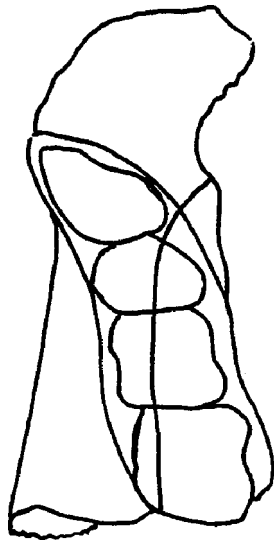
A consideration of interspecies variation shows that prognathic extant pongids, in general, possess straight parallel tooth rows, and according to the data published by Petit-Maire (1974), long, narrow palates. In these taxa, considerable tooth surface is placed anterior to the root of the zygomatic. In the mandible, tooth rows are also straight and often parallel; the overall appearance is long and narrow. However, there is variation in all these features and the nature of this variation is significant. In female extant pongids, with diminutive canines, the anterior portions of the tooth rows (from I2 to P3) may be curved toward the midline. In other female specimens, the tooth rows remain straight, but converge slightly towards the midline. With slightly curved rows, the overall appearance in both maxilla and mandible is that of an elongated parabola. With convergent but straight rows, the overall appearance is slightly V-shaped. In contrast to females (especially true in Gorilla), nearly the opposite is found for some males. In the maxilla, male tooth rows may curve outwardly in

the region around P3 and C1. Alternately, tooth rows may be straight, but angle outwardly. Similar patterns are observed for some male mandibles; in the region around P3 and C1, the tooth rows curve or angle outwards.

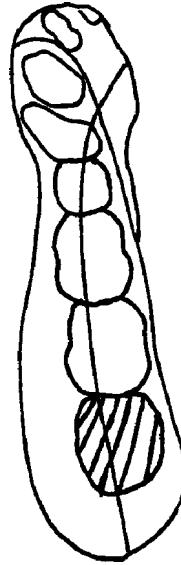
All, or most, of this sex variation is probably related to the size and angulation of maxillary and mandibular canines. Although female C1 may angle laterally, the root is not relatively large. On the other hand, male C1 roots are disproportionately large, and lateral angulation seems to affect the entire tooth row. In fact, the presence of large mandibular C1 may direct the tooth row in a direction opposite to the inferior half of the mandibular corpus. Seen from the occlusal level, this configuration can be likened to an elongated X (Figure 8).

Since there is sex variation within extant pongid taxa, interspecific comparisons must be controlled. Further, if comparisons between fossil specimens of known sex (canines present) also show similar sex variation then perhaps tooth row patterns can be used as sexing criteria for less complete specimens (i.e., those lacking canines).

Ancestral (Proconsul), like extant pongids, has, in general, straight tooth rows in both maxillae and mandible, and a V-shaped pattern is most common. However, there are several exceptions, especially in the maxillae. Predictably, the Moroto palate (UMP 62-11), with the largest canines of any (Proconsul) specimen (see canine



GSI No.18039



YPM 13811

Figure 8 Male (No.18039) and female (YPM 13811) mandibles are compared. Note the differences in the curvature of the tooth row relative to the contour of the inferior half of the respective corpora (indicated by a line drawn through the dentition).

section) has anteriorly divergent tooth rows. Similarly, BMNH 16647 (type of D. nyanzae) has nearly parallel tooth rows, but a relatively smaller canine (than UMP 62-11). It also is a male specimen. This, and the absence of female specimens with either parallel or anteriorly divergent tooth rows, suggests similar sex variation occurs in these Early Miocene pongids; and perhaps tooth row patterns can be used to sex less complete specimens. However, it must be noted that some male specimens have V-shaped rows. Lastly, according to the data presented by Petit-Maire (1974), (Proconsul) palates were long and narrow like Gorilla.

Looking now at the later australopithecine sample, their palates are shorter and broader (Petit-Maire 1974) and tooth rows curved and anteriorly convergent. However, here too, there is great variation, but it cannot be related to two canine morphotypes. Alternative functional explanations for this variation must be considered. First, some specimens have longer and narrower palates which fall within the chimpanzee range of variation (Petit-Maire 1974), while other specimens have straight tooth rows which may be parallel or slightly V-shaped. Since a majority of the unusual specimens (unusual for a hominid) possess small teeth, perhaps most of this variation can be explained in relation to body size. Perhaps larger individuals like Peninj, ER 729, ER 406, and SK 12 had relatively broader palates and more curved tooth rows

because they had very large posterior teeth. In these larger individuals, more extreme modifications were necessary to maintain or place even greater posterior tooth surface in a relatively posterior position. Broader palates and parabolic tooth rows were structural responses that maintained or increased the amount of posterior tooth surface. Smaller individuals, with lower caloric intakes, required less posterior tooth surface. Their palates are longer and narrower than those of the large individuals, and their tooth rows are less curved. The covariance between body size and these features and the data presented by Petit-Maire (1974) lend support to this model of allometry. However, it must be noted, that while few later australopithecines possess parabolic dental arcades, sensu stricto, all have some or a partial expression of the adaptations to orthognathy, more so than in any pongid.

It is significant that the new and earlier australopithecines from the Afar and Laetolil have more elongate and less curved tooth rows which are either parallel (AL 200-1a) or gently convergent anteriorly (LH 4). This, and the fact that their anterior tooth/posterior tooth proportions fall in or near the dryopithecine range (and outside or at the end of the later australopithecine range), and that their zygomatics insert more posteriorly than in the majority of later australopithecines, suggests different dental function, and sets new expectations for recognizing a Miocene australopithecine ancestor. At the least,

this new material may suggest something about the course of hominid evolution. These points will be reviewed and discussed in the section on adaptive patterns.

Walker and Andrews (1973) have shown that African R1 tooth rows were straight, slightly divergent posteriorly, and that the palate was long and narrow. This set of features characterizes dryopithecines in general, and especially (Sivapithecus). Since the Fort Ternan specimen probably represents a female, perhaps a male, when found, will have more nearly parallel tooth rows.

The pattern of sexual variation noted in extant pongids and (Proconsul) can already be documented in (Sivapithecus) and R2. Female specimens have more nearly V-shaped tooth rows, while males have either parallel or slightly divergent tooth rows anteriorly. Additionally, the elongated X pattern is expressed in males (see Figure 8); their tooth rows may curve in a direction opposite to that of the inferior half of the mandibular corpus. In females (YPM 13811 is figured), the tooth row more closely follows the contour of the inferior half of the mandibular corpus. In R2, the Rudabanyan specimens show a (Sivapithecus)-like pattern. They have straight tooth rows, long, narrow palates and depending upon the sex, slightly V-shaped (RUD 12) or slightly divergent (anteriorly) (RUD 15) tooth rows.

There is a much less complete picture of Indian R1/R2 variation because few specimens are preserved at the mid-

line. However, all Indian R1 (and R2) specimens with two or more teeth, clearly have straight, not medially curved, tooth rows (GSI D.185, YPM 13799, BMNH 15423, No.18064, YPM 13814, GSI D.298). The tooth row of one specimen, GSI D.199 is not entirely straight, but is curved outwards, not towards the midline, moving anteriorly from M_3 to P_4 . The same outward orientation is suggested for less complete YPM 13814 (M_3 - M_1), but without a curve. In addition, the tooth rows of both specimens cross their corpora. The fact that their tooth rows angle outwards is highly suggestive of the presence of large canines, and therefore, both probably represent males (see later section on taxonomy).

While it is not yet possible to reconstruct the shape of the palate, the Indian R2 female specimen D. 298 suggests V-shaped tooth rows. D. 298 is the most complete mandible, preserving both incisor sockets, a tiny canine socket which shows that the root of the C_1 did not descend to the base of the corpus, and P_3 - M_2 crowns. Further, like (Sivapithecus), the tooth row of D.298 closely follows the contour of the mandibular corpus. Thus, the patterns emerging for Indian R1/R2 mirror those seen in (Sivapithecus), Hungarian R2, and African R1. What is even more significant from the standpoint of phylogenetic reconstruction is the fact that all of these Miocene forms are more similar to the earlier australopithecines from the Afal and Laetolil than they are to later australopithecines.

(26,27,28) Short Thick Mandibles, Anteriorly
 Deep Horizontal Rami, Internal Morph-
 ology of the Mandibular Symphysis

Three features of the mandibular corpus have been cited in support of hominid-like masticatory functions in R1: increased mandibular robustness under the molars (Simons 1964; Conroy 1972; Tattersall 1975), anteriorly deepened horizontal rami (Pilbeam 1969a), and development of symphyseal transverse tori unlike those in extant pongids (Pilbeam 1970).

Short Thick Mandibles

Functionally, one could associate thickened mandibular corpora in R1 to australopithecine-like mastication which was probably characterized by powerful vertical compressive forces transmitted through the posterior teeth. These compressive forces include the force of the food on the teeth, and the forces exerted by the muscles of mastication on the mandibular corpus.

The ideal location to measure mandibular robusticity on the mandibular corpus is at M_1 . At this position, in all hominoid taxa, no portion of the ascending ramus is present. Unfortunately, with the exception of two Hungarian R2 specimens, no R1/R2 specimens preserve bone in this region. Therefore, a robusticity index was calculated from measurements at M_2 . At this tooth, in most taxa compared below, the root of the ascending ramus is present, and therefore, indices listed in Table 16 do not

directly reflect the effects of compressive forces. Shorter faced taxa will naturally include a greater portion of ascending ramus at M_2 , and therefore more robust corpora in these forms at M_2 do not necessarily indicate greater vertical compressive forces.

Given these limitations, an index to quantify corpus robustness was devised:

$$I = \left(\frac{\text{thickness of corpus at } M_2}{\text{height of corpus at } M_2} \right) \times 100$$

Looking first at extant pongids (Table 16), there is some, but not considerable, sexual dimorphism in the index. However, within each sex, and between taxa, there is great variation. Examination of the unlisted, raw Gorilla data (height and thickness) indicates that the height of the mandibular corpus at M_2 is much more dimorphic than the index (or thickness). Because dimorphism in corpus height far outweighs dimorphism in corpus thickness, the much shorter female Gorilla mandibles are, on the average, more robust (higher indices) than those of the males. In Pan and Pongo, corpus height dimorphism does not exceed corpus thickness dimorphism, and male indices are consequently, on the average, higher.

Early Miocene (Proconsul) data show that, like Gorilla, female indices are higher. Further, the raw data show that, like Gorilla, dimorphism in corpus height exceeds corpus thickness dimorphism. (Proconsul) has the most gracile mandibular corpora out of all the hominoids

TABLE 16
(MANDIBULAR THICKNESS/MANDIBULAR HEIGHT) X 100
(Taken at M₂)

	FEMALES				MALES			
	(N)	$\bar{X}$	OR	SD	(N)	$\bar{X}$	OR	SD
<u>Pan</u>	(20)	55	45-72	6.9	(20)	60	49-74	6.6
<u>Pongo</u>	(10)	50	44-59	4.4	(10)	56	44-65	5.4
<u>Gorilla</u>	(20)	65	55-83	6.8	(20)	54	45-71	6.8
australopithecines*	(32)	66	55-80	8.6				
R2	(2)	59	57-61	---	(4)	64	52-73	---
R1	(1)	57	---	---	(2)	70	67-73	---
<u>D. sivalensis</u>	(2)	65	61-69	---	(0)	--	---	---
<u>D. indicus</u>	(2)	56	53-59	---	(3)	80	76-85	---
(<u>Proconsul</u>)	(4)	54	47-62	---	(2)	50	44-56	---

*Combined sexes.

considered here, and thus all pongid lineages (except Pongo females) appear to be characterized by increased corpus robustness since the Early Miocene.

The data indicate australopithecine mandibles are generally more robust at M_2 than fossil and extant pongids. However, there is clearly extensive range overlap. Thus, mandibular robustness is a poor taxonomic marker for pongids and hominids. The data show that increased mandibular robustness characterizes both pongid and hominid lineages, if derived from a (Proconsul)-like ancestor.

Similarly, both $R1/R2$ and (Sivapithecus), compared to earlier (and extant) pongids have more robust mandibular corpora and greater sexual dimorphism in the index. Controlling sex, index values for $R1/R2$ are either similar or lower than values for (Sivapithecus). Thus, one cannot use this criterion to indicate a more hominid-like condition in $R1/R2$.

Whatever the functional implications, $R1/R2$ and (Sivapithecus) are similar to australopithecines, and all possess robust mandibles at M_2 when compared to Early Miocene and extant pongids. Sexual dimorphism in $R1/R2$ and (Sivapithecus) is greater than in Pongo or Pan. Additionally, the pattern of dimorphism in $R1/R2$ and (Sivapithecus) is unlike that for (Proconsul) and Gorilla (where female mandibles are more robust).

Anteriorly Deep Horizontal Rami

To date, no functional model has been proposed to

explain the supposedly unique presence of anteriorly deepening mandibular corpora in hominids and R1 (Pilbeam 1969a).

The author collected interspecific data to compare R1/R2, and derive a functional explanation for the observed variation. Mandibular corpus depths at P_4 and M_2 were taken and the ratio between them calculated (Table 17). These locations on the corpus were used because this maximized the number of fossil specimens to compare.

Among extant pongids, almost all mandibular corpora (both males and females) deepened anteriorly. A total of five specimens (two Pan, two Pongo, one Gorilla) exhibited a decrease in corpus height at P_4 (total N of 88). While male mandibles were usually taller, there were no dramatic increases at P_4 . In fact, P_4 depth on Pan female mandibles increased, on the average, 3.6mm, whereas the average male increased only 3.1mm. These data indicate that pongid corpora deepen anteriorly, however, this deepening does not seem to be sexually dimorphic.

Similarly, (Proconsul) males and females did not exhibit appreciable sexual dimorphism, and most corpora (all but one) deepened anteriorly. A comparison between (Proconsul) and extant pongids does not reveal any general trends.

The australopithecine sample also shows the tendency for their corpora to deepen anteriorly like extant and fossil pongids. Thus, this criterion is a poor tax-

TABLE 17
ANTERIORLY DEEPENING MANDIBULAR RAMI

	N	Depth(M ₂)*	Depth(P ₄)	ratio P ₄ /M ₂
<u>Pan</u>	(38)	27.0	30.4	1.12
<u>Pongo</u>	(10)	35.0	36.8	1.05
<u>Gorilla</u>	(40)	35.5	38.6	1.08
australopithecines	(9)	37.9	39.5	1.05
<u>D. indicus</u>	(3)	32.7	35.5	1.08
<u>D. sivalensis</u>	(1)	23.3	26.2	1.12
R2	(5)	23.0	25.1	1.09
R1	(2)	24.3	26.6	1.09
(<u>Proconsul</u>)	(8)	25.2	27.5	1.09

*Mean.

onomic marker, and has, perhaps, little or no functional significance in this context.

Like all other hominoids examined, R1/R2 and (Sivapithecus) mandibles deepen anteriorly. No sexual dimorphism was found, and both closely resemble each other and (Proconsul).

Inferior Transverse Torus

It has been observed that R1 inferior transverse tori are unlike those seen in pongids and similar to australopithecine transverse tori (Pilbeam 1969a; Tattersall 1975).

Unfortunately, little is known about the complex biomechanics of the mandibular symphysis, and further, it is important to point out that pongid and early hominid mandibular symphyses are highly variable. However, when present in pongids (Figure 9), in cross-section, the torus is usually thin or shelf like. In some specimens, this shelf extends back to P_4 , and through its entire length it is the most inferior portion of the mandibular symphysis. In comparison, when present, hominid inferior transverse tori are thicker and more rounded in cross-section (Figure 9), and do not project nearly as far posteriorly. Further, only a portion of their tori is the most inferior point on the mandibular symphysis.

R1/R2 (FT 45, BMNH 15423, GSI D.298) and most (Sivapithecus) specimens that preserve all or part of their mandibular symphyses clearly possess pongid-like

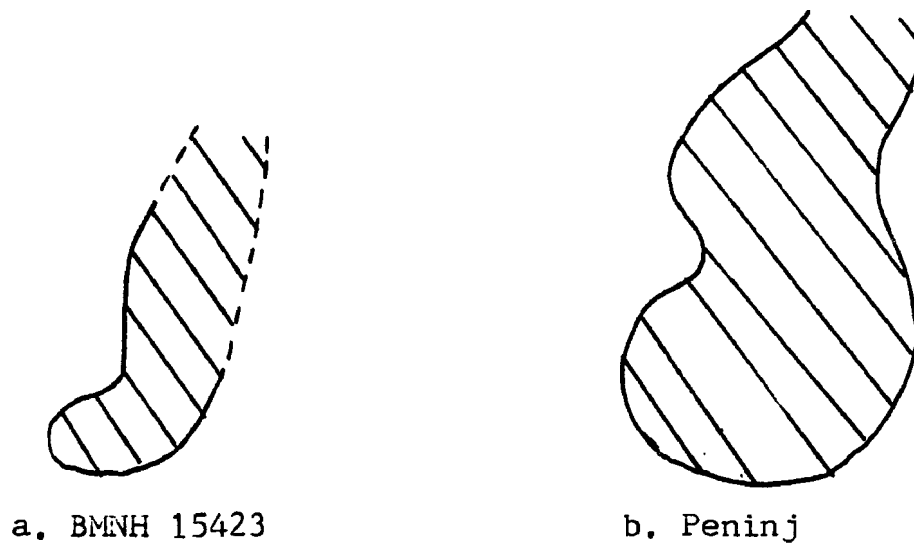


Figure 9a,b Mandibular Symphysis Cross-Sections

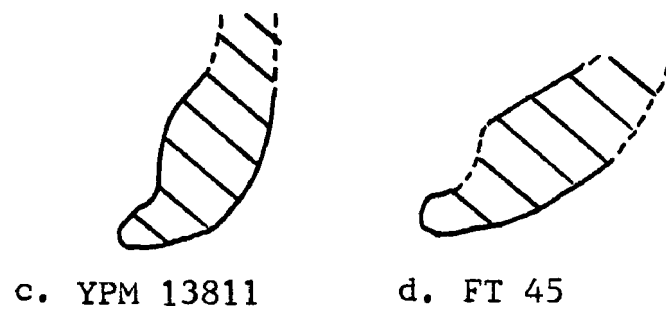


Figure 9c,d Mandibular Symphysis Cross-Sections
(Eurasian and African Specimens)

inferior transverse tori (see Figure 9), when they are present. However, there are exceptions. GSI No.18039 and the new Candir mandible have more hominid-like inferior transverse tori. Thus, the range of symphysis shapes in these Miocene hominoids overlaps the range observed for the earliest undoubted hominids. Unfortunately, one can only speculate at present about the functional significance of the various symphyseal morphologies.

(29,30,31,32,33) Reconstruction of the R1/R2 Face

A short deep face has been reconstructed for R1 (Simons 1972; Tattersall 1975; Conroy 1972) and presumably indicates the importance of powerful posterior tooth loading. However, a mechanical analysis of any masticatory apparatus usually requires a reconstruction of the cross sectional areas, positions, and lines of action of the muscles of mastication as well as an accurate picture of dental morphology. The poorly preserved specimens in R1 and (Sivapithecus) preclude this kind of analysis. No crania are preserved, merely dental and gnathic portions of the face. A mechanical analysis on material in this condition may reflect nothing more than the analyst's bias. In light of this, it will be useful first to discuss the major differences between australopithecine and extant pongid masticatory complexes (based upon complete material), and then examine the fossil evidence to see if and what masticatory patterns are indicated.

It is possible to summarize briefly some important differences between australopithecine and extant pongid masticatory complexes. The morphology of, and relationship between, dentition and cranium suggests that australopithecines were most probably adapted to powerful molar/premolar loading. They appear to have possessed thick molar enamel, and flat, expanded posterior tooth surface (relative to body size). Moreover, canines and premolars no longer provided shearing or puncturing functions.

Instead, the canines were probably used in gripping, and premolars had the singular function of adding surface for crushing and grinding. Further, incisors were small relative to the posterior teeth. Given this morphology, one can postulate selection for large posterior teeth and crushing and grinding functions. However, these adaptations probably varied with body size. For example, larger individuals (larger mandibular corpora) seem to exhibit greater molarization of the premolars, and even smaller anterior teeth relative to the posteriors (or larger posteriors relative to the anteriors).

Additionally, there were many mechanical adaptations for powerful chewing in the skull. M. masseter attached more anteriorly than in most pongids, and the face was usually placed more inferiorly and posteriorly. The result in most specimens (STS 5 a notable exception), was a deeper and more orthognathic face. The wide flare of the zygomatics (also variable) enclosed a large temporal fossa and added a greater lateral component to m. masseter. The area of attachment of this muscle on the zygomatics and gonial angles was usually extensive, and thus indicates that it had a large cross section. M. masseter also provided vertical forces and its line of action, in many specimens, went through all, or most, of the posterior teeth. Again, larger individuals tended to have more anterior origins of this muscle and correspondingly greater molarization of the premolars (Wolpoff 1973). M.

pterygoideus lateralis and m. pterygoideus medialis were also usually large, judging from their extensive attachments on the lateral pterygoid plate. Additionally, the spacious opening for m. temporalis between the zygomatic arch and the lateral wall of the cranium, seen in many specimens, indicates large cross sectional area for this muscle, and power is directly related to cross sectional area. In australopithecines, temporal fossa size shows that m. temporalis was well developed anteriorly as well as posteriorly. The large posterior component on a number of specimens is indicated by a large gutter on the superior side of the zygomatic process of the temporal (ER 406 for example). The large anterior component, however, added vertical crushing force to that of m. masseter and suggests important posterior tooth loading. Often, the combination of small cranium and large m. temporalis resulted in the formation of a sagittal crest, which was also well developed anteriorly.

There is great dental and cranial variation among australopithecines, however, most possessed, more or less, this chewing apparatus designed for posterior tooth loading. With respect to the Afar and Laetolil hominids, it remains to be seen what their entire masticatory complex was like. All indications from the dentition and lower portions of the face suggest a complex less specifically designed for posterior tooth loading. The anterior teeth are relative to the posterior teeth, larger than in the

later australopithecine sample, the tooth rows are elongate, there are fewer adaptations to orthognathy, and there is perhaps greater molar cusp wear asymmetry. All these features indicate greater emphasis on anterior tooth loading than in the later australopithecine sample. Thus, it may be that the powerful posterior tooth loading apparatus seen in the later australopithecines is a more recent development.

Perhaps a considerable part of the variation in the masticatory complex of the later australopithecines could be explained in relation to body size variation and allometry. Larger individuals were more robust, had much larger posterior teeth (proportionately smaller anterior teeth), greater molarization of the premolars, and more anterior attachments for m. masseter. The caloric requirements of larger individuals necessitated proportionately larger muscles and posterior tooth surface, relative to cranial size.

The known postcrania also suggest a wide range in body size, however, the mandibles and posterior tooth size ranges, relative to those postcrania, indicate a large chewing apparatus (when compared to pongids).

In contrast, extant pongids do not exhibit australopithecine-like masticatory adaptations. Extant pongid anterior teeth are hypertrophied (in Pan troglodytes and Pongo both incisors and canines are large; in Gorilla, only canines) relative to their posterior teeth. Canines

and unmolarized premolars are high cusped and have shearing and puncturing functions. Flat posterior tooth occlusal planes are not characteristically found in pongids, and relative to body size, extant pongid posterior teeth are small.

With respect to cranial and facial architecture, the zygomatic arch originates more posteriorly and great flare may be absent. Thus, the proportion of tooth surface, anterior to the origin of the zygomatic, is great relative to tooth surface under, or behind it (m. masseter originates more posteriorly). Also in extant pongids, m. temporalis is well developed posteriorly and its major line of action passes through the anterior teeth during anterior tooth loading. On the other hand, the anterior moiety of this muscle, which contributes compressive force during posterior tooth loading, is less well developed. As a consequence, sagittal crests, when present, usually are well developed posteriorly, less so anteriorly. Thus, most of the adaptations designed to maximize powerful posterior tooth loading are less well developed in extant pongids. The positions and arrangements of the muscles of mastication, and size of the anterior teeth, suggest a system designed for anterior tooth loading.

Obviously, the above summaries are based upon considerable quantities of relatively complete cranial materials. The relative muscle masses, the directions of pull, and their relative positions were known in addition

to dental information. In contrast to this situation, in R1/R2 and (Sivapithecus), most of the pertinent cranial information is unavailable. The morphology and metrics of their dentitions are largely known, but only a small, and perhaps insignificant, part of the architecture of the skull can be determined. What can or cannot be determined about cranial form in R1/R2 and (Sivapithecus) from the existing sample, and its functional significance, is discussed below.

The deep orthognathic face reconstruction of R1 has been supported by a number of workers (Simons 1972; Conroy 1972; Walker and Andrews 1973; Andrews and Walker 1976; Tattersall 1975). The features supposedly demonstrating this condition are vertical ascending rami, anterior coronoid processes, high zygomatics on the maxilla, high maxillary sinuses, and anterior origins of the zygomatics.

Roberts and Tattersall (1974) have pointed out some of the mechanical advantages of a deep, orthognathic face for powerful posterior tooth loading. A posterior and inferior position of the face relative to a superior and anterior position for the back of the skull results in a configuration favorable to the exertion of powerful vertical forces. Conversely, a long skull with prognathic face (more anterior and superior), and the back of the cranium in a more posterior and inferior position, maximizes the horizontal components of the muscles of mas-

tication (particularly m. temporalis) and is designed for anterior tooth loading. Given this additional functional framework, it is now appropriate to examine the individual features of the facial skeleton of R1/R2.

Vertical Ascending Ramus, Anterior Coronoid Process

It has been proposed that more nearly vertical ascending rami characterize deeper faced taxa like R1 and australopithecines, while prognathic extant pongids possess more posteriorly angled ascending rami.

Simple observation and measurement of ascending rami angles in pongids and australopithecines contradicts this notion. The ascending rami in Gorilla and Pongo ($\bar{x}=88^{\circ}$ for $N=10$ Gorilla, $\bar{x}=84^{\circ}$ for $N=10$ Pongo) are nearly vertical and compare favorably with australopithecines ($\bar{x}=84^{\circ}$, $N=10$). Thus there is no expectation that deeper faces are necessarily indicated by the ascending ramus angle, at least within the hominoids measured.

Prior statements about R1 were based upon specimens that preserved only the broken bases of their ascending rami which were barely preserved enough to rise past the alveolar margin. Certainly, any statements about the angle at which they were placed, and the relative position of their coronoid processes, were conjectural. However, new Pakistan specimens of (Sivapithecus) and the Hungarian materials preserve ascending rami that cross the alveolar margin. From these specimens one can show that the ascending rami crossed the alveolus at the anterior portion of M3, and

that the angle of ascent approached 90° . The crossing at M3 is slightly more anterior than in most extant pongids, and may suggest a slightly shorter face for both R2 and (Sivapithecus).

High Insertion of the Zygomatic

The position of the zygomatic above the tooth row has also been used to support the proposed deep face reconstruction of R1. However, among more prognathic and presumably shallower faced extant pongids, the zygomatics insert high on the maxillae. This is especially so in Gorilla and Pongo, both deeper faced than Pan. Additionally, many extant pongids have higher insertions than most australopithecines. However, both extant pongids and hominids are unlike Early Miocene (Proconsul). In these fossil pongids, zygomatics inserted far down on the face, just above the alveolar margin. Thus in both hominid and pongid lineages there has been a trend towards higher zygomatic insertion. It is also important to point out that two Afar specimens, preserving part of the zygomatic process on the maxillae, show a fairly low insertion compared to the later australopithecine sample.

In R1, FT 46 and GSI D.185 preserve all or part of the inferior roots of their zygomatics. The African specimen (FT 46) has a much lower insertion than the Indian specimen (D.185). However, both are higher than in (Proconsul). This is another feature where African R1 differs from Indian R1/R2, and shows greater similarities to

ancestral (Proconsul). While it is true that zygomatics are higher in R1/R2 than in (Proconsul), it is also apparent that a similar trend characterizes (Sivapithecus). Specimens GSI D.1 and GSI D.196 (and a new, but as yet undescribed, maxilla from Pakistan, GSP 11708) show higher zygomatics, relative to the occlusal plane, than D.185 (maximum for R1/R2). Correcting for size (the (Sivapithecus) species are larger than R1/R2), the zygomatics would probably be in approximately the same position in both.

Thus in all pongid and hominid lineages since the Early Miocene there has been a trend towards higher zygomatics. However, in this context, no significant functional differences can be inferred between R1/R2 and (Sivapithecus). And, lastly, while R1/R2 and (Sivapithecus) zygomatics are higher than in (Proconsul), they are placed lower on their maxillae than in most extant pongids and australopithecines.

It has also been suggested that high maxillary sinuses in R1/R2 indicate a deep face because it shows that there was a great distance from orbit to tooth row. Unfortunately, it is difficult to test that hypothesis because unless the sinus is exposed, it is impossible to determine its relative position. X-rays are necessary to compare interspecifically. Moreover, a sinus placed further away from the tooth row may indicate little about the total depth of the face. Sinuses could be in a relatively

high position on a shallow face, or as suggested, part of a totally deepened face. It can be noted, however, that a few (Proconsul) specimens show a much lower position for the sinus when compared to R1/R2 (D.185 for example) and (Sivapithecus) (D.1, D.196, and GSP 11708). Thus, if high sinuses indicate a deep face, this condition characterizes both R1/R2 and (Sivapithecus).

Anterior Zygomatic

The relative position of the zygomatic on the maxilla, in the parasagittal plane, almost certainly has functional significance. A more anterior position places the origin of m. masseter more anteriorly. Consequently, this increases its lever arm, and greater crushing and grinding surface is placed under or behind this muscle.

Data (Table 18) show that compared to australopithecines, extant pongids have, in general, more posteriorly situated zygomatics. In addition, since pongid anterior teeth are relatively large (in Pan and Pongo both incisors and canines are large relative to the posterior teeth, while in Gorilla, only the canines are especially large), and australopithecine posteriors greatly expanded, there is even greater functional difference between them, which is not reflected in the data in Table 18.

Similarly, when R1/R2 and (Sivapithecus) are compared to extant pongids, one finds that the former two have more anterior origins (M^1/M^2 or at M^1) for m. masseter. Again, the total gestalts of R1/R2 and (Sivapithecus) faces are

TABLE 18: MOST ANTERIOR POSITION FOR $\bar{M}$. MASSETER ON THE ZYGOMATICS (in %)

% originating at: p^4		p^4/M^1	M^1	M^1/M^2	M^2	M^2/M^3
<u>Gorilla</u>	male (42)	---	2.0	14.0	74.0	10.0
	female (44)	---	---	16.0	82.0	2.0
<u>Pongo</u>	male(7)	---	---	28.5	71.5	---
	female (8)	---	---	12.5	75.0	12.5
<u>Pan</u>	male (19)	---	---	21.0	63.0	16.0
	female (46)	---	2.0	4.0	70.0	24.0
australopith- ecines	combined sexes (12)	8.3	25.0	8.3	16.6	---
R1	male (0)	---	---	---	---	---
	female (2)	---	---	100.0	---	---
R2	male (0)	---	---	---	---	---
	female (2)	---	---	100.0	---	---
(<u>Sivapithecus</u>)	male (2)	---	---	50.0	50.0	---
	female (1)	---	---	100.0	---	---

not wholly reflected by these data. Compared to Pan and Pongo, these Middle Miocene forms had relatively smaller anterior teeth (or relatively larger posterior teeth), and compared to Gorilla and (Proconsul), relatively smaller canines (incisors are similar in size relative to the posterior teeth). Thus, R1/R2 and (Sivapithecus) have on the average, more anterior origins for m. masseter and less tooth surface anteriorly (more posteriorly), than extant or other fossil pongids. Like R1/R2 and (Sivapithecus), new Afar specimens have more dryopithecine-like dental proportions (anterior tooth surface relative to posterior tooth surface) with zygomatics that begin at M^1 and M^1/M^2 (Johanson and Taieb 1976). These are very similar patterns. However, in contrast to the later australopithecine sample, R1/R2 and (Sivapithecus) have relatively larger anterior teeth and zygomatics which begin at a more posterior position.

In sum, the preserved portions of the R1/R2 and (Sivapithecus) faces allow a few functional conclusions. Probably, the most supportable is, that in both, posterior tooth loading is more important than in any extant or Early Miocene pongid, and this represents a similarity to early undoubted hominids (especially the earliest part of the sample). The more anterior origin of m. masseter and greater proportion of posterior tooth surface under or behind this muscle (when compared to extant and Early Miocene pongids) supports this conclusion. Additionally,

the extreme lateral flare of the zygomatics seen on D.185, FT 45/46, and a new large undescribed (Sivapithecus) specimen suggest a strong lateral component for m. masseter, and perhaps a spacious temporal fossa to accomodate the ascending ramus and large m. temporalis. Both features are seen in many australopithecine crania. Further, a shorter face (shorter than in extant pongids) may also be indicated by the slightly more anterior ascending ramus, short premaxilla, and small anterior teeth. Small anterior teeth and snouts in R1/R2 and (Sivapithecus) suggest a narrow face (also deduced for (Proconsul)). The evidence for a deep face is more inconclusive because high zygomatics are, and high maxillary sinuses could be, found on shallower faced hominoids.

Placing the above conclusions about the R1/R2 (and (Sivapithecus)) face into the total cranial picture, one is still left with unanswered functional questions. These unanswered questions revolve around the relationship of the face to the posterior cranial component. Observation of hominoids, and primates in general, show a multiplicity of face/posterior cranium relationships. Just within the hominoids, gibbons have short faces and long, low posterior cranial components, chimps have both long, low anterior and posterior components, Gorillas have shorter and deeper faces (like Orangs), but long and low posterior components, and australopithecines generally have short faces and relatively high posterior cranial components.

However, some australopithecines, like STS 5, look more like chimps. Thus, there is no expectation that the relationship between face and posterior cranial region can be determined from the face alone. Relatively complete crania for R1/R2 and (Sivapithecus), indicating the position of the face and posterior cranial component, are therefore prerequisites for a total functional analysis.

CHAPTER VII

COMPARISONS OF ADAPTIVE PATTERNS

Given this understanding of the R1/R2 features in a comparative framework, the purpose of this section is to interrelate these individual features into an adaptive and morphological pattern which can then be compared to adaptive and morphological patterns of (Sivapithecus), (Proconsul), australopithecines, and extant pongids. It is reasonable to base taxonomic and phylogenetic conclusions upon these comparisons. In this synthesis, R1 and R2 are considered together because the preceding analysis shows that their individual features are nearly identical.

Adaptive Pattern of R1/R2

The R1/R2 premaxilla houses the roots of small dryopithecine-like incisors, and new Hungarian specimens (RUD 12 and RUD 15) confirm small maxillary incisor crowns relative to posterior teeth. According to Hylander's (1975) extensive comparisons among anthropoids, small incisors are not usually associated with large fruit feeding. Moreover, the less than 60° angle of central incisor implantation in R1/R2 further suggests a non-hominid stripping and husking function. Thus, while the possibility of a large fruit diet is unlikely, the anterior teeth of R1/R2 suggest that its diet could have included small fruits, meat, insects, and herbivorous materials such as leaves, grass, buds, seeds, shoots, bark, and stem

and pith portions of vegetation. Almost any extant pongid's diet includes most of these items (Schaller 1963; Jones and Pi 1971; Teleki 1973; Suzuki 1975; Rodman 1974), although in differing frequencies; Pan and Pongo are primarily large fruit and insect eaters, Gorilla a herbivore.

Additionally, important behavioral and dietary information can be inferred from the R1/R2 C/P₃ complex. Canine sexual dimorphism is indicated from the combined R1/R2 and Hungarian samples, and two distinct canine morphotypes are present (contrast female FT 46 with RUD 15 and perhaps YPM 11309, both males). One can only presume these canines had agonistic and defensive functions similar to those in most of the Old World Anthropoids. That they were sharp, pointed, and projecting, obviates the need for any inferences about the possibility of tool use for defence or intraspecific aggression in this taxon. Further, only slight sexual dimorphism for most teeth (other than the canines) is indicated (see discussion of species in the next section), and is comparable to Pan dimorphism. With respect to diet, wear patterns on canines and P₃ in R1/R2, especially the Hungarian specimens, strongly indicate puncturing, cutting, and shearing. Additional shear is indicated on P³, not cusp blunting as in australopithecines. Thus C₁¹ and P₃³ were designed to slice and puncture, adaptations found in herbivorous or frugivorous extant pongids, and not in presumed small,

hard, object feeders like Gigantopithecus and australopithecines. A diet which requires a dramatic maximization of crushing and grinding tooth surface cannot be reconstructed for R1/R2.

The slight sexual dimorphism found in R1/R2 species (see next section) might suggest arboreal existence for the taxon because small arboreal primates tend to be less dimorphic than closely related terrestrial forms.

The morphology and wear pattern of R1/R2 molars also illuminates possible dietary adaptations for the sample while eliminating (as primary selective agents) some of the food items included in the list above. R1/R2 molars, characterized by bunodont crowns, provide mortar and pestle occlusion. This suggests grinding and crushing were important. Additionally, the posterior teeth could be considered expanded relative to the anterior teeth, another adaptation that could indicate the increasing importance of crushing and grinding. However, bunodonty is not observed in primates that specialize in two dietary items: leaves and grass. Leaf eating colobines, and Gorilla, and grass eating gelada baboons (90-95% of gelada diet consists of grass), contra Jolly (Dunbar 1976), have high cusped molars and extensive enamel crests connecting the high cusps. Further, in these taxa, when wear perforates the enamel, alternating enamel/dentin/enamel surfaces are exposed. These provide excellent cutting and shearing action. This morphological pattern also characterizes

many mammalian herbivores (grass feeding ungulates, for example). Thus, the (presumed) thick enamel, bunodont R1/R2 molars are not designed for grass or leaf eating. That is not to say that these items were not included in the R1/R2 diet, but rather R1/R2 was not primarily adapted to their mastication. Consequently, the items one could include as basic staples in the R1/R2 diet are small fruits, seeds, insects, meat buds, bark, and stem and pith portions of vegetation. It is interesting to note that Ailuropoda (giant panda), which masticates bamboo (pith and stem), has bunodont molars as well as expanded posterior teeth like R1/R2.

In addition, the evidence for rapid attrition diet (inclusion of grit and grass) for R1/R2 can be considered negative, or at best inconclusive. First, R1/R2 molars and premolars exhibit asymmetric occlusal wear, unlike many australopithecines. Asymmetric molar/premolar cusp wear is characterized by greater lingual than buccal cusp wear on maxillary teeth, and greater buccal than lingual cusp wear on mandibular cheek teeth, and this asymmetry increases from M3 to M1; virtually all R1/R2 specimens exhibit this type of wear (D.298 an exception). Further, in the section on molar wear, flatter wear (as opposed to asymmetric wear), which characterizes many australopithecine posterior teeth prior to enamel perforation, was interpreted as a possible adaptation to rapid attrition, reducing wear per unit tooth surface by involving greater

total tooth surface during chewing. Alternately, it was also considered an expression of selection to expand crushing and grinding functional tooth surface. Whatever the functional implications, R1/R2 exhibits more pongid-like molar/premolar wear; much potential crushing and grinding surface was used for shearing, and blunting wear is absent on many surfaces. Second, steep and moderate molar wear gradient frequencies in the total R1/R2 sample are most similar to frequencies obtained for contemporary and extant pongids, not australopithecines or baboons. Moreover, the one young adult specimen (D.185) has only a slight gradient also suggesting slower attrition diet for R1/R2. All of this indicates that the R1/R2 diet did not include much grit or grass (silica content); absence of the latter also previously deduced from molar morphology. Much of the grit in primate diets is derived from foods found on or in the ground.

The remaining aspects of the lower portion of the R1/R2 face support the aforementioned dietary reconstruction. Thick mandibular corpora may indicate powerful vertical compressive forces exerted during posterior tooth loading. The slightly more anterior position of the zygomatic indicates a slightly more anterior origin for m. masseter than in most pongids. This more anterior origin increases the lever arm of the muscle, and places greater crushing and grinding surface under or behind it. The relatively large posterior teeth in R1/R2 also contributed

to the amount of crushing and grinding tooth surface under or behind m. masseter. Further, the portion of the zygomatic preserved on D.185 extends laterally a great distance without curving posteriorly. An equivalent portion of zygomatic in Pan or (Proconsul) would have already curved posteriorly (Gorilla and Pongo are like R1/R2). This lateral flare may be indicative of a wide temporal fossa, and indirectly might also indicate a large m. temporalis. The anterior moiety of this muscle adds to vertical compressive forces during posterior tooth loading.

Thus, all of these facial adaptations point to more powerful vertical compression than is seen in pongids generally. The dietary items just listed as possible major staples could have been the selective agents. However, it should also be noted that many australopithecine-like adaptations (those seen in the later sample) to powerful posterior tooth loading are absent in R1/R2. Adaptations to orthognathy in the shape of the palate and dental arcades are lacking. Moreover, vital information about the position of the face relative to the posterior cranial component is unavailable, and the size of the masticatory apparatus relative to body size is unknown. Thus, while a few hominid-like adaptations (to posterior tooth loading) characterize the known parts of the dentition and face, the majority of features are non-hominid, while others are still unknown. Based on wear patterns and the absence of adaptations to rapid attrition (with the ex-

ception of thick enamel) and molar morphology, it is unlikely grass and grit were included extensively in the diet. Further, it is clear that the R1/R2 shearing and puncturing C/P₃ complex was dimorphic and designed for agonistic and defensive functions, which makes it unnecessary to suggest tool use for these behaviors. Lastly, a low degree of sexual dimorphism in the dentition (see below) is indicated. Among dentally small primates, generally, arboreal forms tend to exhibit less sexual dimorphism than closely related terrestrial forms. The possibility that R1/R2 was arboreal is made more likely by the existence of a long, curved phalange, found at Rudabanya, which may be attributable to R2.

Unfortunately, paleoecological reconstructions of R1/R2 sites do not provide clear cut answers about the sort of niche(s) it was occupying. African R1, found at Fort Ternan (along with (Proconsul)), cannot be certainly associated with open country or forest adapted faunal elements (Andrews and Walker 1976). However, as Van Couvering and Van Couvering noted (1976), it was not until a forest corridor opened up during the Middle Miocene that hominoids spread to Eurasia. Further, the Arabian route led to warm and wet forested regions in the Near East, India, and South Asia. This route was probably taken by ancestral African R1. Thus, at the time of migration, R1/R2 preferred warmer and wetter tropical forests. This is opposite to some recent interpretations (Simons 1976).

However, in a number of works, others have also associated R1/R2 with tropical rainforest environments (Simons and Pilbeam 1965,1972; Simons 1972; Pilbeam 1969,1972).

Subsequent to migration, R2 populations expanded to slightly cooler areas like Hungary. It is also possible that R1/R2 gave rise to populations in Turkey (De Bonis, et. al. 1974,1975; Tekkaya 1974; Tekkaya and Andrews 197) and Greece (Von Koenigswald 1972) which may have encountered more open conditions.

Comparison of R1/R2 and (Proconsul)

There appear to be a number of adaptive differences between R1/R2 and (Proconsul), however, basic adaptive and morphological similarities cannot be underestimated.

In the anterior dentition, both possess relatively small angled incisors (in small premaxillae) which were probably used for stripping and husking. Although canines are relatively reduced in R1/R2, both C/P₃ complexes are designed for puncture and shear and presumably similar agonistic and defensive functions. Similarly, R1/R2 and (Proconsul) P³s have dual function; there is blunting wear on the internal cusp, and shearing wear on the external cusp (paracone). Thus, both have similarly designed anterior teeth and P₃³, and large fruit can be ruled out as a major staple in their respective diets. (Proconsul) molars possess more complicated surfaces (cingula, extra grooves), but the functional significance of this is unknown. Despite these surface detail differences, R1/R2 and (Proconsul) molars are low crowned and low cusped; neither have extensive crests between cusps. Thus, on the basis of molar morphology, grass and leaves are probably just as unlikely as primary staples for (Proconsul) as they are for R1/R2. However, the (Proconsul) diet could have included (like R1/R2) as primary dietary items, small fruits, seeds, meat, buds, insects, bark, and stem and pith portions of vegetation. While M2/M3 appears to be the preferred chewing site in (Proconsul) and R1/R2, (Proconsul) man-

dibular molars are slightly narrower, and maxillary molars slightly broader. R1/R2 may have thicker molar enamel, but as yet no definite adaptive implications are warranted.

Molar wear patterns in R1/R2 and (Proconsul) are identical; there is unequal buccal and lingual cusp wear. Steep and moderate molar wear gradients are absent in young adults. Again, this last feature may indicate slow rates of occlusal attrition for both. Additionally, the tooth rows of R1/R2 and (Proconsul) tend to be V-shaped for females and more parallel for males, and both exhibit long and narrow palate shapes. Thus, they both lack some adaptations to orthognathy with respect to these features. R1/R2 has a slightly deeper palate, and most specimens possess simian shelves (Candir mandible an exception). However, the precise functional significance of these features is unknown.

The remaining aspects of the dentitions and faces of R1/R2 and (Proconsul) are somewhat more different than those discussed above, but all are probably related to slightly more powerful posterior tooth loading in R1/R2. R1/R2 has relatively larger posterior teeth, more robust mandibular corpora, more anterior position of the zygomatics (and presumably m. masseter), and slightly more posterior tooth surface under or behind the origin of m. masseter (and consequently less tooth surface anterior to its origin than in (Proconsul)). The greater lateral flare for the preserved portion of the zygomatics (larger m.

temporalis) in R1/R2 suggests a broader face than (Proconsul) in that region, and perhaps a greater lateral component for m. masseter. Further, the more vertical ascending ramus in R2 (almost 90° in Hungarian R2 specimen RUD 2 and around $70-75^{\circ}$ in two (Proconsul) specimens, RU 1674 and 1948,50), and slightly more anterior position of ascension for the ascending ramus, suggests that the long and narrow palate of R2 was in a more inferior and posterior position relative to the top of the face than in (Proconsul).

In sum, both R1/R2 and (Proconsul) lack dental specializations and/or wear patterns associated with large fruit, leaf, and grass eating. Both could have masticated small fruits, seeds, meat, buds, bark, and stem and pith portions of vegetation. However, since R1/R2 appears to be better equipped for more powerful posterior tooth loading, then perhaps frequencies of hard or tough materials in its diet were higher than in (Proconsul). Conversely, the (Proconsul) diet may have included higher frequencies of softer items like small fruits.

If a phyletic relationship between (Proconsul) and (Dryopithecus) exists, then both R1/R2 and (Proconsul) were wide ranging hominoids that probably occupied a variety of niches as do wide ranging macaques and baboons. Perhaps, both R1/R2 and (Proconsul) had a preference for tropical rainforest at the time of faunal interchange, and subsequently gave rise to animals, with similar morpho-

logical patterns, that survived in cooler and dryer niches in Western Europe ((Dryopithecus)) and in Southwest Asia (Rudabanya was probably cooler and dryer than India during the Middle Miocene). That R1/R2 and (Proconsul) were likely omnivores makes it plausible that wide ranging populations would not necessarily become dentally distinct from each other.

Comparison of R1/R2 and (Sivapithecus)

The analysis of individual features clearly shows that the preserved portions of the smaller R1/R2 and larger (Sivapithecus) species are virtually identical. Therefore, the preceding analysis of the adaptive pattern of R1/R2 holds equally for (Sivapithecus); virtually identical dietary and paleoecological reconstructions are indicated.

(Sivapithecus) and R1/R2 possess relatively small, angled incisors presumably used for stripping and husking, and there is canine reduction relative to posterior teeth. Additionally, pongid-like shearing and puncturing are indicated in their sexually dimorphic C/P₃ complexes. Thus, agonistic and aggressive functions can be ascribed to this region of the dentition for both. They exhibit dual function P³ and similar trends in molar shape and morphology. Both possess bunodont molars which show a predominance of occlusal wear on either buccal (mandibular molars) or lingual (maxillary molars) cusps. Their molar wear gradient distributions are similar, in that young adults show most frequently slight gradients (perhaps an indication of a slow rate of occlusal attrition). They both lack most australopithecine adaptations to orthognathy in the shape of the palate and tooth rows, and display identical sex variation in tooth row orientation (see discussion of sexual dimorphism below). Compared to (Proconsul), they both have more anterior and higher in-

sections of their zygomatics, greater lateral flare of the zygomatics, higher maxillary sinuses, and more robust mandibular corpora. Both have short and narrow snouts, and there are indications that they also possess broad upper facial regions. Again, some of these are perhaps adaptations to powerful posterior tooth loading, and in some respects, (Sivapithecus) is even more hominid-like than R1/R2.

Like R1/R2, the inferred diet of (Sivapithecus) could have included small fruits, seeds, meat, insects, buds, bark, and stem and pith portions of vegetation. Leaves, grass, and large fruits can be ruled out as primary staples -- both for identical reasons. Neither appears to have the dental specializations seen in extant pongids.

The data and morphological comparisons leave little doubt that R1/R2 and (Sivapithecus) are closely related. Eurasian R1/R2 and (Sivapithecus) morphological patterns are nearly identical, and they probably collectively represent one Eurasian adaptive radiation. This is supported by the fact that if the (Proconsul) pattern is taken to characterize the ancestral character state, all derived features of R1/R2 and (Sivapithecus) are shared. These shared derived features (of R1/R2 and (Sivapithecus)) are: 1) slight increase in the angle of central incisor implantation, 2) increase in subnasal prognathism, 3) relative reduction of canines when sex is taken into account (or relative expansion of the posterior teeth), 4) loss of

projecting paracone on P^3 , 5) general loss of molar cingula (Candir an exception), 6) simplification of molar surfaces (loss of extra grooves and crests, etc.), 7) slightly increased bunodontia, 8) increased relative broadness of mandibular molars, 9) decreased relative broadness of maxillary molars, 10) increased enamel thickness(?), 11) increased mandibular robustness under the molars, 12) development of simian shelves or occasionally transverse tori like those of hominids (Candir and No. 18039), 13) less convergent tooth rows, anteriorly, 14) more anterior position for the zygomatics, 15) higher insertion of the zygomatics, 16) greater lateral flare of the zygomatics (broader upper facial region), 17) deeper palate, 18) higher maxillary sinuses, 19) shorter and deeper(?) faces. African R1, where preserved, shares all of these features except 15 and 17, and its canine is not as reduced. Additionally, all other known features of R1/R2 and (Sivapithecus) are similar or identical, but they are primitive retentions inherited from some early dryopithecine stock, like (Proconsul). Thus, all features which distinguish R1/R2 from (Proconsul) also distinguish (Sivapithecus) from (Proconsul), and all primitive features are shared. One can only conclude recent common ancestry and close phylogenetic relations are indicated for R1/R2 and (Sivapithecus).

Lastly, since differences between R1/R2 and (Sivapithecus) adaptive and morphological patterns cannot

- . be demonstrated, conclusions reached for R1/R2 in the comparisons which follow, apply equally to (Sivapithecus).

Comparison of R1/R2 and Australopithecines

Major adaptive differences can be demonstrated between R1/R2 and australopithecines, but there are some parallelisms, especially with the early part of the australopithecine sample, which may have phylogenetic significance (see conclusions). One must also be aware that there are many vital pieces of information lacking in the R1/R2 record.

Unlike R1/R2, the subnasal prognathism of australopithecines is great despite the presence of even relatively smaller incisors in most specimens (the Afar and Laetoli hominids have slightly larger, dryopithecine sized incisors, relative to cheek teeth). As suggested earlier, the great length of anterior snout in australopithecines may be related to elongated posterior tooth roots. This seems to be an even more likely possibility when one considers (Sivapithecus) which also appears to have elongated posterior tooth roots indicated by high maxillary sinuses, and small (Proconsul)-like incisors, yet a longer forefacial region than (Proconsul). R1/R2 incisors are both relatively larger than those of all but a few early australopithecines, and more angled, and consequently better designed for stripping and husking. However, one early australopithecine specimen, AL 200-1a, has stripping wear on its incisors. Additionally, major dietary and behavioral differences between R1/R2 and

australopithecines can be inferred from their contrasting C/P₃ complexes. While some relative reduction does characterize R1/R2 canines, they are not nearly as reduced as most australopithecine canines. Here too, the early part of the australopithecine sample overlaps with the low end of the Miocene hominoid range. However, more significantly, there are important dietary and behavioral differences that can be inferred from their respective C/P₃ complexes. The R1/R2 complex, including two canine morphotypes and sexual dimorphism in relative canine size, has shearing, puncturing, and agonistic and defensive functions, while the australopithecine complex, without two canine morphotypes and clearcut sexual dimorphism in relative canine size, has primarily gripping and crushing functions. Wear patterns reflect these different uses. The early part of the australopithecine sample contains a few specimens (LH 6, LH 4) with some shear on their canines. Thus, while some earlier australopithecines may have a dominant buccal cusp on P₃, it is blunted by wear (some of the Laetolil specimens have blunting and some shearing wear), and never acts primarily as a shearing surface for C¹ or P³ (as it does in R1/R2). Further, R1/R2 P₃s are not molarized teeth, and the importance of shear, as opposed to crushing and grinding, is indicated by the dual function of the R1/R2 P³. Again, australopithecines have lost the shearing function on the buccal cusp of their P³s (and molarized P₃), probably because of the increased

importance of crushing and grinding (both australopithecine P^3 cusps are blunted by wear). Moreover, while R1/R2 and australopithecine molars are bunodont, R1/R2 molars almost always have predominantly buccal cusp wear on mandibular molars, and lingual cusp wear on maxillary molars. Many australopithecine molars and premolars are worn flat, and even those that do not (especially in the Afar and Laetolil samples) have blunting wear on all posterior tooth cusps. This suggests a greater need and use of total tooth surface for crushing and grinding in australopithecines. These contrasting patterns of posterior tooth wear are consistent with the functional interpretations of their respective C/ P_3 complexes. R1/R2 and australopithecine molar wear gradient distributions are different; most young adult australopithecines exhibit moderate or steep molar wear gradients, while the few young adult R1/R2 specimens have slight gradients. Thus, if this is any reflection of attrition rates and/or delayed maturation, a high rate and/or slow maturation is indicated for australopithecines, and a slow rate and/or rapidly erupting molars are indicated for R1/R2. Moreover, australopithecines, unlike R1/R2, possess dental arcade and palatal adaptations to orthognathy. On the other hand, R1/R2 and australopithecine mandibular corpora are robust at M_2 , and this may suggest powerful vertical compression in both during posterior tooth loading. Additionally, m. masseter

attachment is more anterior in R1/R2 than in most pongids, and there is proportionately greater posterior tooth surface under or behind its origin. However, australopithecine m. masseters are commonly found in an even more anterior position (P^4/M^1), and the proportion of posterior tooth surface under or behind the origin is greater than in R1/R2. Most australopithecines exhibit much higher zygomatic insertions as well, and although a few specimens (STS 5, for example) have longer and shallower faces, most possess deep, orthognathic faces and well developed anterior m. temporalis.

To sum up the respective patterns, R1/R2 is basically a short, narrow snouted dryopithecine with a few adaptations for powerful posterior tooth loading while retaining stripping, husking, shearing, and puncturing functions at I1, I2, C1, and P3. The R1/R2 C/P₃ complex is designed and used as it is in pongids, for agonistic display and defensive functions. Australopithecines, on the other hand, have virtually lost these anterior tooth (and P3) functions, decreased the proportion of anterior tooth surface, and increased the grinding and crushing surface of their posterior teeth (especially compared to body mass), modified the shape of the tooth row, palate, and face to promote orthognathy, moved m. masseter far anteriorly and laterally, and increased the size of the anterior moiety of m. temporalis. All these changes were designed to

increase compressive forces during posterior tooth loading, and include greater dental surface for crushing and grinding. Lastly, australopithecines are savannah dwellers, R1/R2 probably a forest (tropical and subtropical) form.

It is important to note that any of the above conclusions derived from comparisons between R1/R2 and australopithecines, hold equally for (Sivapithecus).

Comparison of R1/R2 and Extant Pongids

A. Gorilla

The major discernable morphological and adaptive differences between Gorilla and R1/R2 are found in the molars. Both possess abbreviated premaxillae, small incisors, similarly angled maxillary central incisors, cutting, shearing and puncturing C/P₃ complexes, and dual function P³. While male Gorilla canines are relatively larger (compared to the posterior teeth), R1/R2 canines have the same agonistic and defensive functions. In the molar region, leaf eating (primary staple) Gorilla has high crowned, high cusped occlusal relief with well developed crests (for a hominoid), unlike the bunodont molars of R1/R2. Moreover, the effective shearing action of Gorilla molars is enhanced by rapid enamel perforation which produces alternating enamel/dentin/enamel surfaces. Thus, Gorilla molars are shearing; R1/R2 molars crushing and grinding. On the other hand, molar wear gradient frequency distributions are not dissimilar and may suggest slow occlusal attrition. Similarly, both possess unequal buccal and lingual molar cusp wear and neither exhibits adaptations to orthognathy with respect to palate shape or tooth row orientation. Although R1/R2 has generally more robust mandibular corpora, and slightly more anterior origin for m. masseter, both have high zygomatics that flare laterally. The snout of R1/R2 is narrower, but the Gorilla face (and palate) is deep, and not uncommonly,

the anterior moiety of m. temporalis is well developed (temporal lines meet far forward on the frontal). Thus, both seem to have some adaptations to powerful posterior tooth loading. The major differences appear to be related to size and the leaf eating habits of Gorilla.

B. Pongo

With the exception of the anterior teeth, R1/R2 and Pongo masticatory apparati are similar. Pongo, a large fruit eater (primary staple), has relatively larger incisors and expanded premaxillae to house their roots. However, the angle of maxillary central incisor implantation is the same. As a consequence of incisor hypertrophy and relatively larger canines, the anterior snout of Pongo is broader. Although Pongo canines are larger relative to the posterior teeth than in R1/R2, their respective C/P₃ complexes are similarly designed for puncturing, shearing (P³ retains dual functions in both), agonistic, and defensive functions. Further, R1/R2 and Pongo molar crowns are bunodont. They exhibit unequal wear on buccal and lingual molar cusps (although I have observed a few old adult Pongo specimens with very flat wear), and molar wear gradient distributions appear comparable. Like Gorilla, Pongo has a fairly deep face which is short compared to Pan, high zygomatic insertion, and great lateral zygomatic flare. Additionally, in Pongo, the posterior cranial component is high and anteriorly placed, relative to the face. The orientation probably allows m. temporalis to contribute

considerable force during posterior tooth loading. R1/R2, on the other hand, has slightly more anterior origin for m. masseter than Pongo, and greater tooth surface posterior to or under its origin, and considerably less tooth surface anterior to its origin than in Pongo. R1/R2 also has more robust mandibular corpora. Again, while both exhibit some adaptations related to powerful posterior tooth loading, neither possess adaptations to orthognathy with respect to palate shape and tooth row orientation.

C. Pan

Unlike Gorilla, Pongo, and R1/R2, Pan appears to lack all adaptations to powerful posterior tooth loading. Otherwise, its dentition is much like that of Pongo. It is also primarily a large fruit eater. Pan and R1/R2 central incisors are similarly angled, but only in Pan are the premaxillae and tooth crowns expanded. Pan canines are larger (P. paniscus has much smaller canines than P. troglodytes) relative to the posterior teeth than in R1/R2, but both retain cutting, puncturing, and social functions (P^3 also dual function). They share somewhat similar bunodont molar morphology, unequal molar cusp wear patterns, and similar molar wear gradient frequency distributions. Neither display adaptations to orthognathy in palatal shape or tooth row orientation. However unlike Pongo, Pan has lower zygomatic insertion, very little zygomatic flare, and a long shallow face. Additionally, Pan mandibles are more gracile at M_2 than in R1/R2. Thus, Pan seems to have

little or no adaptations to powerful posterior tooth loading, unlike R1/R2, Pongo, or Gorilla.

In sum, the adaptive and morphological patterns of smaller R1/R2 and larger (Sivapithecus) are indistinguishable. Both are slightly different from (Proconsul) (especially with respect to the features interpreted as adaptations to more powerful posterior tooth loading). While R1/R2 (and (Sivapithecus)) exhibits some australopithecine features, most of its morphology is pongid-like (pongid is used in the broad sense here). However, R1/R2 (and (Sivapithecus)) differs in some respects from the specialized large fruit eating extant pongids like, Pan and Pongo (especially in the size of the anterior dentition and the number of adaptations to powerful posterior tooth loading), and from leaf eating Gorilla (major differences here are related to specialized leaf eating molar morphology of Gorilla).

Thus, a basically pongid-like masticatory apparatus is suggested for R1/R2 (and (Sivapithecus)), and a tropical/subtropical forest herbivore/omnivore niche is most likely at the time of faunal exchange between Africa and Eurasia.

Analysis of the R1/R2 Sample at the Species Level

In this section, the R1/R2 sample is dealt with at the species level. However, formal taxonomic revisions and generic-level decisions will be made in the next section.

Eurasian R1/R2

In order to simplify taxonomic problems, the Eurasian R1/R2 sample will be considered first, then African R1. Since the Hungarian material is morphologically and temporally similar to Indian R1/R2, according to the descriptions by Kretzoi (1975), and observations of photographs of the originals and metrics by this author, it is grouped with the Indian R1/R2 sample. Other Eurasian hominoids, Bodvapihceus, D. macedonensis, D. giganteus, and G. bilaspurensis are not considered in this species level analysis, but will be included later in the general discussion of phylogenetic relationships among Middle Miocene hominoids.

Given the current disagreements about which specimens are to be included in the Eurasian R1/R2 sample, and in order to proceed with an objective taxonomic analysis, prior taxonomic assessments for Indian and Hungarian hominoid specimens (all materials included in Ramapithecus, Rudapithecus, D. sivalensis, and D. indicus) are disregarded, and it is assumed that all Eurasian material is sampled from one species; this is the paleontological

null hypothesis (Simpson 1961). In order to reject the null hypothesis (to erect more than one species), it must be shown that it is unlikely all specimens could be sampled from a single species.

One method of testing the null hypothesis is by comparing the amount of variation in the fossil sample with that of known species. To this end, published Pan, Pongo, and Gorilla data (Mahler 1973) were used for comparison. Sufficiently large samples of fossils were available only for the posterior teeth (P3-M3), and coefficients of variation for the cross sectional area (mesiodistal length X buccolingual breadth) for each tooth are listed below and compared to similar published data for extant pongids (Tables 19 and 20).

Comparisons of the pooled sexes samples show for each tooth that the fossil sample contains greater variation than in any extant pongid species. Pongo comes close for a few teeth, but this is probably a result of the unusually great sexual dimorphism within this Asian pongid. Otherwise, much greater variation is found within the fossil sample.

In a second set of comparisons (within-sex variation), the fossil sample consists of all those specimens this author felt confident in assigning a sex. In extant pongids, for many features, bimodal distributional patterns can be observed, each mode representing a sex. For example, in Pan, Pongo, and Gorilla, there are two canine

TABLE 19
COMPARISON OF VARIATION
(pooled sexes)

Mandibular P_3 - M_3 (Cross Sectional Areas)

	P_3	P_4	M_1	M_2	M_3
Eurasian	N=10	N=18	N=17	N=19	N=21
Hominoid	x=88.5	x=73.8	x=113.1	x=142.3	x=159.0
Fossils	SD=35.9	SD=18.3	SD=27.0	SD=46.2	CV=50.3
	CV=40.6	CV=24.8	CV=24.6	CV=32.5	CV=31.5
<u>Gorilla</u>	N=362	N=362	N=374	N=370	N=335
	x=191.8	x=148.2	x=208.7	x=262.3	x=252.5
	SD=35.0	SD=21.4	SD=24.7	SD=34.2	SD=38.3
	CV=18.3	CV=14.4	CV=11.8	CV=13.0	CV=15.2
<u>Pongo</u>	N=129	N=132	N=139	N=133	N=110
	x=146.6	x=126.2	x=154.0	x=176.6	x=170.0
	SD=33.0	SD=22.5	SD=23.0	SD=29.9	SD=32.8
	CV=22.5	CV=17.9	CV=15.1	CV=16.9	CV=19.3
<u>Pan</u>	N=233	N=233	N=231	N=221	N=218
	x=85.4	x=70.9	x=107.8	x=114.7	x=99.2
	SD=11.5	SD=8.4	SD=11.4	SD=13.5	SD=16.2
	CV=13.4	CV=11.9	CV=10.6	CV=11.8	CV=16.3

TABLE 20
COMPARISON OF VARIATION
(pooled sexes)
Maxillary P³-M³ (Cross Sectional Areas)

	P ³	P ⁴	M ¹	M ²	M ³
Eurasian	N=9	N=9	N=15	N=15	N=11
Hominoid	x=87.7	x=80.8	x=126.7	x=132.6	x=134.9
Fossils	SD=19.5	SD=17.3	SD=20.7	SD=45.9	SD=33.5
	CV=22.3	CV=21.4	CV=16.3	CV=34.6	CV=24.8
<u>Gorilla</u>	N=406	N=404	N=409	N=409	N=363
	x=174.3	x=162.3	x=224.1	x=256.9	x=223.3
	SD=24.1	SD=19.6	SD=25.8	SD=33.9	SD=34.2
	CV=13.8	CV=12.1	CV=11.5	CV=13.2	CV=15.3
<u>Pongo</u>	N=126	N=125	N=138	N=134	N=112
	x=129.2	x=121.3	x=161.3	x=170.4	x=154.4
	SD=20.0	SD=17.6	SD=23.6	SD=27.7	SD=29.1
	CV=15.5	CV=14.5	CV=14.6	CV=16.2	CV=18.8
<u>Pan</u>	N=321	N=300	N=313	N=334	N=299
	x=84.2	x=76.0	x=115.5	x=109.9	x=91.2
	SD=10.0	SD=9.2	SD=11.5	SD=15.0	SD=16.9
	CV=11.9	CV=12.0	CV=9.9	CV=13.6	CV=18.5

morphotypes, and a variety of other features in the mandible and maxilla associated with the dimorphism in this tooth. Using these and similar criteria, 25 fossil specimens were sexed. For each specimen, sex was determined from all, or a combination of, most of the following criteria: canine size and morphology, size and extent of the canine root or socket (if the canine crown was not preserved), height and thickness of the mandibular corpus under the molars (a large buccinator groove can be found on all specimens with male canines, a small groove on specimens with female canines), height of the mandibular corpus around the canine, and convergence of the tooth rows (see detailed discussion on sexual variation in dental arcade shape in the preceding analysis). Male mandibles are: D.189, No. 18039, D.197, AMNH 19412, AMNH 19411, RUD 2, RUD 17, D.199, an undescribed mandible fragment from India. Female mandibles include: YPM 13811, BMNH 15423, D.298, AMNH 19413, and two new Pakistan mandibles (field nos. 4857, 6160). Male maxillae include: D.1, D.196, D.191 (associated with No.18039), RUD 15, and new Pakistan specimen (field no.) 11704. Female maxillae include: D.185, RUD 12, YPM 13799, D.299/300, and new Pakistan specimen (field no.) 11708. A more detailed discussion of sexing and sexual dimorphism is given in a later section.

The estimates of within-sex variation for the fossil sample were compared to those of each extant pongid taxon (Tables 21 and 22). Again, for each tooth, both fossil

TABLE 21
COMPARISON OF VARIATION

(within sexes)

Mandibular C_1 - M_3 (Cross Sectional Areas)

		C_1	P_3	P_4	M_1	M_2	M_3
<u>Fossil</u>							
<u>Sample</u>							
Male	N=6	7	9	5	7	5	
	x=91.7	92.9	76.3	111.2	158.7	147.1	
	SD=39.4	32.2	18.9	37.1	56.2	51.9	
	CV=42.9	34.7	24.8	33.4	35.4	35.3	
Female	N=1	2	4	5	6	3	
	x= --	---	64.3	100.9	126.6	---	
	SD= --	---	24.0	20.8	29.2	---	
	CV= --	---	37.3	20.6	23.0	---	
<u>Gorilla</u>							
Male	CV=16.1	12.6	13.1	10.7	11.5	12.6	
Female	CV=12.8	11.7	11.4	9.6	10.4	11.9	
<u>Pongo</u>							
Male	CV=14.3	16.7	14.5	12.7	12.8	14.9	
Female	CV=17.8	16.5	15.7	11.1	13.2	14.3	
<u>Pan</u>							
Male	CV=17.7	12.2	11.7	10.0	11.8	15.9	
Female	CV=19.5	11.4	11.5	10.7	11.5	15.8	

TABLE 22
COMPARISON OF VARIATION
(within sexes)
Maxillary C¹-M³ (Cross Sectional Areas)

	C ¹	P ³	P ⁴	M ¹	M ²	M ³
<u>Fossil Sample</u>						
Male	N=11	3	4	5	4	2
	x=145.2	---	79.6	118.4	156.6	---
	SD=50.7	---	13.7	22.6	30.8	---
	CV=34.9	---	17.2	19.0	19.7	---
Female	N=1	4	4	4	4	2
	x= --	87.8	76.3	130.1	146.7	---
	SD= --	21.8	18.8	27.3	37.8	---
	CV= --	24.8	24.7	21.0	25.8	---
<u>Gorilla</u>						
Male	CV=16.3	12.7	10.9	10.6	11.9	12.8
Female	CV=13.2	11.0	10.6	9.9	11.1	13.5
<u>Pongo</u>						
Male	CV=16.3	12.2	10.4	11.2	12.1	13.8
Female	CV=15.4	12.3	12.5	11.5	13.6	14.6
<u>Pan</u>						
Male	CV=19.8	11.2	11.3	9.7	13.4	18.8
Female	CV=25.1	11.8	12.1	10.0	13.3	17.7

sexes contained greater variation than any extant pongid sex.

Both types of comparison show that the fossil sample contains too much variation to be considered derived from one species. Hence, the evidence supports rejection of the null hypothesis; two or more species are present.

The next task is to determine whether a two species model can be rejected. In order to do this, the fossil sample has to be partitioned into two subsets. Fortunately, there are gaps in the total sample which conveniently separate into three subsets; small, medium, and large. A combination of small and large subsets (representing one species, the medium subset the second species) yields greater variation than in the total sample and therefore this (two species) combination (small specimens/large specimens, and medium specimens) is handily rejected. This leaves two possibilities to test the two species hypothesis: the small and medium sized specimens represent one species, the large specimen subset the other, or the small specimens represent one species, and a combined medium/large sample represents the second. Stated in another way, the small and large specimen subsets clearly represent two different species. The question which arises next, is whether or not the medium sized specimens can be excluded from either.

Since an already small total sample must be reduced as a consequence of partitioning, only combined sex samples

(for small/medium and medium/large) are large enough to derive estimates of variation. These were derived for both two-species possibilities (Tables 23 and 24). In only two comparisons in the mandible did the variation in Pongo, the most sexually dimorphic extant pongid, exceed that in the fossil subsets. Otherwise, for all other teeth, both possibilities contained greater variation than is found within species of extant pongids.

In the maxilla (Table 24), only the small/medium subset was large enough to calculate the CV. For each tooth (P^3-M^2), the fossil subset contained greater variation than is found in any extant pongid species.

I suggest that these comparisons, and those below, support rejection of the two species hypothesis. Therefore, three or more species are present in this sample, and the medium sized specimens should be considered sampled from the third species. At this point it appears that small, medium, and large sized species are present; however, it is not possible to estimate variation within each of these subsets to determine if they could be further subdivided because N is too small. Each subset appears to be somewhat homogeneous, and, furthermore, there are no convenient points to partition each of the subsets. Thus, at present, there is not enough data to properly test the three species hypothesis. The subsets are taken to represent three different species and are referred to here as small, medium, and large until formally named

TABLE 23
COMPARISON OF VARIATION
(pooled sexes)
Mandibular P₃-M₃ (Cross Sectional Areas)

		P ₃	P ₄	M ₁	M ₂	M ₃
Subsets						
Small/ Medium	N=7	11	17	17	15	
	x=69.1	62.6	99.8	120.0	130.1	
	SD=14.4	11.9	19.0	22.2	30.6	
	CV=20.8	19.6	19.0	18.5	20.3	
Medium/ Large	N=7	10	17	13	15	
	x=98.9	80.1	116.6	153.8	163.8	
	SD=25.2	17.1	16.0	37.7	32.3	
	CV=26.2	21.4	13.8	24.5	19.7	
<u>Gorilla</u>	CV=18.3	14.4	11.8	13.0	15.2	
<u>Pongo</u>	CV=22.5	17.9	15.1	16.9	19.3	
<u>Pan</u>	CV=13.4	11.9	10.6	11.8	16.3	

TABLE 24
COMPARISON OF VARIATION
(pooled sexes)
Maxillary P³-M³ (Cross Sectional Areas)

	P ³	P ⁴	M ¹	M ²	M ³
<hr/>					
Subset					
Small/	N=6	8	10	6	4
Medium	x=79.3	77.8	122.5	132.6	---
	SD=16.5	15.6	19.7	23.9	---
	CV=20.8	20.1	16.1	18.0	---
<u>Gorilla</u>	CV=13.8	12.1	11.5	13.2	15.3
<u>Pongo</u>	CV=15.5	14.5	14.6	16.2	18.8
<u>Pan</u>	CV=11.9	12.0	9.9	13.6	18.5
<hr/>					

TABLE 25
 CALCULATION OF $\overline{cv}$
 Mandibular Dentition (Males)

	C_1	P_3	P_4	M_1	M_2	M_3
<u>Gorilla</u>	CV=16.1	12.6	13.1	10.8	11.5	12.6
<u>Pongo</u>	CV=14.3	16.6	14.4	12.7	12.8	14.9
<u>Pan</u>	CV=17.7	12.0	11.6	10.0	11.8	15.9
	$\overline{cv}$ =16.0	13.8	13.0	11.2	12.0	14.5

(next section).

Further support for the three species model can be derived from a consideration of the distances between subset means (small, medium, large) for each sex. Distances can be expressed in terms of numbers of standard deviations from one mean to the next . This is done below for male and female mandibles separately. In addition, coefficients of difference (Mayr 1969) are also calculated below for pooled sexes.

Male Mandibles

Since the male mandibular subsets are too small to calculate variation (as are all other subsets), extant pongid data were used to derive estimates of standard deviations for each fossil subset mean. For each extant pongid tooth area (C_1-M_3), an average coefficient of variation ($\overline{cv}$) was calculated (Table 25). This $\overline{cv}$ was multiplied by each subset mean (the result divided by 100) to obtain a standard deviation estimate for that fossil mean (SD_{est}) (see Table 26 below). The SD_{est} for each tooth was then used to determine the number of standard deviations from: (1) small subset mean to medium subset mean (using the SD_{est} of the small subset), (2) medium subset mean to small subset mean (using the SD_{est} of the medium subset), (3) medium subset mean to large subset mean (using the SD_{est} of the medium subset), and (4) large subset mean to medium subset mean (using the SD_{est} of the large subset). The results are listed for each tooth in

TABLE 26
 MALE MANDIBLES: MEAN TOOTH AREAS
 AND SD_{est}^*

	C_1	P_3	P_4	M_1	M_2	M_3
Small						
Males	(1)	(2)	(2)	(2)	(2)	(2)
$\bar{X}=58.1$	57.2	56.5	76.3	95.1	97.9	
$SD_{est}=9.2$	7.9	7.4	8.5	11.4	14.2	
Medium						
Males	(3)	(2)	(4)	(2)	(2)	(2)
$\bar{X}=88.1$	82.6	68.8	103.5	137.3	161.3	
$SD_{est}=14.1$	11.4	8.9	11.6	16.5	23.4	
Large						
Males	(1)	(3)	(3)	(2)	(3)	(1)
$\bar{X}=167.6$	123.8	99.8	149.9	215.4	217.1	
$SD_{est}=26.8$	17.1	12.9	16.8	25.8	31.4	

$$*SD_{est} = \frac{\overline{cv}(\bar{X})}{100}$$

TABLE 27
 DISTANCES BETWEEN SUBSET TOOTH AREA MEANS*
 (expressed in number of SDs)

	C ₁	P ₃	P ₄	M ₁	M ₂	M ₃
from;						
Small to Medium	3.26	3.21	1.64	3.20	3.70	4.46
Medium to Small	2.12	2.22	1.37	2.34	2.55	2.70
Medium to Large	5.63	3.61	3.48	4.00	4.73	2.38
Large to Medium	2.96	2.40	2.40	2.76	3.02	1.77

*Male Mandibles

Table 27.

Looking at the male mandible subsets (Table 27), it is apparent that almost half of the calculated distances are greater than 3 standard deviations, and another 10 (of 24) fall between 2.1 and 3.0 standard deviations (this would correspond to the upper or lower 2% of a normal distribution). These data clearly support the hypothesis that the three subsets represent males of three different species; they are measurably distinct from each other, and sortable. One might expect some overlap in ranges between these subsets if tooth size is normally distributed in the three species. However, since 95% of the specimens in a normal distribution will fall within 2 standard deviations of the mean, it is likely that the overlap will never be great. Thus, in most cases, sorting will be possible by first sexing specimens, and then comparing them metrically.

Female Mandibles

A similar procedure was used to sort and show distances between small, medium, and large species females (for the mandibular dentition). The $\overline{cvs}$ were calculated from female extant pongid data, and SD_{est} s were calculated for each tooth, and then used to determine the number of standard deviations from one subset mean to the next (Table 28).

Results in Table 28, where comparisons were possible, show that in 5 of 16 cases, over 3 standard deviations

TABLE 28
 DISTANCES BETWEEN SUBSET TOOTH AREA MEANS*
 (expressed in number of SDs)

	P ₃	P ₄	M ₁	M ₂	M ₃
from;					
Small to Medium	3.46	2.25	4.55	3.52	---
Medium to Small	2.36	1.73	3.10	2.48	---
Medium to Large	---	4.45	2.35	2.42	2.53
Large to Medium	---	2.82	1.88	1.89	1.87

*Female Mandibles

separated means. Another 7 fell between 2.24 and 2.82 standard deviations, and four between 1.73 and 1.89 standard deviations (this corresponds to the extreme 8.5 -6.0% of a normal distribution). These data also show the three subsets are distinguishable, and support the three species hypothesis.

One additional mandibular comparison is available. Estimates of posterior tooth surface area, P_3-M_3 , for male mandibles are presented below, together with $\overline{cv}$ s derived from extant pongids, and SD_{est} s.

	Small	Medium	Large
P_3-M_3	383.1	553.5	806.0
$\overline{cv}$	10.7	10.7	10.7
SD_{est}	41	58	86

This information was similarly used to determine numbers of standard deviations from one mean to another; small/medium 4.14, medium/small 2.93, medium/large 4.36, large/medium 2.93. These results also support the three species indicated by similar statistical tests on individual tooth areas.

Coefficients of Difference

To further support the erection of three species, coefficients of difference (CD) between pooled sex subsets were calculated. The CD, defined by Mayr (1969), is used to determine subspecies status and is calculated by the following formula:

$$CD = \frac{\text{Mean}(b) - \text{Mean}(a)}{SD_a + SD_b}$$

Mayr suggests that a CD of 1.28 indicates 90% joint non-overlap and subspecies status for the two compared samples. (a CD of 1.76 indicates 96% joint non-overlap). Using this formula, CDs were calculated between small, medium, and large subsets (pooled sexes) using standard deviations calculated from the fossil samples. These CDs, listed in Table 29, show that for all but one comparison, more than 1.28 CDs separated the fossil subsets, and in some cases more than 2 CDs separated them. These CDs are greater than those calculated between Pan paniscus and Pan troglodytes, which are considered by this author to be separate species.

Until formally named, these species will be referred to simply as small, medium and large. It can also be noted now that the small species is the same as R2; medium and large species are D. sivalensis and D. indicus, respectively. The medium species also includes some Indian R1 specimens (D.199, No.18064, YPM 13833, D.118/119, BMNH 13264).

TABLE 29
COEFFICIENTS OF DIFFERENCE*
(pooled sexes)

	P ₃	P ₄	M ₁	M ₂	M ₃
CD between;					
Small N=(3)	(5)	(4)	(7)	(5)	
and Medium 2.56	1.19	3.00	1.46	1.30	
N=(5)	(5)	(12)	(8)	(8)	
Medium N=(5)	(5)	(12)	(8)	(8)	
and Large 1.93	2.20	2.03	1.61	1.56	
N=(3)	(4)	(3)	(6)	(6)	

*

$$CD = \frac{\text{Mean}(b) - \text{Mean}(a)}{SD_a + SD_b}$$
 (calculated above for mandibular teeth only)

Sexual Dimorphism

Estimates of sexual dimorphism for each of the three species were calculated for the larger mandibular samples. A few additional, but less complete, specimens were included to increase sample size. Sex assignments were less certain for these specimens.

For each tooth, the female mean cross-sectional area was divided by the male mean. This ratio was also calculated for extant pongid, australopithecine, (Proconsul), and baboon posterior teeth (Table 30). Estimates of sexual dimorphism for australopithecines were derived from Wolpoff (197).

A discussion of morphological dimorphism will follow this metric description.

Small Species

Posterior tooth area dimorphism estimates for the small species are listed below:

	P ₃	P ₄	M ₁	M ₂
female	$\bar{X} = 51.3 (1)$	48.4 (2)	73.7 (1)	94.4 (2)
male	$\bar{X} = 57.0 (2)$	56.6 (2)	76.3 (2)	103.9 (4)
ratio	.90	.85	.96	.90

Compared to the various taxa listed in Table 30, Pan is most similar. However, the estimates for the fossil species are based upon only a few specimens, and therefore any conclusions based on these estimates must

TABLE 30
ESTIMATES OF DIMORPHISM
(Mandibular Dentition)

	C ₁	P ₃	P ₄	M ₁	M ₂
<u>Papio</u>	.37	.49	.85	.84	.82
<u>Gorilla</u>	.50	.74	.86	.90	.87
<u>Pongo</u>	.59	.73	.82	.82	.82
<u>Pan</u>	.65	.87	.95	.96	.98
<u>D. africanus</u>	.60	.73	.71	.82	.86
australopithecines	.79	.82	.84	.81	.77

Female Tooth Area $\bar{X}$ /Male Tooth Area $\bar{X}$

be considered very tentative. One tentative conclusion is that if these three species are derived from (Proconsul), there has been a decrease in the magnitude of dimorphism. The same conclusion can be derived from comparisons of medium and large species dimorphism below with taxa listed in Table 30. In sum, all three species appear to have slight dimorphism, like Pan. This is important in considering the comparisons used to reject the one and two species hypotheses. Pooled sexes variation in Pan is the lowest for the three extant pongids used in the comparisons.

Medium Species

	C_1	P_3	P_4	M_1	M_2
female $\bar{X} =$	52.8 (1)	74.5 (1)	62.3 (1)	108.8 (3)	126.4 (5)
male $\bar{X} =$	88.2 (3)	82.2 (3)	82.3 (3)	114.2 (2)	145.1 (5)
ratio	.60	.91	.91	.95	.87

Large Species

	P_4	M_1	M_2
female $\bar{X} =$	97.9 (1)	135.4 (1)	165.6 (2)
male $\bar{X} =$	99.8 (3)	149.8 (2)	215.4 (3)
ratio	.98	.90	.77

Morphological Dimorphism

A discussion of morphological dimorphism can be presented simultaneously for all three species because

they exhibit identical patterns of sex variation expressed at differing sizes. In the mandible, males possess large projecting canines, and the root socket for this tooth (when crown is absent) reaches far down into the mandibular corpus (e.g. specimens RUD 17, D.189/13828/D.190, AMNH 19411, D.197). Further, these male mandibles have tooth rows that are less convergent anteriorly, and exhibit an elongated (X) appearance with the mandibular corpus (see section above on tooth row shapes analysis). Specimens AMNH 19412, D.199, NO 18039, in addition to the above male mandibles, exhibit extreme examples of this male character. It was noted earlier that this outward angling of the tooth row is probably related to the unusually large male canine, and therefore is an important sexing criterion. Additionally, in the region around M2/M3, male mandibles have extensive buccinator grooves and very thick mandibular corpora. Lastly, in comparison to females of their respective species, males also possess very tall corpora at the symphysis (for example, male AMNH 19411 and female YPM 13811).

In contrast to males, female mandibles exhibit a distinct, predictable suite of features. Their canines are very small, and roots (sockets) do not extend far into their shallow corpora (YPM 13811, D.298, Field No. 6160, 4857). Further, female tooth rows do not angle outwards in relation to the corpus, but rather follow it (D.298,

YPM 13811, BMNH 15423, AMNH 19413, Field No. 6160). Thus, they have more V-shaped tooth rows, while male tooth rows are more nearly parallel, or perhaps slightly divergent anteriorly. Lastly, female mandibular corpora at M_2 and M_3 have small buccinator grooves, and are slender when compared to males (e.g. female AMNH 19413 and male YPM 13828).

In the maxilla, canine size, and morphology, and curvature of the tooth rows are sexually dimorphic. The male's canine is a larger tusklike tooth with projecting crown and long root which extends far up into the maxilla (RUD 15, D.1, D.196, Field No. 11704). Further, this large tooth usually effects the curvature of the tooth row. This can be demonstrated best on specimens D.196 and RUD 15. They possess medially curving M^3-M^1 , but at P^4-C^1 the tooth rows curve outward. Female maxillae like YPM 13799, D.185, and 11708 must have had relatively small canine crowns like RUD 12 because the sockets are tiny and do not project far up into the maxilla. Their tooth rows are also convergent anteriorly, giving them a slight V-shaped appearance (as in RUD 12).

In sum, one pattern of sexual dimorphism for all three fossil species emerges from the preceding analysis. First, the magnitude of dimorphism, compared to (Proconsul) is reduced. Second, all three species display pongid-like rather than hominid of Gigantopithecus-like dimorphism with respect to canine size, canine morphology, and

curvature of the tooth rows. However, unlike extant pongids, there appears to be, in the three fossil forms, greater differences in robustness between male and female mandibular corpora at M_2 - M_3 (especially see buccinator groove differences). Further, for the entire Eurasian sample, canine size, and morphology (roots and sockets), tooth row orientation, corpus robustness at M_2 - M_3 , and symphysis height appear to be good sexing criteria.

African R1

This material has been considered separately from the Eurasian species for a number of reasons. First, it is geographically distant and probably older than the Eurasian materials. Second, African R1 exhibits a greater number of (Proconsul)-like retentions, it has fewer shared derived features in common with the Eurasian materials, and it possesses a somewhat unusual and distinct mandibular symphysis. Third, African R1 may actually be the ancestor of the Eurasian species, and thus separate analysis may better establish its phylogenetic relationships.

Assuming African R1 and Eurasian species represent a group of closely related taxa (perhaps ancestor/descendant), then there appear to be two major events which should be reflected in the taxonomy: group origin and adaptive radiation (presumably represented by African R1 and Eurasian species, respectively). The group's adaptive radiation seems to be a Eurasian, not an African, phenomenon. The absence, in the African Middle Miocene, of this group's adaptive radiation could be a consequence of potentially competing taxa like D. africanus and D. nyanzae which are already present when African R1 appears (these (Proconsul) species are also found at Fort Ternan) (Andrews and Walker 1976). Alternately, the African record for the Middle Miocene is very incomplete and one could consider the above negative evidence.

Specimens included by Walker and Andrews (1973, 1975) in African R1 are: FT 45/46/47, FT 7, FT 48, FT 3318, and FT 8. The last two specimens, one an isolated right C_1 and the other a fragment of an unerupted left C^1 , cannot be confidently included in this sample. They could just as easily be (Proconsul) canines. However, there are three additional specimens, RU 1692, MB 107, and BMNH 16649 (all possibly from Maboko Island) that could be included in African R1.

These three specimens have a long history in the literature. They were first described by Le Gros Clark and Leakey (1951), and placed in Sivapithecus africanus (BMNH 16649, the type). Later, Leakey erected "Kenyapithecus africanus" and placed them in that taxon along with other newly found specimens. Subsequently, Pilbeam (1969b) demonstrated that "K. africanus" was invalid and suggested that all included specimens be placed within (Proconsul). This author contends that all but these three specimens should be considered (Proconsul) specimens.

BMNH 16649, a left maxillary fragment with P^3-M^1 crowns, has no certain provenience. It was reported found on Rusinga Island, but subsequent analysis of the adhering matrix indicates Maboko Island may be the more likely place of origin. Maboko is dated between 15 and 16 mya on the basis of fauna (D.R. Pilbeam, personal communication). A fairly large C^1 socket is indicated,

much larger than would be necessary for the C^1 of FT 46/47, and perhaps represents a male. Additionally, M2 was in occlusion (there is an interproximal wear facet on M1), and M3 was probably just erupting. Wear on M1 is very slight, and consequently, a slight molar wear gradient is indicated. Besides D.185 (from the small species), this would be one of the few young adult R1 specimens and it also has a slight gradient; this may be indicative of slow occlusal attrition (absence of grass or grit in the diet). A number of features support its inclusion with African R1 as opposed to (Proconsul). Morphologically, M1 lacks the extensive and elaborate (Proconsul) cingulum and has a less complicated crown surface. This tooth, and the premolars, are the same size as homologues on the Fort Ternan R1 specimens. Additionally, the zygomatic arch shows m. masseter originates at the anterior part of M1, further forward than most specimens included in small, medium, and large Eurasian species or FT 46/47. This clearly distinguishes it from (Proconsul), where zygomatics usually arise at M2 or behind. Further, BMNH 16649, MB 107, and RU 1692 have long maxillary molars, unlike broad (Proconsul) molars and they are compared below to similar sized

D. nyanzae (breadth/length x 100):

	<u>D. nyanzae</u>	MB 107	FT 46/47	RU 1692	BMNH 16649
M ¹	(4) x=122.0 OR=115.3-126.9	102.7	102.9	---	109.0
M ²	(4) x=114.0 OR=110.4-119.6	---	100.0	96.0	---

The data show the molars of BMNH 16649, MB 107, RU1692, and FT 46/47 to be similar in shape as well as in size, and distinguishable from similar sized maxillary molars of D. nyanzae. RU 1692 (locality unknown), an isolated right M², and MB 107 (Maboko Island), an isolated left M¹, are also morphologically identical to homologues on FT 46/47. They lack (Proconsul)-like cingula, have less complicated crown surfaces, and are lower cusped. MB 107, if included in African R1, would represent the earliest specimen in that sample.

While the zygomatic is fairly low on BMNH 16649, and palate shallow, these are features which also characterize African R1 (when compared to the Eurasian species). BMNH 16649 has slightly larger teeth than FT 46/47, but this is expected since they probably represent male and female (C¹ sockets are also dimorphic). Thus, the African R1 sample that is compared here to the Eurasian species includes FT 46/47/45, FT 7, FT 48, BMNH 16649, MB 107, and RU 1692.

Since the Eurasian species are morphologically (and adaptively) similar metric variants of each other, possible placement of African R1 into any of these younger forms should be based first on metric criteria. When metrics are considered, it is the medium species that is closest in size to African R1 (see Table 31 below). Next, a morphological comparison between African R1 and the medium species is required in order to decide on separate

TABLE 31
CROSS SECTIONAL AREAS (POOLED SEXES)
(Maxillary Teeth)

	P ³	P ⁴	M ¹	M ²
Medium Species	$\bar{X}=99.0$ N=2	88.1 3	135.2 3	158.6 2
African R1	$\bar{X}=98.9$ N=1	80.0 2	117.2 3	143.3 2
Small Species	$\bar{X}=69.4$ N=4	65.2 4	101.9 4	115.2 3

species status for African R1.

Although metrically similar, the African R1 sample and medium species differ in a number of features. African R1 has much lower zygomatic insertion on the maxilla, shallower palate, and morphologically distinct female C¹. In addition, African R1 has an unusual mandibular symphysis cross section, slightly lower molar crowns, and narrower maxillary molars.

The first two features (lower insertion of the zygomatic arch and shallower palate) show African R1 to be similar to (Proconsul), and perhaps underline the geologically earlier position for this material. The different canine (only female C¹ is known for African R1) morphologies (although both exhibit a female pattern) are probably unlikely to occur within a species. Similarly, the symphyseal morphology of African R1 is very different from that of the medium species (and large and small species as well). The African R1 symphysis is more heavily buttressed and more horizontally oriented. Lastly, a comparison of the unworn African R1 maxillary molars shows that their crowns are lower and narrower (Breadth/Length) than those of the medium species.

This author suggests that these differences are sufficient to separate African R1 from the medium Eurasian species. Additionally, the possible ancestral status of African R1 would be better reflected taxonomically, if placed in a separate taxon; therefore, this is done

formally in the next section.

In sum, two R1/R2 species have been recognized here: an earlier and possibly ancestral African form, and a smaller and later Eurasian taxon (R2 = small species). The small species appears to be one metric variant of an adaptive radiation which occurred in Eurasia. The shared features of the three Eurasian species support the idea that they collectively represent a later radiation, while the few (Proconsul)-like retentions in African R1 (plus the unusual mandibular symphysis) suggest it was not part of this Eurasian radiation. This radiation probably dates back as far as the Chinji, where all three species are reported, and certainly their synchronous existence is established at Haritalyangar (Pilbeam, personal communication) in the Nagri.

The recent finds from Turkey (Tekkaya 1974; Tekkaya and Andrews 1976; De Bonis, et.al. 1974, 1975) and Greece (von Koenigswald 1972), as well as Gigantopithecus, are also probably part of this radiation. Careful study of this new material will almost certainly show a more complex picture of this group's phylogenetic history.

Analysis of R1/R2 at the Generic Level

Analysis of R1/R2 species (African R1 and small species = R2) at the generic level necessarily requires a consideration of their adaptive and morphological patterns, geological setting, and probable phylogenetic relationships. However, before this is done, there must be a well defined framework into which African R1 and R2 can be placed. Specifically, this framework involves two closely related forms: geologically earlier (Proconsul), and contemporary (Sivapithecus).

This author suggests that (Proconsul) and (Sivapithecus) represent two major adaptive radiations of dryopithecines. On one hand, (Proconsul) species eventually invaded Europe via a North African (Gibraltar) land connection giving rise to (Dryopithecus) species D. laietanus and D. fontani (an additional larger species may also be present in Spain (Crusafont-Pairo and Golpe-Posse 1972)). This phyletic association is suggested by a new (but as yet undescribed) Spanish (Proconsul) specimen which predates (Dryopithecus) in Europe, and by the fact that (Dryopithecus) and (Proconsul) appear to share a number of features. They both possess more slender mandibular corpora, relatively larger canines (than (Sivapithecus), thinner molar enamel (enamel perforation occurs only after slight occlusal wear in (Dryopithecus)), well defined molar cingula (although some D. laietanus specimens have more weakly developed molar cingula), and

more pointed and higher molar/premolar cusps (less bunodont than (Sivapithecus)). More complete study of the European materials is necessary to clarify relationships.

On the other hand, African R1, which is contemporary with (Proconsul) species D. africanus and D. nyanzae at Fort Ternan, is geologically older but morphologically very similar to Eurasian (Sivapithecus). Presumably, it migrated from Africa, via the Arabian Peninsula, into South Eurasian tropis and subtropics, and subsequently gave rise to another adaptive radiation of hominoids which includes small, medium, and large species and probably Gigantopithecus (schematically represented in Figure 11).

Since there are a number of adaptive differences suggested in the faces and dentitions of (Proconsul) and (Sivapithecus) and probably correspondingly different niche preferences, and different adaptive radiations involved, raising (Sivapithecus) back to genus is considered justified, while maintaining phyletically related (Proconsul) and (Dryopithecus) as subgenera of Dryopithecus. Sivapithecus has priority because it is the genus of the first named specimen of the group (Pilgrim 1910) and S. indicus is the type species. Accordingly, by any definition of the category genus (morphological, adaptive, or phylogenetic) the small species (=R2) and African R1 should be included within the proposed genus Sivapithecus. The comparisons by features and by patterns clearly support their inclusion; R2 as a metric variant of

other contemporary Eurasian Sivapithecus species, and African R1 as a possible ancestor to all three later forms.

Taxonomic Revisions

Order: Primates Linneaus 1758 (1758, p.20)

Suborder: Anthropoidea Mivart 1864 (1864, p.635)

Family: Pongidae Elliot 1913 (1913, errata page)

Subfamily: Dryopithecinae Gregory and Hellman 1939
(1939, p.370)

Genus: Sivapithecus Pilgrim 1910 (1910, p.163)

Known distribution: Middle Miocene of East Africa,
Middle to Late Miocene of
Southern Eurasia.

Diagnosis: Slightly more vertically implanted maxillary central incisors and greater premaxillary prognathism than in Dryopithecus. Canines reduced relative to the posterior teeth when compared to Dryopithecus. Sivapithecus also possesses bunodont molars which generally lack well developed cingula and other enamel surface complications like those seen in (Proconsul). Compared to Dryopithecus, Sivapithecus has generally more robust mandibular corpora under the molars, simian shelves (differs only from (Proconsul) for this feature) and deeper palate. Sivapithecus zygomatic arches are inserted more anteriorly and higher on the maxillae, and show greater lateral flare than in Dryopithecus.

Contained

Species: 1) Sivapithecus africanus Le Gros Clark and
Leakey

2) Sivapithecus brevirostris Lewis

3) Sivapithecus sivalensis Lydekker

4) Sivapithecus indicus Pilgrim

Discussion: Four species are presently included in this genus. Two of the included species, S. africanus and S. brevisrostris contain specimens which were generally placed in "Ramapithecus." The preceding analysis has shown there are no genus-level adaptive or morphological differences in the known parts of "Ramapithecus" and Sivapithecus, and thus a generic distinction is unwarranted; "Ramapithecus" is formally sunk. Sivapithecus has priority over "Ramapithecus."

The African species of Sivapithecus is in some ways different (depth of palate, symphysis morphology) from Eurasian species and is a possible ancestor to all three. S. brevisrostris, S. sivalensis, and S. indicus appear to be metric variants of each other and probably represent a Eurasian adaptive radiation.

Sivapithecus is closely related to Dryopithecus and was probably derived from early members of this genus ((Proconsul) sp.).

African Species

- 1) Sivapithecus africanus Le Gros Clark and Leakey 1951
(1951, p.261)

Kenyapithecus wickeri Leakey 1962 (1962, p.690)

Kenyapithecus africanus Leakey 1967 (1967, p.157)

Ramapithecus wickeri Andrews 1971 (1971, p.192)

Type: BMNH 16649; left maxillary fragment with P^3-M^1 and roots for M^2 , $\frac{1}{2}$ socket for C^1 .

Hypodigm: Type and FT 45/46/47, FT 8, FT 7, RU 1692, MB 107.

Distribution: Kenya, Fort Ternan and Maboko Island, Middle Miocene.

Diagnosis: A medium sized dryopithecine, similar in size to S. sivalensis. Morphology of its mandibular symphysis is distinct from that of Eurasian species of Sivapithecus; it is more heavily buttressed and horizontally oriented. S. africanus has a lower zygomatic insertion and shallower palate than other Sivapithecus species and narrower maxillary molars. Known female C^1 morphologically different from homologue in S. sivalensis. Otherwise, diagnosis is same as that for the genus.

Eurasian Species

2) Sivapithecus brevirostris Lewis 1934

Dryopithecus punjabicus Pilgrim (in part) 1910
(1910, p.63)

Ramapithecus brevirostris Lewis 1934 (1934, p.163)

Bramapithecus thorpei Lewis 1934 (1934, p.173)

Bramapithecus? sivalensis Lewis 1934 (1934, p.174)

Dryopithecus laietanus (in part) Simons and Pilbeam
1965 (1965, p.124)

Ramapithecus punjabicus (in part) Simons and Pilbeam
1965 (1965, p.136)

Rudapithecus hungaricus Kretzoi 1975 (1975, p.579)

Type: YPM 13799; right maxillary fragment with P^3-M^2 and roots (or root sockets) for C^1 , I^2 , and I^1 .

Hypodigm: Type and GSI D.185, D.186, D.187, D.298, No. 18068, YPM 13814, YPM 13806, YPM 13809, YPM 13830, BMNH 15423, RUD 1, RUD 2, RUD 12, RUD 15, RUD 17.

Distribution: Later Middle Miocene of Hungary, Pakistan, and India.

Diagnosis: Smallest species presently known from the Eurasian adaptive radiation of Sivapithecus. Relatively smaller canines than in any other presently recognized Sivapithecus species. Otherwise, diagnosis is the same as it is for the genus. Mandibular posterior teeth cross sectional area means are P_3 54.9 (N=3); P_4 54.0 (N=5); M_1 74.3 (N=4); M_2 99.2 (N=7); M_3 107.0 (N=5); estimate of pooled sexes P_3 - M_3 summed areas is 390 mm².

Discussion: The type of "R. punjabicus", D.118/119, is included in the hypodigm of S. sivalensis on the basis of metrics. It probably represents a female of S. sivalensis because it has only a small buccinator groove, a more gracile mandibular corpus under the molars, and, relative to most other specimens included in the hypodigm of S. sivalensis, smaller teeth. The next available type is YPM 13799 (Lewis 1934, p.163) and hence the name S. brevirostris is appropriate. Other specimens once considered in the hypodigm of "R. punjabicus"; YPM 13833, D.199, BMNH 13264, and No.18064 are also too large to be included in S. brevirostris, and are therefore included in

the next largest species, S. sivalensis. This procedure is believed valid because there is only one major criterion which separates species of Eurasian Sivapithecus (when canines are absent), size.

3) Sivapithecus sivalensis Lydekker 1879

Paleopithecus sivalensis Lydekker 1879 (1879, p.33)

Dryopithecus punjabicus (in part) Pilgrim 1910
(1910, p.63)

Dryopithecus chinjiensis Pilgrim 1915 (1915, p.25)

Paleosimia rugosidens Pilgrim 1915 (1915, p.29)

Dryopithecus pilgrimi Brown, Gregory, and Hellman
1924 (1924, p.1)

Dryopithecus cautleyi Brown, Gregory, and Hellman
1924 (1924, p.5)

Paleopithecus? sylvaticus Pilgrim 1927 (1927, p.9)

Ramapithecus hariensis Lewis 1934 (1934, p.166)

Sugrivapithecus salmontanus Lewis 1936 (1936, p.168)

Sugrivapithecus gregoryi Lewis 1936 (1936, p.450)

Ramapithecus punjabicus (in part) Simons and Pilbeam
1965 (1965, p.136)

Type: GSI D.1; maxilla with roght C¹, damaged P³ and P⁴, and M¹-M³, roots for left M¹-M³, right I² and ½ root socket for I¹.

Hypodigm: Type and D.118/119, D.177, D.180, D.181, D.188, D.199, D.299/300, D.301, D.304-7, D.313-4, No. 18041-2, No.18064-7, No.18069-70, YPM 13807, YPM 13811, YPM 13813, YPM 13825, YPM 13832, YPM 13836, BMNH 13264, AMNH 19411-2, AN 612.

Distribution: Later Middle Miocene, early Late Miocene of India, Pakistan, and China.

Diagnosis: Medium sized species of Sivapithecus similar in size to S. africanus, but differs in showing a more vertically oriented mandibular symphysis, deeper palate, higher zygomatic insertion on the maxilla, broader maxillary molars, and female C^1 with more well developed lingual cingulum. Canines relatively larger than in S. brevisrostris. Otherwise, diagnosis is the same as it is for the genus. Mandibular posterior teeth cross sectional area means are; P_3 80.0 (N=4); P_4 72.0 (N=5); M_1 110.8 (N=12); M_2 135.4 (N=10); M_3 145.1 (N=10); estimate of pooled sexes P_3 - M_3 summed areas is 545 mm^2 .

4) Sivapithecus indicus Pilgrim 1910

Sivapithecus indicus Pilgrim 1910 (1910, p.63)

Dryopithecus? frickae Brown, Gregory, and Hellman
1924 (1924, p.3)

Sivapithecus himalayensis Pilgrim 1927 (1927, p.2)

Sivapithecus orientalis Pilgrim 1927 (1927, p.5)

Dryopithecus sp. Pilgrim 1927 (1927, p.7)

Sivapithecus middlemissi Pilgrim 1927 (1927, p.8)

Dryopithecus keijuanensis Woo (in part) 1968
(1968, p.38)

Sivapithecus aiyengari Prasad 1962 (1962, p.89)

Type: GSI D.176, right lower M_2 .

Hypodigm: Type and GSI D.178, D.179, D.189-92, D.196-98,
D.238, D.303, D.308, D.309, No.18039-40, YPM
13827-28, YPM 13834, YPM 13835, YPM 13837, BMNH
13364-66.

Distribution: Later Middle Miocene of India and Pakistan.

Diagnosis: Large species of Sivapithecus, slightly

larger dentally than D. major. Canines relatively larger than in S. sivalensis. Otherwise, diagnosis is the same as it is for the genus. Mandibular posterior teeth cross sectional area means are: P_3 123.8 (N=3); P_4 99.6 (N=4); M_1 145.0 (N=3); M_2 199.0 (N=6); M_3 196.4 (N=6); estimate of pooled sexes P_3 - M_3 summed areas is 765 mm^2 .

CHAPTER VIII

CONCLUSIONS

"Ramapithecus"

Two species of specimens formerly allocated to "Ramapithecus" (formally sunk) have been recognized here: Sivapithecus africanus and S. brevirostris. These species have been shown to be morphologically and adaptively inseparable from other Sivapithecus species (S. indicus and S. sivalensis). African S. africanus appears to be the earliest Sivapithecus species, and may be the ancestor of the Eurasian adaptive radiation of the genus. S. brevirostris is the smallest species within that Eurasian radiation, and can probably be considered a size variant of the other two recognized species.

Sivapithecus' species diet could have included small fruits, seeds, meat, bark, buds, insects, and stem and pith portions of plants. None appears to possess a dental apparatus specifically designed to masticate large fruits, leaves, or grass, nor is there any evidence for a highly abrasive diet (no grit or grass). All possess the same few adaptations to powerful posterior tooth loading: thick mandibular corpora under the molars, more anteriorly situated m. masseter, large m. temporalis(?), and larger posterior teeth relative to the canine. Otherwise, most of the other known features of the dentition and face can be considered resemblances to a majority of other dryopithecines: relatively small incisors which were procumbent

and angled to the tooth row, narrow anterior snout, a C/P₃ complex designed for puncturing, shearing, agonistic, and aggressive functions, dual function P³ (blunting and shearing wear), bunodont molars, a predominance of lingual and buccal cusp wear on the maxillary and mandibular molars, respectively, pongid-like molar wear gradients in young adults, and absence of adaptations to orthognathy in the shape of the palate (long and narrow) and tooth rows (straight and nearly parallel to anteriorly divergent for males, straight and more convergent anteriorly for females).

The major australopithecine adaptations cannot be inferred for either S. africanus or S. brevirostris. There are no archeological materials (manuports or artifacts) or evidence of base camps, nor is there any evidence for bipedalism. To the contrary, small curved phalanges recovered by Kretzoi (1975) in Hungary, if referrable to S. brevirostris, suggest the opposite possibility; S. brevirostris was an arboreal species. This is consistent with the preferred niche, tropical and subtropical forests, and with the low level of sexual dimorphism suggested in the preceding analysis. Further, essential behavioral changes are not indicated in the C/P₃ complex. S. brevirostris and S. africanus relied, like closely related taxa, on morphologically (and metrically) dimorphic canines to maintain intragroup order, and perhaps

interspecific defense.

Another important australopithecine characteristic is delayed maturation, as seen in the dental eruption pattern (Mann 1968, 1975), not in molar wear gradient distributions. In S. africanus and S. brevirostris there are no juvenile specimens known, and therefore the pattern of eruption is unknown directly for these taxa. However, a new juvenile Pakistan specimen (GSP 11536/7), probably referable to D. indicus, appears to have a pattern more similar to that of chimps, than australopithecines. Thus, if true, S. africanus, the proposed ancestor of S. indicus, is likely to have had a similarly fast or faster rate of tooth eruption, while contemporary S. brevirostris was probably much like S. indicus.

The molar wear gradient data show that the Sivapithecus species considered in detail share a similar distribution of gradients. Young adult specimens (BMNH 16649, D.185, YPM 13811, D.196) display little or no gradients, and older adult specimens develop them in comparable frequencies (between Sivapithecus species considered). However, uncontrollable factors such as enamel thickness, enamel hardness, preferential tooth use, and varying rates of occlusal attrition diminish the significance of the molar wear gradient data. It is interesting to note that the new large Turkish specimens described by de Bonis, similar in size to S. indicus, display moderate

gradients in young adult specimens (RPI 54 and RPI 55), unlike all other Sivapithecus species considered. In addition, the Turkish materials suggest a high degree of sexual dimorphism within that sample.

In sum, Sivapithecus is a short and narrow snouted ape, perhaps also possessing a broad upper face and some adaptations to powerful posterior tooth loading. The species recognized show little sexual dimorphism and probably preferred tropical or subtropical forest environments, at least at the time of faunal exchange between Africa and Eurasia. The migratory route was a forest corridor (Van Couvering and Van Couvering 1976) which led to other forested environments. It is equally probable that ultimately, Sivapithecus species became wide ranging and existed in a number of environments, perhaps like baboons or macaques. Some of the newly described materials from Greece and Turkey may represent Sivapithecus species living in dryer and more open environments, which replaced many of the forested regions of Eurasia, during the late Middle and Late Miocene.

Phylogenetic Conclusions

It is appropriate to consider implications about the hominid/pongid split arising from the preceding analysis. However, first it is important to point out and incorporate the phylogenetic scheme derived for pongids and hominids based upon comparative studies of living representatives.

These phenetic studies have suggested that the lineage leading to Pongo diverged first, and then another divergence occurred between the common ancestors of Pan, Gorilla, and hominids (Figure 10). Thus, there are two splitting points that are of primary interest and three lineage origins (Pongo, African apes, Hominids). Given this as the most likely phylogenetic alternative based upon a phenetic approach, two schemes involving the fossil forms discussed in this work seem most likely.

In the first phylogenetic reconstruction, the early division between (Proconsul) and Sivapithecus is considered the split between African pongids and hominids (Figure 11). One of the (Proconsul) species gives rise to the Western European (Dryopithecus) radiation from which eventually a Pongo ancestor presumably migrated to Asia after 9mya since there is yet no record of it in explored 9-13my old deposits in Southern Eurasia. Sivapithecus cannot be the Pongo ancestor in this scheme because that would violate the given phenetic interpretation by making Pongo, rather than the African apes, more closely related to hominids. The route for the Pongo ancestor may appear to some to be

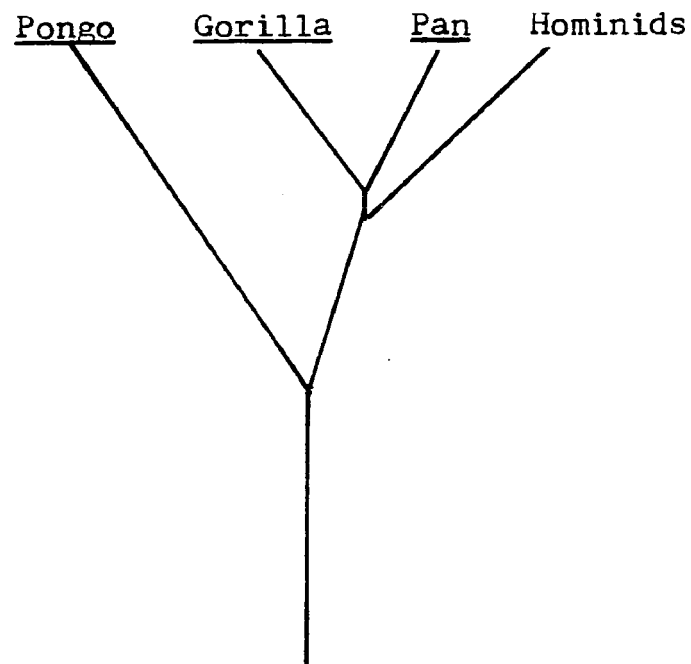


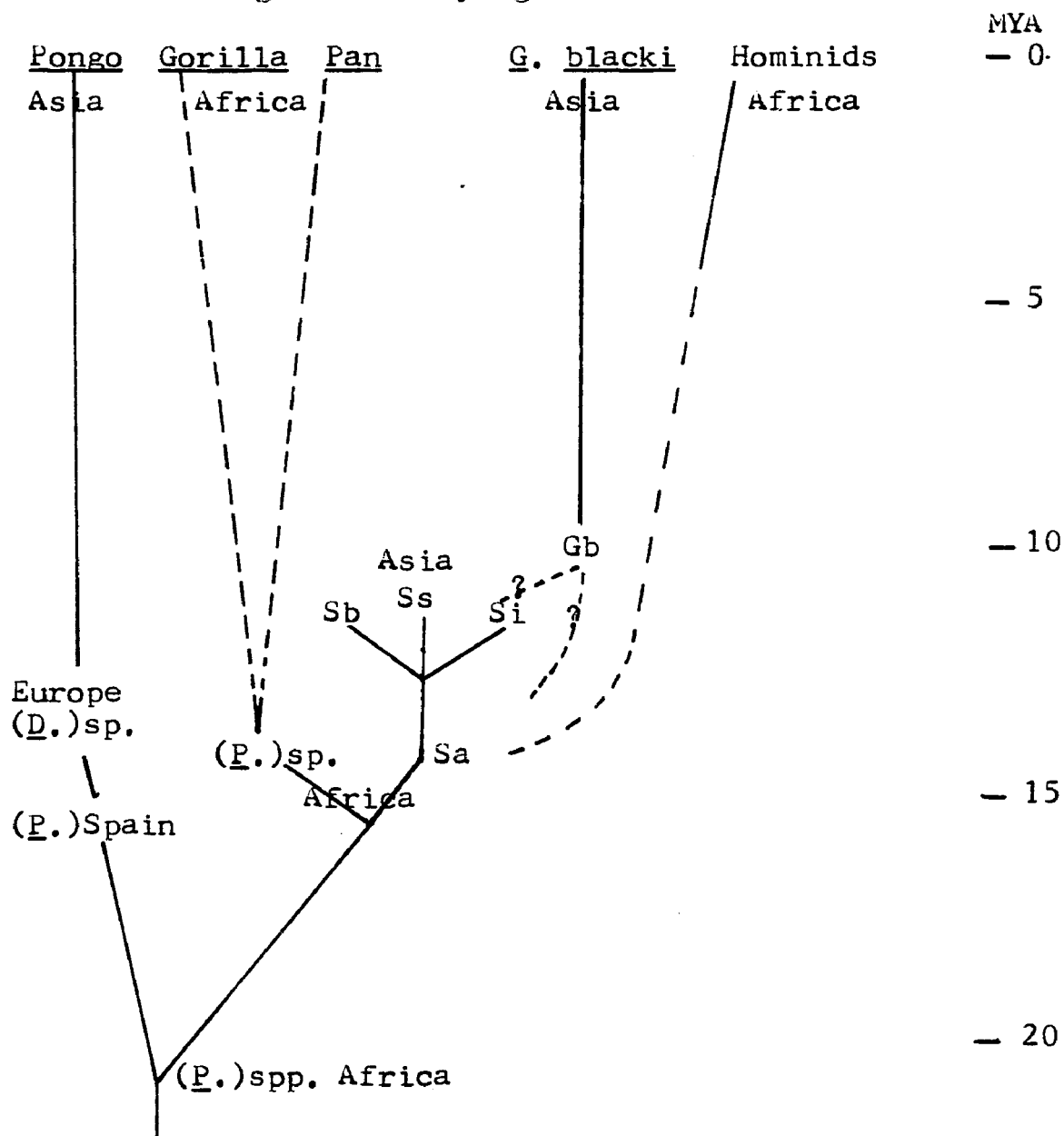
Figure 10 Relationships Between Great Apes and
Man (based upon phenetics)

unlikely, however, a similar explanation might equally apply to the migration of European gibbons like Pliopithecus to Southeast Asia. Pliopithecus is in many respects like modern gibbons, and it is at present the only logical choice geographically for the ancestor of extant hylobatids. Thus, at present, since one must conclude that this European form migrated from Europe to Southeast Asia after 9 mya, a similar explanation could be used to derive Southeast Asian Pongo from European (Dryopithecus). Moreover, as a consequence of the geographic isolation of Africa after the Middle Miocene, it becomes increasingly unlikely that a Pongo ancestor could be derived from that continent. Thus, probably either a Pongo ancestor is endemic to South Asia in the Middle Miocene (in this scheme it is not one of the Sivapithecus species, and therefore it is unknown in the Asian fossil record), or it existed in Western Europe.

Referring again to Figure 11, with the Pongo lineage diverged, the common ancestor of Pan, Gorilla, and hominids is represented by another (Proconsul) species which by 15 mya has given rise to Sivapithecus (represented at Maboko). The African pongid lineage (Pan and Gorilla) is represented by a (Proconsul) species, and African Sivapithecus gives rise to African hominids and Eurasian Sivapithecus and Gigantopithecus.

A phyletic relationship between Sivapithecus and hominids can readily be supported on the basis of shared characters in the known portions of the face and dentition.

Figure 11 Phylogenetic Scheme #1



Abbreviations: (P.)-(Proconsul), (D.)-(Dryopithecus)

Sa-Sivapithecus africanus, Sb-Sivapithecus

brevirostris, Ss-Sivapithecus sivalensis,

Si-Sivapithecus indicus, Gb-Gigantopithecus

bilaspurensis

These resemblances are even greater when one compares Sivapithecus to the new, and geologically earlier (3-3.75 mya), australopithecines from the Afar and Laetolil. Morphologically, Sivapithecus and early australopithecine P4-M3 do not differ, although the latter still show more blunting occlusal wear. Further, P₃, in these early australopithecines, shows more numerous similarities to Sivapithecus than can be found when comparing the later hominid sample with Sivapithecus. Early australopithecine P₃s exhibit greater buccal cusp dominance, angulation with the tooth row, one specimen (LH 4) is reported to have interlocked with the maxillary canine (buccal face wear) preventing mesial drift of the mandibular posterior teeth, and the roots occasionally bifurcate at the alveolus (also LH 4). However, P₃ in these early hominids also displays blunting wear, unlike Sivapithecus.

In the anterior dentition of the early australopithecine sample, both incisors and canines are generally larger than in the later australopithecine sample, relative to the posterior teeth, and in many instances, fall in or near the Sivapithecus ranges (see sections on relative canine size and relative incisor size). One of the Laetolil specimens also possesses a diastema between I² and C¹, and one of the Afar specimens exhibits stripping wear on its incisors. However, unlike Sivapithecus, the early australopithecine canine tips are blunted and worn to the occlusal level rapidly, two distinct canine mor-

phototypes are not present, and there is no clear bimodality in relative canine size.

Additionally, this newly described early hominid material exhibits higher frequencies of elongate and more narrow tooth rows and palates, more V-shaped dental arches, more gracile mandibular corpora, and more posteriorly situated zygomatic arches. Although some of these Sivapithecus-like features can be found in the later australopithecine sample (particularly smaller individuals) their frequencies appear to be much higher in this earlier sample. Thus, it becomes increasingly easy to support a phyletic relationship on morphological grounds between Sivapithecus and early hominids when the earliest australopithecines are considered. Certainly, similarities between Sivapithecus and australopithecines are more numerous than between (Proconsul) and australopithecines.

The known distribution of australopithecines and the zoogeographic information provided by Cooke and Coryndon and Savage support an African origin for australopithecines. At present, australopithecines are only known from Africa and even contemporary circum-Mediterranean sites like Pikermi and early Villafranchian faunas have failed to yield a single undoubted australopithecine find. While early hominids are found in Java, even if one were to argue that these specimens represent later australopithecines, there is none that can be dated earlier

than 1.9 mya. That the faunal migrations from Africa to Eurasia were interrupted in the Middle to Late Miocene supports the likelihood that Sivapithecus populations in Africa became isolated from those in Asia and speciation followed. Ultimately, a Sivapithecus species in Africa gave rise to australopithecines in that region and by 1.9mya these hominid populations had migrated as far as Java. In Asia, during the Middle and Late Miocene, Sivapithecus species radiated first throughout the forested areas, and perhaps later into more open and dryer niches that were replacing the forests. Gigantopithecus, and possibly the new Turkish specimens, described by De Bonis, represent later species of this radiation that occupied the ever expanding dryer and cooler niches. Parallel expansion of Sivapithecus in Africa led to the origin of australopithecines.

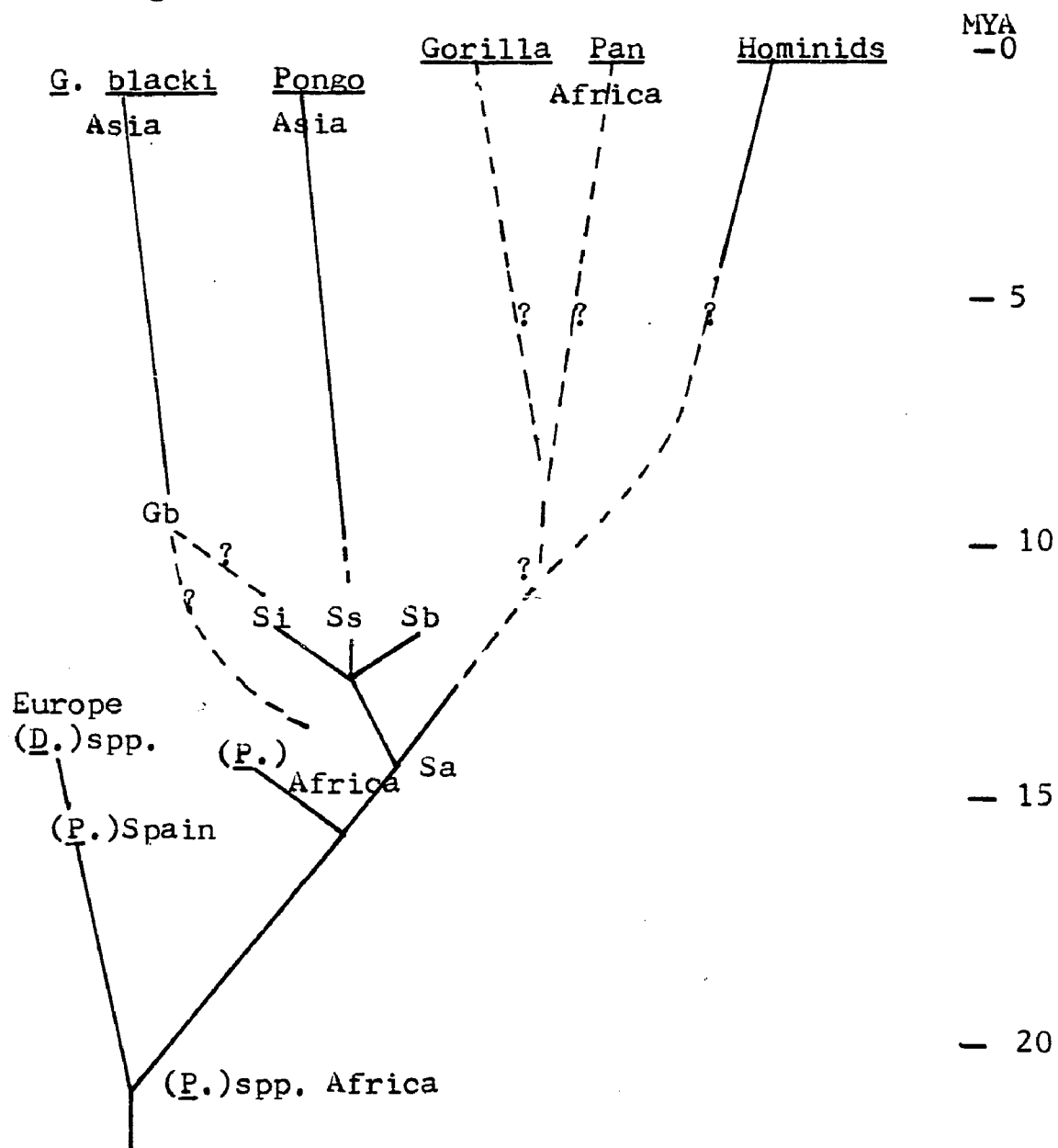
However, the data presented here clearly support the idea that a parallel development of australopithecines in Eurasia and Africa, starting after the commencement of (partial or complete) geographic isolation, 12 mya, is unlikely. When Eurasian and African Sivapithecus populations became isolated, there were few australopithecine adaptations in either. In fact, the same statement can be made for the 9½ million year old Sivapithecus species at Haritalyangar (found near the Nagri/Dhok Pathan boundary). They were forest populations, perhaps arboreal (Hungarian phalanges are curved), there is no evidence

of base camps, manuports or artifacts, there is no evidence for delayed maturation, nor is there any change in the function of the C/P₃ complex. One would have to suggest the very unlikely possibility that complex system and behavioral changes arose independently in order to derive australopithecines in both areas. With the alternate explanation, one is left with a single derivation of these unique adaptations in a region from which australopithecines are already known; this is the simplest explanation and one that can be tested by exploring Plio/Pleistocene deposits in Eurasia.

Lastly, according to this suggested phylogeny, an African (Proconsul) species gives rise to the African pongids. This too is based on characters shared by these fossil and extant pongids; relatively larger canines, retention of molar cingula, more gracile mandibles, and more posterior insertions of the zygomatics (at M² and M³). A Pan/Gorilla split could have occurred almost any time after 15 mya. Collecting in West and Central Africa will be necessary before more definitive conclusions can be reached about the phylogeny of African pongids.

The second phylogenetic scheme (Figure 12), considered possible but less likely by the author, places the two break points later in time. First, the Pongo lineage is derived from one of the Eurasian Sivapithecus species. From a geographical standpoint this might be

Figure 12 Phylogenetic Scheme #2



Abbreviations: (P.)-(Proconsul), (D.)-(Dryopithecus),

Sa-Sivapithecus africanus, Sb-Sivapithecus

brevirostris, Ss-Sivapithecus sivalensis,

Si-Sivapithecus indicus, Gb-Gigantopithecus

bilaspurensis

— 25

more likely than the previously suggested phyletic relationship between European (Dryopithecus) and Pongo. It is conceivable that a dietary generalist like Sivapithecus could have evolved into a large fruit eating form like Pongo.

With the Pongo lineage isolated in Eurasia after the Middle Miocene, the common ancestor of the African pongids and australopithecines is represented by an African Sivapithecus species, and a split between them could have occurred anytime between 12 and 5 mya. Despite the fact that there are many dental similarities between Sivapithecus and australopithecines, and between (Proconsul) and extant African pongids, it is still possible that Sivapithecus gave rise to both. Sivapithecus is not an australopithecine, but rather a dryopithecine without the clearcut dental specializations seen in extant African apes or early hominids.

The shared locomotor adaptations among the living great apes and man also support a later divergence. The presence of these shared characters can be most simply (but not necessarily correctly) explained as a consequence of common inheritance. The fact that (Proconsul) does not exhibit these characters makes the earlier divergences, suggested in the first scheme, less likely because it necessitates the explanation that the shared locomotor adaptations arose independently.

It is also possible to partially combine both schemes. Orangs could, following scheme 1, be descended from European (Dryopithecus), while, following scheme 2, Sivapithecus in Africa gave rise to both African apes and australopithecines.

Thus, at present, it is not possible to eliminate one of the schemes. Clearly, the most significant information lacking in the fossil record revolves around the ancestry of the great apes. It is conceivable that many of the australopithecine adaptations arose in the Late Miocene. If true, earlier populations were dryopithecine-like, and therefore could be in the ancestry of the African apes. Only by recognizing the earliest evidence of the African ape lineages can we determine the dates of divergence.

APPENDIX 1A

S. africanus Maxillae

Side	L	R	R	L	R
Specimen	FT 46*	FT 47	RU 1692	BMNH+ 16649	MB 106
C ¹ L	9.6	---	---	---	---
B	8.6	---	---	---	---
P ³ L	---	---	---	8.6	---
B	---	---	---	11.5	---
P ⁴ L	7.0	---	---	7.6	---
B	10.5	---	---	11.4	---
M ¹ L	10.7	10.5	---	10.0	10.9
B	10.9	10.8	---	10.9	11.2
M ² L	11.6	12.0	12.2	---	---
B	11.6	12.0	11.7	---	---
M ³ L	---	---	---	---	---
B	---	---	---	---	---

*Measurements taken from Andrews and Walker (1976).

+Measurements taken from a cast.

APPENDIX 1A
S. africanus Mandibles

Side Specimen	L FT 45	R FT 7	R FT 48
C ₁ L B	--- ---	--- ---	--- ---
P ₃ L B	10.9 6.6	--- ---	--- ---
P ₄ L	8.2 8.4	8.2 9.0 (est.)	--- ---
M ₁ L B	--- ---	10.3 10.0	--- ---
M ₂ L B	--- ---	--- ---	11.2 9.3
M ₃ L B	--- ---	--- ---	--- ---

APPENDIX 1B

S. brevirostris Maxillae

Side	R	L	L	L	R
Specimen	GSI D. 185	GSI D. 186	GSI D. 187	GSI 18068	YPM 13799
C ¹ L	---	---	---	---	---
B	---	---	---	---	---
P ³ L	7.0	---	---	---	7.5
B	9.1	---	---	---	10.3
P ⁴ L	6.3	---	---	---	6.8
B	8.8	---	---	---	9.9
M ¹ L	10.4	---	---	---	10.0
B	10.8	---	---	---	10.7
M ² L	10.4	---	9.5	---	10.1
B	11.0	---	10.5	---	11.7
M ³ L	---	9.3	---	8.5	---
B	---	11.0	---	9.8	---

APPENDIX 1B

S. brevirostris Maxillae

Side	L	L	L	R
Specimen	YPM 13809	RUD 12	RUD 15	RUD 15
I ¹ L	---	7.3	---	9.0
B	---	7.2	7.2	7.3
I ² L	---	---	5.3	5.4
B	---	---	6.6	6.3
C ¹ L	11.4	8.4*	10.0*	---
B	8.3	6.6*	7.5*	---
P ³ L	---	6.2	7.1	7.0
B	---	10.0	10.5	---
P ⁴ L	---	6.1	6.6	6.7
B	---	10.3	11.4	11.5
M ¹ L	---	9.2	8.7	8.8
B	---	10.5	10.6	---
M ² L	---	---	10.1	9.9
B	---	---	---	11.4
M ³ L	---	10.3	---	---
B	---	12.0	---	---

*Measurements taken from a photo by the author, see text
for discussion.

APPENDIX 1B

S. brevirostris Mandibles

Side	R	R	L	L	L
Specimen	GSI D. 298	YPM 13806	YPM 13814	YPM 13830	BMNH*
C ₁ L	---	---	---	---	---
C ₁ B	---	---	---	---	---
P ₃ L	9.5	---	---	---	---
P ₃ B	5.4	---	---	---	---
P ₄ L	6.0	---	---	7.6	7.1
P ₄ B	6.9	---	---	7.8	7.8
M ₁ L	9.1	---	---	---	8.2
M ₁ B	8.1	---	---	---	---
M ₂ L	10.2	10.9	11.0	---	9.7?
M ₂ B	9.0	10.1	10.5	---	10.0?
M ₃ L	---	11.0	11.8	---	10.4
M ₃ B	---	9.1	10.8	---	---

*Measurements provided by D.W. Frayer.

APPENDIX 1B

S. brevirostris Mandibles

Side	L	R	L	L	R
Specimen	RUD 1	RUD 2	RUD 2	RUD 17	RUD 17
I ₂ L	---	---	---	5.0	---
I ₂ B	---	---	---	7.2	---
C ₁ L	---	9.5*	---	8.7	8.8
C ₁ B	---	7.4*	---	6.0	6.6
P ₃ L	---	9.0	---	9.7	10.0
P ₃ B	---	5.6	---	6.5	6.4
P ₄ L	7.9	7.6	---	7.5	7.6
P ₄ B	9.5	7.0	---	8.1	7.9
M ₁ L	8.6	9.1	9.1	9.6	9.5
M ₁ B	8.3	8.0	8.3	8.6	8.4
M ₂ L	9.4	10.1	9.9	11.0	10.6
M ₂ B	9.5	8.5	8.5	9.7	9.9
M ₃ L	11.8	10.9	11.0	11.4	10.8
M ₃ B	9.5	8.4	---	9.5	9.7

*Estimates based upon both right and left canines.

APPENDIX 1C

S. sivalensis Maxillae

Side	R	R	L	R	R
Specimen	GSI D. 1	GSI D. 188	GSI D. 299/300	GSI D. 299/300	GSI D. 301
C ¹ L	13.2	---	10.7	11.0	---
B	10.9	---	8.4	9.2	---
P ³ L	---	---	8.8	8.8	---
	---	---	10.9	11.0	---
P ⁴ L	7.5	---	---	7.5	---
B	11.4	---	---	11.2	---
M ¹ L	10.8	---	---	10.9	12.0
B	12.0	---	---	12.3	12.5
M ² L	12.2	---	---	11.7	---
B	12.9	---	---	13.7	---
M ³ L	11.4	11.0	---	11.0	---
B	10.5	11.7	---	12.7	---

APPENDIX 1C

S. sivalensis Maxillae

Side	L	R	R	L	R
Specimen	GSI D. 307	GSI D. 313	GSI 18064	GSI 18065	GSI 18070
C ¹ L	12.8	---	---	---	---
B	8.9	---	---	---	---
P ³ L	---	---	---	---	---
B	---	---	---	---	---
P ⁴ L	---	---	---	8.2	---
B	---	---	---	12.2	---
M ¹ L	---	10.4	11.2	---	---
B	---	12.1	12.2	---	10.7
M ² L	---	---	12.2	---	---
B	---	---	13.2	---	---
M ³ L	---	---	11.6	---	---
B	---	---	12.2	---	---

APPENDIX 1C

S. sivalensis Maxillae

Side	R
Specimen	YPM 13807
C ¹ L	---
B	---
P ³ L	---
B	---
P ⁴ L	---
B	---
M ¹ L	10.0
B	11.3
M ² L	12.2
B	13.0
M ³ L	---
B	---

APPENDIX 1C

S. sivalensis Mandibles

Side	R	L	R	L	R
Specimen	GSI D. 118	GSI D. 119	GSI D. 177	GSI D. 180	GSI D. 181
C ₁ L	---	---	---	---	---
C ₁ B	---	---	---	---	---
P ₃ L	---	---	---	---	---
P ₃ B	---	---	---	---	---
P ₄ L	---	---	8.7	---	---
P ₄ B	---	---	9.8	---	---
M ₁ L	---	---	12.0	11.5	12.3
M ₁ B	---	---	10.4	9.5	10.1
M ₂ L	---	11.6	13.2	---	---
M ₂ B	---	9.6	12.2	---	---
M ₃ L	12.8	---	---	---	---
M ₃ B	10.4	---	---	---	---

APPENDIX 1C

S. sivalensis Mandibles

Side	L	R	L	L	L
Specimen	GSI D. 199	GSI D. 304	GSI D. 305	GSI D. 306	GSI D. 314
C ₁ L	---	---	---	---	---
C ₁ B	---	---	---	---	---
P ₃ L	---	---	---	---	---
P ₃ B	---	---	---	---	---
P ₄ L	7.5	---	---	---	---
P ₄ B	9.4	---	---	---	---
M ₁ L	10.6	11.6	10.9	10.6	---
M ₁ B	---	9.3	9.5	9.9	---
M ₂ L	12.0	---	---	---	---
M ₂ B	11.0	---	---	---	---
M ₃ L	12.9	---	---	---	13.5
M ₃ B	11.2	---	---	---	12.0

APPENDIX 1C

S. sivalensis Mandibles

Side	L	R	R	L	L
Specimen	GSI 18041	GSI 18042	GSI 18067	GSI 18069	AMNH 19411
C ₁ L	---	---	---	---	10.0
C ₁ B	---	---	---	---	8.8
P ₃ L	---	---	---	---	11.3
P ₃ B	---	---	---	---	7.2
P ₄ L	---	---	---	7.7	---
P ₄ B	---	---	---	9.0	8.2
M ₁ L	12.1	---	---	---	---
M ₁ B	10.1	---	---	---	---
M ₂ L	---	12.7	---	---	---
M ₂ B	---	10.5	---	---	---
M ₃ L	---	---	12.3	---	---
M ₃ B	---	---	9.7	---	---

APPENDIX 1C
S. sivalensis Mandibles

Side	R	L	L	L	R
Specimen	AMNH 19411	AMNH 19412	YPM 13811	YPM 13813	YPM 13825
C ₁ L	10.6	10.5	8.8	---	---
C ₁ B	8.7	8.6	6.0*	---	---
P ₃ L	---	11.7	---	---	---
P ₃ B	---	7.2	5.0*	---	---
P ₄ L	8.4	8.1	7.6	---	---
P ₄ B	8.5	9.0	8.2	---	---
M ₁ L	---	10.9	11.3	11.0	11.1
M ₁ B	---	9.5	9.3	9.6	9.4
M ₂ L	---	12.5	12.1	---	12.8
M ₂ B	---	11.4	10.5	---	9.6
M ₃ L	---	14.6	---	---	---
M ₃ B	---	12.2	---	---	---

*Estimated.

APPENDIX 1C

S. sivalensis Mandibles

Side	R	L	L	R
Specimen	YPM 13832	YPM 13833	YPM 13836	BMNH* 13264
C ₁ L	---	---	---	---
C ₁ B	---	---	---	---
P ₃ L	---	---	---	---
P ₃ B	---	---	---	---
P ₄ L	---	---	---	---
P ₄ B	---	---	---	---
M ₁ L	---	---	---	---
M ₁ B	---	---	---	---
M ₂ L	12.8	---	---	---
M ₂ B	11.6	---	---	---
M ₃ L	---	13.9	12.8	13.3
M ₃ B	---	11.9	10.0	11.0

*Measurements provided by D.R. Pilbeam.

APPENDIX 1D

S. indicus Maxillae

Side	L	L	R	R	R
Specimen	GSI D. 191	GSI D. 192	GSI D. 196	GSI D. 238	GSI D. 308
C ¹ L	---	16.3	14.5	15.4	15.5
B	---	10.2	12.7	12.5	11.0
P ³ L	---	---	---	---	---
B	---	---	---	---	---
P ⁴ L	---	---	---	---	---
B	---	---	11.8	---	---
M ¹ L	10.3	---	11.0	---	---
B	12.0	---	12.5	---	---
M ² L	13.0	---	13.2	---	---
B	14.0	---	14.5	---	---
M ³ L	---	---	12.8	---	---
B	---	---	13.8	---	---

APPENDIX 1D

S. indicus Maxillae

Side	R	L	L	R	L
Specimen	GSI D. 309	YPM 13827	YPM 13834	YPM 13835	YPM 13837
C ¹ L	---	---	---	---	---
B	---	---	---	---	---
P ³ L	---	---	---	---	8.9
B	---	---	---	---	11.4
P ⁴ L	---	---	---	---	---
B	---	---	---	---	---
M ¹ L	---	---	11.5	---	---
B	---	---	12.4	---	---
M ² L	---	---	---	12.8	13.8
B	---	---	---	15.5	15.2
M ³ L	12.1	13.0	---	---	---
B	12.9	13.8	---	---	---

APPENDIX 1D

S. indicus Maxillae

Side	R	R
Specimen	BMNH* 13365	BMNH* 13366
C ¹ L	---	---
B	---	---
P ³ L	---	---
B	---	---
P ⁴ L	---	---
B	---	---
M ¹ L	11.3	11.3
B	13.1	13.3
M ² L	---	---
B	---	---
M ³ L	---	---
B	---	---

*Measurements provided by D.R. Pilbeam.

APPENDIX 1D
S. indicus Mandibles

Side	L	L	R	L	R
Specimen	GSI D. 197	GSI D. 198	GSI D. 303	GSI 18039	GSI 18040
C ₁ L	---	---	---	---	---
C ₁ B	---	---	---	---	---
P ₃ B	13.7	---	---	13.3	---
P ₃ L	8.7	---	---	8.3	---
P ₄ L	8.4	---	---	8.7	---
P ₄ B	11.5	---	---	11.2	---
M ₁ L	12.5	---	---	12.2	---
M ₁ B	11.9	---	---	---	---
M ₂ L	15.9	13.0	---	15.6	15.5
M ₂ B	13.5	12.3	---	14.3	14.0
M ₃ L	---	14.9	15.5	---	16.0
M ₃ B	---	13.3	11.8	---	13.4

APPENDIX 1D

S. indicus Mandibles

Side	L	L	L
Specimen	AMNH 19413	YPM* 13828	BMNH** 13364
C ₁ L	---	14.7	---
B	---	11.4	---
P ₃ L	---	15.4	---
B	---	9.2	---
P ₄ L	9.5	9.4	---
B	10.3	11.2	---
M ₁ L	12.2	12.9	---
B	11.1	11.7	---
M ₂ L	13.8	15.1	---
B	12.4	13.8	---
M ₃ L	14.2	16.2	15.1
B	12.8	13.4	12.2

*Composite of D.189/D.190 and YPM 13828.

*Measurements provided by D.R. Pilbeam

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