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# Morphometric Analysis of Extant and Miocene Fossil Pongid Mandibles

BY

© Julie Lindgren Cormack

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF ARTS

DEPARTMENT OF ANTHROPOLOGY

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Date: 14th August 1985

Along with morphology or structure, let us add size.... structure is quality, while size is quantity.... how can one classify animals on the basis of size? In any one genus, for instance, one can find an extremely large range of sizes.... size may be an important difference between two species in one genus and have consequences which permeate into its ecology, its reproductive activities, its evolutionary progress, its development, its physiological activities....

J.T. Bonner (1965:7)

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Morphometric Analysis of Extant and Miocene Fossil Pongid Mandibles, submitted by Julie Lindgren Cormack in partial fulfilment of the requirements for the degree of Master of Arts.

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(Supervisor)

L. M. Fedigan..............................

Michael C Mahaney..............................

G.H. Sperber..............................

Date: 14 August 1985

# Abstract

The primary purpose of this thesis is to examine interspecific, subspecific, and sexual variation in the size of the mandible in five extant pongid groups. As expected, gorillas are the largest, orang-utans intermediate, and chimpanzees the smallest in size. Bornean orang-utans and highland mountain gorillas are the largest of their respective genera. Males normally have bigger mandibles than females.

A secondary purpose is the comparison of metrical similarities between the mandible of extant pongids to those mandibular fragments presently belonging to the fossil <u>Ramapithecus</u>/<u>Sivapithecus</u> group. Examination of a possible anatomical association between orang-utans and the Miocene fossils involves the use of the multivariate statistical approach known as discriminant analysis. As well, the ranges of metrical variation in the lower jaw in the sample of modern primates are plotted as a series of graphs in which the fossil measurements are fitted. Using the discriminant analysis technique 62% of the Miocene mandibular fragments fit within the morphological size range of <u>Pan</u>. This result suggests an affiliation with <u>Pan</u> in terms of biological distance, body size, or dietary similarities.

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# Chapter I

## Purpose

The main purpose of this thesis is to examine the interspecific, subspecific, and sexual levels of morphometric variation of the mandible in a sample of five extant pongid groups. A secondary intent involves the comparison, based on measurements, of middle to late Miocene hominoid fossil mandibles presently identified in the published literature as either *Ramapithecus* or *Sivapithecus*, to the five skeletal samples of extant pongids. The approach of categorizing taxonomically unknown fossils in terms of living counterparts is founded in the present trend in physical anthropology of the use of comparative research. A brief discussion of the history leading to this approach is examined below.

## Historical development of comparative research

Traditionally, comparative research stressed morphological similarities and differences between fossils and extant primates. This emphasis occurred because many of the first palaeoanthropologists were trained initially in anatomy (for example, Davidson Black, Raymond Dart and Grafton Elliot Smith). Thus, these scholars brought their own expertise to the new field of human origins research. These studies of anatomical similarities and differences might be considered as part of the first phase in the development of an overall comparative methodology. This primary phase was noted for its emphasis on description and typology of fossil remains and was a period of data collection and organization.

> ...all that can be done with the initial descriptive information is to gain a first understanding, a sense of problem, and a preliminary classification. To go further requires an elaboration of theory and method along different lines.
>
> (Washburn 1953:715)

With an increase in both quantity and quality of individual fossil fragments, it became apparent that palaeoanthropology was entering the beginning stages of an analytical and interpretative phase (Phase 2). This change was most definitely influenced by Washburn's 1953 publication entitled "The strategy of physical anthropology", which stressed rigor in methodology and presentation. During this period, comparative analyses based on the anatomy of extant primates were still important. However, a simple description of the fossils was no longer satisfactory.

The desire for more information by early anthropologists, (for example, on the stratigraphy and geology of specific fossil localities) brought an influx of scholars from outside palaeoanthropology. This acceptance of other disciplines such as palynology, geology, zoology, and molecular biology could be termed the beginnings of a "multi-disciplinary approach" to the study of early hominoids (Phase 3).

The first major application of this new approach occurred in 1967, when F.C. Howell co-directed a large-scale field excavation project in the Omo Valley, Ethiopia. This international field operation involved French, Kenyan, American, and Ethiopian scholars (Arambourg et al. 1967, 1969; Howell 1968).

Although the study of anatomical similarities between fossils and modern representatives continued in the third phase, a new emphasis was manifest. The likeness in morphology between primate skeletons and fossils fragments led to the belief that analogous social patterns also existed. As a result, the behaviour of non-human primates, as determined by various field studies, was used as a model to provide some insight into the behaviour of early hominoids. For instance, some present models attempt to examine: (1) the evolution of a hunting behaviour (Hill 1982; Washburn and Lancaster 1968); and (2) the origin of the family unit (Gough 1975; Lovejoy 1981).

## History of collection of fossil hominoids

The most recently discovered facial remains (Andrews and Tekkaya 1980; Pilbeam 1982; Pilbeam and Smith 1981; Wu 1983), and more complete postcranial evidence (Pilbeam *et al.* 1977, 1980) of middle to late Miocene fossils have shown striking gross morphological similarities, especially in terms of cranial size and proportions, to extant *Pongo* skeletal material. On the basis of this possible anatomical affinity, most scholars today have placed *Sivapithecus* (including *Ramapithecus*) on a direct ancestral line to the orang-utan. The new evidence, plus a recent re-organization and re-examination of the middle to late Miocene hominoid material, seems to have confirmed this affiliation. A brief synopsis of this change in interpretation follows.

The original discovery of *Ramapithecus* in India in 1932 resulted in the establishment of two separate species (Lewis 1934): *Ramapithecus brevirostris* nd *Ramapithecus harensis*. Since most of the preliminary finds of *Ramapithecus* included only small jaw fragments and teeth, the taxonomic assessment of these fossils was based solely on dental/gnathic features. Although many of the individual teeth of the ramapithecines were very human-like, later discoveries of more complete jaws showed a greater similarity to the apes.

This change in opinion began with the reconstruction of a newly discovered mandibular fragment from Fort Ternan, Kenya, KNM-FT 45 (Andrews 1971). Since the symphyseal region was preserved on this specimen, Walker and Andrews (1973), using mirror image replicas, were able to reconstruct the shape of the dental arcade. The results of previous attempts at determining ramapithecine dental arcade shape showed tendencies towards the human trait of a more parabolic tooth row. In contrast to these results, Walker and Andrews (1973) found that their reconstructed jaw had ape-like parallel tooth rows. Later discoveries of complete jaws supported this new interpretation, and consequently the original belief that this genus was ancestral to the human line (Lewis 1934, 1937; Simons 1977; Simons and Pilbeam 1965) shifted with the recovery of more middle to late Miocene fossil remains.

Before the discovery of the first _Ramapithecus_ another Miocene fossil was known from India. This fossil primate, investigated by Lydekker (1879), was originally identified as _Paleopithecus_ _sivalensis_. Today, it is more commonly known as _Sivapithecus_. This fossil represented a more robust and larger primate than _Ramapithecus_, and therefore most scholars considered this genus to be a pongid ancestor (Pilbeam _et al._ 1977;

Simons and Pilbeam 1965). However, with the shift in interpretation of <u>Ramapithecus</u> from a hominid to a pongid ancestor it was suggested that there were affinities between these two fossil genera (Ciochon and Corruccini 1982, 1983; Greenfield 1979; Kay 1982; Kay and Simons 1983; Lipson and Pilbeam 1982; Pickford 1977; Pilbeam 1980; Pilbeam <u>et al.</u> 1977; Ward and Pilbeam 1983; Wolpoff 1982).

At present, there are two issues under debate regarding the taxonomic and ancestral position of these two fossils. The first issue deals with whether there is a relationship between <u>Ramapithecus</u> and <u>Sivapithecus</u>. Since the major localities of these fossil discoveries, mainly in Indo-Pakistan and China, show stratigraphic contemporaneity, then this may provide the geological evidence as to why these two genera might be related.

In terms of morphological similarity, if the fossil evidence of these two genera only indicate differences in size, and not proportion, then these two originally separately classified fossils may have to be combined into a single genus. Because the term <u>Sivapithecus</u> was proposed originally in 1910 (Pilgrim 1910), the rule of historical priority in the naming of taxa dictates that a single genus classification would adopt the earlier title (Greenfield 1979; Kay 1982).

Differences in size between Ramapithecus and Sivapithecus may be an indication of sexual dimorphism, and therefore these might represent a single species. For instance, if the two genera are combined, then the larger sivapithecines might be interpreted as males, whereas the smaller ramapithecines may be examples of females (Wu 1983; Wu and Xu 1985). Another interpretation suggests that if the two genera are distinctive, then each genera would include male and female variants not yet identified (Wu and Oxnard 1983a, 1983b).

The second issue deals with the problem of ancestry. Most scholars believe that these fossils are pongid ancestors (general references include: Andrews 1982; Andrews and Cronin 1982; Lipson and Pilbeam 1982; Martin and Andrews 1982; Pilbeam 1983; Wolpoff 1982; Wu 1983). More specifically, Pilbeam et al. (1977) noted that the Ramapithecidae (his term for Ramapithecus and Sivapithecus fossils) were ancestral to Australopithecus and therefore to Homo. However this view changed and Pilbeam (1983, 1984) now sees strong anatomical similarities between the Miocene fossils and modern orang-utans. Andrews and Tekkaya (1980) initially claimed a strong Ramapithecus (including Sivapithecus) relationship to Pongo.

In contrast to both of these interpretations, Kay (1982) and Kay and Simons (1983) state that ramapithecines (including *Sivapithecus*) share the following six characteristics with early australopithecines: (1) broad mandibular corpora; (2) thick enamelled molars; (3) reduced canine size; (4) reduced canine sexual dimorphism; (5) buccolingually broad, mesiodistally short upper canines; and (6) an enlargement of the P3 metaconid. According to the authors, these dental/gnathic similarities mean that ramapithecines are good cladistic ancestors for *Australopithecus* and *Homo*.

## Structure and function of the mandible

Traditionally, research on the mandible has not been as extensive as studies of the dentition. Even with the availability of the mandible as the second most common structure, after the dentition, in the recovery of fossil remains, research on this bone has been minimal. It was, therefore decided to examine the lower jaw in this thesis research.

The adult primate mandible is a single bone, which together with the cranium forms the skull. The mandible is considered the only moveable bone in the skull with exception of the auditory ossicles. It is the region of temporo-mandibular articulation between the cranium and the lower jaw which allows this movement. The combination of the flexible ligaments in the temporomandibular joint and the insertion of particular muscles on the mandible are the precise features which provide the impetus for jaw movement. Since the mandible is most significantly involved with mastication (or the operation of chewing), a brief description of the major masticatory muscles is provided.

The muscles of mastication are: the temporalis; masseter; medial pterygoid; and lateral pterygoid. The origin of the temporalis muscle is the temporal line, temporal fossa, and overlying fascia, which often in pongids is located along the mid-sagittal position of the cranium. This muscle inserts on the internal surface of the coronoid process of the mandible and the anterior margin of the ascending ramus. The function of the temporalis muscle involves actively pulling the mandible backward, and thus closing the jaw. Another muscle which aids in the closing of the jaw is the masseter muscle, which originates from the zygomatic arch, and inserts on the external face of the ascending ramus. The origin of the medial pterygoid muscle is located on the medial aspect of the lateral pterygoid plate of the sphenoid bone, all of which is found at the base of the cranium. The point of insertion of this muscle is the internal surface of the gonial angle. The only masticatory muscle whose function is opening the jaw is the lateral pterygoid muscle. This muscle originates from the lateral aspect of the lateral pterygoid plate of the sphenoid bone. It inserts into the neck of the mandibular condyle.

The most obvious function of the mandible is as a bony structure capable of holding the deciduous and adult sets of teeth. On a broader scale, the mandible, because of its position as part of the oral cavity, is involved predominantly in the overall operation of mastication. During any phase of chewing the mandible functions as a lever by providing antero-posterior and lateral movements. Minor functions of the mandible are related to movement involved with facial expressions and vocalizations.

Structure and function of the mandible are related. A change in a particular structural element of the mandible, such as the laceration of one of masticatory muscles, the loss of a condyle, the loss of teeth may lead to a deviation from the normal functional operation. The relationship between structure and function arises because of the "plastic" nature of the primate mandibular form (Symons 1951). This plasticity is a result of: (1) continuous changes in the mandibular form during ontogeny [growth]; and (2) structural alterations which can change the function or cause dysfunction [environment]. In other words, the mandible, in comparison to any other bone in the skeleton will respond more strongly to structural changes induced by either growth or environmental demands (Symons 1951). In order to further understand the potential effects of the "plastic" nature of the mandible, specific examples of ontogenetic and environmental factors are discussed.

The most regular ontogenetic change of the mandible occurs with the loss of teeth during the process of aging. Jensen and Palling (1954) noted that the loss of teeth in elderly humans resulted in an increase in the size of the gonial angle. This change, described as a flattening of the gonial angle, was directly affected by the exertion on the mandible of the masseter and medial pterygoid muscles. According to Rogers and Applebaum (1941) and Scott (1954), loss of teeth also resulted in a decrease in the size of the coronoid process.

Environmental factors such as the effects of trauma, disease, malocclusion, or dietary change might also alter the structure of specific components of the mandible, or of the mandible as a whole bone. Examples of trauma and dietary change follow.

Trauma defined as an injury to the body caused by shock, would include the laceration of a single muscle or a group of muscles. The most frequent experiment using masticatory muscles is the removal of the temporalis muscle. The four studies mentioned herein (Avis 1959; Boyd *et al.* 1967; Horowitz and Shapiro 1951; Washburn 1947) generally demonstrated the same results. All of these studies noted that the coronoid process, on which the temporalis muscle normally inserts, disappeared completely or reduced somewhat in size. The "loss" of this mandibular element was due to resorption since the coronoid process was well-formed before the removal of the muscle. Avis (1959) and Washburn (1947) also found that the nuchal crest decreased in size with [illegible] severing of the temporalis muscle. Boyd *et al.* (1967) stated that the removal of muscles decreased or eliminated the amount of blood supply to a particular region of bone. Consequently, this bone was incapable of growing or being maintained due to the lack of nourishment.

Removal of the masseter muscle from its point of origin on the zygomatic arch also resulted in a reduction of bone size (Horowitz and Shapiro 1955). This decrease in the size of the mandible clearly led to malocclusion of the teeth.

Since trauma is defined as an injury caused by shock, it would be appropriate to include the removal of bony components as part of this label. A study by Sarnat and Engel (1951) demonstrated the trauma involved in the removal of a single mandibular condyle. The results of that research produced asymmetrical deformities of the mandible, such as a very short and wide ascending ramus. According to these authors, the shift in the shape of the ramus affected the overall position of the mandible, which clearly led to malocclusion. As compensation for the loss of the condyle, the coronoid process increased in thickness and height. Surprisingly, Sarnat and Engel (1951) noted that mandibular function was not seriously impaired.

Change in diet has also been used as a criterion for structural alterations in the mandible (Corruccini and Beecher 1982, 1984). As with the preceding example, primates were used as the experimental animals. Both of these dietary studies showed similar results. Animals fed on soft diets suffered from more incidences of malocclusion, as well as mandibular and incisal overjet. Corruccini and Beecher (1982, 1984) believed that the mastication of soft foods provided little stimulus for development, and as a result, the structure of the mandible atrophied. Soft diets also led to more variability in mandibular ramal breadths, and in the size of the mandibular condyle.

In order to discriminate among three pongid species based upon variation in the size of the mandible and of mandibular components, it is necessary to show that the metrics used assess species-specific differences and not differences resulting from trauma, disease, and/or dietary practices experienced by individuals during ontogeny. If these influences, as described in the above examples, can be controlled for, then any attempt to separate the three species using mandibular size will be based on the normal hereditary variation that exists within (for example, sexual differences) and between (for example, phylogenetic differences) the groups. In other words, factors of growth such as the loss of teeth due to aging, or environmental factors such as a change in diet affect individual variation. Therefore, it is these influences that should not be part of the variation which normally defines a particular genus or species. If these factors affecting the individual can be accounted for in a study where groups are being compared, then the comparison is based on the normal phylogenetic variation which originally separates the groups.

In this research, allometric differences between juveniles and adults are "eliminated" by using only adults in the statistical analysis. Environmental influences are more difficult to detect because of the unavailability of particular details regarding each pongid specimen. For instance, it is impossible to test for malocclusion without the corresponding maxilla for each mandible. The effects of natural trauma (not induced by experiments) on pongid lower jaws is also difficult to assess because of the lack of detailed studies on this subject.

The issue of dietary change affecting certain features of the mandible is more complex because of the influence of various geographical localities for the collection of the primate specimens. Although the collections catalogue indicated that most of the extant pongids were originally from the wild, there can be no confirmation as to the food sources. However, it can be assumed that because most of the specimens were from the wild, these primates would have probably followed "normal" dietary regimes. According to Corruccini and Beecher (1982, 1984) if the primate specimens measured show a great degree of variability in ramal breadth measurement, then these primates might have consumed soft diets.

I am confident in the reduction of possible deviant environmental factors on the extant pongid specimens because of their probable habitat in the wild, and hence the lack of such influences as an abnormal soft diet or experimental trauma affecting these primates. If however, such factors were involved, then any deviations in structure from the norm would have been noted while taking measurements. None were identified.

## Sexual dimorphism

In highly sexual dimorphic primates, such as orang-utans and gorillas, males can weigh up to twice as much as females (Napier and Napier 1967). If there is an association between body weights and the size of skeletal components, the jaw for instance, then these differences in body size should also affect the size of the mandible.

A comparison of male/female differences within a single species has been explained in terms of a sexual selection theory (Darwin 1871). This idea proposed that competition existed between members of one sex (usually males) for access to the other sex. Certain dimorphic features, such as canine size, or particular behaviours made male primates more attractive to females and more feared among other males. The theory of sexual selection is only one idea. Other proposals to explain male/female size variation include: increased frugivory (Leutenegger and Cheverud 1985), polygyny (Leutenegger and Cheverud 1985), and terrestrial habitat on open savanna (Crook and Gartlan 1966; Krantz 1982). These three factors have been proposed as contributing to higher levels of sexual dimorphism in certain primate societies.

As mentioned earlier, the size variation between the Miocene hominoids may reflect sexual differences, whereby _Ramapithecus_ represents females, and _Sivapithecus_ represents males. If this relationship is confirmed, then using theories of extant pongid sexual dimorphism, predictions of diet and habitat could be assessed for these Miocene fossils. Existing sexual differences in diet of chimpanzees (Galdikas and Teleki 1981; McGrew 1979), and orang-utans (Galdikas and Teleki 1981) may demonstrate similar adaptations of the Miocene fossils. It would be more difficult to account for certain behaviours such as mating practices, or competition for sexual privileges within a Miocene fossil society.

## _History of mandibular research_

Interest in this region of the cranium probably came about with dissection of non-human primates. These dissections led to publications of skeletal descriptions (Anderson 1906), as well as details on the musculature of the lower jaw. This basic knowledge on structure was essential for understanding the masticatory operation in non-human primates (Hiiemae 1984; Hiiemae and Kay 1972; Jablonski 1981; Kay and Hiiemae 1974; Smith 1984; Ward 1974). Similar research on the chewing mechanism in modern humans has also been studied (Gingerich 1979; Hildebrand 1931; Hylander 1975; Simon 1974).

Today, much of the research on the human mandible deals with clinical questions. For instance, the examination and surgical correction of the temporomandibular joint syndrome, defined as an improper positioning of the condyle in the mandibular fossa, is an important component of dentistry. As well, studies continually view the muscles involved in mastication (Moller 1966) and the changes due to the growth of the human mandible. In 1977, Anderson et al. proposed an extension of a growth study by suggesting that the human lower jaw could be used in an estimation of age, sex, and body size of individual children.

Specific regions of both the human and primate mandible have been of particular interest. These anatomical features include: the chin (Mijsberg 1930;

Wolff 1984); the dento-alveolar arch (Lavelle and Flinn 1972; Owen 1969); the mandibular condyle (Smith et al. 1983a, 1983b); the mandibular corpus (Smith 1982, 1983); the mandibular fossa (Ashton and Zuckerman 1954; Hinton 1979); the mandibular symphysis (Beecher 1977; Goodman 1968); the mental foramen (Montagu 1954; Simonton 1923); the torus mandibularis (Mayhall 1983); and the temporomandibular joint (Demes 1984).

In summary, modern human mandibular studies deal mainly with clinical problems or certain regional features. Although non-human primate research also deals with specific local features, it more commonly examines the muscular structure and function of the mandible (Dechow and Carlson 1982; Dechow et al. 1983; Franks et al. 1982; Nemeth et al. 1983).

As with studies of modern pongid and human lower jaws, research on fossil mandibles also began with descriptions (Andrews 1971; Leakey 1970; Martin and Andrews 1984; Simons 1964; Xu and Lu 1979; Zwell 1972). Once a mandible or mandibular fragment was discovered, it was described and compared with living representatives and other similar fossils. This procedure of analysis was, and still is used for human and non-human primate fossil material.

Only very recent interpretative research on the fossil mandible has stressed specific regions or features. For example, White (1977) and Chamberlain and Wood (1985) analyzed the mandibular corpus in Plio-Pleistocene hominids; Picq (1983) looked at the temporomandibular joint in mainly Pleistocene hominids; and Benz (1980) and Wolpoff (1975) both published on the evolutionary changes in the early hominid mandible. Specific work on fossil pongid mandibles has only been recently introduced by Smith (1980).

In general, mention of the mandible of fossil hominids or pongids usually appears in the context of a larger and more detailed "craniofacial analysis". This type of discourse normally covers topics such as: maxillo-facial (Ward and Pilbeam 1983); palato-facial (Corruccini and Henderson 1978; McHenry *et al.* 1980); and cranial base studies (Anderson and Popovich 1983).

## Hypotheses to be tested

### EXTANT PONGID SPECIES CAN BE DISCRIMINATED ON THE BASIS OF INTERSPECIFIC AND SEXUAL VARIATIONS IN MANDIBULAR MORPHOLOGY

The primary hypothesis in this research tests the idea that extant pongid jaws can be distinguished interspecifically and sexually on the basis of size and dimension. The general assumption in this research is that there are discriminations of size between chimpanzees, gorillas, and orang-utans. This relationship of size in the mandible is more clearly understood by examining the overall body size of these primates. A comparison of general body size shows that gorillas are the largest, orang-utans intermediate, and chimpanzees the smallest. It is assumed that this order would be maintained with the measurement of body parts, in this case, the mandible.

The effects of experimentally induced soft diets on the primate mandibular form are known (Corruccini and Beecher 1982, 1984). However a comparison between dietary regime and size of the primate mandible has yet to demonstrate a relationship. In other words, it is difficult to relate the mainly folivorous diet of large mandibular-sized gorillas to the smaller mandibular-sized orang-utans and chimpanzees which regularily subsist on fruit.

Comparison of overall body size shows that male primates are larger than females (Kavanagh 1983; Napier and Napier 1967). As with the association between genera, this order is thought to be consistent with the examination of a particular body part. Based on these assumptions, it is expected that measurements taken on the extant pongid lower jaw will reflect interspecific and sexual size variation consistent with that variation demonstrated in a comparison of body size.

## A COMPARISON OF THE SIZE OF THE MANDIBLE BETWEEN EXTANT PONGIDS AND MIOCENE FOSSILS ILLUSTRATES A MORPHOLOGICAL CLOSENESS TO THE MODERN ORANG-UTAN (PONGO PYGMAEUS)

A secondary hypothesis to be tested in this study states that, mandibular measurements taken on Miocene fossils are statistically related to the same measurements on extant pongid lower jaws. More specifically, the mandibular measurements from fossils belonging to Ramapithecus/Sivapithecus cluster statistically around the same measurements of one of the three pongids in the control sample. Since many scholars believe that ramapithecines and sivapithecines are ancestral to *Pongo*, it is expected that this statistical clustering will be the most apparent between these two groups. The underlying assumption of this hypothesis is based on previous studies which demonstrate facial and dental similarities between these Miocene fossils and *Pongo* (Pilbeam 1982).

## Chapter 2

### Materials

The extant materials analyzed for this study included two separate samples of pongid mandibles. The larger sample, initially totalling 185 individuals, included three genera, Gorilla, Pongo, and Pan. This sample was further divided into two subspecies of Gorilla and two subspecies of Pongo. Herein, this group of 185 extant pongid mandibles will be regarded as the "data base" since it provided measurement data necessary to predict the species (and sex) of test mandibles. Two groups of test mandibles used included a smaller sample of seven modern pongid jaws, referred to as the "test sample", and 29 mandibular fragments from the Miocene Epoch, presently identified as either Ramapithecus or Sivapithecus.

The strength of the apparent anatomical association between these fossils and extant pongids, demonstrated the need to compare between these two groups. Although a comparison of fossil mandibles to modern human jaws was not examined, this type of study might have been an important indicator of any human affinity of the Miocene fossils. The inclusion of Gorilla and Pan in the data base was essential to broaden the pongid morphological comparison. Gorillas and chimpanzees were not considered descendants of the Miocene fossils because of the evidence of molecular data. The molecular phylogeny based on, but not exclusively including, immunological and nucleic acid data has indicated that Pongo diverged from the chimpanzee-gorilla-human lineage about eight to ten million years B.P. (Cronin 1983; Gribbin and Cherfas 1982). This date is generally consistent with the date for the Miocene fossils. As well, Gorilla and Pan are believed to have split from the main stem leading to hominids approximately four to five million years B.P. (Cronin 1983; Gribbin and Cherfas 1982).

The major sample of extant primate mandibular measurement data used in this thesis was collected at the National Museum of Natural History, Smithsonian Institution in Washington D.C., where the largest North American sample of extant pongid skeletons is presently housed. Since this collection contained specimens obtained from the late 1800s up to the present day, the collectors and original localities of the skeletal remains were diverse. This diversity should indicate that the measurements taken on the sample of extant pongid lower jaws is likely representative of normal size variation.

Measurements of all available mandibles were taken over a nine-day period in February, 1984. A total of 185 jaws were studied, but an additional thirty mandibles, out on loan, could not be analyzed. The Master Catalogue of Pongidae Skeletons provided by Dr. Richard Thorington Jr., Curator of Mammals, listed among other details, information on taxonomic classification, sex, and age for most of the mandibles.

The Smithsonian Institution collection included juveniles and adults, both of which were measured, even though juveniles were not included in the statistical analyses. The age identification approach taken here involved the numerical coding of the data base mandibles into one of five distinct categories (adapted from Shea 1983), with totals of each group given below:

| | | | |
|---|---|---|---|
| 1 | Adult | Full dentition | 141 |
| 2 | Juvenile | M2-partial eruption | 26 |
| 3 | Unknown | - | 0 |
| 4 | Adult (questionable) | C, M3 erupting | 14 |
| 5 | Juvenile (questionable) | M2-fully erupted | 4 |

Numeric codes 4 (questionable adult) and 5 (questionable juvenile) represented my interpretation of transitional growth stages. These two categories were only used when the age information was not available in the Master Catalogue of Pongidae Skeletons. Since all mandibles could be aged using one of four categories, as shown above, it was found that numeric code 3 (unknown age) was unnecessary.

Due to the relatively large degree of sexual dimorphism in great apes, it was important to identify the sex of each individual mandible. This information was either written on the bone itself, or listed in the Master Catalogue. Sex was also numerically coded, as shown below. Totals of each group are given.

| | | |
|---|---|---|
| 1 | Male | 90 |
| 2 | Female | 73 |
| 3 | Unknown | 10 |
| 4 | Male (questionable) | 7 |
| 5 | Female (questionable) | 5 |

Sex codes 4 (questionable male) and 5 (questionable female) were my interpretation of sex, when this information was not available. Since the genera involved in this study were sexually dimorphic, it was presumed that sex codes 4 and 5 could be developed, using considerations for differences of canine size, canine socket size, or general robusticity of the jaw. If the details of sex were not available, then the mandible was classified as being of an unknown sex. Table 1 illustrates the breakdown of age and sex for each of the five extant pongid groups which comprise the data base.

As mentioned earlier, a second, smaller sample of seven modern pongid mandibles was measured. This sample was taken from three sources: Department of Anthropology, University of Alberta; Dentistry Museum, University of Alberta; and the Zoology Museum, University of Calgary. The Department of Anthropology provided two examples of adult *Pongo* (one male, one female),* as well as an adult male *Pan* mandible. An articulated juvenile *Pan* specimen was used from the Dentistry Museum. The mandibles from the Zoology Museum, University of Calgary originally came from the Calgary Zoo. These included an adult female *Gorilla*, an adult male *Pongo*, and a juvenile *Pan*.

Data collection of the fossil mandibular measurements normally required the use of secondary sources. Measurements of the mandibles were taken from the published literature because of the large quantity and diverse locations of the original and good cast fossil material found throughout North America and Asia. Some information on fossil material was also gathered through correspondence with individuals investigating

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* The *Pongo* specimens were on loan from the Department

the Miocene Epoch. Because of the large amount of variability in the types of fossil mandibular fragments discovered, there could be no standard region of the jaw which was commonly measured. However, the listing of fossil material used in this study (Appendix 1) indicates that the postcanine region was quite common. It would therefore follow that measurements in this area of the jaw would also be quite common.

Fossils classified as either Ramapithecus or Sivapithecus, and for which mandibular material and measurements were available, were included in this study. The extensive fossil collections from Lufeng, China, were not included because of the inaccessibility of the necessary measurement data. The Kenyapithecus wickeri evidence from Fort Ternan, Kenya (KNM-FT 7, KNM-FT 45) was also excluded because of their probable dryopithecine affinities (Pickford 1984, personal communication). Appendix 1 lists and describes the fossil material used in the project. This appendix also documents the changes in taxonomic classification for each of the fossils over the past few decades.

## Methods

The measurements and non-dimensional observations on extant pongid mandibles and the measurements taken on the Miocene fossils used human anatomical landmarks, and followed standard human osteometric techniques. A maximum of 34 measurements were considered for each extant pongid mandible in the data base and each of the seven cases in the test sample (Table 2; Figure 1). Measurements were taken with Mitutoyo dial calipers (Model #505-646) calibrated to 0.02 mm. Three of the measurements (ramus height, gonial angle, and maximum length) were taken on a "standard" goniometer, or mandibular board. Four non-metric characteristics (Table 3) were studied on the extant pongid samples only.

Although measurements provided quantitative details on specific regional aspects of mandibular variation, photographs often better illustrated observed features, such as general shape or certain non-dimensional traits. For this reason, it was decided to take a minimum of three aspects (left lateral, occlusal, and posterior) for each mandible in the data base. This task resulted in a catalogue of 635 black and white photographs of the available pongid mandibles in the Smithsonian Institution collection.

The technique for the photographs involved the use of a piece of black velvet for a backdrop, its location dependant upon the aspect of the photograph. A 35 mm

Canon AT-1 camera with a 50 mm lens, without flash, and loaded with Kodak Plus-X 125 film, was attached to a small tripod. For extra lighting, a single 24-inch fluorescent tube was placed directly behind the camera.

Since this research emphasizes measurements, it is appropriate to examine particular measurements; discussing problems, sources of reduced measurement precision*, and to offer suggestions for similar future morphometric analyses. Specific measurements are discussed in five separate categories: use of the goniometer; corpus height and breadth measurements for postcanine teeth; use of certain landmarks; anterior measurements; and posterior measurements.

The purpose of using a goniometer was to illustrate the shape relationships between ramus height, gonial angle, and maximum length of the mandible. These relationships were very difficult to assess if the mandible was too large to fit properly on the goniometer, as was the case with many of both genders of orang-utan and gorilla mandibles (Plate 1). For these primates, it was often necessary to set the dial calipers on the mandibular board at the same angle as

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*The phrase "reduced measurement precision" implies a reduction in exactness in the value of particular measurements. The term "error" is not used in this context because it implies that the measurement, and its corresponding value, are wrong.

the vertical steel upright in order to measure ramus height correctly. Therefore, the degree of precision in this goniometer measurement was affected by the size of the lower jaw. In comparison to the rest of the measurements, the values for ramus height and maximum length which were taken on the goniometer were not as precise because they were only calibrated to the closest millimeter.

Since the vertical steel upright on a goniometer is immobile, it is assumed that the mandible to be measured is symmetrical. This assumption had important implications because it meant that this component of the goniometer could not account for either absent or uneven condyles, or absent or uneven gonia. The lack of symmetrically oriented condyles or gonia, especially in chimpanzee and gorilla mandibles, caused the bones to move laterally while being measured. This movement made it necessary to use only the most posteriorly positioned condyle for reference in placing the jaw on the goniometer.

As outlined above, the problem of "fit" on the mandibular board was a major factor in reducing measurement precision. This situation could have been remedied with the construction of a larger sized instrument with a flexible vertical steel upright which could be altered according to right and left side separately, in order to fit asymmetrical condyles or gonia. This type of goniometer would be ideal because it could identify measurement variation between the sides of the lower jaw, thus possibly illustrating certain unilateral differences in masticatory operation.

Slight variations of corpus height and corpus breadth measurements may have been a result of limited osteometric experience on the part of the researcher. It seemed that measurements on the left half of the mandible were more difficult to take than on the right half of the jaw. This difference might have been a reflection in the way the bone was held while taking measurements. More specifically, the balance of the bone in the hand seemed more awkward with the taking of left side measurements. Lack of teeth and broken alveoli made it more difficult to estimate the exact mid-tooth placement of some corpus height and breadth measurements. Large tooth roots, especially in gorillas, caused alveolar bulging which interfered with, and increased the size of, the corpus. The position of the simian shelf and genial tubercles also interfered with corpus height under P3. This interference was observed as a flattening of the inferior border in the area of the P3 which continued posteriorly. The result of measuring in this region led to inflated corpus height measurements (Plate 2). The location and angle of the anterior border of the ramus in relation to M3 corpus breadth made this measurement difficult (Plate 3).

The problems mentioned above merely illustrate observations in the measurement technique of corpus height and breadth. Unless the methods of taking measurements in this area of the mandible were to be changed, the influence of such features as genial tubercles, lack of teeth, reduced alveoli, and simian shelf projection must be considered.

The use of landmarks is an effective and standard approach in osteometry. Montagu (1960:48) defined gnathion as, "the middle point on the lower border of the mandible" and gonion as, "the most lateral external point of junction of the horizontal and ascending rami of the lower jaw". In this study the application of the gonion and gnathion was questioned, because these definitions were subjective and in the case of the gonion, did not account for the effects of muscle markings. Hence, these landmarks were difficult to locate precisely.

In contrast to Montagu´s definition of these human landmarks, Duerst (1926; as referred to by von den

Driesch (1976)) suggested that the position of the gonion in animals such as suid, bovids, and equids be divided into at least two anatomical landmarks: gonion caudale and gonion ventrale. The former term was defined as "the most aboral [posterior] point of the mandible", and the latter term defined as "the most basal point of the mandible" (von den Driesch 1976:53). These two "new" landmarks are less subjective than the placement of the single gonial angle because they each have their own reliable reference point. In the case of the gonion caudale, its position is located on a horizontal plane directly behind the most posterior point on the third molar, at the level of the alveolar bone. The position of the gonion ventrale is determined by measuring an exact vertical line from the highest point on the coronoid process. The location of a gonial angle "proper" could be assessed more precisely by finding the exact mid-point of these two "new" landmarks.

Although Montagu's definitions were used for the measurement of bigonial breadth and symphysis height, it might be suggested that more precise definitions, especially with regards to the gonial landmark proposed originally by Duerst (1926), be considered for future morphometric studies of pongids.

Anterior measurements were taken in the symphyseal region. Since some lower jaws were cut at the mid-line, symphysis measurements were difficult to take. In orang-utans, the simian shelf often exhibited a large, single genial tubercle which hindered the measurement of the symphysis breadth. Since pongid mandibles have a characteristically large, flattened simian shelf, which increased symphysis breadth, it was considered appropriate to take two breadth measurements in this region. The first measurement was taken parallel to the external surface of the symphysis (SymBE) and the second was taken parallel to the internal surface of the symphysis (SymBI).

The large size and varied shape of gorilla mandibles often created problems in such posterior measurements as ramus height, minimum ramus width, and bigonial breadth. Ramus height was difficult to measure because of the almost 90 degree gonial angle in gorilla jaws (Plate 4). This vertical L-shape of the gonial angle meant that the location of a straight line measurement from the highest point on the condyle to inferior border was not standardized. As mentioned previously, the large size of gorilla mandibles in relation tc the small goniometer made the ramus height measurement hard to assess precisely. Since many gorilla mandibles had a strongly convex-shaped anterior border of the ramus, the exact placement of the minimum ramus width measurement also varied. Bigonial measurements were strongly influenced by the shape and amount of gonial flaring in all three pongid genera, especially gorillas.

Reduced precision for two non-metric posterior observations was also considered. First, the general shape of the gonion, as presently defined, could be surveyed from the posterior aspect in terms of either the particular angle or the complete ramus (Plate 5). Examination of the precise gonial angle tended to make the observed inversion or eversion of this region more severe. A strongly inverted gonial angle would probably be affected by a heavy medial pterygoid muscle, whereas the masseter muscle, which inserts on the external surface of the gonion would have an influence on the eversion of this area of the jaw. If the gonial angle was viewed as part of the whole ramal structure, then any inversion or eversion caused by the effects of muscles of this region would have appeared less definite. Second, the position of the M3 in relation to the anterior border of the ramus, when viewed laterally, was entirely dependant upon the level at which the researcher was examining the specimen.

The above discussion illustrates possible sources of imprecision by a single observer, yet there are also difficulties in the use of other researchers' techniques. Although measurements were based on standardized anatomical landmarks based on the human mandible, variation in the names of these measurement variables occurred. For instance, the terms "breadth" and "height" could be synonymous with "thickness" and "length", or "depth" respectively. A misunderstanding of these terms might result in imprecise measurement values.

A more serious problem was the different way in which measurements were taken by various researchers. This difficulty, known as "experimenter error" could only be resolved if a single person took all measurements. Since this is usually impossible, it is necessary to understand that this type of error may always affect one's results. The general assumption in the comparative use of standard anatomical landmarks is that they will reduce, but not eliminate, the amount of "experimenter error".

## Statistical applications

The numeric analysis of the Smithsonian Institution collection of 185 lower jaws involved using the

Statistical Package for the Social Sciences, Version X (1983). This SPSSX package was selected because of its regular application in anthropological research and because it contained the required procedures for the analysis of the data. Four procedures were used: plot, discriminant analysis, condescriptive, and breakdown. According to van Vark (1984), classification of unknown specimens, on the basis of morphology, can be determined using either a visual comparison or following a multivariate statistical approach. In this research both methods (visual and multivariate) were employed, and were recognized under the labels "plot" and "discriminant analysis", respectively. The two other procedures, "condescriptive" and "breakdown", were used in the computation of descriptive statistics for the data base. A discussion of the four SPSSX procedures, as well as brief comments on ratios, follows. Each of these topics is examined in terms of why they are used, and what general information they provide.

## DESCRIPTIVE STATISTICS

The procedure known as "breakdown" was an appropriate technique because it calculated descriptive statistics from the measurement information in the data base in terms of certain sub-groupings (for example, male _Pongo_ _pygmaeus_ _pygmaeus_). Before this technique was run, the sub-groups had to be defined. The initial separation of the data base was using the taxonomic classification of species. The next required level of separation was due to sexually dimorphic differences in the size of the jaws. Since the variation in size was also important between adults and juveniles, these two age categories were mutually exclusive. Hence, the data base of 185 mandibles was broken down by species, sex, and age. Descriptive statistics could be calculated for any combination of these three sub-groups.

Similar results for the calculation of descriptive statistics were obtained using the procedure known as "condescriptive". This approach was used in conjunction with the breakdown procedure since it provided a greater variety of descriptive statistics including minimum/maximum values, and ranges of measurement values.

## RATIOS

Although the breakdown and condescriptive procedures analyzed the pongid data base variation using single measurements, these procedures were not capable of determining relationships between variables. The study of a relationship between two measurements constitutes the use of an index. Bass (1971:55) defined an index as, "the ratio of the width to the length of an object". The single index used in this study was the mandibular corpus shape, which compared corpus breadth with corpus height, and was calculated as follows (Kay 1982)* :

$$100 \text{ X } \frac{\text{M1-M2 Height}}{\text{M1-M2 Breadth}}$$

PLOT

A visual interpretation of the descriptive statistics (more specifically, the range of measurement values), was illustrated by a graphics procedure called "plot". The results of this approach provided 34 separate two-dimensional graphs, that is, one graph for each measurement variable. Three sets of graphs were plotted, where each set accounted for a distinct age group: adults only, juveniles only, and a series of combination plots including measurement values for both adults and juveniles. Only the adult graphs were used for comparison to the test mandibles.

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* A discussion of this ratio also appeared in Kay and Simons (1983).

The format of the graphs is shown in Figure 2, and explained as follows. The horizontal, or X axis represents the range of measurement values for a specific variable. The vertical, or Y axis identifies the five types of primates in the data base. Thus, each graph illustrates the range of values for a single measurement variable between the five pongid groups. The range of values for any particular species is further broken down by sex ("1" for males, "2" for females). Note that, in Figure 2 the range of sexual variation has been simplified from a series of "1´s" and "2´s" to a single line with either the letter "m" or the letter "f" denoting sex. Therefore, these graphs function as visual "keys" not only showing the extent of variation of one measurement variable between groups, but also providing comparison between the sexes within groups.

The graphs produced by plot were used in the following way. A measurement value from a mandible belonging either to a case in the test sample of seven modern lower jaws or a mandibular fragment from the Miocene Epoch, was located visually on the horizontal axis of the graph with the corresponding measurement variable. A line from this measurement value point on the horizontal axis was run vertically through each of the five extant pongid ranges. Whenever this vertical line, representing a specific measurement value, crossed within the range of one or more of the five groups, its position within the group was noted. In the case of some measurement variables, the two sex ranges overlapped in an extant pongid group. This region of intersection between the sexes was known as the male/female range, and was designated by an asterisk in subsequent tables. Therefore, for any of the five groups, a single value might fall within one of the following three sex categories - male (M); male/female (*); or female (F).

Using the plot approach, a prediction of species (and sex) for each of the mandibles in the test sample, or Miocene mandibular fragments was based on the "total" number of times a measurement value crossed within the morphological boundaries of the extant pongids for that measurement variable. The more often a case from the test sample, or Miocene mandibular fragment fell within a particular group (or a particular sex category), the more confident the prediction was.

## DISCRIMINANT ANALYSIS

The multivariate statistical method used in this study was discriminant analysis. This technique examined the differences between two or more groups while considering several variables simultaneously. Although for this research, five extant pongids were identified as groups, it might have been possible to combine the Bornean and Sumatran orang-utans and the highland mountain and lowland gorillas into their respective species. An assumption in discriminant analysis states that there is <u>within-group homogeneity</u>. Since these two groups of pongids were originally separated at the subspecies level because of geographical, physical, and colour modifications, (Napier and Napier 1967) it was felt that if they were combined, there would a loss of this homogeneity.

In this thesis, variables were identified as the 34 measurements. The ability of this multivariate technique to include all 34 mandibular measurements together was known as the "direct approach" to discriminant analysis. An alternative to this approach was to determine which of the 34 measurement variables provided the strongest discrimination between the five groups. Although this option would decrease the number of measurement variables to a more manageable size, there was no guarantee that the top discriminators would correspond with those measurement variables available for the fossils.

Discriminant analysis is based on the use of Fisher's (1936) linear function. Campbell (1984:179) defined this function as, "the linear combination of the original variables which maximize the distance between the population means, relative to the within-populations variation". In this study, the above phrase "original variables" was represented by 34 measurements, and a "population" referred more specifically to each of the five extant pongid groups. Now, Campbell's quote could be altered to state that the integration of 34 measurement variables was primarily used to define the range of morphological variation in each of the five types of primates while explaining separation between these groups.

The algorithm for discriminant analysis is represented as

$$Z = A^{1}X^{1} + A^{2}X^{2} + \ldots + A^{n}X^{n} + K$$

where Z is the discriminant score for each group, A is the classification coefficient for a particular measurement variable, X is the corresponding measurement value, and K is a constant value which is assessed for each group.

Each classification coefficient represents the relative contribution of its associated measurement variable to a particular pongid group. Since there were five groups, each containing 34 measurement variables, one linear discriminant analysis produced 170 (34 measurements multiplied by 5 groups) classification coefficients.

As noted in the algorithm, discriminant analysis also calculated a constant value for each of the five pongid groups. Kachigan (1982:18) generally defined a constant as, "the invariable characteristics of objects which differentiate one class of objects from another". More specifically, the constant computed during the discriminant analysis procedure represented a numeric value which, in combination with the classification coefficients precisely defined any of the five extant pongid groups.

Classification and prediction are the two main functions of discriminant analysis (Brown 1984; Klecka 1975, 1980). For both of these functions of discriminant analysis, only those mandibles in the data base identified as male or female adult, or male or female questionable adult were used. I shall refer to classification as the test for internal consistency, and prediction as the test for external consistency. An explanation of these two functions follows.

### Classification: the test for internal consistency

It was unreasonable to attempt to predict the taxonomic and sexual affiliations of unknown mandibular specimens using the data base for comparison until the classification of the mandibles in the data base were examined. In other words, how were the jaws in the data base classified if examined on the basis of measurement comparison with each other? The solution to this question involved running the discriminant analysis program twice, once for males and once for females, in order to determine the percentage of mandibles in the data base that were accurately sexed and taxonomically grouped. The results are presented in Chapter 3.

### Prediction: the test for external consistency

The prediction of an unknown mandibular specimen to a particular extant pongid group involved the calculation of Fisher's classification coefficients for only those measurement variables available for each case in the test sample, or for a single Miocene mandibular fragment. For example, if three measurements were obtained for an unknown mandibular specimen, then Fisher's classification coefficients were computed for only those three variables. Coefficients and a constant were calibrated for all of the five extant pongid groups. The coefficients were then multiplied by their respective raw measurement values for the unknown specimen. These new values (classification coefficient multiplied by measurement value (or $A^{1} X^{1}$)) were added together with the constant value for the corresponding group, thus producing five discriminant scores. Each discriminant score was unique for each extant pongid group. Once these scores were compared, the largest discriminant score represented the predicted group membership for the unknown mandibular specimen.

The sample of 185 modern pongid mandibles from the Smithsonian Institution was considered initially as the primary data base from which all calculations and predictions were derived. However, as the following discussion illustrates, certain groups were eliminated from this total. For example, all juvenile mandibles, totalling 24 and including those classified as questionable juveniles, were excluded from the analysis to prevent skewing of the measurement values. Since 22 of the mandibles could not be sexed accurately, these individuals were excluded from the analysis. Therefore, the primary data base included 139 mandibles (77 males; 62 females).

A further reduction in the sample size occurred as a result of the discriminant analysis procedure which eliminated cases with missing values. Thirty-three percent, or 55 out of the 139 cases, were excluded because of the limiting restrictions of the SPSSX program to deal with missing values. Hence, the final sample size consisted of 84 mandibles (46 males; 38 females). Although this small but "pure" sample was used, there was an alternative.

The alternative involved the calculation of the average (or mean) for each of the missing measurement variables, keeping the pongid groups and male-female classification distinct. These averages were then substituted for the missing measurement values in each of the 55 cases. Since this option would increase the sample size from 84 to 139, it "altered" the data by removing any error caused by the missing values. In other words, cases which might normally be excluded from the study because of their missing values, would seemingly fit into the normal range of variation with the use of this option. Therefore, the decision of which alternative to use was between a small "pure" sample or a large "altered" sample with fitted averages. It was decided to use the unaltered "pure" sample as the data base. Consideration was also given to the fact that the range of mandibular variation in the data base would be used against measurements of Miocene fossils dating approximately ten million years ago. An altered data base might increase error in this application.

## Chapter 3

## Results

The purpose of this chapter is to present and discuss the results of the statistical analyses. Since each of the three samples in this study are used for different reasons (for explanation, see page 23), the results are organized according to these groups. Discussion of the statistical analyses for each of the three groups is examined in terms of the following categories: descriptive statistics; plot; and discriminant analysis. Because of the small sizes of the test sample and the Miocene fossils, descriptive statistics are not calculated, and therefore are not discussed for these two groups. Most of the results referred to are presented in tabular form and should be consulted regularly throughout the reading of this chapter.

### Smithsonian Institution data base

Descriptive statistics were calculated for this large data base in order to illustrate the range of morphological variation of mandibular measurements. The variation was examined in terms of metric measurements, non-metric observations, and ratios.

## DESCRIPTIVE STATISTICS

### A. Measurements

Mean values and standard deviations were calculated for each of the 34 measurements (Table 4). These univariate statistics were determined separately for males (Table 4.1) and females (Table 4.2). A comparison of these average values in Table 4 provides details on the morphological variability of extant pongid mandibles. This variability is interpreted on three levels: interspecific, subspecific, and sexual.

### Interspecific comparisons

This level of variation referred to the average measurement differences between the five groups of extant pongids. One way of examining interspecific variation would involve the direct comparison of average measurement values listed in Tables 4.1 and 4.2 between the five extant pongid groups. Since it would be necessary to consider each variable and both sexes separately, this approach would require 68 distinct interpretations (34 variables multiplied by 2 sexes). Consequently, this technique would be tedious, and not particularly informative because relationships among variables could not be assessed. Therefore it was decided to examine interspecific variation by using another method.

This alternative technique was based on how the mean values, for a single measurement variable and one particular sex, RANKED between each of the five extant pongid groups. By examining the ranking position of subspecies for a single variable, it would be possible to find relationships between variables with similar ranking orders. For instance, comparing the five average measurement values for the variable "bicondylar width", the ranking order of the male extant pongids in the data base, listed from highest average to lowest average, were: *Gorilla gorilla beringei*, *Gorilla gorilla gorilla*, *Pongo pygmaeus pygmaeus*, *Pongo pygmaeus abelli*, and *Pan troglodytes*. If the variable "maximum length" also had the same ranking order, then it would be feasible to consider a relationship between the length and width of the mandible in the five pongid groups.

Before interpreting the results, it was necessary to determine the ranking order, from highest to lowest mean value, for each of the 34 measurement variables. As with the calculation of univariate statistics where the sexes were recognized separately, this ranking procedure identified males and females distinctly. Consequently, the ranking order for each of the 34 variables was considered twice, once for males, and once for females. The ranking of this total of 68 variables could be summarized into 12 distinctive ranking orders. These 12 rankings, plus their frequency of occurrence for both males and females are listed in Table 5. The discussion on interspecific comparisons was based entirely on the information listed in Table 5. For details on exact mean values, Tables 4.1 and 4.2 should be consulted.

Using body size, it has been observed that gorillas are the largest, orang-utans are intermediate, and chimpanzees are the smallest pongids. The NORM or expected trend in this size-based comparative analysis of these pongids was that gorillas would have the largest mandibular measurement values and chimpanzees the smallest. Orang-utan average mandibular measurement values were therefore located between the measurement values of Pan and Gorilla. This "expectation" showed for the measurements of both male and female pongid mandibles.

According to Table 5, 19 measurement variables taken on the data base of male pongid jaws and 12 measurements taken on the data base of female pongid jaws followed this NORM. In only six measurement variables did the highest average values not belong to one of the two gorilla subspecies. These variables were: foramen mentalia width in males (Table 5, vi); symphysis height in females (Table 5, viii); gonial angle measurements (male and female) (Table 5, ix, x); left M2 height in females (Table 5, xi); and right M3 breadth in males (Table 5, xii). *Pongo pygmaeus pygmaeus* had the highest values for the measurement of foramen mentalia width and symphysis height; whereas *Pongo pygmaeus abelli* had the largest measurement averages for the left M2 height and the right M3 breadth. The gonial angle measurements were the largest in *Pan*.

In the four measurement variables in which orang-utans had the largest mean values, one of the gorilla subspecies always had the second highest mean value. The difference between the first and second means were: 1.29 mm - foramen mentalia width; 0.14 mm - symphysis height; 0.35 mm - left M2 height; 0.14 mm - right M3 breadth. Since these quantities were small, an increase in the number of measured jaws might have illustrated better the expected trend towards the largest mandibles existing in gorillas.

The fact that *Pan* had both of the largest gonial angle averages probably reflects true interspecific differences in the measurement of this mandibular region of extant pongids. This observation will be examined more closely later. The remainder of this section deals with variations in the ranking orders from the expected or NORMal trend.

The first variation from the NORM occurred as a result of a switching of positions #2 and #3; that is, between the smallest of the gorilla subspecies (Gorilla gorilla gorilla) and the largest of the orang-utan subspecies (Pongo pygmaeus pygmaeus). Ten measurement variables taken on male pongid jaws and two measurement variables taken on female pongid jaws conformed to this ranking order (Table 5, i).

Of the ten variables for male pongids, nine were postcanine corpus height measurements. The only height measurement not included was the left M2. In this case, BOTH Pongo pygmaeus pygmaeus and Pongo pygmaeus abelli average values (39.96 mm and 35.75 mm, respectively) were larger than the mean value for Gorilla gorilla gorilla (35.63 mm). Although the difference in the mean value of the left M2 corpus height between the lowland gorilla and the Sumatran orang-utan was only 0.12 mm, 4.33 mm separated the gorilla and Pongo pygmaeus pygmaeus. The small difference between the average values of Gorilla gorilla gorilla and Pongo pygmaeus abelli (0.12 mm) was not significant. The ranking of the left M2 measured in males did not correspond exactly to the other nine corpus height variables because of the slightly higher mean value in Pongo pygmaeus abelli (Table 5 iii). With an increase in sample size, this variable would most likely follow the trend of the other nine postcanine corpus heights.

As noted above, nine of the ten measurement variables taken on male pongid jaws were corpus height measurements. The tenth variable, also a height measurement, was symphysis height. The large symphysis measurement in orang-utans was probably related to the mean values for nine of the ten corpus heights. This association between a large symphysis height and large corpus height might indicate a need for structural balance during the process of mastication.

The two measurement variables taken on female pongid jaws were also postcanine corpus height measurements (left P3 and right P3). Since there were a total of ten postcanine corpus height measurements, the ranking order of the other eight should be examined. As with the left M2 height in males, the mean measurement corpus height values for the left P4, right P4, left M1, and right M1 were greater in BOTH Pongo pygmaeus pygmaeus and Pongo pygmaeus abelli as compared to the average values for Gorilla gorilla gorilla (Table

5, iii). Now, six of the ten corpus height measurements on female pongid jaws have been accounted for. Three of the remaining four height measurements also had greater averages between the two subspecies of Pongo when compared to the mean values for Gorilla gorilla gorilla. However, the ranking order of these three corpus height measurements were separate because the order of Pongo pygmaeus pygmaeus and Pongo pygmaeus abelli was reversed (Table 5, v).

The fourth and last of the corpus height measurements, left M2, had the following mean value ranking order: Pongo pygmaeus abelli, Gorilla gorilla beringei, Pongo pygmaeus pygmaeus, Gorilla gorilla gorilla, Pan troglodytes (Table 5, xi). This order might represent inter- and sub- specific variation, but, because of the consistency in the other postcanine measurements, it would be more probable to suspect [illegible]rs in measuring technique. This suspicion can be strengthened because, as noted earlier, the corpus measurements taken on the left side of the mandible were more awkward to measure.

In summary, the mean values of all twenty corpus height measurements were larger in the two subspecies of Pongo if compared to the smaller of the gorilla subspecies, Gorilla gorilla gorilla. In other words, the corpus height region in orang-utan mandibles was larger than the same area in the lowland gorilla. In addition, the ranking order of only four of these twenty measurements on female jaws (corpus heights of the right M2, left M2, right M3, and left M3) were larger in Pongo pygmaeus abelli than in Pongo pygmaeus pygmaeus (Table 5, v, xi).

The second most common ranking order from the NORM occurred with a re-arrangement of the Pongo subspecies. Pongo pygmaeus pygmaeus, normally the larger of the two subspecies, had average measurement values LOWER than those of Pongo pygmaeus abelli. This order never occurred in male pongids, though it appeared in the measurement of female pongid jaws eight times (Table 5, ii). The measurements involved were: bicondylar width, maximum length, right ramus height, left and right coronoid process height, and three corpus breadth variables.

Twenty-nine of the 34 measurement variables had ranking orders in which the mean values of the two subspecies of female Pongo were not separated by any of the other three groups. Of these 29, 11 (including the eight variables counted here) listed the mean values of Pongo pygmaeus abelli first. This likeness in the mean values of 29 measurement variables taken on female Pongo *pygmaeus pygmaeus* and *Pongo pygmaeus abelli* demonstrates a similarity in size. If these mean values were not significantly different then, this similarity might have provided justification in combining these two separate subspecies into one.

The fourth most common ranking order from the NORM included only two measurement variables: bigonial width in male pongids, and the internal measurement of the symphysis breadth in female pongids (Table 5, iv). The inclusion of both of these variables did not seem to indicate any clear trend. It was noted however, that of the four symphysis breadth measurements (external and internal, male and female), only the internal manner of taking this measurement on female pongids did not follow the expected trend of size order. Since the internal manner of measuring the symphysis breadth did not conform to the NORMal ranking order, its use might be questioned.

The sixth and seventh ranking orders occurred in the measurement of the foramen mentalia width (Table 5, vi, vii). Neither of these ranking orders were consistent with the normal trend of *Gorilla gorilla beringei* having the largest sized mandibular feature. The variability between these two ranking orders might represent true interspecific and sexual distinctions of the five pongids. However, because of closeness of the average measurement values, a more likely interpretation would be that the differences in the ranking orders were a reflection of a small sample size. An increase in sample size might either correct or confirm this variability.

The ninth and tenth ranking orders were significant because the largest average was found in the smallest sized primate (Table 5, ix, x). The extreme obtuse values for gonial angle in male and female _Pan_ was observed while originally measuring the bones. In Comas (1960), the degree of variation in the pongid gonial angle ranged from 95 degrees to 118 degrees. This range seems consistent with the results herein.

### _Subspecific comparisons_

Comparisons at this level occurred between either _Pongo pygmaeus pygmaeus_ and _Pongo pygmaeus abelli_ or between _Gorilla gorilla gorilla_ and _Gorilla gorilla beringei_. The normal trend in body size comparison demonstrated that _Pongo pygmaeus pygmaeus_ and _Gorilla gorilla beringei_ were the largest of their respective genera. This trend seemed to be apparent in the comparison of mandibular size. Within _Pongo_, 32 of a total of 34 measurement variables taken on males were consistently larger in Pongo pygmaeus pygmaeus. Measurements taken on female orang-utans did not show this trend as strongly, since only 22 of the 34 measurement variables were larger in Pongo pygmaeus pygmaeus.

Differences between the two gorilla subspecies showed exactly the same trend for both sexes. Normally, Gorilla gorilla beringei was the larger of the two subspecies. Of 34 measurement variables only two, foramen mentalia width and gonial angle, were larger in Gorilla gorilla gorilla.

Sexual comparisons

Examination of the mandibles for each species and each sex showed a definite trend for male pongid jaws to be larger than female pongid jaws. This trend was confirmed by comparing the average values for each measurement between the sexes, and within each of the five pongid groups. Only nine of the 170 (34 variables multiplied by five groups) measurement variables were larger in the female pongids. Five of these nine variables occurred in the chimpanzee mandible: gonial angle, right ramus height, left M2 breadth, left M3 breadth, and right M3 height. It was not surprising to find large mean values in the female chimpanzee mandibles, because of the similarity in jaw size to the male *Pan* mandible. With the likeness in jaw size between the male and female chimpanzees, it would be expected that a comparable relationship would exist with overall body size proportions.

Three of the remaining four measurement variables which had larger values in females as compared to males were in *Gorilla gorilla beringei*. These variables were: symphysis breadth (external), left M2 breadth, and right M2 height. The differences of the male measurements to the female values in two of these variables was slight: 0.36 mm - symphysis breadth, external; 0.71 mm - left M2 breadth. However, the difference between the male and female measurement values for the right M2 height was 7.97 mm. This extreme difference was probably due to difficulty in measuring, since such variation did not occur elsewhere.

The fourth and last measurement variable with a higher female than male value was the measurement of the bigonial width in *Pongo pygmaeus abelli*. The difference of 5.78 mm may have also been due to inaccuracies of measuring. The larger standard deviation for males, as well as the small sample size, should be noted.

## B. Non-metric observations

Frequencies, with conversion into percentages, were calculated for each of the four non-dimensional observations (Table 6.1 (males) and 6.2 (females)). As with the metric data, both adults and questionable adults were included in the computation of non-metric observations. Because of the lack of non-metric characteristics in Miocene mandibular fragments, these features were not of significant value in this research at this time. The discussion is organized in terms of: the position of the M3; gonial angle; and the number of mental foramina (right and left sides).

Two potential problems with the data in Tables 6.1 and 6.2 were: (1) the small sample size, and therefore lack of noticeable trends between the groups; and (2) the subjectivity of some of the variables.

The second problem could have been solved in two manners. The first approach would require being more general in the alternatives chosen for each variable. For example, the number of alternatives for "the position of the M3 in relation to the anterior border of the ramus" might be changed from seven to only four degrees (anterior to border; covered 1/2; covered totally; and not available). A second approach would consider only using the presence or absence of specific traits. In the case of the variable, "M3 position in relation to the anterior border", presence would infer a complete view of the M3 anterior to the ramus, and absence would imply that the M3 was hidden behind the ramus.

The manner in which the variable, "position of the M3" was observed was also too subjective since the height at which the mandible was examined would vary for each individual specimen. The lack of standardization in the form of the gonial angle also led to problems of subjectivity (see page 36 for discussion).

i. Position of the M3

The position of the M3 for the five groups showed a slight tendency towards this tooth being totally visible or partially covered (defined as 1/2 or 1/4), by the anterior border of the ramus. This observation was true for both male and female pongids.

The variable, "third molar position" did not show any important distinctions between the five groups since the sample sizes were too small to precisely assess the most common position of the third molar. For instance, the inclusion of the six unavailable individual *Pongo pygmaeus pygmaeus* lower jaws might have better indicated the highest frequency.

The "position of the M3 in relation to the anterior border of the ramus" was distinctive in male gorilla mandibles. Sixty-two percent and 64% of the molars were anterior in Gorilla gorilla gorilla and Gorilla gorilla beringei, respectively. These high value percentages were definitely related to the extreme verticality of the anterior border of the ramus.

The "position of the M3 in relation to the anterior border of the ramus" in female gorillas was not as clear as that described for males. This increased variability between subspecies, of the location of the M3 related to the anterior border of the ramus might be a indication of measuring subjectivity or, a true (functional?) difference distinguishing the sexes.

ii. Gonial angle

It was hypothesized that the highest frequency of gonial shape would be "straight". Inversion or eversion of this area might be indicative of muscle attachment requirements. For instance, heavy chewing muscles such as the temporalis have a large surface area, and with frequent and powerful use in certain pongids cause the region of muscular origin to develop a bony crest. If one masticatory muscle can have such an effect on the bony structure, then it would be reasonable to examine the effects of other powerful chewing muscles.

As mentioned in Chapter 1, the gonial region is an area where two of the four major masticatory muscles insert, the masseter (on the external surface), and the medial pterygoid (on the internal surface). If these two muscles were constantly being exercised, then these attachment regions might need greater surface areas and increased rugosity to hold muscular strands.

The high percentage of eversion at the gonion in male _Gorilla gorilla beringei_ (63.6%) as compared to _Pongo_ (10.7%) or _Pan_ (30.0%) might illustrate the strength of highly powerful masseter muscles. The seemingly vertical anterior border of the ramus in gorillas could be related functionally to the strong everted gonia, as a necessary requirement for stable and balanced masticatory operation.

Group variation in the shape of the gonial angle might not have shown as clearly in Tables 6.1 and 6.2 because of the lack of substantial difference in the definition of terms. For example, 60.7% of male _Pongo pygmaeus pygmaeus_ mandibles were identified as having a straight gonial angle shape, whereas 57.1% of male _Pongo pygmaeus abelli_ mandibles indicated slight inversion. How does the term "straight" differ from the term "slight inversion"?

It was interesting to note that the highest frequency of gonial angle shape in both male and female <u>Gorilla gorilla gorilla</u> mandibles was straight; whereas the highest frequency in male and female <u>Gorilla gorilla beringei</u> mandibles was identified as a slightly everted gonial shape. Although these differences might have represented inaccuracies in term definitions, they probably indicated true variation reflecting specific functional muscular requirements.

Sexual differences of the gonial angle shape did not appear overly strong in any of the five extant pongid groups.

### iii. Number of mental foramina

Based on human comparison, it was thought that a single mental foramen, one for each side, would be the most common tendency in extant pongids. Although one foramen in pongids was very common in this research, Simonton (1923) found that multiple foramina, defined as two or three, occurred in 39% of orang-utans, 15% in chimpanzees, and 27% in gorillas.

The results of this research are:

Multiple foramina (2 or 3)

| | Left side | | | | Right side | | | |
|---|---|---|---|---|---|---|---|---|
| | M | | F | | M | | F | |
| | % | N | % | N | % | N | % | N |
| *P.p.p.* | 35.7 | (10) | 53.9 | (14) | 42.9 | (12) | 50.0 | (13) |
| *P.p.a.* | 14.3 | (1) | 25.0 | (2) | 25.0 | (1) | 37.5 | (3) |
| *P.t.* | - | | - | | - | | 9.1 | (1) |
| *G.g.g.* | 14.3 | (3) | 36.4 | (4) | 9.5 | (2) | 45.5 | (5) |
| *G.g.b.* | 100.0 | (11) | 66.6 | (4) | 63.7 | (7) | 83.4 | (5) |

The results listed in the above table show some similarity to data provided by Simonton (1923). Direct comparison was difficult because of the few numbers of pongid mandibles with the characteristic series of multiple foramina.

By examining the above table, it can be noted that *Pan* had the least frequent number of multiple mental foramina. This follows Simonton (1923). Although the percentage of multiple mental foramina in the two subspecies of orang-utan vary, the frequency of this trait in *Pongo pygmaeus pygmaeus* was close to the single value of 39% proposed by Simonton (1923). It was awkward to compare the gorilla values in the table above to those established by Simonton (1923) because of the range of values extending from 9.5% to 100.0%. Yet, if the percentages are averaged out for Gorilla gorilla gorilla (27%), this value equates the percentage suggested by Simonton (1923).

One mental foramen was usually the most common in four of the five extant pongid groups (both sexes). The exception was Gorilla gorilla beringei which consistently appeared to have more than a single mental foramen. Single and double mental foramina were easy to identify. Triple (usually in a triangular formation) and more than triple implied a group with no apparently dominant foramen.

Subspecifically, Gorilla gorilla beringei stood out from Gorilla gorilla gorilla in terms of having more multiple mental foramina. If all multiple mental foramina are functional as transporters of sensory nerves, then a larger sized primate (Gorilla gorilla beringei) with a big jaw would require more foramina.

There was more consistency in the frequency of numbers of multiple mental foramina between the sexes than subspecifically. This observation was especially true when the percentage of multiple mental foramina (two or three) were combined (see table above). It was interesting to note the greater frequency of multiple mental foramina in females.

## C. Ratios

As mentioned in Chapter 2, the single ratio tested was the mandibular corpus shape. According to Kay (1982)[*], if the index value was equal to or less than 160, the mandibular corpus shape was defined as shallow/broad. If on the other hand, the index value was greater than 160, the mandible had a deep/narrow corpus shape. Table 7 lists the index values determined from the pongid data base, as well as those indices published by Kay (1982). Before considering the significance of these results, three important distinctions between the measurement technique of Kay and of the approach taken herein must be mentioned.

First, as noted in the equation (see page [illegible] the height and breadth measurements were examined at the mid-point <u>between</u> the M1 and M2. This was the method used by Kay (1982). In this study, the corpus measurements were taken at the mid-point of <u>each</u> postcanine tooth. Therefore, height and breadth measurements for both the first and second molars had to be used. Note that in Table 7, columns 1 and 3 provide the mean indices for the first molars; whereas columns 2 and 4 list the mean index values for the second molars.

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[*] The results in Kay (1982) were also published in Kay and Simons (1983).

In order to compare these results with Kay (1982), the two index values, one for M1 and one for M2, had to be added together and then averaged. The average values (indicated in the brackets in Table 7) were then considered equivalent for comparison with the indices produced by Kay (1982).

Second, Kay (1982) made no mention of whether the measurements he used were consistently taken on one particular side of the lower jaw. Because this research measured the right and left sides separately, four ratios (ultimately reduced to two, because they were averaged) were calculated for every group (see Table 7).

Third, Kay (1982) did not examine subspecific or sexual variation in his extant pongid sample. The absence of any consideration of sex differences meant that the average index values produced by Kay (1982) must be compared to the indices for both males and females. In the case of Pongo or Gorilla comparisons, index values for both subspecies must also be examined.

As indicated, direct comparison of my results with Kay (1982) was rather difficult mainly because of organizational differences. However, three comparisons are discussed:

(1) The single most important similarity between the two sets of results was that Pongo consistently had

the largest mean index values. All pongids, with the exception of female gorillas, had indices larger than 160, and therefore could be characterized as having deep/narrow mandibular corpus shapes.

(2) Since the indices for the two subspecies of Gorilla varied from 147.4 to 184.0, it was impossible to compare these values to the single average of 179 determined by Kay (1982). Note that the range produced by Kay (1982) had minimum and maximum values of 150 to 204, respectively. Although this range was not exactly the same as the results herein, the great distance between minimum and maximum values probably indicated that both males and females were measured.

(3) The mean index values for Pan troglodytes were less than those determined by Kay (1982). There seemed to be more consistency in the values produced in this study (minimum - 171.4; maximum - 177.6) than compared to the range (165-199) listed by Kay (1982).

A comparison of the interspecific variation in the average ratios between the left and right half of extant pongid mandibles indicated that ratios on the left side of the jaw were greater than those on the right side. The single exception to this observation occurred in female Gorilla gorilla beringei mandibles. It is possible that unilateral mastication might strengthen one side of the jaw, and thus have an effect on bony development. This idea could be tested by examining the mandibular corpus shape along all postcanine teeth, in order to establish whether there truly is variation between the shape of jaw sides.

Further discussion of the results in Table 7 is primarily organized according to the side on which the measurement is taken. As before, the average values in the brackets are the basis for analysis. The results of the ratios measured on the left half of the jaw are examined first. Later discourse deals with the right side results.

Interspecific differences in the ratios between the five pongid groups confirmed the consistency in mandibular measurements of <u>Pongo</u>, the similarity in likeness of mandibular measurements of <u>Pan</u>, and the large degree of variability in the mandibular measurements of <u>Gorilla</u>.

More detailed subspecific comparison of <u>Pongo</u> showed that female orang-utans had larger mandibular corpus shape indices than their male counterparts. The small degree of difference between the ratios of female <u>Pongo</u> might justify the combination of these two groups. Since the amount of variation between male orang-utans was greater, there would be more hesitation in joining the subspecies in this case.

The expected trend of males having greater ratios occurred in both subspecies of gorillas. However, it was normally thought that Gorilla gorilla beringei would have the largest ratio because it had the greatest sized mandible. This was not true in the case of the females. At present, there is no explanation for this. The greater distance in the ratios between males and females in gorillas probably confirmed the higher amount of overall sexual dimorphism in body size.

The lack of strong differences in the value of the ratios of Pan indicated a similarity in this mandibular morphological feature between males and females. It was apparent on the basis of this interpretation as well as analysis of the other measurements, and non-metric observations, that Pan was the least sexually dimorphic pongid.

The ratios determined for the right side of the mandible followed precisely the results and discussion on the ratios of the left side. In other words, female Pongo ratios were greater than their male counterparts. The ratios of Pan were very similar to each other, thus confirming the lack of sexual dimorphism in the mandible of this primate. The only difference between the right and left side analysis occurred in the female Gorilla.

The right side ratio in female *Gorilla gorilla beringei* was greater than in *Gorilla gorilla gorilla*.

Summary

Analysis of measurements, non-metric observations, and the mandibular corpus shape ratio support the following summary statements on the variation of extant pongid mandibles:

[illegible] Gorillas had the largest sized mandibles, then orang-utans, and finally, chimpanzees.

(2) *Gorilla gorilla beringei* and *Pongo pygmaeus pygmaeus* were the largest of their respective genera.

(3) Males usually had the largest sized jaw in all of the five pongid groups. This was strongly apparent in the more highly sexually dimorphic great apes, such as gorillas, and orang-utans. Chimpanzees which were characterized as being less sexually dimorphic did not exhibit great morphological variation in the size or dimensions of the mandible between males and females.

(4) In cases of mandibular measurement variables where any one of the above explanations did not seem true, problems of small sample size or difficulties in measuring may have been involved.

## PLOT

The plot technique provided graphic illustrations of the genus, subspecies, and sexual levels of variation. However, in contrast to the descriptive statistics, this method used individual measurement values instead of averages. Individual measurement values were more important because the distribution of these values with[illegible]e measurement variable could be pinpointed.

Using a typ[illegible] example of the plot output (Figure 2), genus, subspecies, and sexual variation are briefly described. Genus variation is detailed first. In Figure 2, the range of bicondylar width measurement values in Pan were located closer to the left side of the graph, and therefore nearer to the low end of the measurement scale. The same variable for the larger Gorilla was located at the right side of the graph, thus indicating larger measurement values. Simply stated, the size of a specific measurement variable on the mandible seemed to reflect the overall size of the primate. This same type of interpretation was possible for subspecies comparison.

This right/left and large/small relationship was also apparent in the examination of sexual differences within a single extant pongid group. For example, the range of male measurements were often positioned toward the right side of the graph; whereas female measurements were generally located nearer the left side of the graph.

Closer examination of the sexual differences between subspecies revealed a sexually dimorphic trend. In highly sexually dimorphic pongids (gorillas and orang-utans), there was little to no overlap of the sexes in a particular subspecies of the measurement values for a single variable. However, in chimpanzees which were much less sexually dimorphic primates, many of the measurement values overlapped between both sexes. This overlapping, also identified as a lack of strong male/female differences in measurement values for the same variable in Pan was noted in Figure 2.

## DISCRIMINANT ANALYSIS

As explained in Chapter 2, the discriminant analysis procedure was used ultimately as a multivariate statistical technique to predict the taxonomic classification of unknown mandibles. However, before the mandibles in the data base were used for predictions, the test for internal consistency or "classification" had to be tested. This required two tests for internal consistency, one for 46 males, and a second for 38 females.

The outcome of both tests resulted in a 100% accuracy in the classification of groups and sex. This meant that the test for internal consistency confirmed the sex, and taxonomic grouping of every one of the 46 male and 38 female pongid mandibles originally identified by the Smithsonian Institution. With this confirmation, there should be confidence in the application of the measurements of the pongid mandibles in the data base to the taxon and sex prediction of unknown lower jaws. Internal consistency for age was also confirmed since all known juveniles in the data base were already excluded. The results of testing external consistency (using the data base to predict the taxon and sex of unknown mandibles) is discussed in the context of the two sections dealing with the test samples.

## Test sample - U. of Calgary; U. of Alberta

Descriptive statistics were not calculated for this test sample because of the small size of the group. However, as the function of this sample was to test the external consistency of plot and discriminant analysis approaches, the results of both techniques are discussed.

PLOT

The exact procedure used in the plot technique is described in Chapter 2, and is not reviewed here. The results of the plot approach for this test sample are listed in Table 8. The values in Table 8 represent the total number of times measurement values for a particular test case fit within the morphological range of any of the five extant pongid groups. For each group, a value could belong to a male (M), male/female (*), or female (F) category.

With the exception of Case Number 5, there was no clear trend of taxon and sex prediction in any of the other seven test cases (Table 8). This situation will be understood more clearly with the following brief remarks on each of the individual test cases.

Case Number 1 was not markedly recognized as a female gorilla, because not only did most of the measurement values fit into the male/female range, but, a large number of the values were spread between three of the group (Pongo pygmaeus pygmaeus, Pongo pygmaeus abelli, and Gorilla gorilla gorilla).

Case Numbers 2 and 7, both juveniles, did not show any trend toward a certain taxon or sex. The reason for this was because of a lack of enough measured juvenile mandibles as part of the data base.

Case Number 3 seemed to be accurately predicted as a male. However it was difficult to judge whether it was an orang-utan or a gorilla, because of the large quantity of measurement values which fell in the range of both genera. Case Number 4, a male Pan, consistently fit within the range of Pan, although not necessarily in the male range. Case Number 5, known to be female Pongo, seemed to fit comfortably into the morphological range of the female Pongo pygmaeus pygmaeus. Case Number 6 showed strong tendencies toward the morphological range of the male orang-utan, yet 15 measurement values fell within the range of the two subspecies of male gorillas.

An apparent problem in this approach was the large number of variables which fit within the male/female (*) range. This problem was noted by the sizeable number of values in the column labelled with the asterisk. Although this difficulty was found in all five of the extant pongid groups, it was not strongly manifest in Gorilla gorilla beringei because of the small number of values from the test cases which fit in the range of this pongid. Clearly, the information in this table demonstrated that there was insufficient separation in the morphology of the mandible between male and female hominoids. A lack of differentiation was also evident between the five groups. Both of these problems may have been remedied partially with a substantial increase in the number of measureable mandibles in the data base, thereby leading to a better definition of the normal range of pongid mandibular morphological variation.

## DISCRIMINANT ANALYSIS

As with the plot method, discriminant analysis was described in Chapter 2 (see pages 42-49) and ~~need~~ not be repeated here. If the sex of an unknown case in the test sample was known, then the calculation of the discriminant score was based on this known sex. In other words, a jaw belonging to a male orang-utan, would calculate a discriminant score based on the 46 adult male mandibles from the Smithsonian Institution data base. The sex of five of the cases in the test sample were known.

In the other two cases, the sex of the jaw was unknown. This fact was not surprising since these two cases (Nos. 2 and 7) were juveniles. In the instance of an unknown sex, both male (based on 46 mandibles) and female (based on 38 mandibles) sets of Fisher's classification coefficients were used. Hence, two sets of linear functions were determined.

The result of the discriminant analysis procedure correctly predicted the species membership in four out of the seven cases. Three of the tests cases (Nos. 1, 3, and 5) were not assessed correctly, and these problem cases are dealt with below.

Case Number 3, which was a male orang-utan was predicted to be a male gorilla. The calculations were reviewed three times, resulting in no changes in the final assessment. A possible explanation for this final prediction was that Case Number 3 had a very large mandible which fell within the size range of a male gorilla. This idea may be substantiated by examining the plotted results of this individual in Table 8. This lower jaw fitted within the range of a male <u>Gorilla gorilla gorilla</u> a total of 15 times. Therefore, these measurements probably skewed the outcome of the discriminant analysis toward the larger male gorilla.

Case Number 1, a female gorilla, and Case Number 5, a female orang-utan were also classified incorrectly. The former was predicted to fit more within the range of <u>Pongo</u> and the latter fitted more in the range of <u>Gorilla</u>. These cases were tested twice, resulting in the same prediction. According to the plot this prediction was surprising, since there was no obvious trend toward the pred[illegible] group. Therefore, in these cases, there must have been an external influencing factor.

One interpretation is that the procedure discriminant analysis did not work for these two cases. If the statistical procedure is at fault, it may have been a result of the low tolerance level* of the LtM3H (left third molar corpus height), LtM3B (left third molar corpus breadth), and RtM3B (right third molar corpus breadth) measurements which removed them from the analysis. With a decrease in the tolerance level from the normal level of 0.001 to 0.00001, two of these measurement variables (LtM3H, LtM3B) were forced back into the analysis. However, the RtM3B variable was not entered because of its extremely small tolerance level. Further increase was not considered because of the risk of computational inaccuracies in the calculation of a discriminant score.

Exclusion of the three problem variables altered the prediction of Case Number 1, which as a result was correctly identified as a female Gorilla. Since the prediction for Case Number 5 did not change, another factor must be involved.

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*The SPSSX User's Guide (1983:632) defined tolerance as the "proportion of its within-groups variance not accounted for by other variables in the analysis". Klecka (1980:57) stated that "the tolerance for a variable not yet selected is one minus the squared multiple correlation between the variable and all variables already entered, when the correlations are based on the within-groups correlation matrix".

Case Number 5, a female orang-utan, was measured at the Department of Anthropology, University of Alberta. The previous habitat of this pongid was unknown. However, if it spent most of its life, especially during ontogeny, at a zoo, then certain structural changes in the mandible could develop. For instance, the consumption of soft foods could slightly modify mandibular structure compared to wild primates which subsist on hard diets (Corruccini and Beecher 1982, 1984). As well, this pongid may have suffered from certain skeletal deficiencies as a result of lack of exercise, or the influence of parasites. These factors of captivity might have altered the normal structure of the mandible, therefore affecting the classification of this specimen.

## Miocene fossil hominoid sample

As mentioned previously, Appendix 1 describes the Miocene fossils used in this research. This appendix includes the numerous taxonomic classifications for each fossil, plus a series of measurements (in millimeters) included in this study. Due to the small number and larger variety of measurement variables for each fossil, it was impossible to calculate descriptive statistics for this group. However, the results of a comparison between the ratios of Sivapithecus indicus and Sivapithecus sivalensis developed by Kay (1982) are compared to ratios of five individual Miocene fossil fragments (Table 9). As well, the results of plot (Table 10) and discriminant analysis (Table 11) are examined. Table 12 is a summary of the taxonomic predictions using both the plot and discriminant analysis approaches for the 29 Miocene fossils. This table also lists the percentage of cases which are correctly classified for the available measurement variables.

## RATIOS

Since Kay (1982) determined the mandibular corpus shape ratio for two sets of fossils, it was decided to use some of the individual specimens from this study as a comparison (Table 9). Kay (1982) was clearly confident of his classification of Sivapithecus indicus and Sivapithecus sivalensis fossils because of his calculation of the mandibular corpus shape ratios within these two groups with no mention of which fossils were included in either group. Because of the fragmentary nature of the fossil record, it would have been more appropriate and more precise to determine the ratio on the basis of single individual fragments.

Generally, the values calibrated in this study for the individual fossil specimens were greater than the two single group ratios determined by Kay (1982). GSI D 298 and YPM 13811 were most recently classified as *Sivapithecus sivalensis* (see Appendix 1). The ratio of the first specimen (GSI D 298) fits most closely with its "proper" taxonomic group. However, YPM 13811 greatly exceeded the calculated ratio for its respective classification, if it is considered *Sivapithecus sivalensis*.

The remaining three fossils (GSP 11706, GSP 13165, and ONGC V 790) were all classified most recently as *Sivapithecus indicus*. The ratios calculated for these fossils did not fit into the mean ratio proposed by Kay (1982) for this group.

It is suggested that more individual fossils be examined in terms of this ratio in order for this technique to become valuable. Once other ratios are developed, similarities in ratio values could also be used to demonstrate close taxonomic affiliations.

## PLOT

The prediction results using the plot approach have been listed in Table 10. Calculation of totals for each of the three sex groups (male (M); male/female (*); and female (F)) was not deemed valuable because of the few measurement variables available for each fossil. Before contending, with the plot results, three important concerns are discussed. These are listed below.

(1) Occasionally, some of the measurement variables, especially corpus height and breadth, did not make reference to the particular side on which a measurement was taken. The side was not difficult to determine if only fragmented segments of the fossil jaw were available. However, in the case of complete mandibles (for example, GSP 4622/4857, GSP 9564/9905/9901/9977, and GSP 15000), it was impossible to assess which side a specific measurement came from. On that account, both sides have to be considered in the computation of plot and discriminant analysis.

(2) Another complication involved mandibular measurement variables which had two or more values. The difference between the two values ranged from 0.5 mm to 3.7 mm for publications by the same senior author, and 0.4 mm to 1.8 mm for publications between different senior authors. This variation was accounted for since all of the values were tested using the plot method.

(3) A final concern dealt with the problem of measurement variables which did not fall within the range of any of the five extant pongid groups. These

variables were identified by a blank space under all of the extant pongid group columns in Table 10 and were checked as to why they might not fall within the range determined in this research for the Smithsonian Institution data base. The result of these checks showed that many of these "problem measurement values" were originally described in different terms from that proposed in this study. The superscript numbers beside each of these values in Table 10 referred to a terminological qualification of the measurement variable. These qualifications were listed on the facing page to Table 10. The differences in terminology did not affect the plot results because each variable was considered separately. Yet, because discriminant analysis involved the combination of all variables entered, an error in terminology might skew the results. Hence, any variables which did not fit within the morphological range determined by plot, were excluded from the discriminant analysis method.

As with the test sample, the results of the plot analysis of the Miocene fossil mandibular fragments seemed to confirm the large amount of size variability that normally exists in modern pongid mandibles. The absence of specific classifications was probably due, once again, to the large number of variables which fall within the male/female (*) range.

## DISCRIMINANT ANALYSIS

Table 11 shows the ranking of the three best taxonomic predictions for each of the 29 Miocene mandibular fragments using discriminant analysis. It is important to remember that only those measurement values which fit into the plot are used in the discriminant analysis. Since many of the fossils were not identified as being of a particular sex in the published literature, the discriminant score was tested for both sexes.

Eighteen of 29 (62%) of the Miocene fossils fitted more within the anatomical range of the chimpanzee. Six of the fossils (GSI D 18039, GSP 4230, GSP 4622/4857, GSP 15000, GSP 15629, ONGC V 790) did not fit obviously into any of the five extant pongid groups. GSP 13808 was the only Miocene fossil tested whose mandibular measurements fell within the range of the Gorilla. Only four of the 29 Miocene fossils were within the range of Pongo. These four cases included: GSP 9564/9905/9901/9977, GSP 11706, GSP 16077, and GSP 17125. The specific predictions for each of the 29 Miocene fossil fragments follows.

The basis for a discussion on this subject is found in Table 10 (plot results) and Table 11 (discriminant analysis results). If a sexual classification was considered for a fossil, the literature review reference was listed in Appendix 1. Brief comments are made on the species and sexual prediction for each of the fossils.

Graecopithecus freybergi: The single measurement variable available for this fossil indicated a morphological similarity with Pan, using both plot and discriminant analysis approaches. Martin and Andrews (1984) suggested that this fossil might be female. The plot results showed no indication of this prediction.

AMNH 19411: The majority of the plot results belonged to Pan. This prediction was confirmed by discriminant analysis. There was no prediction for sex in the literature review.

AMNH 19413: There was no indication in the plot results of the final prediction of Pan determined by discriminant analysis. There was no prediction for sex in the literature review.

BMNH 15423: The majority of the plot results belonged to Pan. This prediction was confirmed using discriminant analysis. Greenfield (1977) suggested that this fossil might be female. The plot results indicated that the three measurements fell within the female range twice out of a total of six times (33%).

<u>GSI</u> <u>D</u> <u>118/119</u>: The majority of the plot results belonged to <u>Pan</u>. This prediction was confirmed using discriminant analysis. Greenfield (1977) suggested that this fossil might be female. The plot results indicated that the two measurements fell within the female range thrice out of a total of four times (75%).

<u>GSI</u> <u>D</u> <u>177</u>: There was no indication in the plot results of the final prediction of <u>Pan</u> determined by discriminant analysis. The alternating positions of the second and third predictions between the two subspecies of <u>Pongo</u> might have reflected the patterns of morphological similarity in these mandibular measurements of these two groups. There was no prediction for sex in the literature review.

<u>GSI</u> <u>D</u> <u>197</u>: There was no indication in the plot results of the final prediction of <u>Pan</u> determined by discriminant analysis. The alternating positions of the second and third predictions between the two subspecies of <u>Pongo</u> might have reflected the patterns of morphological similarity in these mandibular measurements of these two groups. There was no prediction for sex in the literature review.

<u>GSI</u> <u>D</u> <u>199</u>: The single measurement variable available for this fossil indicated a morphological

similarity with Pan, using both plot and discriminant analysis approaches. Greenfield (1977) suggested that this fossil might be male. The plot results indicated no evidence for this prediction.

GSI D 298: The majority of the plot results belonged to Pan. This prediction was confirmed using discriminant analysis. There was no prediction for sex in the literature review.

GSI D 18039: The variability of the plot results was also present in the discriminant analysis results. Therefore, no species prediction was readily obvious. Greenfield (1978) suggested that this fossil might be male. The plot results indicated that the two measurements fall within the male range twice out of a total of six times (33%).

GSP 4230: The variability of the plot results was also present in the discriminant analysis results. Therefore, no species prediction was readily obvious. There was no prediction for sex in the literature review.

GSP 4622/4857: The variability of the plot results was also present in the discriminant analysis results. Therefore, no species prediction was readily available. Note: If the number of categories in the discriminant analysis approach were reduced, trends towards a particular species may have become more evident. This problem was a direct result of the lack of side designation in the measurement variables. Greenfield (1979) suggested that this fossil might be female. The plot results indicated that the 11 measurement alternatives, accounting for the testing of sides, as well as the varying measurement values, fell within the female range 21 out of a total of 32 times (65.6%).

*GSP 9563/9902*: There was no indication in the plot results of the final prediction of *Pan* determined by discriminant analysis. Greenfield (1979) suggested that this fossil might be female. The plot results indicated that the three measurement alternatives fell within the female range twice out of a total of six times (33%).

*GSP 9564/9905/9901/9977*: There was no indication in the plot results of the final prediction of *Pongo* determined by discriminant analysis. There was no prediction for sex in the literature review.

*GSP 11706*: The majority of the plot results were evident in both subspecies of *Pongo*. This prediction was confirmed using discriminant analysis. There was no prediction for sex in the literature review.

*GSP 13165*: There was no indication in the plot results of the final prediction of *Pan* determined by discriminant analysis. There was no prediction for sex in the literature review.

GSP 13566: The majority of the plot results belonged Pan. This prediction was confirmed using discriminant analysis. There was no prediction for sex in the literature review.

GSP 13808: The single measurement variable available for this fossil indicated a morphological similarity with Gorilla, using both plot and discriminant analysis approaches. There was no prediction for sex in the literature.

GSP 13875: The majority of the plot results belonged to Pan. This prediction was confirmed using discriminant analysis. There was no prediction for sex in the literature review.

GSP 14951: The single measurement variable available for this fossil indicated a morphological similarity with Pan, using both plot and discriminant analysis approaches. There was no prediction for sex in the literature review.

GSP 15000: The variability of the plot results was also present in the discriminant analysis results. Therefore, no species prediction was readily obvious. Note: If the number of categories in the discriminant analysis approach were reduced, trends towards a particular species may have become more evident. This problem was a direct result of the lack of side designation in the measurement variables. Pilbeam (1982) suggested that this fossil might be male. The plot results indicated that the 23 measurement alternatives, accounting for the testing of sides, as well as varying measurement values, fell within the male range 22 out of a total of 68 times (32.4%).

<u>GSP</u> <u>15397</u>: The majority of the plot results belonged to <u>Pan</u>. This prediction was confirmed using discriminant analysis. There was no prediction for sex in the literature review.

<u>GSP</u> <u>15629</u>: The variability of the plot results was also present in the discriminant analysis results. Therefore, no species prediction was readily obvious. There was no prediction for sex in the literature review.

<u>GSP</u> <u>16077</u>: There was no indication in the plot results of the final prediction of <u>Pongo</u> determined by discriminant analysis. There was no prediction for sex in the literature review.

<u>GSP</u> <u>17125</u> The majority of the plot results were evident in both subspecies of <u>Pongo</u>. This prediction was confirmed using discriminant analysis. There was no prediction for sex in the literature review.

<u>ONGC V 790</u>: The variability of the plot results was also present in the discriminant analysis results. Therefore, no species prediction was readily obvious. There was no prediction for sex in the literature review.

<u>PUA 1047-69</u>: There was no indication in the plot results of the final prediction of <u>Pan</u> determined by discriminant analysis. There was no prediction for sex in the literature review.

<u>YPM 13811</u>: The majority of the plot results belonged to <u>Pan</u>. This prediction was confirmed using discriminant analysis. Simons and Pilbeam (1965) and Greenfield (1978, 1979) suggested that this fossil might be female. The plot results indicated that the eight measurement alternatives, accounting for varying measurement values, fell within the female range nine out of a total of 16 times (56.3%).

<u>YPM 13814</u>: The majority of the plot results belonged to <u>Pan</u>. This prediction was confirmed using discriminant analysis. There was no prediction for sex in the literature review.

## <u>Discussion</u>

The visual approach (plot) confirmed the existence of interspecific, subspecific, and sexual variation in the mandibular morphology of the extant pongid data base. The multivariate statistical technique, discriminant analysis, used for testing classification accurately determined the taxon and sex of extant pongid mandibles belonging to the data base.

In the discriminant analysis test of prediction of the 29 Miocene fossil fragments, the results did not *precisely* verify the hypothesis. This failure to generate a specific prediction was influenced by the absence of enough discrimination between the five extant pongid groups. In addition, the lack of apparent (as in *Pan*) or strong (as in *Pongo*) sexually dimorphic differences in the mandibular morphology was also recognized as a factor. The absence of more precise definitions of metric variation in the mandible might have been remedied with an increase in the size of the data base. As well, the incorporation of more individuals would have led to better defined ranges of normal variation of measurements and features in extant pongid mandibles.

# Chapter 4

This final chapter examines a series of considerations which affected the method and outcome of this research. The discussion is organized according to the two original hypotheses which are presented in the introductory chapter. The closing paragraphs examine new areas of investigation for future pongid morphometric studies.

## HYPOTHESIS 1:

## EXTANT PONGID SPECIES CAN BE DISCRIMINATED ON THE BASIS OF INTERSPECIFIC AND SEXUAL VARIATIONS IN MANDIBULAR MORPHOLOGY

The examination of this hypothesis involved comparative tests of the "size" of certain mandibular features between five extant pongid groups. Interspecific, subspecific, and sexual variation in the measurements and non-metric observations of extant great ape mandibles was noted. These different levels of variation could be used to distinguish, generally, the five pongid groups. The calculation of a mandibular corpus shape ratio provided less separation between the groups.

The main difficulty in taking measurements of extant pongid mandibles was the problem of bone size.

Measuring instruments and the actual measurement variables considered were based solely on osteometric techniques applied to humans. Therefore, there was no consideration made for the more robust size of pongid mandibles, or of accentuated features such as muscle markings, big genial tubercles, and alveolar bulges.

Two important considerations in the statistical approach were: the problem of sample size; and the difficulty resulting from limitations in the selected discriminant analysis procedure. A larger (and yet, still representative) sample size was needed to enhance the separation between subspecies and between sexes. An increase in the number of individuals in the data base might also have better defined the range of morphological variation of extant pongid mandibles by making the outlying values more distinctive.

The use of a statistical program other than the *Statistical Package for the Social Sciences, Version X* (1983) might have included cases with missing variables, which would have resulted in the retention of 55 of the mandibles within the analysis.

## HYPOTHESIS 2:

## A COMPARISON OF THE SIZE OF THE MANDIBLE BETWEEN EXTANT PONGIDS AND MIOCENE FOSSILS ILLUSTRATES A MORPHOLOGICAL CLOSENESS TO THE MODERN ORANG-UTAN (PONGO PYGMAEUS)

The visual and multivariate statistical methods used in this study failed to demonstrate the "present" taxonomic interpretations, using the size of the mandible, of a sample of Miocene hominoid fragments. Even though 62% of the Miocene fossil mandibles tested fitted most closely the morphological range of the chimpanzee mandible, to immediately change the classification of these fossils on this basis would be erroneous. Yet, this association of *Ramapithecus* and *Sivapithecus* to the chimpanzee must be significant.

One manner of interpreting this relationship is to say that it represents a measure of biological distance, whereby the Miocene fossils *are* ancestral to *Pan*. This research was not the first to suggest such an association. Bilsborough (1971) clearly stated that the ramapithecine maxilla, YPM 13799, was similar to *Pan* in dimensions of the dental arcade (including palatal breadth at the canine, fourth premolar, and molar), the curvature of the incisors, and the length of the diastema. Morbeck (1983) claimed a similar structural relationship between the size of the ramapithecine humerus from Rudabanya, Hungary (RUD 53) and the humerus of extant pongids. Of a total of 16 measurements taken on this fossil, 15 fell within the range of <u>Pan</u>, and 13 fit in the range of <u>Pongo</u>. Clearly, the ranges of morphological variation of the extant pongid humerus were not distinct enough for a comparison to a fossil specimen.

Another means of interpreting this relationship between the Miocene fossils and <u>Pan</u> involves a comparison of body size. It has been assumed throughout this study, that a large-sized primate, such as a gorilla, has a large mandible and a small primate, like a chimpanzee, has a smaller mandible. If 62% of the Miocene fossil mandibular fragments fit within the size range of <u>Pan</u>, then it should be feasible that such a sized-based relationship would also affect body size.

A major work involving the prediction of body size of Miocene fossils was attempted in 1980 by Richard J. Smith. In his dissertation, Smith who used details on extant pongid body size, diet, cranial measurements, and phylogenetic classification discovered that his body weight predictions of <u>Ramapithecus</u> (ranging from 16.7 kg to 57.0 kg) and <u>Sivapithecus</u> (ranging from 57.5 kg to 64.5 kg) were highly variable. Although the individually predicted body weight values were speculative, this research did confirm the results of other studies which demonstrate that Ramapithecus is smaller than Sivapithecus.

On the basis of postcranial evidence, Pilbeam (1979) predicted that Ramapithecus would have weighed 20 kg and Sivapithecus, 40 kg. Andrews (1981) suggested that modern baboons were a reliable comparison for the body weight of Ramapithecus, and that orang-utans were a good model for the body weight of Sivapithecus. As noted by Smith (1980), Pilbeam (1979) and Andrews (1981) also predicted Ramapithecus to be the smaller of the two fossil forms.

Because of the variation in the predicted body weights for the Miocene fossils, there was some difficulty in comparing them to the weight of modern pongids. This problem will be dealt with by not using the specific predicted weights developed by Smith (1980), and instead emphasis will be placed on the results by Pilbeam (1979) and Andrews (1981).

It was also awkward to compare the predicted weights with those of modern pongids, since many field studies of living primates indicated large degrees of variation in body weight. This problem should be alleviated by using the body weights of modern pongids listed only in Napier and Napier (1967).

Napier and Napier (1967) stated that on average, male Pan weighs 49 kg, and female Pan weighs 41 kg, whereas the weight of Pongo pygmaeus abelli ranged from 69 kg in males to 37 kg in females. The weights of Pongo pygmaeus pygmaeus were not included because of an original miscalculation by Lyon.

The prediction of 20 kg for Ramapithecus body weight put forth by Pilbeam (1979) was much less than either modern Pan or Pongo values. A 40 kg weight prediction for Sivapithecus fitted more within the modern pongid weight classification.

According to Napier and Napier (1967), the body weight of Papio anubis is between 22-30 kg for males, and 11-15 kg for females. These weight values did not correspond exactly to Pilbeam's (1979) prediction of Ramapithecus weighing about 20 kg. The body weight prediction by Andrews (1981) suggested that Ramapithecus was a small ancestor if compared to the body weight of extant chimpanzees.

On the basis of the above discussion, it seemed that similarity in the size of fossil mandibles to Pan did not necessarily demonstrate a likeness in body weight. This observation might reflect differences in the body proportions between extant pongids and Miocene fossils. One must be aware of the problem of comparison between fossils which existed for at least seven million years (8 mya to 14 mya) compared to modern chimpanzees which, according to molecular data, split from the human-ape lineage about four to five million years ago.

A final means of explaining the possible true relationship of Miocene fossils to Pan involves a comparison of diet. Corruccini and Beecher (1982, 1984) demonstrated that similarities in diet would have an effect on the structure of the mandible. Although their research mainly dealt with influence of soft diets, the impact of frugivory and folivory should reflect variation in certain components of the masticatory apparatus. Most studies of this variation have emphasized the structural differences in the tooth morphology.

Specific proposals have been put forth regarding the dietary adaptation of the Miocene fossils. Kay (1977) claimed that Ramapithecus and Sivapithecus indulged in eating fruit. Andrews and Aiello (1984) also believed that sivapithecines (including ramapithecines) were frugivores. These two predictions are similar to the normal dietary regime of Pan and Pongo. Therefore, in the comparative examination of Miocene fossils to the extant pongids, a likeness in dental structure demonstrates similarities in diet. Clearly, the next step would be to determine the structural differences in the mandible between modern folivores and frugivores. Once this variation was assessed, then a comparison of jaw structure to Miocene fossils would be appropriate.

Although it was not the purpose to suggest new taxonomic categories for the fossils, the importance of this research lay in the realization that if Ramapithecus and Sivapithecus were ancestral or in some way related morphologically to the modern orang-utan, then this association might be evident in a simple comparative study.

All of the above discussion is based on the assumption that the similarity between the Miocene fossils and modern chimpanzees is a measure of biological distance. If, however this relationship of the Miocene fossils to Pan is not a measure of biological distance, then this may indicate a source of error in methodology.

Clearly, in this multivariate statistical approach, the computation of a discriminant score is the basis of the taxonomic prediction of unknown mandibles. Corruccini (1975:3) stated that this approach is, "not designed to indicate relative affinities of unrelated individuals or to the parent populations...., or *to be applied to outside groups not included in the original function computations*" (my emphasis). If biological distance is not a factor, then Corruccini (1975) may have provided a reason why the use of discriminant analysis in this study concluded that 62% of the Miocene fossils fitted more aptly in the range of *Pan*, rather than toward the expected group of orang-utans (*Pongo*).

Predictions of sex were difficult to determine because of the very recent addition of this factor to Miocene fossil interpretations. Although Greenfield (1977, 1978, 1979) was the only author who consistently attempted to provide sex classification for some of the Miocene fossils, there was little information beyond his research.

An important concern in this type of prediction is how to define the male versus the female in terms of fossils. If one bases the comparison on living primates, then size difference could be used to distinguish the sexes. In other words, does a large bone necessarily represent a male individual, and a small bone a female? The amalgamation of *Ramapithecus* and *Sivapithecus* results in a possibility that size differences between these two groups may actually be accounted for by sexual dimorphism. Whether the sex classification of fossils is based on a single specimen, or on a group of large-sized (and possibly of similar taxonomic classification) primates, little research can be done until the exact differences between the sexes can be established.

As a result of the literature search for measurement values of some of the Miocene hominoid mandibular fragments, three inconsistencies in the collection of measurement data were noted. These three factors are: (1) differences in the measurement techniques between researchers sometimes resulted in at least two values for one measurement variable; (2) although there are standard landmarks and terms used for osteometric analysis, there existed variation in the names of some of the measurement variables; and (3) often, there was no attempt to identify the side of the bone on which a measurement was taken. The effect of these inconsistencies on this research meant that all of these options had to be considered. For instance, if two or more values were available for one measurement, both values were tested using plot and discriminant analysis. Where the terms of measurement variables were different from those presented herein, these measurement variables were excluded from the analysis. Finally, the lack of side designation of certain measurement variables meant that both right and left sides had to be investigated. These aforementioned factors must be resolved before future morphometric research in this area can continue.

The above discussion has dealt primarily with considerations of the present research. The following brief discourse looks at alternative ways to approach future morphometric analyses.

Although non-dimensional features are examined in the extant pongid data base, there is no comparison with the same characteristics in the Miocene fossils. This could be an important area of research because it might lead to a better understanding of how muscles attached, or tubercles affected the masticatory process in fossil Hominoids. Photographs illustrating particular aspects would be of great assistance in such a project.

Another application of this approach might consider only juvenile fossils. It would be imperative to accurately define ~~this~~ age category, and probably necessary to divide it into various sub-groups, such as fetal, newborn, immature, and sub-adult. These types of analyses are inappropriate until more fossils of young individuals are identified and described.

Similar analyses, but using different features of the mandible or another part of the skeleton, might substantiate or disprove the results of the thesis. The results of a different statistical approach may provide valuable information influencing the outcome of this research.

Finally, once this approach is refined, a statistical application to other fossil groups could have important ramifications in terms of taxonomic and/or sexual predictions.

# Tables

| Age | P.p.pygmaeus |  |  |  | P.p.abelli |  |  |  | P.troglodytes |  |  |  | G.g.gorilla |  |  |  | G.g.beringei |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | A | J | A? | J? | A | J | A? | J? | A | J | A? | J? | A | J | A? | J? | A | J | A? | J? |
| Sex |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| M | 24 | 3 | 4 | 1 | 6 | 3 | 1 | - | 9 | 3 | 1 | 1 | 21 | 1 | - | - | 11 | 1 | - | - |
| F | 21 | 7 | 5 | - | 7 | 1 | 1 | - | 11 | 2 | - | - | 1[illegible] | - | 1 | - | 6 | - | - | 1 |
| ? | - | 1 | 1 | - | - | - | - | - | 3 | 4 | - | - | - | - | - | - | 1 | - | - | - |
| M? | 1 | - | - | - | - | - | - | - | 1 | - | - | - | 4 | - | - | - | 1 | - | - | - |
| F? | 2 | - | - | - | - | - | - | - | 1 | - | - | 1 | 1 | - | - | - | - | - | - | - |
| Total No. in species |  |  |  | 70 |  |  |  | 19 |  |  |  | 37 |  |  |  | 38 |  |  |  | 21 |

Table 1. Data base: Age and sex breakdown

## Table 2.

### Measurement variables included in study (after Brothwell 1981:82-84; Montagu 1960:51-52)

| | |
|---|---|
| Bicondylar Width:<br>(BiConW) | Diameter between most external points of the mandibular condyles. |
| Bigonial Width:<br>(BiGW) | Distance between gonia. |
| Foramen Mentalia Width:<br>(ForAW) | From the most anterior point of one mental foramen to another. |
| Minimum Ramus Width:<br>((Rt)RamW) | Smallest distance between the anterior and posterior borders of the ascending ramus. (left and right side; measured independently) |
| Symphysis Height:<br>(SymH) | Distance between infradentale and gnathion. |
| Symphysis Breadth:<br>(SymB(E)) | Maximum thickness of the symphysis, excluding the genial tubercles and the simian shelf (external and internal measurement) |
| Maximum Mandibular Length:<br>(MaxL) | Distance between the most posterior points on the condyles to the most anterior point of the mandible. Since this length is measured on the mandible board, it accounts for the angle of the gonia. |
| Gonial Angle:<br>(GonA) | The angle between the condyles to the gonia and the base of the mandible. |
| Ramus Height:<br>((Rt)RamH) | Height of the ramus from top of condyle to the base of the mandible. (left and right side; measured independently) |

| | |
|---|---|
| Coronoid Process Height: ((Rt)CorH) | Height of the ramus from top of coronoid process to the base of the mandible. (left and right side; measured independently) |
| Corpus Height* : ((Rt)P3H) | Height from inferior border (base) of mandible to alveolar crest on buccal surface of middle of post-canine tooth to be measured. |
| Corpus Breadth* : ((Rt)P3B) | Maximum breadth under postcanine tooth to be measured. |

* Corpus height and corpus breadth measurements were taken under each of the premolars and molars on both sides of the mandible.

## Table 3.

### Non-metric observations included in study

M3 position to anterior border of the mandibular ramus:

- M3 - anterior to border
  - covered 1/4
  - covered 1/2
  - covered 3/4
  - trace visible
  - totally hidden
  - not available

Gonial angle shape:

- straight
- inversion - slight
  - marked
- eversion - slight
  - marked
- not available

Number of mental foramina (left and right side; sides checked independently)

- single
- double
- triple
- more than triple
- not available

| Variable | P.p.pygmaeus |  |  | P.p.abelli |  |  | P.troglodytes |  |  | G.g.gorilla |  |  | G.g.beringei |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | $\bar{x}$ | SD. | N. | $\bar{x}$ | SD. | N. | $\bar{x}$ | SD. | N. | $\bar{x}$ | SD. | N. | $\bar{x}$ | SD. | N. |
| BiConW | 135.57 | 9.46 | 19 | 124.96 | 7.43 | 06 | 102.60 | 8.13 | 07 | 137.08 | 8.06 | 17 | 147.17 | 4.77 | 11 |
| BiGW | 112.47 | 11.65 | 23 | 81.55 | 35.77 | 06 | 90.67 | 9.83 | 07 | 113.79 | 14.93 | 18 | 137.69 | 7.34 | 10 |
| ForAW | 51.42 | 4.21 | 24 | 47.71 | 3.64 | 06 | 44.06 | 2.63 | 08 | 50.13 | 4.73 | 21 | 48.39 | 2.53 | 11 |
| LtRamW | 60.92 | 5.14 | 24 | 56.65 | 7.74 | 06 | 45.34 | 3.21 | 08 | 66.80 | 5.58 | 19 | 76.50 | 5.13 | 10 |
| RtRamW | 61.86 | 5.50 | 24 | 57.34 | 7.35 | 06 | 45.83 | 3.12 | 09 | 66.33 | 4.12 | 18 | 74.87 | 5.01 | 10 |
| SymH | 66.62 | 6.66 | 24 | 59.16 | 7.46 | 06 | 44.76 | 5.12 | 07 | 63.59 | 5.94 | 21 | 70.41 | 4.63 | 11 |
| SymBE | 26.75 | 5.03 | 24 | 20.80 | 2.90 | 06 | 18.15 | 1.43 | 08 | 29.38 | 3.67 | 21 | 33.66 | 2.85 | 11 |
| SymBI | 22.08 | 2.36 | 24 | 19.45 | 2.08 | 06 | 17.61 | 1.53 | 08 | 26.49 | 2.05 | 21 | 31.09 | 2.36 | 11 |
| MaxL | 130.36 | 10.00 | 22 | 127.17 | 14.32 | 06 | 100.88 | 8.89 | 08 | 149.05 | 15.40 | 20 | 166.10 | 10.35 | 10 |
| GonA | 109.82 | 4.90 | 22 | 110.83 | 6.65 | 06 | 111.63 | 8.77 | 08 | 99.40 | 8.99 | 20 | 98.30 | 7.72 | 10 |
| LtRamH | 87.16 | 7.57 | 20 | 81.09 | 8.24 | 06 | 64.57 | 6.60 | 07 | 92.21 | 12.26 | 19 | 117.89 | 7.84 | 10 |
| RtRamH | 87.96 | 8.54 | 19 | 82.58 | 8.12 | 06 | 63.75 | 5.99 | 08 | 93.90 | 13.70 | 18 | 118.21 | 6.62 | 10 |
| LtCorH | 98.54 | 7.65 | 21 | 93.91 | 11.80 | 06 | 64.40 | 4.74 | 08 | 115.12 | 10.03 | 16 | 127.36 | 6.97 | 08 |
| RtCorH | 98.61 | 7.41 | 21 | 94.56 | 12.46 | 06 | 63.97 | 4.03 | 09 | 116.26 | 10.02 | 18 | 129.18 | 8.35 | 09 |
| LtP3H | 49.85 | 4.94 | 23 | 42.66 | 4.88 | 06 | 33.56 | 3.47 | 07 | 47.73 | 4.28 | 21 | 52.08 | 3.73 | 10 |
| LtP3B | 22.35 | 2.38 | 24 | 20.08 | 2.62 | 06 | 17.67 | 1.79 | 07 | 27.44 | 3.30 | 21 | 31.23 | 2.67 | 11 |
| RtP3H | 50.54 | 4.70 | 24 | 42.99 | 5.69 | 06 | 33.63 | 3.80 | 08 | 47.57 | 4.46 | 21 | 51.69 | 5.29 | 10 |
| RtP3B | 22.58 | 1.37 | 24 | 20.24 | 2.85 | 06 | 17.44 | 1.34 | 08 | 25.98 | 2.45 | 21 | 28.72 | 2.76 | 11 |

Table 4.1 Date base: Averages and standard deviations of measurements on male pongid mandibles (measured in millimeters)

| Variable | <u>P.p.pygmaeus</u> | | | <u>P.p.abelli</u> | | | <u>P.troglodytes</u> | | | <u>G.g.gorilla</u> | | | <u>G.g.beringei</u> | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $\bar{x}$ | SD. | N. | $\bar{x}$ | SD. | N. | $\bar{x}$ | SD. | N. | $\bar{x}$ | SD. | N. | $\bar{x}$ | SD. | N. |
| LtP4H | 45.10 | 4.73 | 23 | 37.82 | 5.48 | 06 | 30.41 | 2.58 | 07 | 41.62 | 3.71 | 21 | 45.61 | 3.20 | 11 |
| LtP4B | 18.89 | 1.78 | 23 | 17.93 | 1.91 | 06 | 15.76 | 0.92 | 07 | 21.27 | 2.20 | 21 | 24.96 | 1.27 | 11 |
| RtP4H | 45.20 | 4.75 | 24 | 38.22 | 5.66 | 06 | 30.69 | 2.92 | 07 | 42.10 | 3.83 | 21 | 45.83 | 4.10 | 11 |
| RtP4B | 19.25 | 1.80 | 24 | 18.04 | 2.06 | 06 | 15.80 | 0.98 | 07 | 21.10 | 1.92 | 21 | 24.03 | 1.67 | 11 |
| LtM1H | 42.15 | 4.33 | 23 | 35.[illegible] | 5.57 | 06 | 26.99 | 4.59 | 07 | 38.57 | 3.17 | 21 | 43.80 | 2.73 | 11 |
| LtM1B | 18.25 | 1.98 | 23 | 17.04 | 0.77 | 06 | 14.46 | 0.58 | 07 | 19.84 | 1.69 | 21 | 22.72 | 1.85 | 11 |
| RtM1H | 42.55 | 4.71 | 24 | 37.08 | 5.91 | 06 | 28.78 | 2.88 | 08 | 39.60 | 3.46 | 21 | 44.43 | 3.07 | 10 |
| RtM1B | 18.41 | 1.67 | 24 | 17.89 | 0.53 | 06 | 15.11 | 0.93 | 08 | 20.93 | 2.07 | 21 | 23.21 | 2.01 | 10 |
| LtM2H | 39.96 | 3.94 | 24 | 35.75 | 5.99 | 06 | 26.51 | 1.32 | 08 | 35.63 | 2.88 | 21 | 41.65 | 2.82 | 11 |
| LtM2B | 20.13 | 2.18 | 24 | 18.75 | 1.21 | 06 | 15.13 | 1.37 | 08 | 22.08 | 1.98 | 21 | 24.20 | 2.27 | 11 |
| RtM2H | 40.25 | 4.68 | 24 | 36.61 | 6.41 | 06 | 25.96 | 1.50 | 08 | 36.87 | 2.84 | 20 | 42.22 | 3.38 | 09 |
| RtM2B | 21.19 | 2.04 | 24 | 21.02 | 1.59 | 06 | 16.56 | 1.84 | 08 | 23.05 | 2.12 | 20 | 24.31 | 2.01 | 10 |
| LtM3H | 41.15 | 3.90 | 23 | 36.58 | 6.44 | 06 | 28.53 | 1.94 | 08 | 38.20 | 2.60 | 21 | 43.88 | 5.40 | 09 |
| LtM3B | 24.28 | 2.64 | 24 | 23.56 | 3.31 | 06 | 17.80 | 1.36 | 08 | 25.15 | 2.18 | 21 | 26.49 | 2.39 | 10 |
| RtM3H | 41.02 | 4.44 | 23 | 36.67 | 5.71 | 06 | 26.57 | 1.44 | 09 | 38.36 | 2.83 | 20 | 44.67 | 2.92 | 09 |
| RtM3B | 24.61 | 1.95 | 23 | 26.06 | 2.74 | 06 | 18.14 | 1.32 | 09 | 25.49 | 1.93 | 20 | 25.92 | 2.00 | 10 |

| | P.p.pygmaeus | | | P.p.abelli | | | P.troglodytes | | | G.g.gorilla | | | G.g.beringei | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Variable | x̄ | SD. | N. | x̄ | SD. | N. | x̄ | SD. | N. | x̄ | SD. | N. | x̄ | SD. | N. |
| BiConW | 111.45 | 6.33 | 19 | 115.43 | 7.18 | 06 | 101.66 | 6.04 | 06 | 120.15 | 6.64 | 09 | 129.95 | 8.48 | 06 |
| BiGW | 89.29 | 7.07 | 19 | 87.33 | 8.13 | 07 | 85.12 | 2.04 | 07 | 94.70 | 9.05 | 09 | 120.92 | 8.76 | 05 |
| ForAW | 42.79 | 3.95 | 20 | 41.84 | 5.30 | 07 | 43.50 | 2.62 | 10 | 44.82 | 4.04 | 10 | 37.48 | 1.64 | 06 |
| LtRamW | 48.63 | 3.33 | 19 | 45.38 | 4.42 | 06 | 42.97 | 3.32 | 08 | 55.27 | 4.62 | 09 | 60.28 | 3.11 | 06 |
| RtRamW | 48.41 | 3.26 | 20 | 45.69 | 4.14 | 06 | 43.44 | 3.04 | 08 | 55.58 | 5.08 | 09 | 59.77 | 1.83 | 06 |
| SymH | 53.46 | 2.57 | 21 | 51.30 | 2.31 | 07 | 40.63 | 3.60 | 10 | 52.11 | 6.39 | 10 | 53.32 | 2.41 | 05 |
| SymBE | 21.79 | 3.40 | 21 | 19.23 | 2.71 | 07 | 16.22 | 2.10 | 10 | 25.56 | 3.38 | 10 | 34.02 | 4.14 | 06 |
| SymBI | 18.54 | 1.86 | 21 | 14.88 | 1.49 | 07 | 15.80 | 1.96 | 10 | 22.65 | 2.40 | 10 | 26.97 | 1.43 | 06 |
| MaxL | 106.76 | 5.40 | 21 | 108.29 | 6.75 | 07 | 99.25 | 3.81 | 08 | 131.89 | 6.17 | 09 | 136.83 | 5.67 | 06 |
| GonA | 109.29 | 4.97 | 21 | 102.14 | 7.45 | 07 | 113.50 | 3.93 | 08 | 96.56 | 4.56 | 09 | 96.33 | 5.09 | 06 |
| LtRamH | 78.17 | 4.19 | 20 | 77.79 | 4.07 | 07 | 63.25 | 5.82 | 08 | 82.45 | 8.07 | 09 | 98.26 | 5.87 | 06 |
| RtRamH | 77.85 | 4.96 | 20 | 77.86 | 3.83 | 06 | 65.50 | 5.36 | 06 | 81.76 | 7.59 | 09 | 97.66 | 5.32 | 06 |
| LtCorH | 82.94 | 5.19 | 19 | 84.16 | 3.64 | 06 | 63.12 | 2.56 | 09 | 96.15 | 8.56 | 09 | 104.62 | 3.74 | 05 |
| RtCorH | 81.41 | 4.84 | 20 | 83.49 | 3.55 | 06 | 62.48 | 4.17 | 08 | 96.19 | 8.04 | 09 | 104.90 | 3.21 | 06 |
| LtP3H | 40.93 | 2.99 | 21 | 39.02 | 2.24 | 07 | 30.28 | 2.59 | 10 | 39.89 | 3.85 | 10 | 42.62 | 2.27 | 05 |
| LtP3B | 18.49 | 1.63 | 21 | 17.12 | 1.96 | 07 | 16.47 | 4.54 | 11 | 22.90 | 2.41 | 10 | 26.93 | 1.18 | 05 |
| RtP3H | 41.74 | 3.05 | 20 | 39.21 | 1.99 | 07 | 30.94 | 2.60 | 10 | 40.44 | 4.13 | 10 | 43.36 | 1.70 | 06 |
| RtP3B | 18.25 | 2.13 | 20 | 16.94 | 1.32 | 07 | 15.40 | 1.39 | 10 | 21.53 | 1.61 | 10 | 24.50 | 1.36 | 06 |

Table 4.2 Data base: Averages and standard deviations of measurements on female pongid mandibles (measured in millimeters)

| Variable | P.p.pygmaeus $\bar{x}$ | SD. | N. | P.p.abelli $\bar{x}$ | SD. | N. | P.troglodytes $\bar{x}$ | SD. | N. | G.g.gorilla $\bar{x}$ | SD. | N. | G.g.beringei $\bar{x}$ | SD. | N. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| LtP4H | 37.09 | 3.16 | 21 | 35.31 | 1.50 | 07 | 27.84 | 2.69 | 10 | 34.66 | 3.84 | 10 | 37.29 | 3.93 | 05 |
| LtP4B | 16.12 | 1.75 | 21 | 15.78 | 1.89 | 07 | 14.44 | 1.61 | 11 | 19.31 | 1.89 | 10 | 22.86 | 1.39 | 05 |
| RtP4H | 37.43 | 3.63 | 20 | 35.55 | 1.44 | 07 | 28.13 | 2.74 | 10 | 34.77 | 3.92 | 10 | 37.51 | 0.82 | 05 |
| RtP4B | 16.13 | 1.67 | 20 | 16.31 | 1.92 | 07 | 14.34 | 1.26 | 10 | 19.14 | 1.44 | 10 | 21.52 | 0.72 | 06 |
| LtM1H | 35.04 | 2.49 | 21 | 33.82 | 1.50 | 07 | 26.62 | 2.23 | 11 | 32.70 | 3.39 | 10 | 35.32 | 3.45 | 05 |
| LtM1B | 15.40 | 1.49 | 21 | 15.38 | 2.05 | 07 | 14.09 | 1.48 | 11 | 19.21 | 1.02 | 10 | 22.27 | 0.65 | 06 |
| RtM1H | 34.78 | 2.61 | 21 | 33.82 | 1.89 | 07 | 26.63 | 2.58 | 10 | 32.58 | 3.87 | 10 | 36.25 | 1.41 | 06 |
| RtM1B | 15.66 | 1.35 | 21 | 15.92 | 2.50 | 07 | 14.10 | 1.28 | 10 | 19.45 | 0.52 | 10 | 21.59 | 0.49 | 06 |
| LtM2H | 33.69 | 2.64 | 21 | 34.20 | 1.37 | 07 | 25.04 | 2.08 | 11 | 31.03 | 3.22 | 10 | 33.85 | 2.33 | 05 |
| LtM2B | 16.76 | 1.23 | 21 | 16.22 | 1.83 | 07 | 15.29 | 1.04 | 11 | 21.71 | 1.59 | 10 | 24.91 | 1.31 | 06 |
| RtM2H | 33.46 | 2.72 | 21 | 34.18 | 1.24 | 07 | 25.24 | 2.69 | 09 | 30.96 | 3.20 | 10 | 34.25 | 0.82 | 06 |
| RtM2B | 17.45 | 1.72 | 21 | 17.59 | 2.56 | 07 | 15.98 | 0.66 | 09 | 21.48 | 1.93 | 10 | 23.21 | 1.41 | 06 |
| LtM3H | 35.27 | 3.06 | 21 | 36.30 | 1.70 | 07 | 26.92 | 2.05 | 10 | 34.59 | 3.64 | 10 | 36.60 | 2.12 | 04 |
| LtM3B | 21.02 | 2.21 | 21 | 20.04 | 1.94 | 07 | 18.26 | 1.51 | 10 | 24.83 | 1.13 | 10 | 26.28 | 0.89 | 04 |
| RtM3H | 34.76 | 2.85 | 21 | 35.79 | 2.26 | 07 | 26.72 | 2.66 | 09 | 34.40 | 3.39 | 10 | 37.10 | 0.68 | 05 |
| RtM3B | 21.73 | 2.07 | 21 | 21.52 | 3.45 | 07 | 17.95 | 1.34 | 09 | 25.18 | 0.65 | 10 | 25.54 | 1.85 | 05 |

| Ranking Orders: from highest to lowest mean values | Frequency of Occurrence: | |
|---|---|---|
| | Males | Females |
| NORM (expected trend):<br>G.g.b. - G.g.g. - P.p.p. - P.p.a. - P.t. | 19 | 12 |
| i) G.g.b. - P.p.p. - G.g.g. - P.p.a. - P.t. | 10 | 2 |
| ii) G.g.b. - G.g.g. - P.p.a. - P.p.p. - P.t. | - | 8 |
| iii) G.g.b. - P.p.p. - P.p.a. - G.g.g. - P.t. | 1 | 4 |
| iv) G.g.b. - G.g.g. - P.p.p. - P.t. - P.p.a. | 1 | 1 |
| v) G.g.b. - P.p.a. - P.p.p. - G.g.g. - P.t. | - | 3 |
| vi) P.p.p. - G.g.g. - G.g.b. - P.p.a. - P.t. | 1 | - |
| vii) G.g.g. - P.t. - P.p.p. - P.p.a. - G.g.b. | - | 1 |
| viii) P.p.p. - G.g.b. - G.g.g. - P.p.a. - P.t. | - | 1 |
| ix) P.t. - P.p.a. - P.p.p. - G.g.g. - G.g.b. | 1 | - |
| x) P.t. - P.p.p. - P.p.a. - G.g.g. - G.g.b. | - | 1 |
| xi) P.p.a. - G.g.b. - P.p.p. - G.g.g. - P.t. | - | 1 |
| xii) P.p.a. - G.g.b. - G.g.g. - P.p.p. - P.t. | 1 | - |
| Total: | 34 | 34 |

Table 5. Data base: Ranking orders for measurements

| Variable | P.p.p. |  | P.p.a. |  | P.t. |  | G.g.g. |  | G.g.b. |  |
|---|---|---|---|---|---|---|---|---|---|---|
|  | Freq | % | Freq | % | Freq | % | Freq | % | Freq | % |
| M3 - Ant. to border | 9/28 | 32.1 | 2/7 | 28.6 | 4/10 | 40.0 | 13/21 | 61.9 | 7/11 | 63.6 |
| Covered 1/4 | 5/28 | 17.9 | 2/7 | 28.6 | 5/10 | 50.0 | 8/21 | 38.1 | 3/11 | 27.3 |
| Covered 1/2 | 7/28 | 25.0 | 1/7 | 14.3 | - | - | - | - | - | - |
| Covered 3/4 | - | - | 1/7 | 14.3 | - | - | - | - | - | - |
| Trace visible | 1/28 | 3.6 | - | - | - | - | - | - | - | - |
| Totally hidden | - | - | - | - | - | - | - | - | - | - |
| Not available | 6/28 | 21.4 | 1/7 | 14.3 | 1/10 | 10.0 | - | - | 1/11 | 9.1 |
| Gonial angle shape |  |  |  |  |  |  |  |  |  |  |
| Straight | 17/28 | 60.7 | 2/7 | 28.6 | 7/10 | 70.0 | 14/21 | 66.7 | 3/11 | 27.3 |
| Inversion-slight | 8/28 | 28.6 | 4/7 | 57.1 | - | - | 2/21 | 9.5 | 1/11 | 9.1 |
| -marked | - | - | 1/7 | 14.3 | - | - | - | - | - | - |
| Eversion-slight | 3/28 | 10.7 | - | - | 3/10 | 30.0 | 5/21 | 23.8 | 7/11 | 63.6 |
| -marked | - | - | - | - | - | - | - | - | - | - |
| Not available | - | - | - | - | - | - | - | - | - | - |

Table 6.1 Data base: Frequency and percentage calculations of observations on male pongid mandibles

| Variable | P.p.p. |  | P.p.a. |  | P.t. |  | G.g.g. |  | G.g.b. |  |
|---|---|---|---|---|---|---|---|---|---|---|
|  | Freq | % | Freq | % | Freq | % | Freq | % | Freq | % |
| Left side - No. mental foramina |  |  |  |  |  |  |  |  |  |  |
| Single | 17/28 | 60.7 | 2/7 | 28.6 | 10/10 | 100 | 18/21 | 85.7 | - | - |
| Double | 7/28 | 25.0 | 1/7 | 14.3 | - | - | 3/21 | 14.3 | 7/11 | 63.6 |
| Triple | 3/28 | 10.7 | - | - | - | - | - | - | 4/11 | 36.4 |
| More then triple | 1/28 | 3.6 | - | - | - | - | - | - | - | - |
| Not available | - | - | 4/7 | 57.1 | - | - | - | - | - | - |
| Right side - No. mental foramina |  |  |  |  |  |  |  |  |  |  |
| Single | 16/28 | 57.1 | 2/7 | 28.6 | 9/10 | 90.0 | 19/21 | 90.5 | 4/11 | 36.4 |
| Double | 8/28 | 28.6 | 1/7 | 14.3 | - | - | 2/21 | 9.5 | 3/11 | 27.3 |
| Triple | 4/28 | 14.3 | - | - | - | - | - | - | 4/11 | 36.4 |
| More than triple | - | - | - | - | - | - | - | - | - | - |
| Not available | - | - | 4/7 | 57.1 | 1/10 | 10.0 | - | - | - | - |

| Variable | P.p.p. | | P.p.a. | | P.t. | | G.g.g. | | G.g.b. | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Freq | % | Freq | % | Freq | % | Freq | % | Freq | % |
| M3 - Ant. to border | 2/26 | 7.7 | 2/8 | 25.0 | 6/11 | 54.5 | 1/11 | 9.1 | 1/6 | 16.7 |
| Covered 1/4 | 5/26 | 19.2 | 4/8 | 50.0 | 2/11 | 18.2 | 7/11 | 63.6 | 3/6 | 50.0 |
| Covered 1/2 | 10/26 | 38.5 | 1/8 | 12.5 | 1/11 | 9.1 | 2/11 | 18.2 | 1/6 | 16.7 |
| Covered 3/4 | 3/26 | 11.5 | - | - | - | - | - | - | - | - |
| Trace visible | - | - | - | - | - | - | - | - | - | - |
| Totally hidden | - | - | - | - | - | - | - | - | - | - |
| Not available | 6/26 | 23.1 | 1/8 | 12.5 | 2/11 | 18.2 | 1/11 | 9.1 | 1/6 | 16.7 |
| Gonial angle shape | | | | | | | | | | |
| Straight | 16/26 | 61.5 | 4/8 | 50.0 | 6/11 | 54.5 | 6/11 | 54.5 | 2/6 | 33.3 |
| Inversion-slight | 10/26 | 38.5 | 4/8 | 50.0 | 5/11 | 45.5 | 4/11 | 36.4 | - | - |
| -marked | - | - | - | - | - | - | - | - | - | - |
| Eversion-slight | - | - | - | - | - | - | - | - | 4/6 | 66.7 |
| -marked | - | - | - | - | - | - | - | - | - | - |
| Not available | - | - | - | - | - | - | 1/11 | 9.1 | - | - |

Table 6.2 Data base: Frequency and percentage calculations of observations on female pongid mandibles

| Variable | P.p.p. |  | P.p.a. |  | P.t. |  | G.g.g. |  | G.g.b. |  |
|---|---|---|---|---|---|---|---|---|---|---|
|  | Freq | % | Freq | % | Freq | % | Freq | % | Freq | % |
| Left side - No. mental foramina |  |  |  |  |  |  |  |  |  |  |
| Single | 10/26 | 38.5 | 4/8 | 50.0 | 11/11 | 100 | 7/11 | 63.6 | - | - |
| Double | 8/26 | 30.8 | 1/8 | 12.5 | - | - | 2/11 | 18.2 | 2/6 | 33.3 |
| Triple | 6/26 | 23.1 | 1/8 | 12.5 | - | - | 2/11 | 18.2 | 2/6 | 33.3 |
| More than triple | 1/26 | 3.8 | - | - | - | - | - | - | 2/6 | 33.3 |
| Not available | 1/26 | 3.8 | 2/8 | 25.0 | - | - | - | - | - | - |
| Right side - No. mental foramina |  |  |  |  |  |  |  |  |  |  |
| Single | 10/26 | 38.5 | 3/8 | 37.5 | 10/11 | 90.9 | 6/11 | 54.5 | 1/6 | 16.7 |
| Double | 6/26 | 23.1 | 2/8 | 25.0 | 1/11 | 9.1 | 4/11 | 36.4 | 4/6 | 66.7 |
| Triple | 7/26 | 26.9 | 1/8 | 12.5 | - | - | 1/11 | 9.1 | 1/6 | 16.7 |
| More than triple | 2/26 | 7.7 | - | - | - | - | - | - | - | - |
| Not available | 1/26 | 3.8 | 2/8 | 25.0 | - | - | - | - | - | - |

This research:

| Groups: | LtM1 | | LtM2 | RtM1 | | RtM2 | Kay (1982):<br>Average/<br>Number |
|---|---|---|---|---|---|---|---|
| P.p.p. (28) (male) | 223.34 | (207.61554) | 191.89107 | 221.8925 | (202.15518) | 182.41786 | Pongo pygmaeus<br>(20)<br>$\bar{x}$ = 204<br>(165-235) |
| P.p.p. (26) (female) | 226.67192 | (211.68) | 196.68808 | 221.51423 | (205.24173) | 188.96923 | |
| P.p.a. (7) (male) | 207.27857 | (196.39) | 185.50143 | 204.58 | (187.33929) | 170.09857 | |
| P.p.a. (8) (female) | 221.21125 | (214.55875) | 207.90625 | 213.87625 | (205.93741) | 197.99857 | |
| P.t. (10) (male) | 183.165 | (177.63639) | 172.10778 | 187.65889 | (171.36056) | 155.06222 | Pan troglodytes<br>(12)<br>$\bar{x}$ = 183<br>(165-199) |
| P.t. (11) (female) | 190.01818 | (176.99455) | 163.97091 | 189.484 | (173.61534) | 157.74667 | |
| G.g.g. (21) (male) | 194.93762 | (178.6981) | 162.45857 | 190.23381 | (175.75616) | 161.2785 | Gorilla gorilla<br>(13)<br>$\bar{x}$ = 179<br>(150-204) |
| G.g.g. (11) (female) | 168.38091 | (154.93591) | 141.49091 | 165.69273 | (153.89864) | 142.10455 | |
| G.g.b. (11) (male) | 194.21091 | (183.96728) | 173.72364 | 192.436 | (183.063) | 173.69 | |
| G.g.b. (6) (female) | 158.89 | (147.443) | 135.996 | 167.95333 | (158.01) | 148.06667 | |

Table 7. Data base: Mandibular corpus shape ratios
(Average indices in brackets)

This table represents the total number of measurements which overlap the three sex groups, for each test case.

M - male

* - male/female

F - female

In two cases, the individual mandibles are not considered adults, and therefore both are compared to adult and juvenile plots (graphs developed from the data base). Superscripts "a" and "b" refer to the use of the juvenile graphs and the adult graphs, respectively.

| Case Number | Actual Classification | Species Totals P.p.p. F | | | P.p.a. F | * | M | P.t. F | * | M | G.g.g. F | * | M | G.g.b. F | * | M |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | F | * | M | | | | | | | | | | | | |
| 1 | Female Gorilla | 6 | 18 | 9 | 4 | 13 | 9 | - | 2 | 6 | 4 | 22 | 4 | 6 | 3 | 4 |
| $2^a$ | Pan (juvenile) | 2 | 14 | 2 | - | - | 3 | 4 | 2 | 3 | - | - | - | - | - | - |
| $2^b$ | Pan (juvenile) | 4 | - | - | 3 | 1 | 1 | 4 | 1 | - | - | - | - | 1 | - | - |
| 3 | Male Pongo | 2 | 12 | 15 | 1 | 4 | 18 | - | 2 | 1 | 4 | 11 | 15 | 7 | 6 | 8 |
| 4 | Male Pan | 7 | 1 | - | 5 | 3 | - | 12 | 11 | 1 | 1 | 1 | 1 | - | - | - |
| 5 | Female Pongo | 16 | 9 | 2 | 5 | 12 | 12 | 1 | 10 | 13 | 12 | 7 | 2 | 1 | 2 | 3 |
| 6 | Male Pongo | - | 8 | 26 | - | 5 | 15 | 1 | 2 | - | 2 | 15 | 15 | 8 | 4 | 15 |
| [illegible] | Pan (juvenile) | - | 16 | 4 | - | - | 5 | 1 | 2 | 4 | - | - | - | - | - | - |
| $7^b$ | Pan (juvenile) | 5 | - | - | 3 | 2 | - | 6 | 5 | 1 | - | - | - | 1 | - | - |

Table 8. Test sample: Plot results

This research:

| | | Mandibular corpus shape: |
|---|---|---|
| GSI D 298 | M2H - 22.5<br>M2B - 15 | $\frac{22.5}{15} \times 100 = 150.0$ |
| GSP 11706 | M1H - e. 34<br>M1B - e. 17 | $\frac{34}{17} \times 100 = 200.0$ |
| GSP 13165 | M1H - e. 30<br>M1B - e. 15 | $\frac{30}{15} \times 100 = 200.0$ |
| ONGC V 790 | M1H - 37.5<br>M1B - 20 | $\frac{37.5}{20} \times 100 = 187.5$ |
| YPM 13811 | M1H - 25.6<br>M1B - 13* | $\frac{25.6}{13} \times 100 = 196.9$ |

* measured in the middle of the tooth

Kay (1982):

S. indicus - 154
(from Siwalik sample
totalling 7)

S. sivalensis - 152
(from Siwalik sample
totalling 6)

Table 9. Miocene fossils: Mandibular corpus shape ratios

This table lists the fossils, and their corresponding measurement values. The symbols under each of the five subspecies columns indicates how a specific variable fits within that subspecies.

The symbols are:
M - male

* - male/female

F - female

Superscript footnote references:

1. measured on the anterior face
2. measured anterior to tooth
3. "thickness of jaw in front of root of ascending ramus" (Gregory and Hellman 1926)
4. measured as the vertical diameter of the symphysis
5. measured as the maximum antero-posterior width
6. measured as the symphysis depth
7. measured as the breadth at M2
8. measured as the symphysis length
9. measured as the breadth at M2
10. taken as a distal measurement
11. measured as the symphysis depth
12. measured as the corpus depth
13. "horizontal distance from the most anterior point to posterior border of ramus" (Preuss 1982)
14. measured as corpus thickness
15. measured as symphysis depth
16. measured as corpus height
17. measured as corpus height
18. taken as a maximum measurement
19. measured as the breadth

Table 10. Miocene fossils: Plot results

| Fossil | Measurements (mm.) | | Species<br>P.p.p. | P.p.a. | P.t. | G.g.g. | G.g.b. |
|---|---|---|---|---|---|---|---|
| Graecopithecus freybergi | RtM3H | 25 | | | * | | |
| AMNH 19411 | SymH | 43 ① | | | * | | |
| | | 42.6 | | | * | | |
| | SymBE | 17.8 | F | * | * | | |
| | | 17 | F | * | * | | |
| | SymBI | 17.8 | F | M | * | | |
| | | 17 | F | * | * | | |
| AMNH 19413 | LtM3H | 31 ② | F | M | M | F | |
| | LtM3B | 19 ③ | * | * | * | | |
| BMNH 15423 | LtM2H | 23 | | | F | | |
| | LtM3H | 26.6 | | M | * | | |
| | LtP4H | 31 | | M | * | F | |
| GSI D 118/119 | (Rt)M3B | 19.8 | F | F | * | | |
| | (Lt)M2H | 23.4 | | | F | | |

| Fossil | Measurements (mm.) | | Species | | | | |
|---|---|---|---|---|---|---|---|
| | | | P.p.p. | P.p.a. | P.t. | G.g.g. | G.g.b. |
| GSI D 177 | RtP4B | 15 | F | F | * | | |
| GSI D 197 | LtP3H | 32.8 | | | * | | |
| | LtP4H | 35.5 | F | * | | * | |
| | LtP4B | 14.5 | F | F | F | | |
| | LtM2H | 27.8 | F | M | * | F | |
| GSI D 199 | LtP4B | 13 | | | F | | |
| GSI D 298 | SymH | 30 ④ | | | | | |
| | SymBE | 12 ⑤ | | | | | |
| | SymBI | 12 ⑤ | | | | | |
| | RtM2H | 22.5 | | | F | | |
| | RtM2B | 15 | F | F. | * | | |
| GSI D 18039 | LtM2B | 25 | M | | | M | * |
| | LtP3B | 20 | * | * | * | | |

| Fossil | Measurements (mm.) | | Species | | | | |
|---|---|---|---|---|---|---|---|
| | | | P.p.p. | P.p.a. | P.t. | G.g.g. | G.g.b. |
| GSP 4230 | RtM3H | 30.5 | F | M | | F | |
| | RtM3B | 23.5 | * | * | | M | M |
| | | 22.8 | * | F | | M | M |
| GSP 4622/4857 | (Lt)P4B | 13 | | | F | | |
| | (Rt)P4B | 13 | | | F | | |
| | SymH | 31 ⑥ | | | | | |
| | | 30 ⑥ | | | | | |
| | SymBE | 14.5 | | | F | | |
| | | 15 | | | F | | |
| | SymBI | 14.5 | | F | F | | |
| | | 15 | | F | F | | |
| | (Lt)M3H | 27.3 | F | M | * | | |
| | | 31 | F | M | M | F | |
| | (Rt)M3H | 27.3 | F | | * | | |
| | | 31 | F | M | | F | |

| Fossil | Measurements (mm.) | | Species | | | | |
|---|---|---|---|---|---|---|---|
| | | | P.p.p. | P.p.a. | P.t. | G.g.g. | G.g.b. |
| | (Lt)M2B | 48 ⑦ | | | | | |
| | (Rt)M2B | 48 ⑦ | | | | | |
| | (Lt)M3B | 19.5 | * | * | F | | |
| | | 20 | * | * | F | | |
| | (Rt)M3B | 19.5 | F | F | * | | |
| | | 20 | F | F | F | | |
| GSP 9563/9902 | SymH | 33 ⑧ | | | | | |
| | SymBE | 17 | F | * | * | | |
| | SymBI | 17 | F | * | * | | |
| GSP 9564/9905/ 9901/9977 | (Lt)P4B | 15.5 | F | F | * | | |
| | | 16 | F | * | * | | |
| | (Rt)P4B | 15.5 | F | * | * | | |
| | | 16 | F | * | M | | |
| | SymH | 52.5 | F | * | M | * | F |
| | | 52 | F | * | M | * | F |

| Fossil | Measurements (mm.) | | Species | | | | |
|---|---|---|---|---|---|---|---|
| | | | P.p.p. | P.p.a. | P.t. | G.g.g. | G.g.b. |
| | SymBE | 20 | F | * | * | | |
| | SymBI | 20 | * | M | M | | |
| | (Lt)M3H | 42.5 | M | M | | M | M |
| | | 40 | * | M | | M | M |
| | (Rt)M3H | 42.5 | M | M | | M | M |
| | | 40 | M | M | | M | |
| | (Lt)M2B | 47 ⑨ | | | | | |
| | (Rt)M2B | 47 ⑨ | | | | | |
| | (Lt)M3B | 24 | * | M | | * | M |
| | | 26 | M | M | | * | * |
| | (Rt)M3B | 24 | * | * | | * | * |
| | | 26 | M | * | | * | * |
| | (Lt)P4H | 43.5 | * | M | | M | M |
| | | 43 | * | M | | M | M |
| | (Rt)P4H | 43.5 | * | M | | M | M |
| | | 43 | * | M | | M | M |

| Fossil | Measurements (mm.) | | Species | | | | |
|---|---|---|---|---|---|---|---|
| | | | P.p.p. | P.p.a. | P.t. | G.g.g. | G.g.b. |
| GSP 11706 | RtM1 H | 34 | * | * | M | * | |
| | RtM1 B | 17 | * | F | | | |
| | RtM3H | 34 | F | * | | * | |
| | RtM3B | 24 | * | * | | * | * |
| GSP 13165 | RtP4B | 15 | F | F | * | | |
| | RtM1 H | 30 | | M | * | F | |
| | RtM1 B | 15 | F | F | * | | |
| | RtP4H | 34 | F | * | M | * | |
| GSP 13566 | RtM3H | 24.5 | | | * | | |
| | RtM3B | 19.5 | F | F | * | | |
| GSP 13808 | RtM1 B | 20 | M | | | * | M |

| Fossil | Measurements (mm.) | | Species<br>P.p.p. | P.p.a. | P.t. | G.g.g. | G.g.b. |
|---|---|---|---|---|---|---|---|
| GSP 13875 | RtP4H | 26 | | | F | | |
| | RtP4B | 13.5 | | | F | | |
| | RtM3H | 23 ⑩ | | | F | | |
| | RtM3B | 19 ⑩ | F | F | * | | |
| | SymH | 31.5 ⑪ | | | | | |
| | SymBE | 15 | | | F | | |
| | SymBI | 15 | | F | F | | |
| GSP 14951 | RtM3H | 21.5 ⑫ | | | | | |
| | RtM3B | 16.5 | | | * | | |
| GSP 15000 | (Lt)P4H | 37 | F | * | | * | F |
| | (Rt)P4H | 37 | * | * | | * | F |
| | (Lt)P4B | 16 | F | * | * | | |
| | | 14.3 | F | F | F | | |
| | (Rt)P4B | 16 | F | * | M | | |
| | | 14.3 | F | | * | | |
| | (Lt)M3H | 34 | F | * | | * | * |
| | (Rt)M3H | 34 | F | * | | * | |

| Fossil | Measurements (mm.) | | Species | | | | |
|---|---|---|---|---|---|---|---|
| | | | P.p.p. | P.p.a. | P.t. | G.g.g. | G.g.b. |
| | (Lt)M3B | 28.5 | M | | | M | M |
| | | 26.7 | M | M | | M | * |
| | (Rt)M3B | 28.5 | | M | | | M |
| | | 26.7 | M | * | | M | * |
| | (Lt)RamH | 108 | | | | M | |
| | (Rt)RamH | 108 | | | | M | |
| | (Lt)RamW | 60 | M | M | | * | F |
| | (Rt)RamW | 60 | M | M | | * | F |
| | SymH | 42 | | | * | | |
| | | 44 | | | * | F | |
| | SymBE | 20 | F | * | * | | |
| | | 21 | * | * | | F | |
| | SymBI | 20 | * | M | M | | |
| | | 21 | * | M | | F | |
| | MaxL | 130 ⑬ | M | M | | * | |

| Fossil | Measurements (mm.) | | Species | | | | |
|---|---|---|---|---|---|---|---|
| | | | P.p.p. | P.p.a. | P.t. | G.g.g. | G.g.b. |
| GSP 15397 | LtP4H | 29 | | | * | | |
| | LtP4B | 13.5 | | | F | | |
| | LtM3H | 28.5 | F | M | * | | |
| | LtM3B | 14 ⑭ | | | | | |
| GSP 15629 | SymH | 35 ⑮ | | | | | |
| | SymBE | 18 | F | * | * | | |
| | SymBI | 18 | F | M | * | | |
| GSP 16077 | LtM3H | 19.8 ⑯ | | | | | |
| | LtM3B | 22.5 | * | * | | M | |
| | LtP3H | 26.5 ⑰ | | | | | |
| | LtP3B | 13.7 | | | F | | |
| GSP 17125 | RtM3H | 30.6 | F | M | | | |
| | RtM3B | 24.2 | * | * | | * | * |
| | RtP3H | 38.5 | F | * | M | * | |
| | RtP3B | 16.2 | F | F | * | | |

| Fossil | Measurements (mm.) | | Species | | | | |
|---|---|---|---|---|---|---|---|
| | | | P.p.p. | P.p.a. | P.t. | G.g.g. | G.g.b. |
| ONGC V 790 | RtP4H | 42 ⑱ | * | M | | M | M |
| | RtP4B | 19 ⑱ | * | * | | * | |
| | RtM1 H | 37.5 ⑱ | * | M | | * | F |
| | RtM1 B | 20 ⑱ | M | | | * | M |
| | RtM2H | 35 ⑱ | * | * | | M | F |
| PUA 1047-69 | LtP3H | 33.5 | | | * | | |
| | LtP4H | 32.2 | F | M | M | F | F |
| | SymH | 40.4 | F | | | | |
| | SymBE | 15.9 | F | | F | | |
| | SymBI | 15.9 | * | F | F | | |

| Fossil | Measurements (mm.) | | Species | | | | |
|---|---|---|---|---|---|---|---|
| | | | P.p.p. | P.p.a. | P.t. | G.g.g. | G.g.b. |
| YPM 13811 | SymBE | 13.6 | | | F | | |
| | SymBI | 13.6 | | F | F | | |
| | LtM1H | 25.6 | | | * | | |
| | LtP4H | 26 | | | F | | |
| | LtP4B | 11.5 ⑲ | | | | | |
| | LtM1B | 13 | | F | F | | |
| | LtM2B | 16 | F | F | * | | |
| | LtM3B | 19 | * | * | * | | |
| | | 18.6 | F | * | * | | |
| YPM 13814 | LtP4H | 27.5 | | | * | | |
| | LtP4B | 12.5 | | | F | | |

Duplicated variable lists within each fossil indicate one or more values for variables.

If sides are not indicated for specific measurements, then both left and right sides are tested.

Both sexes are considered for all fossils.

Table 11. Miocene fossils: Discriminant analysis results (listing the top three predicted groups)

| Fossil | Measurement Variables | Sex | Species<br>P.p.p. | P.p.a. | P.t. | G.g.g. | G.g.b. |
|---|---|---|---|---|---|---|---|
| Graecopithecus freybergi | RtM3H | M |  | 2 | 1 | 3 |  |
|  | RtM3H | F | 3 |  | 1 | 2 |  |
| AMNH 19411 | SymH - SymBE | M |  | 2 | 1 | 3 |  |
|  | SymH - SymBE | M |  | 2 | 1 | 3 |  |
|  | SymH - SymBE | M |  | 2 | 1 | 3 |  |
|  | SymH - SymBE | M |  | 2 | 1 | 3 |  |
|  | SymH - SymBE | F | 3 | 2 | 1 |  |  |
|  | SymH - SymBE | F | 3 | 2 | 1 |  |  |
|  | SymH - SymBE | F | 3 | 2 | 1 |  |  |
|  | SymH - SymBE | F | 3 | 2 | 1 |  |  |
|  | SymH - SymBI | M | 3 | 2 | 1 |  |  |
|  | SymH - SymBI | M | 3 | 2 | 1 |  |  |
|  | SymH - SymBI | M |  | 2 | 1 | 3 |  |
|  | SymH - SymBI | M | 3 | 2 | 1 |  |  |

| Fossil | Measurement Variable | Sex | Species |  |  |  |  |
|---|---|---|---|---|---|---|---|
|  |  |  | P.p.p. | P.p.a. | P.t. | G.g.g. | G.g.b. |
|  | SymH - SymBI | F |  | 2 | 1 | 3 |  |
|  | SymH - SymBI | F | 2 | 3 | 1 |  |  |
|  | SymH - SymBI | F | 3 |  | 1 | 2 |  |
|  | SymH - SymBI | F | 2 |  | 1 | 3 |  |
| AMNH 19413 | LtM3H - LtM3B | M |  | 2 | 1 | 3 |  |
|  | LtM3H - LtM3B | F | 3 | 2 | 1 |  |  |
| BMNH 15423 | LtM2H - LtM3H - LtP4H | M |  | 3 | 1 | 2 |  |
|  | LtM2H - LtM3H - LtP4H | F |  |  | 1 | 2 | 3 |
| GSI D 118/119 | (Rt)M3B - (Lt)M2H | M |  | 3 | 1 | 2 |  |
|  | (Rt)M3B - (Lt)M2H | F | 3 |  | 1 | 2 |  |
| GSI D 177 | RtP4B | M | 3 | 2 | 1 |  |  |
|  | RtP4B | F | 2 | 3 | 1 |  |  |

| Fossil | Measurement Variable | Sex | Species<br>P.p.p. | P.p.a. | P.t. | G.g.g. | G.g.b. |
|---|---|---|---|---|---|---|---|
| GSI D 197 | LtP3H - LtP4H - LtP4B - LtM2H | M | 3 | 2 | 1 | | |
| | LtP3H - LtP4H - LtP4B - LtM2H | F | 2 | 3 | 1 | | |
| GSI D 199 | LtP4B | M | 3 | 2 | 1 | | |
| | LtP4B | F | 2 | 3 | 1 | | |
| GSI D 298 | RtM2H - RtM2B | M | | 2 | 1 | 3 | |
| | RtM2H - RtM2B | F | 3 | | 1 | 2 | |
| GSI D 18039 | LtM2B - LtP3B | M | 1 | 2 | | 3 | |
| | LtM2B - LtP3B | F | 3 | | | 1 | 2 |
| GSP 4230 | RtM3H - RtM3B | M | 3 | 1 | | 2 | |
| | RtM3H - RtM3B | M | | 1 | 3 | 2 | |
| | RtM3H - RtM3B | F | 2 | 3 | | 1 | |
| | RtM3H - RtM3B | F | 1 | 3 | | 2 | |

| Fossil | Measurement Variable | Sex | Species | | | | |
|---|---|---|---|---|---|---|---|
| | | | P.p.p. | P.p.a. | P.t. | G.g.g. | G.g.b. |
| GSP 4622/4857 | SymBE - LtP4B -<br>LtM3H - LtM3B | M | 3 | 2 | 1 | | |
| | SymBE - LtP4B -<br>LtM3H - LtM3B | M | 3 | 1 | 2 | | |
| | SymBE - LtP4B -<br>LtM3H - LtM3B | F | 3 | 2 | 1 | | |
| | SymBE - LtP4B -<br>LtM3H - LtM3B | F | 3 | 2 | 1 | | |
| | SymBE - RtP4B -<br>RtM3H - RtM3B | M | 3 | 2 | 1 | | |
| | SymBE - RtP4B -<br>RtM3H - RtM3B | M | 3 | 1 | 2 | | |
| | SymBE - RtP4B -<br>RtM3H - RtM3B | F | 2 | 3 | 1 | | |
| | SymBE - RtP4B -<br>RtM3H - RtM3B | F | 1 | 3 | 2 | | |
| | SymBI - LtP4B -<br>LtM3H - LtM3B | M | 3 | 2 | 1 | | |
| | SymBI - LtP4B -<br>LtM3H - LtM3B | M | 3 | 1 | 2 | | |

| Fossil | Measurement Variable | Sex | Species | | | | |
|---|---|---|---|---|---|---|---|
| | | | P.p.p. | P.p.a. | P.t. | G.g.g. | G.g.b. |
| | SymBI - LtP4B - LtM3H - LtM3B | F | 2 | 3 | 1 | | |
| | SymBI - LtP4B - LtM3H - LtM3B | F | 2 | 3 | 1 | | |
| | SymBI - RtP4B - RtM3H - RtM3B | M | 3 | 2 | 1 | | |
| | SymBI - RtP4B - RtM3H - RtM3B | M | 3 | 1 | 2 | | |
| | SymBI - RtP4B - RtM3H - RtM3B | F | 2 | 3 | 1 | | |
| | SymBI - RtP4B - RtM3H - RtM3B | F | 1 | 3 | 2 | | |
| GSP 9563/9902 | SymBE | M | 3 | 2 | 1 | | |
| | SymBE | F | 3 | 2 | 1 | | |
| | SymBI | M | 3 | 2 | 1 | | |
| | SymBI | F | 3 | 2 | 1 | | |

| Fossil | Measurement | Sex | Species | | | | |
|---|---|---|---|---|---|---|---|
| | Variable | | P.p.p. | P.p.a. | P.t. | G.g.g. | G.g.b. |
| GSP 9564/9905/ 9901/9977 | SymH - SymBE - LtP4H - LtP4B - LtM3H - LtM3B | M | 1 | 2 | | 3 | |
| | SymH - SymBE - LtP4H - LtP4B - LtM3H - LtM3B | M | 1 | 2 | | 3 | |
| | SymH - SymBE - LtP4H - LtP4B - LtM3H - LtM3B | F | 1 | 2 | | 3 | |
| | SymH - SymBE - LtP4H - LtP4B - LtM3H - LtM3B | F | 1 | 2 | | 3 | |
| | SymH - SymBE - RtP4H - RtP4B - RtM3H - RtM3B | M | 1 | 2 | | 3 | |
| | SymH - SymBE - RtP4H - RtP4B - RtM3H - RtM3B | M | 1 | 2 | | 3 | |
| | SymH - SymBE - RtP4H - RtP4B - RtM3H - RtM3B | F | 1 | 2 | | 3 | |

| Fossil | Measurement Variable | Sex | Species |  |  |  |  |
|---|---|---|---|---|---|---|---|
|  |  |  | P.p.p. | P.p.a. | P.t. | G.g.g. | G.g.b. |
|  | SymH - SymBE - RtP4H - RtP4B - RtM3H - RtM3B | F | 1 | 2 |  | 3 |  |
|  | SymH - SymBI - LtP4H - LtP4B - LtM3H - LtM3B | M | 1 | 2 |  | 3 |  |
|  | SymH - SymBI - LtP4H - LtP4B - LtM3H - LtM3B | M | 1 | 2 |  | 3 |  |
|  | SymH - SymBI - LtP4H - LtP4B - LtM3H - LtM3B | F | 1 | 2 |  | 3 |  |
|  | SymH - SymBI - LtP4H - LtP4B - LtM3H - LtM3B | F | 1 | 3 |  | 2 |  |
|  | SymH - SymBI - RtP4H - RtP4B - RtM3H - RtM3B | M | 1 | 2 |  | 3 |  |
|  | SymH - SymBI - RtP4H - RtP4B - RtM3H - RtM3B | M | 1 | 2 |  | 3 |  |
|  | SymH - SymBI - RtP4H - RtP4B - RtM3H - RtM3B | F | 1 | 2 |  | 3 |  |

| Fossil | Measurement Variable | Sex | Species | | | | |
|---|---|---|---|---|---|---|---|
| | | | P.p.p. | P.p.a. | P.t. | G.g.g. | G.g.b. |
| | SymH - SymBI - RtP4H - RtP4B - RtM3H - RtM3B | F | 1 | 2 | | 3 | |
| GSP 11706 | RtM1H - RtM1B - RtM3H - RtM3B | M | 2 | 1 | | 3 | |
| | RtM1H - RtM1B - RtM3H - RtM3B | F | 1 | 2 | | 3 | |
| GSP 13165 | RtP4H - RtP4B - RtM1H - RtM1B | M | 3 | 2 | 1 | | |
| | RtP4H - RtP4B - RtM1H - RtM1B | F | 2 | 3 | 1 | | |
| GSP 13566 | RtM3H - RtM3B | M | | 2 | 1 | 3 | |
| | RtM3H - RtM3B | F | 2 | 3 | 1 | | |
| GSP 13808 | RtM1B | M | 2 | 3 | | 1 | |
| | RtM1B | F | | 3 | | 1 | 2 |
| GSP 13875 | SymBE - RtP4H - RtP4B - RtM3H - RtM3B | M | | 2 | 1 | 3 | |
| | SymBE - RtP4H - RtP4B - RtM3H - RtM3B | F | 2 | 3 | 1 | | |

| Fossil | Measurement Variable | Sex | Species | | | | |
|---|---|---|---|---|---|---|---|
| | | | P.p.p. | P.p.a. | P.t. | G.g.g. | G.g.b. |
| | SymBI - RtP4H - RtP4B - RtM3H - RtM3B | M | 3 | 2 | 1 | | |
| | SymBI - RtP4H - RtP4B - RtM3H - RtM3B | F | 2 | 3 | 1 | | |
| GSP 14951 | RtM3B | M | 2 | | 1 | | 3 |
| | RtM3B | F | 2 | 3 | 1 | | |
| GSP 15000 | LtRamW - SymH - SymBE - MaxL - LtRamH - LtP4H - LtP4B - LtM3H - LtM3B | M | 2 | 3 | | 1 | |
| | LtRamW - SymH - SymBE - MaxL - LtRamH - LtP4H - LtP4B - LtM3H - LtM3B | M | 2 | 3 | | 1 | |
| | LtRamW - SymH - SymBE - MaxL - LtRamH - LtP4H - LtP4B - LtM3H - LtM3B | F | 1 | 2 | 3 | | |

| Fossil | Measurement | Sex | Species | | | | |
|---|---|---|---|---|---|---|---|
| | Variable | | P.p.p. | P.p.a. | P.t. | G.g.g. | G.g.b. |
| | LtRamW - SymH - SymBE - MaxL - LtRamH - LtP4H - LtP4B - LtM3H - LtM3B | F | 1 | 2 | | | 3 |
| | RtRamW - SymH - SymBE - MaxL - RtRamH - RtP4H - RtP4B - RtM3H - RtM3B | M | | 3 | | 1 | 2 |
| | RtRamW - SymH - SymBE - MaxL - RtRamH - RtP4H - RtP4B - RtM3H - RtM3B | M | | 3 | | 1 | 2 |
| | RtRamW - SymH - SymBE - MaxL - RtRamH - RtP4H - RtP4B - RtM3H - RtM3B | F | 1 | | 3 | | 2 |
| | RtRamW - SymH - SymBE - MaxL - RtRamH - RtP4H - RtP4B - RtM3H - RtM3B | F | 2 | | 3 | | 1 |

| Fossil | Measurement Variable | Sex | Species P.p.p. | P.p.a. | P.t. | G.g.g. | G.g.b. |
|---|---|---|---|---|---|---|---|
| | LtRamW - SymH - SymBI - MaxL - LtRamH - LtP4H - LtP4B - LtM3H - LtM3B | M | 2 | 3 | | 1 | |
| | LtRamW - SymH - SymBI - MaxL - LtRamH - LtP4H - LtP4B - LtM3H - LtM3B | M | 2 | 3 | | 1 | |
| | LtRamW - SymH - SymBI - MaxL - LtRamH - LtP4H - LtP4B - LtM3H - LtM3B | F | 1 | 2 | 3 | | |
| | LtRamW - SymH - SymBI - MaxL - LtRamH - LtP4H - LtP4B - LtM3H - LtM3B | F | 2 | 3 | | | 1 |
| | RtRamW - SymH - SymBI - MaxL - RtRamH - RtP4H - RtP4B - RtM3H - RtM3B | M | 3 | 2 | | 1 | |

| Fossil | Measurement Variable | Sex | Species | | | | |
|---|---|---|---|---|---|---|---|
| | | | P.p.p. | P.p.a. | P.t. | G.g.g. | G.g.b. |
| | RtRamW - SymH - SymBI - MaxL - RtRamH - RtP4H - RtP4B - RtM3H - RtM3B | M | 3 | 2 | | 1 | |
| | RtRamW - SymH - SymBI - MaxL - RtRamH - RtP4H - RtP4B - RtM3H - RtM3B | F | 1 | | 3 | | 2 |
| | RtRamW - SymH - SymBI - MaxL - RtRamH - RtP4H - RtP4B - RtM3H - RtM3B | F | 2 | | | 3 | 1 |
| GSP 15397 | LtP4H - LtP4B - LtM3H | M | 3 | 2 | 1 | | |
| | LtP4H - LtP4B - LtM3H | F | 3 | 2 | 1 | | |

| Fossil | Measurement Variable | Sex | Species P.p.p. | P.p.a. | P.t. | G.g.g. | G.g.b. |
|---|---|---|---|---|---|---|---|
| GSP 15629 | SymBE | M | 3 | 2 | 1 | | |
| | SymBE | F | 3 | 2 | 1 | | |
| | SymBI | M | 3 | 2 | 1 | | |
| | SymBI | F | 1 | 3 | 2 | | |
| GSP 16077 | LtP3B - LtM3B | M | 3 | 1 | 2 | | |
| | LtP3B - LtM3B | F | 3 | 1 | 2 | | |
| GSP 17125 | RtP3H - RtP3B -<br>RtM3H - RtM3B | M | 2 | 1 | 3 | | |
| | RtP3H - RtP3B -<br>RtM3H - RtM3B | F | 1 | 2 | | 3 | |
| ONGC V 790 | RtP4H - RtP4B -<br>RtM1H - RtM1B -<br>RtM2H | M | 2 | 3 | | 1 | |
| | RtP4H - RtP4B -<br>RtM1H - RtM1B -<br>RtM2H | F | 1 | 3 | | 2 | |

| Fossil | Measurement Variable | Sex | Species P.p.p. | P.p.a. | P.t. | G.g.g. | G.g.b. |
|---|---|---|---|---|---|---|---|
| PUA 1047-69 | SymH - SymBE -<br>LtP3H - LtP4H | M | 3 | 2 | 1 | | |
| | [illegible]mH - SymBE -<br>LtP3H - LtP4H | F | 3 | 2 | 1 | | |
| | SymH - SymBI -<br>LtP3H - LtP4H | M | 3 | 2 | 1 | | |
| | SymH - SymBI -<br>LtP3H - LtP4H | F | 2 | 3 | 1 | | |
| YPM 13811 | SymBE - LtP4H -<br>LtM1H - LtM1B -<br>LtM2B - LtM3B | M | 3 | 2 | 1 | | |
| | SymBE - LtP4H -<br>LtM1H - LtM1B -<br>LtM2B - LtM3B | M | 3 | 2 | 1 | | |
| | SymBE - LtP4H -<br>LtM1H - LtM1B -<br>LtM2B - LtM3B | F | 3 | 2 | 1 | | |
| | SymBE - LtP4H -<br>LtM1H - LtM1B -<br>LtM2B - LtM3B | F | 3 | 2 | 1 | | |

| Fossil | Measurement Variable | Sex | Species [illegible].p. | P.p.a. | P.t. | G.g.g. | G.g.b. |
|---|---|---|---|---|---|---|---|
| | SymBI - LtP4H - LtM1H - LtM1B - LtM2B - LtM3B | M | 3 | 2 | 1 | | |
| | SymBI - LtP4H - LtM1H - LtM1B - LtM2B - LtM3B | M | 3 | 2 | 1 | | |
| | SymBI - LtP4H - LtM1H - LtM1B - LtM2B - LtM3B | F | 3 | 2 | 1 | | |
| | SymBI - LtP4H - LtM1H - LtM1B - LtM2B - LtM3B | F | 3 | 2 | 1 | | |
| YPM 13814 | LtP4H - LtP4B | M | 3 | 2 | 1 | | |
| | LtP4H - LtP4B | F | 3 | 2 | 1 | | |

The 29 Miocene fossils as well as their respective available measurements are listed in columns 1 and 2.

Each fossil was compared to both male and female values for each measurement variable (Column 3).

Column 4 lists the percentage of correctly classified mandibles in the data base, using <u>only those measurements available for specific fossils</u>.

The last two columns summarize the taxonomic predictions for specific fossils, using the two approaches discriminant analysis and plot.

Table 12. Miocene fossils: Summary predictions

| Fossil | Measurements | Sex | Prediction Power | (N) | Predictions using | |
|---|---|---|---|---|---|---|
| | | | | | Discriminant Analysis | Plot |
| Graecopithecus freybergi | RtM3H | M | 50% | (68) | Pan | Pan |
| | RtM3H | F | 35.85% | (53) | Pan | Pan |
| AMNH 19411 | SymH - SymBE | M | 64% | (75) | Pan | Pan |
| | SymH - SymBE | F | 60% | (60) | Pan | Pan |
| | SymH - SymBI | M | 72% | (75) | Pan | Pan |
| | SymH - SymBI | F | 75% | (60) | Pan | Pan |
| AMNH 19413 | LtM3H - LtM3B | M | 54.55% | (66) | Pan | - |
| | LtM3H - LtM3B | F | 60.38% | (53) | Pan | - |
| BMNH 15423 | LtM2H - LtM3H - LtP4H | M | 62.12% | (66) | Pan | Pan |
| | LtM2H - LtM3H - LtP4H | F | 63.46% | (52) | Pan | Pan |
| GSI D 118/119 | (Rt)M3B - (Lt)M2H | M | 54.41% | (68) | Pan | Pan |
| | (Rt)M3B - (Lt)M2H | F | 55.77% | (52) | Pan | Pan |

| Fossil | Measurements | Sex | Prediction Power | (N) | Predictions using Discriminant Analysis | Predictions using Plot |
|---|---|---|---|---|---|---|
| GSI D 177 | RtP4B | M | 45.33% | (75) | Pan | - |
| | RtP4B | F | 40.68% | (59) | Pan | - |
| GSI D 197 | LtP3H - LtP4H - LtP4B - LtM2H | M | 72.60% | (73) | Pan | - |
| | LtP3H - LtP4H - LtP4B - LtM2H | F | 71.67% | (60) | Pan | - |
| GSI D 199 | LtP4B | M | 52.70% | (74) | Pan | Pan |
| | LtP4B | F | 31.15% | (61) | Pan | Pan |
| GSI D 298 | RtM2H - RtM2B | M | 50.68% | (73) | Pan | Pan |
| | RtM2H - RtM2B | F | 52.54% | (59) | Pan | Pan |
| GSI D 18039 | LtM2B - LtP3B | M | 58.67% | (75) | - | - |
| | LtM2B - LtP3B | F | 62.30% | (61) | - | - |
| GSP 4230 | RtM3H - RtM3B | M | 43.28% | (67) | - | - |
| | RtM3H - RtM3B | F | 49.06% | (53) | - | - |

|  |  |  |  | Predictions using |  |
|---|---|---|---|---|---|
| Fossil | Measurements | Sex | Prediction Power (N) | Discriminant Analysis | Plot |
| GSP 4622/4857 | SymBE - LtP4B -<br>LtM3H - LtM3B | M | 79.69% (64) | - | - |
|  | SymBE - LtP4B -<br>LtM3H - LtM3B | F | 73.08% (52) | - | - |
|  | SymBE - RtP4B -<br>RtM3H - RtM3B | M | 78.46% (65) | - | - |
|  | SymBE - RtP4B -<br>RtM3H - RtM3B | F | 76.47% (51) | - | - |
|  | SymBI - LtP4B -<br>LtM3H - LtM3B | M | 78.13% (64) | - | - |
|  | SymBI - LtP4B -<br>LtM3H - LtM3B | F | 84.62% (52) | - | - |
|  | SymBI - RtP4B -<br>RtM3H - RtM3B | M | 76.92% (65) | - | - |
|  | SymBI - RtP4B -<br>RtM3H - RtM3B | F | 86.27% (51) | - | - |

| Fossil | Measurements | Sex | Prediction Power (N) | Predictions using | |
|---|---|---|---|---|---|
| | | | | Discriminant Analysis | Plot |
| GSP 9563/9902 | SymBE | M | 50% (76) | Pan | - |
| | SymBE | F | 45.90% (61) | Pan | - |
| | SymBI | M | 64.47% (76) | Pan | - |
| | SymBI | F | 60.66% (61) | Pan | - |
| GSP 9564/9905/ 9901/9977 | SymH - SymBE - LtP4H - LtP4B - LtM3H - LtM3B | M | 82.81% (64) | Pongo | - |
| | SymH - SymBE - LtP4H - LtP4B - LtM3H - LtM3B | F | 82.35% (51) | Pongo | - |
| | SymH - SymBE - RtP4H - RtP4B - RtM3H - RtM3B | M | 80% (65) | Pongo | - |
| | SymH - SymBE - RtP4H - RtP4B - RtM3H - RtM3B | F | 90% (50) | Pongo | - |
| | SymH - SymBI - LtP4H - LtP4B - LtM3H - LtM3B | M | 89.06% (64) | Pongo | - |

| Fossil | Measurements | Sex | Prediction Power (N) | | Predictions using<br>Discriminant Analysis | Plot |
|---|---|---|---|---|---|---|
| | SymH - SymBI -<br>LtP4H - LtP4B -<br>LtM3H - LtM3B | F | 88.24% | (51) | Pongo | - |
| | SymH - SymBI -<br>RtP4H - RtP4B -<br>RtM3H - RtM3B | M | 83.08% | (65) | Pongo | - |
| | SymH - SymBI -<br>RtP4H - RtP4B -<br>RtM3H - RtM3B | F | 94% | (50) | Pongo | - |
| GSP 11706 | RtM1H - RtM1B -<br>RtM3H - RtM3B | M | 69.70% | (66) | Pongo | Pongo |
| | RtM1H - RtM1B -<br>RtM3H - RtM3B | F | 76.92% | (52) | Pongo | Pongo |
| GSP 13165 | RtP4H - RtP4B -<br>RtM1H - RtM1B | M | 68.92% | (74) | Pan | - |
| | RtP4H - RtP4B -<br>RtM1H - RtM1B | F | 67.24% | (58) | Pan | - |
| GSP 13566 | RtM3H - RtM3B | M | 43.28% | (67) | Pan | Pan |
| | RtM3H - RtM3B | F | 49.06% | (53) | Pan | Pan |

| Fossil | Measurements | Sex | Prediction Power (N) | | Predictions using | |
|---|---|---|---|---|---|---|
| | | | | | Discriminant Analysis | Plot |
| GSP 13808 | RtM1 B | M | 50.67% | (75) | Gorilla | Gorilla |
| | RtM1 B | F | 54.10% | (61) | Gorilla | Gorilla |
| GSP 13875 | SymBE - RtP4H - RtP4B - RtM3H - RtM3B | M | 80% | (65) | Pan | Pan |
| | SymBE - RtP4H - RtP4B - RtM3H - RtM3B | F | 86% | (50) | Pan | Pan |
| | SymBI - RtP4H - RtP4B - RtM3H - RtM3B | M | 83.08% | (65) | Pan | Pan |
| | SymBI - RtP4H - RtP4B - RtM3H - RtM3B | F | 90% | (50) | Pan | Pan |
| GSP 14951 | RtM3B | M | 42.03% | (69) | Pan | Pan |
| | RtM3B | F | 37.74% | (53) | Pan | Pan |

| Fossil | Measurements | Sex | Prediction Power (N) | | Predictions using | |
|---|---|---|---|---|---|---|
| | | | | | Discriminant Analysis | Plot |
| GSP 15000 | LtRamW - SymH - SymBE - MaxL - LtRamH - LtP4H - LtP4B - LtM3H - LtM3B | M | 89.66% | (58) | - | - |
| | LtRamW - SymH - SymBE - MaxL - LtRamH - LtP4H - LtP4B - LtM3H - LtM3B | F | 93.33% | (45) | - | - |
| | RtRamW - SymH - SymBE - MaxL - RtRamH - RtP4H - RtP4B - RtM3H - RtM3B | M | 85.96% | (57) | - | - |
| | RtRamW - SymH - SymBE - MaxL - RtRamH - RtP4H - RtP4B - RtM3H - RtM3B | F | 93.18% | (44) | - | - |
| | LtRamW - SymH - SymBI - MaxL - LtRamH - LtP4H - LtP4B - LtM3H - LtM3B | M | 89.66% | (58) | - | - |

| Fossil | Measurements | Sex | Prediction Power (N) | | Predictions using | |
|---|---|---|---|---|---|---|
| | | | | | Discriminant Analysis | Plot |
| | LtRamW - SymH - SymBI - MaxL - LtRamH - LtP4H - LtP4B - LtM3H - LtM3B | F | 91.11% | (45) | - | - |
| | RtRamW - SymH - *SymBI - MaxL* - RtRamH - RtP4H - RtP4B - RtM3H - RtM3B | M | 87.72% | (57) | - | - |
| | RtRamW - SymH - SymBI - MaxL - RtRamH - RtP4H - RtP4B - RtM3H - RtM3B | F | 95.45% | (44) | - | - |
| GSP 15397 | LtP4H - LtP4B - *LtM3H* | M | 71.21% | (66) | Pan | Pan |
| | LtP4H - LtP4B - *LtM3H* | F | 73.08% | (52) | Pan | Pan |
| GSP 15629 | SymBE | M | 50% | (76) | - | - |
| | SymBE | F | 45.90% | (61) | - | - |
| | SymBI | M | 64.47% | (76) | - | - |
| | SymBI | F | 60.66% | (61) | - | - |

| | | | | | Predictions using | |
|---|---|---|---|---|---|---|
| Fossil | Measurements | Sex | Prediction Power | (N) | Discriminant Analysis | Plot |
| GSP 16077 | LtP3B - LtM3B | M | 58.42% | (69) | Pongo | - |
| | LtP3B - LtM3B | F | 54.72% | (53) | Pongo | - |
| GSP 17125 | RtP3H - RtP3B - RtM3H - RtM3B | M | 78.46% | (65) | Pongo | Pongo |
| | RtP3H - RtP3B - RtM3H - RtM3B | F | 76.47% | (51) | Pongo | Pongo |
| ONGC V 790 | RtP4H - RtP4B - RtM1H - RtM1 B - RtM2H | M | 73.61% | (72) | - | - |
| | RtP4H - RtP4B - RtM1H - RtM1 B - RtM2H | F | 83.64% | (55) | - | - |
| PUA 1047-69 | SymH - SymBE - LtP3H - LtP4H | M | 63.01% | (73) | Pan | - |
| | SymH - SymBE - LtP3H - LtP4H | F | 66.10% | (59) | Pan | - |
| | SymH - SymBI - LtP3H - LtP4H | M | 75.34% | (73) | Pan | - |
| | SymH - SymBI - LtP3H - LtP4H | F | 76.27% | (59) | Pan | - |

| | | | | | Predictions using | |
|---|---|---|---|---|---|---|
| Fossil | Measurements | Sex | Prediction Power | (N) | Discriminant Analysis | Plot |
| YPM 13811 | SymBE - LtP4H - LtM1H - LtM1B - LtM2B - LtM3B | M | 77.94% | (68) | Pan | Pan |
| | SymBE - LtP4H - LtM1H - LtM1B - LtM2B - LtM3B | F | 84.31% | (51) | Pan | Pan |
| | SymBI - LtP4H - LtM1H - LtM1B - LtM2B - LtM3B | M | 83.82% | (68) | Pan | Pan |
| | SymBI - LtP4H - LtM1H - LtM1B - LtM2B - LtM3B | F | 90.20% | (51) | Pan | Pan |
| YPM 13814 | LtP4H - LtP4B | M | 66.22% | (74) | Pan | Pan |
| | LtP4H - LtP4B | F | 65% | (60) | Pan | Pan |

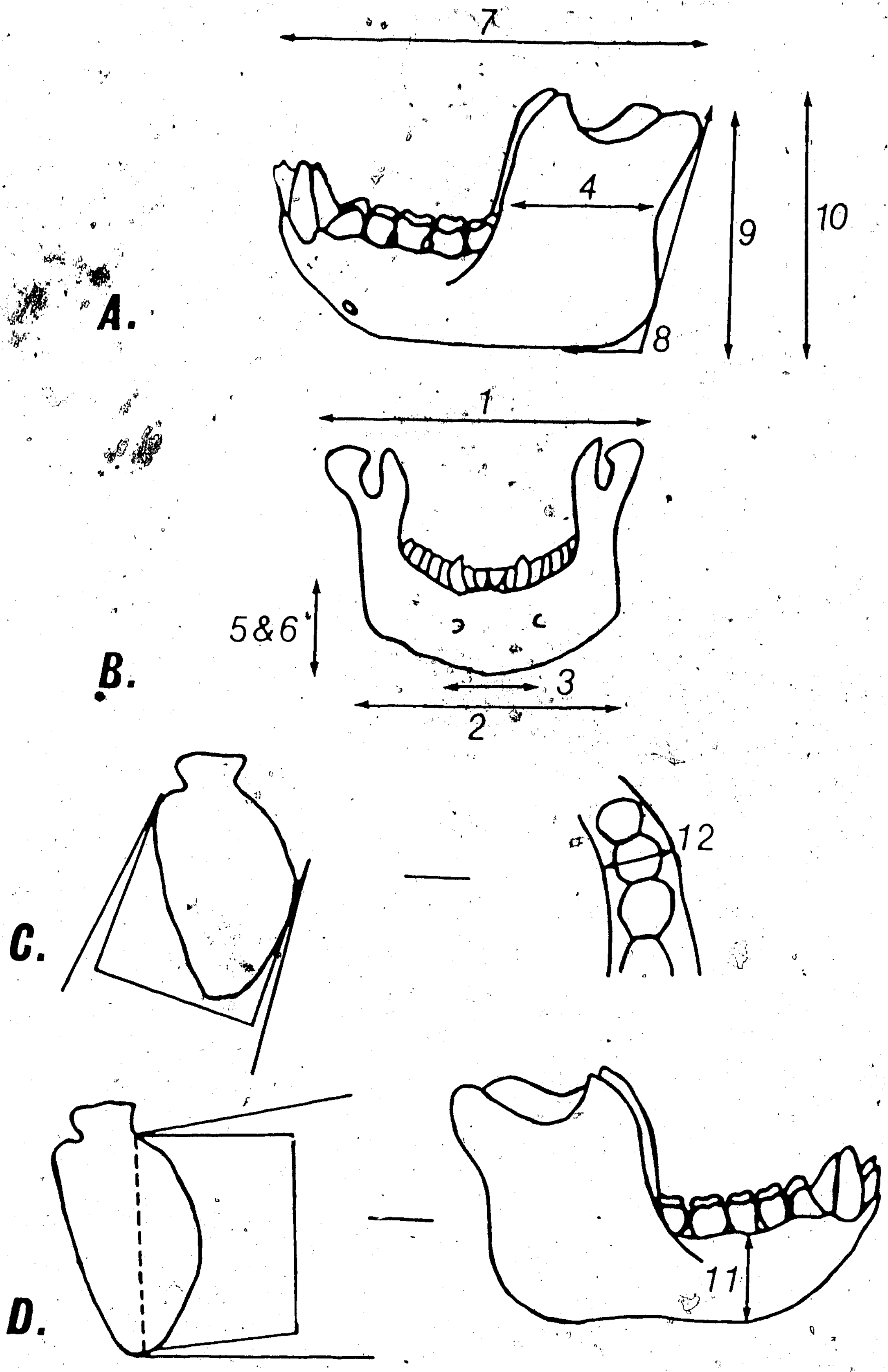
# Figures

Figure 1.

Measurements taken in this study
(adapted from Brothwell 1981:82-84;
Leakey and Leakey 1978:172-73)

Legend

1 - Bicondylar width
2 - Bigonial width
3 - Foramen mentalia width
4 - Minimum ramus width
5 - Symphysis height
6 - Symphysis breadth (external and internal)
7 - Maximum length
8 - Gonial angle
9 - Coronoid process height
10 - Ramus height
11 - Corpus height
12 - Corpus breadth


7
4
9
10
8
A.
1
5&6
B.
3
2
C.
12
D.
11

Species: (identified on vertical axis)

1 - <u>Pongo pygmaeus pygmaeus</u>
2 - <u>Pongo pygmaeus abelli</u>
3 - <u>Pan troglodytes</u>
4 - <u>Gorilla gorilla gorilla</u>
5 - <u>Gorilla gorilla beringei</u>

Sex: m - male
f - female

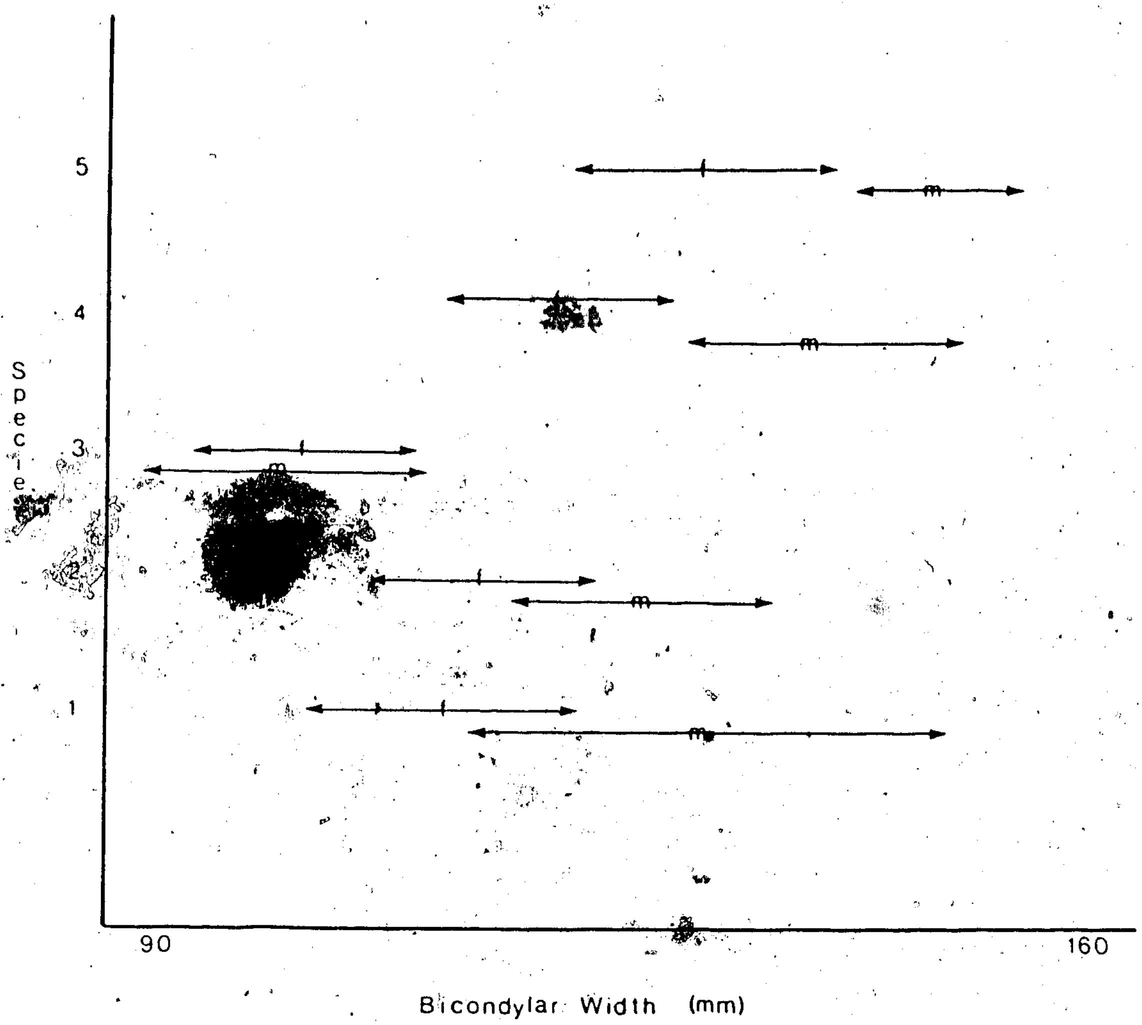
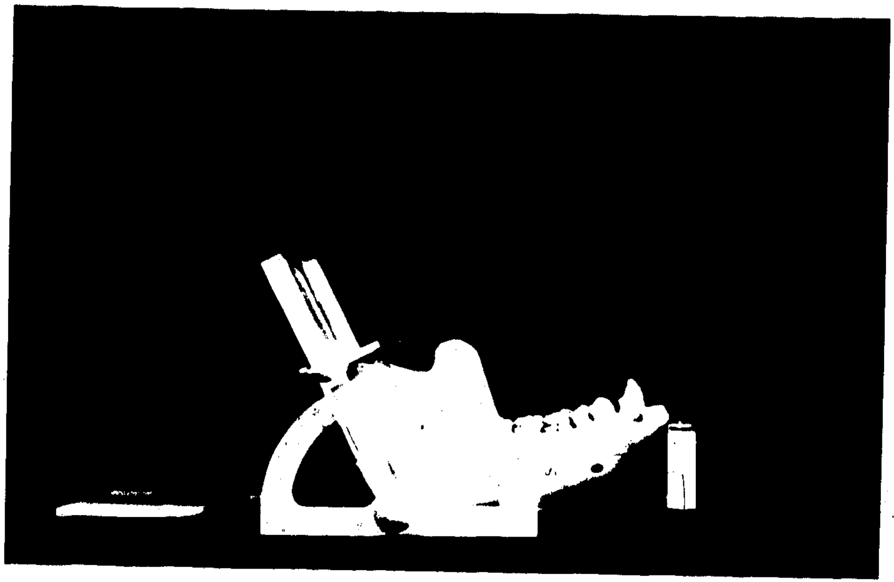


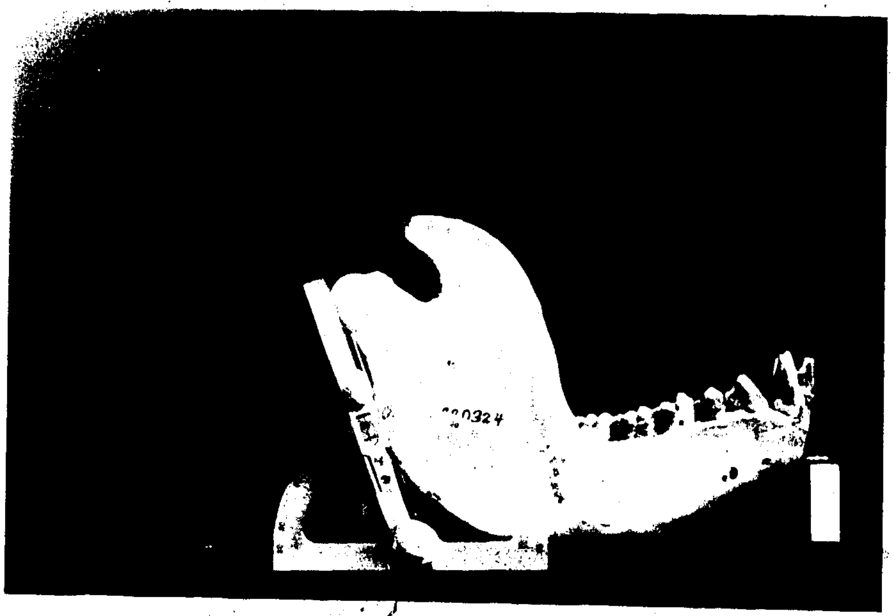
Figure 2. Example of plot graph showing range of morphological variation in extant pongid mandibles between groups, and between sexes

# Photographic plates

Plate 1.

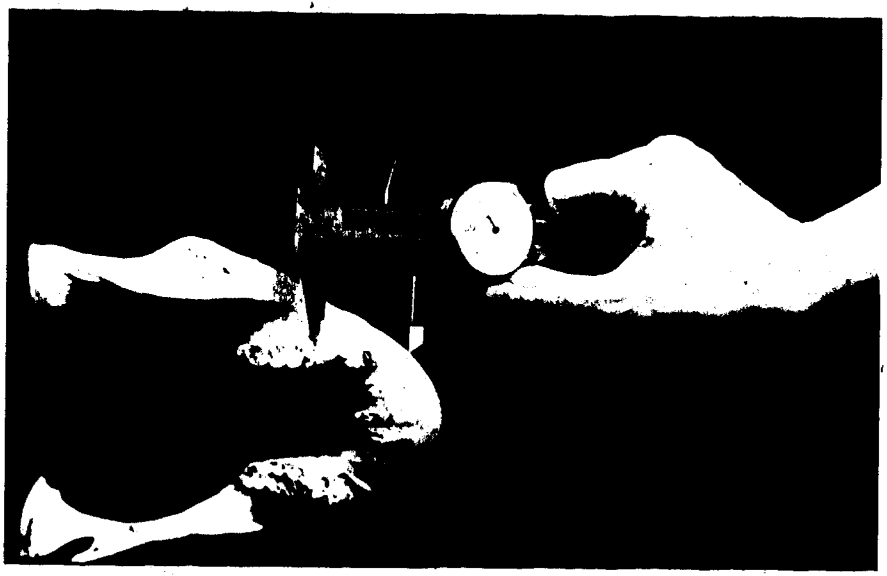


A. Normal fit on goniometer
(Pongo pygmaeus pygmaeus)

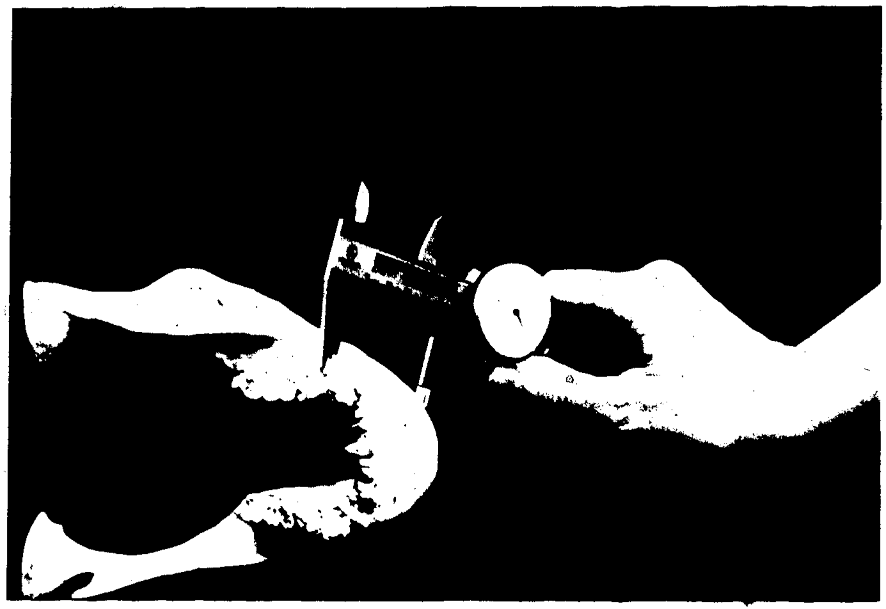


B. Problem fit on goniometer
(Gorilla gorilla gorilla)

Plate 2.



A. Normal corpus height measurement

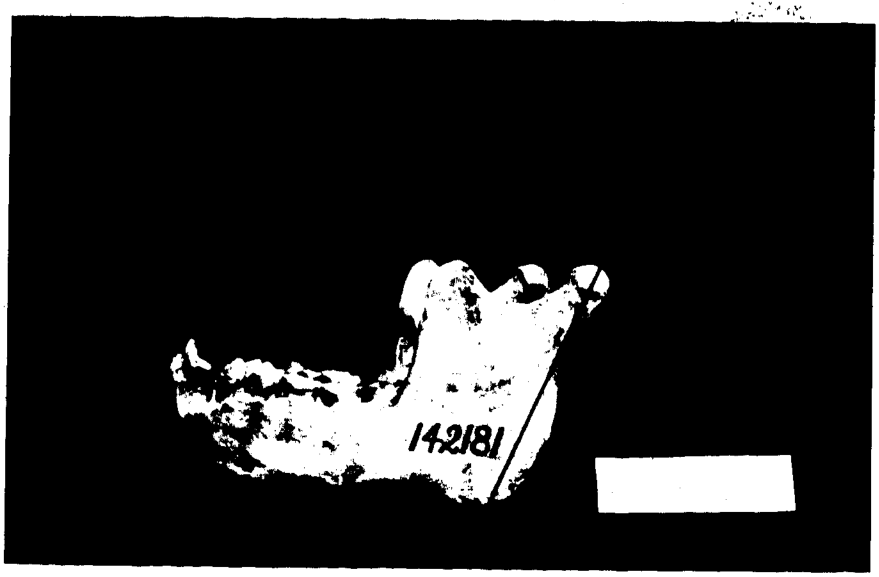


B. Corpus height measurement - taking into account the flattening of the inferior border below P3

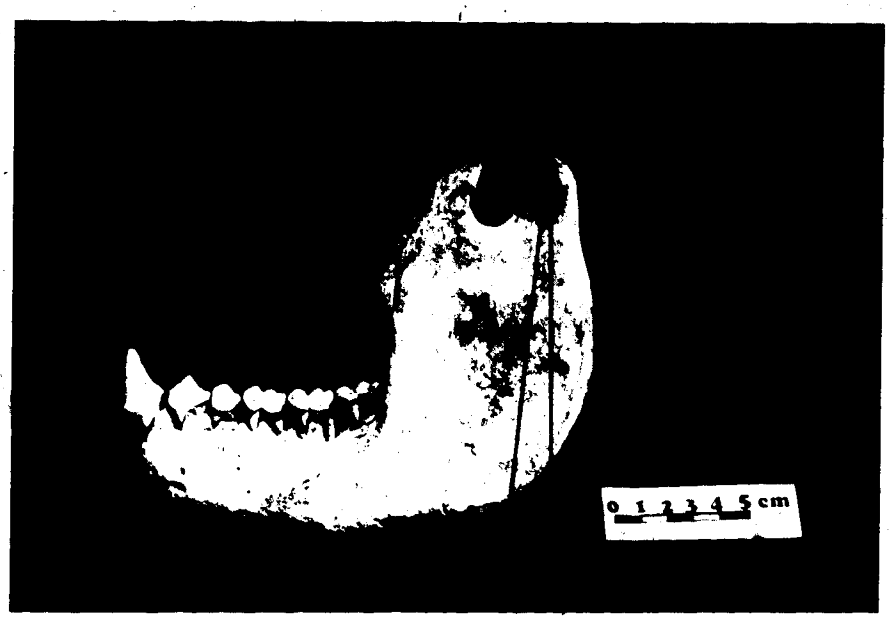
Plate 3.

Photograph illustrating effect of anterior ramal border flaring on corpus breadth measurement of M3

Plate 4.

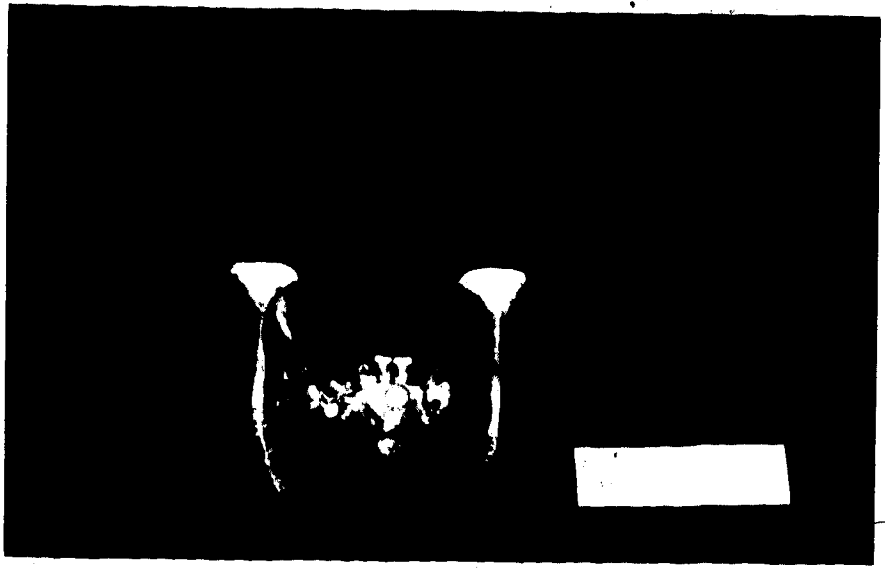


A. Typical orang-utan mandible.
Ramal height takes into account gonial angle

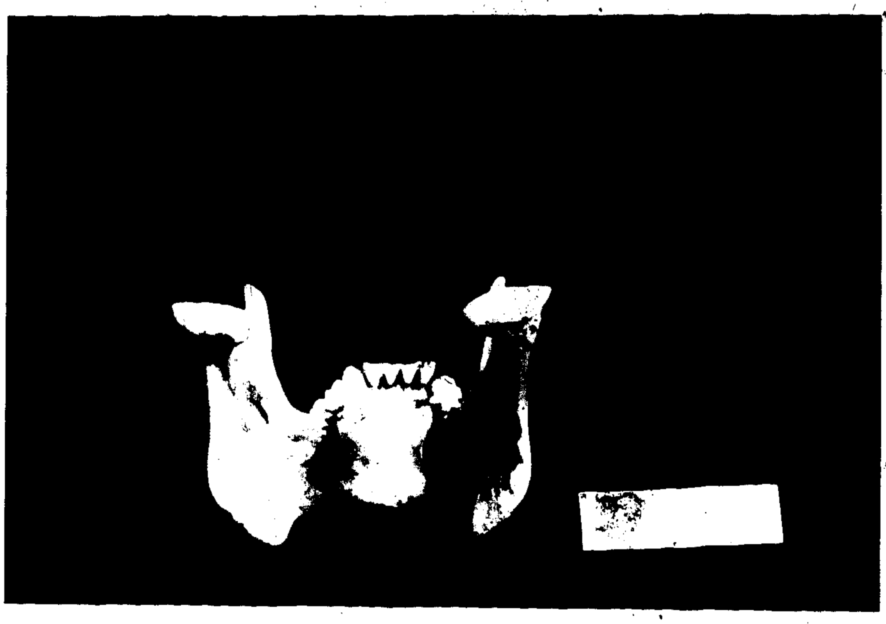


B. Typical gorilla mandible.
Ramal height difficult to measure (a or b)

Plate [illegible].



A. Gonial angle reflecting ramus shape - straight
(*Gorilla gorilla gorilla*)



B. Marked inversion of gonial angle,
excluding ramus shape
(*Pongo pygmaeus pygmaeus*)

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# Appendix 1.

## List of Miocene fossil hominoid mandibular fragments included in this study

Each fossil is anatomically described.

Numerous previous taxonomic classifications for each fossil are also listed.

Measurement variables and values (in millimeters) are presented.

"e" refers to estimated measurement values.

Graecopithecus freybergi

"Bei dem neuen Funde handelt es sich um einen schwer beschadigten Unterkiefer eines alten Individuums; der noch in der Matrix befindlichen Kiefer wurde von mir mir teilweise freigelegt um ein Auseinanderfallen zu verhuten. Beide Mandibelhalften sind vorhanden, rechts P4-M2 (M3 ist abgebrochen), links sind keine Zahne mehr anwesend. Der Symphysenteil ist ganzlich zersplittert. Man erhalt leider den Eindruck, der Kiefer sei erst nach der Entdeckung so schwer beschadigt worden. Die Unterseite des Kiefers ist ebenfalls sehr stark beschadigt; links liegt uber die ganze Lange die Spongiosa frei, rechts ist ein kleiner Teil des Unterrandes zu erkennen" (von Koenigswald 1972:387)

[The hominoid find is a very damaged mandible probably from an elderly individual. Both mandibular halves are present, however there are differences between the sides. The right half includes P4 to M2, with the M3 area broken. The left mandibular half contains no teeth. The symphysis is completely splintered and therefore does not provide a clean break for exact reconstruction.]

| | | |
|---|---|---|
| von Koenigswald | 1972 | Graecopithecus freybergi |
| Andrews and Tekkaya | 1976 | Dryopithecus indicus |

| | | |
|---|---|---|
| Simons | 1976a | Ramapithecus |
| Simons | 1976b | Ramapithecus |
| Simons | 1981 | Ramapithecus |
| Kay | 1982 | Sivapithecus indicus |
| Kay and Simons | 1983 | Sivapithecus indicus |
| Martin and Andrews | 1984 | Sivapithecus meteai (Female?) |

Measurements:

M3 - corpus height (right side): 25
(von Koenigswald 1972)

<u>AMNH</u> <u>19411</u> (cast no. GSI D 193)

"The anterior part of a lower jaw (Amer. Mus. No. 19411), including the symphysis, the alveoli of the incisors, the lower part of both canines and the premolars of both sides; also one condyle" (Gregory/Hellman 1926:26)

| | | |
|---|---|---|
| Brown *et al.* | 1924 | Dryopithecus pilgrimi |
| Gregory and Hellman | 1926 | Dryopithecus pilgrimi |
| Lewis | 1937 | Sivapithecus sivalensis |
| Wadia and Aiyengar | 1938 | Sivapithecus sivalensis |
| Simons and Pilbeam | 1965 | Dryopithecus sivalensis |

| | | |
|---|---|---|
| Pilbeam | 1969b | Dryopithecus |
| Chopra and Kaul | 1975 | Dryopithecus sivalensis |
| Prasad | 1977 | Sivapithecus sivalensis |
| Greenfield | 1977 | Sivapithecus sivalensis |
| Greenfield | 1979 | Sivapithecus sivalensis |
| Kay | 1982 | Sivapithecus sivalensis |
| Kay/Simons | 1983 | Sivapithecus sivalensis |
| Prasad | 1983 | Sivapithecus sivalensis |

Measurements:

Symphysis height (anterior face): e.43 (Gregory and Hellman 1926)

- - 43 (Pilbeam 1969b)

- - 42.6 (Simons and Pilbeam 1965)

Symphysis breadth: 17.8 (Pilbeam 1969b)

17.0 (Simons and Pilbeam 1965)

<u>AMNH</u> <u>19413</u> (cast no. GSI D 195)

"The left half of a mandible (Amer. Mus. No. 19413) lacking the front part but containing P4-M3 in excellent condition" (Gregory and Hellman 1926:27)

| | | |
|---|---|---|
| Brown *et al.* | 1924 | Dryopithecus frickae |
| Gregory and Hellman | 1926 | Dryopithecus frickae |
| Lewis | 1937 | Sivapithecus indicus |
| Wadia and Aiyengar | 1938 | Sivapithecus indicus |
| Simons and Pilbeam | 1965 | Dryopithecus indicus |
| Prasad | 1977 | Sivapithecus indicus |
| Greenfield | 1977 | Sivapithecus indicus |
| Greenfield | 1979 | Sivapithecus indicus |
| Kay | 1982 | Sivapithecus indicus |
| Prasad | 1983 | Sivapithecus indicus |

Measurements:

M3 - corpus height (anterior to tooth): 31 (Gregory and Hellman 1926)

Thickness of jaw in front of root of ascending ramus: 19 (Gregory and Hellman 1926)

BMNH 15423

"Inferiorly, the symphysis is preserved although superiorly the [left] mandible is broken away in front of the roots of P3; posteriorly, the ramus is broken just behind M3 roots. Broken and eroded partial crowns of P4 through M3 are preserved. The first and third molars are in particularly bad condition, having lost their enamel entirely. The roots only of P3 are preserved. The crown of P4 is broken lingually, and heavily worn. Most of the M2 crown is present, although as on P4 the lingual third is missing" (Pilbeam 1969a:1094)

| | | |
|---|---|---|
| Simons | 1964 | Proconsul africanus ? |
| Simons and Pilbeam | 1965 | Dryopithecus laietanus |
| Pilbeam | 1969a | Ramapithecus punjabicus |
| Greenfield | 1974 | Dryopithecus laietanus |
| Conroy and Pilbeam | 1975 | Ramapithecus |
| Greenfield | 1977 | Sivapithecus brevirostris (Female) |
| Greenfield | 1979 | Sivapithecus brevirostris |
| Kay | 1982 | Sivapithecus simonsi |
| Kay and Simons | 1983 | Sivapithecus simonsi |

Measurements:

M2 - corpus height: e.23 (Simons and Pilbeam 1965)

M3 - corpus height: 26.6 (Pilbeam 1969a)

P4 - corpus height: 31 (Pilbeam 1969a)

GSI D 118-119

"The types of the present species are portions of the right and left ramus of the same mandible, the former [GSI D 118] containing M3 with half the broken crown of M2 and the latter [GSI D 119] M2 with the broken crown of M3" (Pilgrim 1915:9)

| | | |
|---|---|---|
| Pilgrim | 1910 | Dryopithecus punjabicus |
| Pilgrim | 1915 | Dryopithecus punjabicus |
| Lewis | 1937 | Bramapithecus punjabicus |
| Wadia and Aiyengar | 1938 | Bramapithecus punjabicus |
| Simons | 1964 | Ramapithecus punjabicus |
| Simons and Pilbeam | 1965 | Ramapithecus punjabicus |
| Prasad | 1969 | Ramapithecus punjabicus |
| Pilbeam | 1969b | Ramapithecus punjabicus |
| Chopra and Kaul | 1975 | Ramapithecus punjabicus |
| Greenfield | 1977 | Sivapithecus sivalensis (Female) |
| Prasad | 1977 | Ramapithecus punjabicus |
| Greenfield | 1979 | Sivapithecus sivalensis |

| | | |
|---|---|---|
| Kay | 1982 | Sivapithecus sivalensis |
| Prasad | 1983 | Ramapithecus punjabicus |
| Prasad (pers. comm.) | 1984 | Ramapithecus punjabicus |

Measurements:

M3 - corpus breadth: 19.8 (Pilgrim 1915)

M2 - corpus height: 23.4 (Pilgrim 1915)

GSI D 177

"....a right mandibular ramus (Ind. Mus. D. 177) from the same locality, containing M1 and M2, PM4, and the broken crowns [illegible] M3 and PM3 with a part of the alveolus of the canine" (Pilgrim 1915:34)

| | | |
|---|---|---|
| Pilgrim | 1915 | Sivapithecus indicus |
| Pilgrim | 1927 | Sivapithecus indicus |
| Lewis | 1937 | Sivapithecus indicus |
| Gregory *et al.* | 1938 | Sivapithecus indicus |
| Wadia and Aiyengar | 1938 | Sivapithecus sivalensis |
| Simons and Pilbeam | 1965 | Dryopithecus indicus |
| Prasad | 1969 | Sivapithecus sivalensis |

| | | |
|---|---|---|
| Prasad | 1977 | Sivapithecus sivalensis |
| Greenfield | 1977 | Sivapithecus sivalensis |
| Kay | 1982 | Sivapithecus indicus |

Measurements:

P4 - corpus breadth: e.15 (Pilgrim 1915)

<u>GSI</u> <u>D</u> <u>197</u>

"Left mandibular ramus" (Prasad 1983:567) "....preserve the symphyseal region and sockets of anterior teeth....preserve left P3 through M2" (Simons and Pilbeam 1971:26)

| | | |
|---|---|---|
| Pilgrim | 1927 | Sivapithecus himalayensis |
| Lewis | 1937 | Sivapithecus indicus |
| Wadia and Aiyengar | 1938 | Sivapithecus indicus |
| Simons and Pilbeam | 1965 | Dryopithecus indicus |
| Prasad | 1969 | Sivapithecus indicus |
| Pilbeam | 1969b | Dryopithecus (Sivapithecus) sivalensis |
| Greenfield | 1977 | Sivapithecus indicus |
| Greenfield | 1979 | Sivapithecus indicus |

| | | |
|---|---|---|
| Kay | 1982 | Sivapithecus indicus |

Measurements:

P3 - corpus height: 32.8 (Pilgrim 1927)

M2 - corpus height: 27.8 (Pilgrim 1927)

P4 - corpus breadth: 14.5 (Pilbeam 1969b)

P4 - corpus height: 35.5 (Pilbeam 1969b)

<u>GSI</u> <u>D</u> <u>199</u>

"....consists of a left mandibular ramus containing P4-M3" (Simons and Pilbeam 1965:90)

| | | |
|---|---|---|
| Pilgrim | 1927 | Paleopithecus sylvaticus |
| Lewis | 1937 | Sivapithecus sivalensis |
| Wadia and Aiyengar | 1938 | Sivapithecus sivalensis |
| Simons and Pilbeam | 1965 | Dryopithecus sivalensis |
| Prasad | 1969 | Sivapithecus sivalensis |
| Pilbeam | 1969b | Dryopithecus (Sivapithecus) sivalensis |
| Simons and Pilbeam | 1972 | Ramapithecus punjabicus |
| Greenfield | 1974 | Dryopithecus sivalensis |
| Prasad | 1977 | Sivapithecus sivalensis |

| | | |
|---|---|---|
| Greenfield | 1977 | Sivapithecus sivalensis (Male) |
| Greenfield | 1979 | Sivapithecus sivalensis |
| Kay | 1982 | Sivapithecus sivalensis |
| Prasad | 1983 | Sivapithecus sivalensis |

Measurements:

P4 - corpus breadth: 13 (Pilbeam 1969b)

<u>GSI</u> <u>D</u> <u>298</u> (cast no. YPM 13870/field no. 618)

"....front part of mandible including right ramus (horizontal) with P3-4, M1-2, and alveoli of C1, I1-2" (Gregory <u>et</u> <u>al.</u> 1938:21)

| | | |
|---|---|---|
| Pilgrim | 1915 | Sivapithecus chinjiensis |
| Gregory <u>et</u> <u>al.</u> | 1938 | Ramapithecus brevirostris |
| Wadia and Aiyengar | 1938 | Ramapithecus cf. brevirostris |
| Simons | 1964 | Proconsul africanus ? |
| Simons and Pilbeam | 1965 | Dryopithecus laietanus |
| Prasad | 1969 | Sivapithecus chinjiensis |
| Pilbeam | 1969b | Ramapithecus punjabicus |

| | | |
|---|---|---|
| Greenfield | 1974 | Dryopithecus laietanus |
| Greenfield | 1977 | Sivapithecus brevirostris |
| Szalay and Delson | 1979 | cf. Sivapithecus sivalensis |
| Kay | 1982 | Sivapithecus simonsi |
| Kay and Simons | 1983 | Sivapithecus simonsi |
| von Koenigswald | 1983 | cf. Ramapithecus |

Measurements:

Vertical diameter of symphysis: e.30 (Simons and Pilbeam 1965)

Max. ant/post width of symphysis: 12 (Simons and Pilbeam 1965)

M2 - corpus height: 22.5 (Simons and Pilbeam 1965)

M2 - corpus breadth: 15 (Simons and Pilbeam 1965)

### GSI D 18039

"....a left mandibular ramus with crowns of P3-M2 (G.S.I. 18039). The incisor alveoli and most of the symphyseal region are present" (Simons and Pilbeam 1965:92)

| | | |
|---|---|---|
| Prasad | 1962 | Sivapithecus aiyengari |
| Simons and Pilbeam | 1965 | Dryopithecus indicus |

| | | |
|---|---|---|
| Prasad | 1969 | Sivapithecus aiyengari/ Sivapithecus indicus |
| Greenfield | 1977 | Sivapithecus indicus |
| Greenfield | 1978 | Sivapithecus indicus (Male) |
| Prasad | 1983 | Sivapithecus indicus |
| Kay and Simons | 1983 | Sivapithecus indicus |
| Prasad (pers. comm.) | 1984 | Sivapithecus indicus |

Measurements:

M2 - corpus breadth: 25 (Prasad 1962, 1967, 1984)

P3 - corpus breadth: e.20 (Prasad 1962, 1967)

GSP 4230

"....consists of part of a right mandible including the corpus and ascending ramus, M2 crown, and M3 root sockets" (Pilbeam *et al.* 1980:9)

| | | |
|---|---|---|
| Pilbeam *et al.* | 1977 | Sivapithecus indicus |
| Pilbeam *et al.* | 1980 | Sivapithecus indicus |
| Kay | 1982 | Sivapithecus indicus |

Measurements:

M3 - corpus height: 30.5 (Pilbeam *et al.* 1977, 1980)

M3 - corpus breadth: 23.5 (Pilbeam *et al.* 1977)
22.8 (Pilbeam *et al.* 1980)

GSP 4622/4857

"....consists of a mandible lacking ascending rami, with the left molars and right M3 intact" (Pilbeam et al. 1980:10)

| | | |
|---|---|---|
| Pilbeam *et al.* | 1977 | Ramapithecus punjabicus |
| Greenfield | 1979 | Sivapithecus (Female) |
| Pilbeam *et al.* | 1980 | Ramapithecus punjabicus |
| Simons | 1981 | Ramapithecus |
| Pickford | 1982 | Ramapithecus punjabicus |
| Kay | 1982 | Sivapithecus sivalensis |
| Kay and Simons | 1983 | Sivapithecus sivalensis |

Measurements:

P4 - corpus breadth: 13 (Pilbeam *et al.* 1977, 1980)
Symphysis height: 31 (Pilbeam *et al.* 1980)
e.30 (Pilbeam *et al.* 1977)
Symphysis breadth: 14.5 (Pilbeam *et al.* 1980)
15 (Pilbeam *et al.* 1977)
M3 - corpus height: 27.3 (Pilbeam *et al.* 1980)
31 (Pilbeam *et al.* 1977)

M2 - corpus breadth: 48 (Pilbeam et al. 1977)

M3 - corpus breadth: 19.5 (Pilbeam et al. 1980)

20 (Pilbeam et al. 1977)

GSP 9563/9902

"...consists of a partial mandible in two pieces, contacting in the region of the right P3. One piece includes the superior part of the right corpus with roots of M3 and P4, and crowns of M1 and M2. The other is a symphyseal portion running to the inferior border, including the crown of P3 and the roots or sockets of the left P4, C, I2, I1, right I1 and I2. Alveoli or roots of the right C and P3 are lost" (Pilbeam et al. 1980:14)

| | | |
|---|---|---|
| Pilbeam et al. | 1977 | Ramapithecus punjabicus |
| Greenfield | 1979 | Sivapithecus (Female) |
| Pilbeam et al. | 1980 | Ramapithecus punjabicus |
| Kay | 1982 | Sivapithecus sivalensis |

Measurements:

Symphysis height: e.33 (Pilbeam et al. 1980)

Symphysis breadth: 17 (Pilbeam et al. 1980)

GSP 9564/9905/9901/9977

"....consists of a mandible lacking the ascending rami, with the crowns of the left P4 through M3 and the roots or sockets of all other teeth" (Pilbeam *et al.* 1980:16).

| | | |
|---|---|---|
| Pickford | 1977 | Sivapithecus indicus |
| Pilbeam *et al.* | 1977 | Sivapithecus indicus |
| Pilbeam *et al.* | 1980 | Sivapithecus indicus |
| Simons | 1981 | Sivapithecus indicus |
| Kay | 1982 | Sivapithecus indicus |
| Kay and Simons | 1983 | Sivapithecus indicus |

Measurements:

P4 - corpus breadth: 15.5 (Pilbeam *et al.* 1977)
16 (Pilbeam *et al.* 1980)
Symphysis height: 52.5 (Pilbeam *et al.* 1977)
52 (Pilbeam *et al.* 1980)
Symphysis breadth: 20 (Pilbeam *et al.* 1977, 1980)
M3 - corpus height: 42.5 (Pilbeam *et al.* 1977)
40 (Pilbeam *et al.* 1980)
M2 - corpus breadth: e.47 (Pilbeam *et al.* 1977)
M3 - corpus breadth: 24 (Pilbeam *et al.* 1977)
26 (Pilbeam *et al.* 1980)

P4 - corpus height: 43.5 (Pilbeam et al. 1977)

43 (Pilbeam et al. 1980)

GSP 11706

"....consists of a right mandibular corpus with molar roots; a tiny portion of M3 enamel remains at the mesiobuccal corner" (Pilbeam et al. 1980:24)

| | | |
|---|---|---|
| Pilbeam et al. | 1977 | Sivapithecus indicus/ Ramapithecus punjabicus |
| Pilbeam et al. | 1980 | Sivapithecus indicus/ Ramapithecus punjabicus |

Measurements:

M1 - corpus height: e.34 (Pilbeam et al. 1980)

M1 - corpus breadth: e.17 (Pilbeam et al. 1980)

M3 - corpus height: e.34 (Pilbeam et al. 1980)

M3 - corpus breadth: e.24 (Pilbeam et al. 1980)

GSP 13165

"....consists of a right mandibular corpus with P4 root and crowns of all three molars. The inferior margin is present from a little mesial to P4 to the mesial part of M2" (Pilbeam et al. 1980:17)

| | | |
|---|---|---|
| Pilbeam et al. | 1977 | Sivapithecus indicus |

| | | |
|---|---|---|
| Pilbeam *et al.* | 1980 | Sivapithecus indicus |
| Kay | 1982 | Sivapithecus indicus |

Measurements:

P4 - corpus breadth: 15 (Pilbeam *et al.* 1977)

M1 - corpus height: e.30 (Pilbeam *et al.* 1980)

M1 - corpus breadth: e.15 (Pilbeam *et al.* 1980)

P4 - corpus height: 34 (Pilbeam *et al.* 1977)

GSP 13566

"....consists of a portion of right mandibular corpus with M2 and M3" (Pilbeam *et al.* 1980:36)

| | | |
|---|---|---|
| Pilbeam *et al.* | 1980 | Sivapithecus indicus |
| Kay | 1982 | Sivapithecus indicus |

Measurements:

M3 - corpus height: 24.5 (Pilbeam *et al.* 1980)

M3 - corpus breadth: 19.5 (Pilbeam *et al.* 1980)

GSP 13808

"....consists of four mandibular fragments, probably from one individual. One piece consists of the inferior portion of a mandibular corpus, representing some 14 of the inferior border. It probably came from a specimen with a shallow robust corpus. Another piece preserves superior parts of the right corpus, and has parts of the crowns of P3 and M1, and the broken roots of P4" (Pilbeam et al. 1980:29)

| | | |
|---|---|---|
| Pilbeam et al. | 1980 | Sivapithecus indicus/ Ramapithecus punjabicus |

Measurements:

M1 - corpus breadth: e.20 (Pilbeam et al. 1980)

GSP 13875

"....consists of an edentulous mandible with right corpus and symphysis to left distal P3. The right ascending ramus is gone. The roots of the right P3 through M2 and of the left P3, and the sockets of the canines and incisors are present (Pilbeam et al. 1980:17)

| | | |
|---|---|---|
| Pilbeam et al. | 1980 | Sivapithecus indicus/ Ramapithecus punjabicus |

Measurements:

Symphysis breadth: 15 (Pilbeam et al. 1980)

Symphysis height: 31.5 (Pilbeam et al. 1980)

P4 - corpus height: 26 (Pilbeam et al. 1980)

P4 - corpus breadth: 13.5 (Pilbeam et al. 1980)

M3 - corpus height (distal): e.23 (Pilbeam et al. 1980)

M3 - corpus breadth (distal): e.19 (Pilbeam et al. 1980)

### GSP 14951

"....consists of a right mandibular corpus with roots of M1 through M3" (Pilbeam *et al.* 1980:37)

| | | |
|---|---|---|
| Pilbeam *et al.* | 1980 | Sivapithecus indicus/<br>Ramapithecus punjabicus |

Measurements:

M3 - corpus height: 21.5 (Pilbeam *et al.* 1980)

M3 - corpus breadth: 16.5 (Pilbeam *et al.* 1980)

### GSP 15000

"....adult, probably male, and consists of most of the left side of the face including a small portion of the frontal bone, the zygomatic arch and temporo-mandibular joint, the maxilla, a virtually entire mandible and the complete dentition" (Pilbeam 1982:232) "Most of the mandible is present, with some breakage, crushing, and distortion. The main damage is at the symphysis where breaking and crushing to the left of the midline obscure some detail. There is internal longitudinal crushing of both corpora, with associated flattening of their inferior border. The left ascending ramus is virtually entire except for the angle, the coronoid process, and part of the condyle; on the right the ascending ramus is less complete, although the angle is present. Overall, to permit accurate reconstruction", (Pilbeam and Smith 1981:4)

| | | |
|---|---|---|
| Pilbeam and Smith | 1981 | Sivapithecus indicus |
| Pilbeam | 1982 | Sivapithecus indicus (Male) |
| Preuss | 1982 | Sivapithecus indicus |
| Kay | 1982 | Sivapithecus indicus |
| Kay and Simons | 1983 | Sivapithecus indicus |

Measurements:

P4 - corpus height: 37 (Pilbeam 1982;
Pilbeam and Smith 1981;
Preuss 1982)

P4 - corpus breadth: 16 (Pilbeam 1982;
Pilbeam and Smith 1981)

14.3 (Preuss 1982)

M3 - corpus height: 34 (Pilbeam 1982;
Pilbeam and Smith 1981;
Preuss 1982)

M3 - corpus breadth: 28.5 (Pilbeam 1982;
Pilbeam and Smith 1981)

26.7 (Preuss 1982)

Ramus height: 108 (Pilbeam 1982;
Pilbeam and Smith 1981)

Ramus width: 60 (Pilbeam 1982;
Pilbeam and Smith 1981)

Symphysis height: e.42 (Pilbeam 1982;
Pilbeam and Smith 1981)

e.44 (Preuss 1982)

Symphysis breadth: e.20 (Pilbeam 1982;
Pilbeam and Smith 1981)

e.21 (Preuss 1982)

Mandibular length ("horizontal distance from most anterior point to posterior border of ramus" Preuss 1982:148): e.130 (Preuss 1982)

GSP 15397

"The specimen is an edentulous left mandibular corpus, broken in the region of I2....details of the symphyseal region are lost, and there is damage to the alveolar region" (Pilbeam *et al.* 1980:38)

Pilbeam *et al.* 1980 Sivapithecus indicus/ Ramapithecus punjabicus

Measurements:

P4 - corpus height: e.29 (Pilbeam *et al.* 1980)

P4 - corpus breadth: e.13.5 (Pilbeam *et al.* 1980)

M3 - corpus height: e.28.5 (Pilbeam *et al.* 1980)

M3 - corpus breadth: e.14 (Pilbeam *et al.* 1980)

GSP 15629

"....consists of a symphyseal fragment with the sockets of the canines, incisors, and right P3, and the right P4 root" (Pilbeam *et al.* 1980:38)

Pilbeam *et al.* 1980 Sivapithecus indicus/ Ramapithecus punjabicus

Measurements:

Symphysis height: e.35 (Pilbeam *et al.* 1980)

Symphysis breadth: e.18 (Pilbeam *et al.* 1980)

GSP 16077

"....left corpus complete from midline to third molar" (Raza *et al.* 1983:52)

| | | |
|---|---|---|
| Kay | 1982 | Sivapithecus sivalensis |
| Raza *et al.* | 1983 | Ramapithecus punjabicus |

Measurements:

M3 - corpus height: 19.8 (Raza *et al.* 1983)

M3 - corpus breadth: 22.5 (Raza *et al.* 1983)

P3 - corpus height: 26.5 (Raza *et al.* 1983)

P3 - corpus breadth: 13.7 (Raza *et al.* 1983)

GSP 17125

"....right corpus, broken obliquely through the symphysis, lacking the tooth crowns but with the roots of the canine to the third molar" (Raza *et al.* 1983:52)

| | | |
|---|---|---|
| Raza *et al.* | 1983 | Sivapithecus indicus ? |

Measurements:

M3 - corpus height: 30.6 (Raza *et al.* 1983)

M3 - corpus breadth: 24.2 (Raza *et al.* 1983)

P3 - corpus height: 38.5 (Raza et al. 1983)

P3 - corpus breadth: 16.2 (Raza et al. 1983)

ONGC V 790

"....a broken right ramus which has been regarded as the holotype. It extends from very near the symphysis to slightly behind M1 whereupon the teeth are situated without any diastema. At the front end of the mandible a deep scraping has removed a considerable part, leaving the hinder end of the alveolus of last incisor (I2) and damaging the antero-external part of the canine root. The crown of canine is missing. The crown of P3 has been broken away and in P4 it is intact. The enamel, however, in the latter was not preserved all over the crown except at the postero-internal corner; but the dentine is fully preserved without any damage and the shape of the crown can be easily made out. The crown of M1 lacks enamel on the lingual side. The dentine, however, is nearly undamaged and the cusps can be easily ascertained. A deep vertical fracture delimits nearly the whole of the mandible behind M1, except in the basal portion, where a part of ramus opposite to M2 is preserved due to the slant nature of the above mentioned fracture." (Pandey and Sastri 1968:207)

| | | |
|---|---|---|
| Pandey and Sastri | 1968 | Sivapithecus lewisi |

| | | |
|---|---|---|
| Prasad | 1969 | Sivapithecus indicus |
| Andrews and Tekkaya | 1976 | Dryopithecus indicus |
| Prasad | 1977 | Sivapithecus |
| Szalay and Delson | 1979 | Sivapithecus indicus |
| Kay | 1982 | Sivapithecus indicus |
| Prasad | 1983 | Sivapithecus indicus |
| Kay/Simons | 1983 | Sivapithecus indicus |
| Prasad (pers. comm.) | 1984 | Sivapithecus indicus |

Measurements:

P4 - corpus breadth (maximum): 19 (Pandey and Sastri 1968)

P4 - corpus height (maximum): 42 (Pandey and Sastri 1968)

M1 - corpus breadth (maximum): 20 (Pandey and Sastri 1968)

M1 - corpus height (maximum): 37.5 (Pandey and Sastri 1968)

M2 - corpus height (maximum): 35 (Pandey and Sastri 1968)

### PUA 1047-69

"The [left] mandibular fragment consisting of P3, P4 partly broken incisors, a canine and the isolated lower left M1" (Chopra 1978:4)

| | | |
|---|---|---|
| Chopra and Kaul | 1975 | Dryopithecus sivalensis |
| Chopra | 1978 | Dryopithecus sivalensis |
| Kay | 1982 | Sivapithecus sivalensis |
| Chopra | 1983 | Sivapithecus sivalensis |

Measurements:

P3 - corpus height (left side): 33.5 (Chopra 1983; Chopra and Kaul 1975)

P4 - corpus height (left side): 32.2 (Chopra 1983; Chopra and Kaul 1975)

Symphysis height: 40.4 (Chopra and Kaul 1975)

Symphysis breadth: 15.9 (Chopra and Kaul 1975)

<u>YPM 13811</u> (cast no. GSI D 294)

"....imperfect left corpus of a young adult (or nearly adult) and probably female lower jaw, with three perfect teeth (PM2, M1, M2) the whole roots of three others (C, PM1, M3), and a small portion of the root of the lateral incisor" (Hrdlicka 1935:37)

| | | |
|---|---|---|
| Lewis | 1934 | Sugrivapithecus salmontanus |
| Lewis | 1937 | Sugrivapithecus salmontanus |
| Wadia and Aiyengar | 1938 | Sugrivapithecus salmontanus |

| | | |
|---|---|---|
| Simons and Pilbeam | 1965 | Dryopithecus sivalensis (Female) |
| Pilbeam | 1969b | Dryopithecus (Sivapithecus) sivalensis |
| Chopra and Kaul | 1975 | Dryopithecus sivalensis |
| Greenfield | 1977 | Sivapithecus sivalensis |
| Greenfield | 1978 | Sivapithecus sivalensis (Female) |
| Greenfield | 1979 | Sivapithecus sivalensis (Female) |
| Kay | 1982 | Sivapithecus sivalensis |
| Prasad | 1983 | Sivapithecus sp. indet. |
| Kay/Simons | 1983 | Sivapithecus sivalensis |

Measurements:

Symphysis breadth (maximum): 13.6 (Hrdlicka 1935)

M1 - corpus height: 25.6 (Simons and Pilbeam 1965)

P4 - corpus height: 26 (Pilbeam 1969b)

P4 - corpus breadth: 11.5 (Pilbeam 1969b)

M1 - corpus breadth (middle of tooth): 13 (Hrdlicka 1935)

M2 - corpus breadth (middle of tooth): 16 (Hrdlicka 1935)

M3 - corpus breadth (middle of tooth): 19
(Hrdlicka 1935)

18.6
(Simons and Pilbeam 1965)

YPM 13814 (cast no. GSI D.295)

"The left ramus bearing M3, M2, the alveolus and roots of M1, and a portion of the alveolus and root of P4" (Lewis 1934:173)

| | | |
|---|---|---|
| Lewis | 1934 | Bramapithecus thorpei |
| Lewis | 1937 | Bramapithecus thorpei |
| Wadia and Aiyengar | 1938 | Bramapithecus thorpei |
| Simons | 1964 | Ramapithecus punjabicus |
| Simons and Pilbeam | 1965 | Ramapithecus punjabicus |
| Prasad | 1969 | Ramapithecus punjabicus |
| Pilbeam | 1969b | Ramapithecus punjabicus |
| Greenfield | 1977 | Sivapithecus brevirostris |
| Greenfield | 1979 | Sivapithecus brevirostris |
| Kay | 1982 | Sivapithecus sivalensis |
| Prasad | 1983 | Ramapithecus punjabicus |

Measurements:

P4 - corpus height: 27.5 (Pilbeam 1969b)

P4 - corpus breadth: 12.5 (Pilbeam 1969b)