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The Mysterious Phylogeny of Gigantopithecus

Perhaps the most questionable attribute given to *Gigantopithecus* is its taxonomic and phylogenetic placement in the superfamily Hominoidea. In 1935 von Koenigswald made the first discovery of a lower molar at an apothecary in Hong Kong. In a mess of "dragon teeth" von Koenigswald saw a tooth that looked remarkably primate-like and purchased it; this tooth would later be one of four looked at by a skeptical friend, Franz Weidenreich. It was this tooth that von Koenigswald originally used to name the species *Gigantopithecus blacki.* Researchers have only four mandibles and thousands of teeth which they use to reconstruct not only the existence of this primate, but its size and phylogeny as well.

Many objections have been raised to the past phylogenetic relationship proposed by Weidenreich, Woo, and von Koenigswald that *Gigantopithecus* was a forerunner to the hominid line. Some suggest that researchers might be jumping the gun on the size attributed to *Gigantopithecus* (estimated between 10 and 12 feet tall); this size has perpetuated the idea that somehow *Gigantopithecus* is still roaming the Himalayas today as Bigfoot. Many researchers have shunned the Bigfoot theory and focused on the causes of the animals extinction. It is my intention to explain the theories of the past and why many researchers currently disagree with them. It will be necessary to explain how the researchers conducted their experiments and came to their conclusions as well.

The Research

The first anthropologist to encounter *Gigantopithecus* was von Koenigswald who happened upon them in a Hong Kong apothecary selling "dragon teeth." Due to their large size one may not even have thought that they belonged to any sort of primate, however von Koenigswald knew better because of the markings on the molar. In 1981 von Koenigswald described again the shape of the molar he came upon and wrote about in 1935.

> This tooth, larger than a gorilla's and the larger orangutan teeth, is markedly different from the orangutan teeth of the same drugstore. The tooth is higher, there are no wrinkles, and the cusps must have been depressed but are rather high and swollen. This unusual type must have belonged to an as-yet-unknown higher primate. (von Koenigswald 1935; von Koenigswald 1981: 38).

Based on his previous knowledge of what tooth characteristics set the anthropoids apart from other primates von Koenigswald named the species *Gigantopithecus blacki* von Koenigswald. The suffix -pithecus in the name *Gigantopithecus* implies that von Koenigswald believed that tooth belonged to a primate and more specifically to an anthropoid (1981).

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There were others that von Koenigswald discussed his finds with, but they presumed by his description of the tooth that it belonged to a giant orangutan (von Koenigswald 1981). In 1944 when Weidenreich was able to look at the teeth (by that time von Koenigswald had acquired 3 more) he was able to discern, even though all they had to use in their calcula-tions were the lower and upper molars, that "*Gigantopithecus* considerably exceeded *Meganthropus in size and robustness*" (Weidenreich 1944: 481).

Aside from the general size estimation made about *Gigantopithecus* Weidenreich carefully examined the occlusal surface noting in particular the pattern similarities found in *Gigantopithecus* and in modern humans. What he noticed was that:

> The patterns of the two third lower molars and that of the upper one are identical with the corresponding pattern of any hominid tooth, including modern man, not only with regard to their general character, but also to minute details; and they are to the same degree quite different from any known recent fossil anthropoid (Weidenreich 1945: 124).

With this information Weidenreich was able to extrapolate information from the teeth that indicated a probable phylogenetic relationship for *Gigantopithecus* in Hominoidea.
It seems that most of the research done on *Gigantopithecus* was done in the early part of this century, and the conclusions drawn from these studies were generally accepted. It was however very important to determine the placement of *Gigantopithecus* in the geologic time scale to get an idea of its diet and possibly more insight into its proper placement in the anthropoid lineage. Dirk Hooijer was able to determine its placement by looking at other fossilized tooth descriptions from the drug store in which von Koenigswald bought the teeth. "The associated fauna strongly suggests the so-called *Stegodon-Ailuropoda* fauna from southern China" (Hooijer 1951: 276). The fauna found with the teeth suggests a time period during the Middle Pleistocene. This knowledge lead him to believe that *Gigantopithecus* was roaming the landscape sometime during the Middle Pleistocene therefore a contemporary of *Stegodon-Ailuropoda*.

Much of this information went unchanged until in the late 1960's when a mandible was found. It wasn't quite as large as the three other *Gigantopithecus* mandibles that had been found earlier, which indicated to researchers that they may have found another genus of primate or possibly another species of *Gigantopithecus*. What they discovered was later determined to be a new species, and it was named *Gigantopithecus bilaspurensis*. This discovery opened new doors to the phylogenetic placement of *Gigantopithecus* because not only was it smaller than *G. blacki* v.K. and found in India, but it has been determined to come from the middle Pliocene. This lead to the reexamination of old research done on *Gigantopithecus* to review the old phylogenies and reconstruct new ones.

Simons and Chopra were intricately involved with the discovery of *G. bilaspurensis* and the subsequent revising of the work done by von Koenigswald, Weidenreich, and Woo earlier this century. They too looked at the teeth for some phylogenetic clue and what they discovered was rather interesting. The canines were not the projecting and dimorphic ones that is expected in a good ape, they were reduced considerably; speculation suggests that this has something to do with diet and a specialization of the teeth for the purpose of grinding. Another deviation from what one would expect to find in the great apes is the form of the P_3

and P_4. The shape of the P_3 "does not exhibit an anterio-lateral extension for sectorial or sharpening action against the posterior wear facet of the upper canine" (Simons and Chopra 1969a: 12). In fact even the P_4 has some peculiarities to it ". . . the trigonid portion of the P_4 is greatly expanded while the talonid is much reduced over what is typical of apes" (Simons and Chopra 1969a: 12). On the other hand, Simons and Chopra note, the molars (M_1-M_3) appear to have a primitive form found in most pongids, where the molars increase in size in breadth and length posteriorly (1969a).

The discovery of *G. bilaspurensis* by Simons and Chopra has opened up, again, the question of the phylogenetic positioning of *Gigantopithecus* to many researchers. David Pilbeam looked as the jaw of *Gigantopithecus* to help visualize some of the phylogenetic connotations found in some specific characteristics. By looking at the buttressing at the mandibular symphysis he noted that "The symphysis was strongly buttressed by superior and inferior transverse tori" (1970: 518). This statement suggests that *Gigantopithecus* possessed an incipient simian shelf or possibly a full simian shelf a characteristic normally associated with the great apes. He made mention of the size of the canines being reduced, as mentioned by Simons and Chopra, however, he went further to say that the ". . . canines were reduced like those of Hominidae (and *Oreopithecus*) they were not incisiform slicing teeth like those of hominids"(Pilbeam 1970: 518).

By looking at the teeth and jaws Pilbeam was able to use a theory brought about by Clifford Jolly in 1966 when discussing the differences in the "dental, mandibular and facial adaptations of the gelada baboons (*Theropithecus*) . . . from those of other baboon (*Papio*)" (Pilbeam 1970: 518). The theory suggests that the differences found in *Theropithecus* came about because of a specialized diet. This lead Pilbeam (1970) to believe that the short deep face of *Gigantopithecus* could be attributed, like *Theropithecus*, *Ramapithecus*, and *Australopithecus* to a need for the powerful mastication mechanisms needed for its proposed diet of bamboo. This terrestrial diet would explain the very worn occlusal surface of *Gigantopithecus*' teeth as well as its robust mandible.

Aside from visually identifying physical attributes of *Gigantopithecus* researchers have conducted numerous versions of multivariate experiments using measurements of the teeth to determine alternative phylogenetic relationships. The idea behind a multivariate experiment is to determine which groups cluster around each other, or in other words which are close enough to imply a phylogenetic relationship. Three important multivariate experiments were conducted by Robinson and Steudel (1973), Corruccini (1975), and Gelvin (1980), each refuting the other, but all very important.

Robinson and Steudel used the multivariate technique to determine the separation between the different groups that they looked at: *Pan, Pongo,* and *Gorilla* including fossil samples of *H. erectus, A. africanus, Paranthropus, G. bilaspurensis,* and *G. blacki* (1975). They chose to keep "the most frequently preserved representative of the anterior dentition, the canine. In addition the sequence *P3-M1* was retained to represent the posterior teeth"(Robinson and Steudel 1973: 573). In this analysis they used measurements that covered the mesio-distal length and bucco-lingual breadth to determine a plausible relationship. What they discovered was that "all four figures show a distinct separation between hominids and pongids, except for the intermediate *G. blacki*"(Robinson and Steudel 1973: 515).

Corruccini as well used multivariate analysis techniques to determine the phylogeny of *Gigantopithecus* comparing his results with others that had done the experiments. He was able to reduce the number of specimens used by excluding the M_3 lengths because they are not present in every *Gigantopithecus* (Corruccini 1975). *Australopithecus* specimens with more than half of the measurements missing were also excluded. However, this did leave the researchers with 17 variables to work with: "bicanine breadth, symphyseal height, corpus height and width, P_4 - M_2 chord, and the length and breadth of I_2 through M_2"(Corruccini 1975: 167). The specimens were separated out by sex as well as by species therefore eliminating the major problem than Corruccini had with Robinson and Steudel's (1973) multivariate experiment, stating that it "can be objected to on the basis of their failure to separate considerations of size and shape. Thus they analyze raw dental measurements, and the results, expectably, are dominated by size" (Corruccini 1975: 169).

One other influential multivariate analysis was conducted by Gelvin in 1980 where he looked at Neogene fossil apes (*Proconsul africanus, P. nyanzae, P. major, Dryopithecus laietanus, Ouranopithecus macedoniensis, Sivapithecus indicus and S. Sivalensis)*, *Gigantopithecus,* and fossil hominids (gracile, robust, and hyper-robust Plio-Pleistocene hominids, and *Homo erectus*). Fossils primates were used instead of extant primates because Gelvin believes that "taxonomic studies of fossils are more effectively performed if their affinities are assessed in the context of other phylogenetically related fossils rather than extant forms (Conroy, 1972; Oxnard, 1972)" (Corruccini 1975: 542). The results that were obtained from the multivariate analysis place *Gigantopithecus* in a cluster with *Australopithecus*, *Homo erectus,* and *Ouranopithecus macedoniensis*. However in one of the canonical variates (canonical variate II) *G. blacki* is separated from the hominids, however, *G. bilaspurensis* was not (Corruccini 1980).

Conclusions of Researchers

In the beginning, von Koenigswald truly believed he had found an anthropoid and as of yet no one has considered that presumption false. What researchers today have a problem with stems from the fact that new information has come about since von Koenigswald considered *Gigantopithecus* to be a hominid. However, in 1981 he wrote ". . . the teeth are too overspecialized to fit into the *Homo* line." (von Koenigswald 1981: 39). He hasn't allowed himself to be fully drawn into some of the newly proposed phylogenetic proposals such as classifying *Ramapithecus* together with *Sivapithecus*, and *Gigantopithecus* as a whole under Ramapithecidae. His feeling is that what has been uncovered about *Ramapithecus* does not lent itself to any "conclusive interpretations" (von Koenigswald 1983: 525).

Weidenreich also came to the same conclusion as did von Koenigswald, he wrote that *Gigantopithecus* should be placed as a hominid because in his opinion the most primitive state was gigantism and not dwarfism. Dwarfism being the most common primitive form of many mammals, Weidenreich proposes his idea based on the fact that ". . . living pygmies do not possess any true primitive features which make them different from taller races; nor do they represent a uniform morphological group, as the theory demands" (Weidenreich 1946: 47).

Simons and Ettel cite that Weidenreich "concluded that they evolutionary line leading to modern man must have run from *Gigantopithecus* by way of *Meganthropus* to *Pithecanthropus* and then to modern *Homo sapiens*" (Simons and Ettel 1970: 77). This supports Weidenreich's theory that giants predated dwarfs in the hominid line, and one can infer from this proposed phylogeny that Weidenreich believed that *Gigantopithecus* was a hominid.

Currently there are few researchers who believe that *Gigantopithecus* was a precursor to modern humans, and tend to place it in Hominoidea by way of the Pongidae. One of Pilbeam discoveries on the jaw of *Gigantopithecus* was transverse tori which would indicate a possibility of a simian shelf, which is found in the great apes, members of the Pongidae. Pilbeam and Simons (1965) believes that orangutans, chimps, and gorillas should be placed in Pongidae as well as *Dryopithecus* and *Gigantopithecus.* His proposed phylogenetic sequence is: "*Dryopithecus indicus* (Late Miocene)_ *D. giganteus* (Early Pliocene)_ *G. bilaspurensis* (Middle Pliocene)_ *G. blacki* (Middle Pleistocene)" (Pilbeam 1970: 517). It is fairly evident from his research and proposed phylogenetic relationship that Pilbeam believes that *Gigantopithecus* is a aberrant pongid (Pilbeam 1970).

Simons (1960) suggested that because of similarities in the relationship of mandible to tooth size, and other tooth characteristics, there was a possibility of a relationship between *Oreopithecus* and *Gigantopithecus* (Simons and Chopra 1969a). Simons and Chopra (1969b) created a tentative phylogeny for *Gigantopithecus.* That *Gigantopithecus* probably deserves to be kept in the family Pongidae, and seen as a specialized branch which had in the past been suggested by von Koenigswald (1935) and by Simons and Pilbeam (1965). However, "HERBERER [1959], DART [1960], and JU-KANG WOO [1962] have taken the position that *Gigantopithecus* is a hominid . . ."(Simons and Chopra 1969b: 141). Simons and Chopra (1969b) attribute this proposed phylogeny (Dart, Herberer, and Woo) to the terrestrial adaptations that both *Gigantopithecus* and *Australopithecus* have developed.

Others that believe the placement of *Gigantopithecus* belongs in Pongidae are Martin (1990) who suggests *Gigantopithecus* is part of the radiation that occurred during the Miocene that developed into the thick enameled great apes "from which the human lineage may have diverged at some point" (Martin 1990: 82). Simons and Ettel (1970) propose that *Gigantopithecus* is a side branch of pongid evolution which includes a "line of enormous apes that became increasingly adapted to a specialized mode of feeding" (Simons and Ettel 1970: 85).

Those that did the multivariate analysis research came to many different conclusions about the phylogeny of *Gigantopithecus.* Robinson and Steudel (1973) proposed that the phylogeny of *Gigantopithecus* was somewhere between pongids and hominids, however they feel that *Paranthropus* is probably the closest to it. This conclusion was made because their results in one analysis show that the *Gigantopithecus* tooth row pattern more closely follows that of *Paranthropus*, except the degree of anterior tooth reduction is greater in *Paranthropus* (Robinson and Steudel 1973). What Corruccini (1975) discovered was that "*Gigantopithecus bilaspurensis* is maximally separated from hominids on the second coordinate, and is approached more closely by *Pongo*" (Corruccini 1975: 170). This suggests he feels *Gigantopithecus* is more closely related to the great apes than to humans. Gelvin (1980) used

different tactics to determine the phylogeny of *Gigantopithecus*, by utilizing fossil data, and not data from extant primates. His conclusions suggest that "dentally *Gigantopithecus* is a hominid or is closely related to hominids"(Gelvin 1980: 560).

Discussion

It seems like an incredible task to try and unearth the phylogeny of a primate that we only have four jaws and thousands of teeth. From the collection researchers have the ability to examine both upper and lower teeth (albeit mostly molars). It is true that you can learn a lot about an animal, especially a primate, by its dentition. The dentition of primates by the Pliocene and Pleistocene had become basically what we see today, for Platyrrhines and Prosimians the dentition is normally 2-1-3-3 (of course there are exceptions), but for Catarrhines the dental formula is *always* 2-1-2-3. By looking at the mandibles and especially the alveoli the researcher can count the number of teeth and determine the taxonomic placement of the primate. In the case of *Gigantopithecus* the dental formula is 2-1-2-3. By determining this all anyone can state is that the dental formula tells us it is a Catarrhine. Looking at the occlusal surface of the molars and the incisors can aid researchers in a taxonomic placement. If the teeth were truly bilophodont (or incipient bilophodont) one could make the assumption that this was not a hominoid, but a cercopithecoid. In the molar sample for *Gigantopithecus* the occulsal surface of the teeth are well worn down from grit in their terrestrial diet of bamboo. However, researchers are still able to discern the complex patterns of the teeth and have determined them to be hominoid like. What does this tell us? That we have a hominoid. The next task is to determine which family *Gigantopithecus* belongs to: Hylobatidae, Pongidae, or Hominidae.

We can exclude the hylobates (gibbons and siamangs) because the largest are about 11 kg and they lack any sexual dimorphism (Fleagle1988). From what researchers can deduce about *Gigantopithecus*' is that it was similar or larger to that of modern gorillas which is considerably larger than the hylobates. The morphology of the mandible can be used to rule out hylobates because *Gigantopithecus* has a parabolic arcade whereas the hylobates have a slight flaring posteriorly. The teeth of the are as well different in the hylobates than in *Gigantopithecus*, for the molars of *Gigantopithecus* are very complex, while the molar teeth of the hylobates are rather simple with low rounded cusps and broad basins (Fleagle 1988), not seen in the *Gigantopithecus* sample.

Before trying to place *Gigantopithecus* in either the Pongids or Hominids one must consider what makes them different from each other. However, even by doing this it would still shed little light on where *Gigantopithecus* fits in, because the differences are more associated with the post cranial skeleton than with the teeth and mandible. However, there is one distinguishing feature. Great apes have a simian shelf located as extremely robust transverse inferior and superior tori. This exaggeration of the tori is not seen in hominids and can be considered a pongid characteristic.

As far as dental characteristics of pongids are concerned they differ among the species. Fleagle (1988) describes the dentition of the orangutan as having cheek which teeth are thickly

enameled and have a crenulated occlusal surface with low, flat cusps. The lateral upper incisors are peg-like, whereas the medial incisors are broad. The canines are described as being sexually dimorphic. On the other hand, the gorilla has thinly enameled molar teeth which have high cusps. Their canines, as well, are large and robust and incisors relatively small. The size of the gorilla and orangutan and the similarities in the parabolic arcade of the jaw lend themselves to having *Gigantopithecus* considered a pongid, as opposed to a hominid.

Hominids are truly characterized by their mode of locomotion, bipedalism. If it were possible to show that *Gigantopithecus* was a biped than it would be easier to place it in this family. In some of the multivariate experiments australopithecines were shown to be similar in tooth form to *Gigantopithecus* but all they really were able to say was, noted by Corruccini (1975), that *Gigantopithecus* was closer to one than to the other. This does not imply certain affiliation with the australopithecines or the gorilla. In some cases sexual dimorphism of males and females was ignored thereby altering the results in a way that might give a false impression of a relationship. There are many reasons why some researchers would place *Gigantopithecus* in the hominid line: the non-sectorial anterior premolar, the bicuspid upper and posterior premolars, the non-projecting canines (with little or no dimorphism in shape), and the thick molar enamel. Yet these similarities only show that it possessed some hominid traits.

I am apt to believe that *Gigantopithecus* rightly belongs with the pongids, simply because there is not enough post cranial evidence to sway my opinion. It is also apparent to me that *Gigantopithecus*, dentally, possess a mosaic of traits that indicate an affiliation with both hominids and pongids. This, however, may be attributed to the diet of *Gigantopithecus*. What is clearly evident is that the skeletal collection of *Gigantopithecus* is severely lacking, and although researchers feel they may have discovered a distal portion of the humerus belonging to *Gigantopithecus* it would still be next to impossible to determine its phylogeny from that. There is always the possibility that *Gigantopithecus* could be a branch in the hominid lineage, but not ancestral to us.

It is apparent to me that because of the parabolic arcade and the simian shelf that *Gigantopithecus* is more likely a pongid than a hominid, simply because you don't find any hominids with a simian shelf, and the size of *Gigantopithecus* seems to place it with the pongids (of course the size is speculative as well). The climate in some areas was more accommodating to certain organisms, and some of the genera we see today were located in other areas during different time periods, and specialized to those areas. I would like to suggest the possibility of *Gigantopithecus* as an Asian gorilla and not an Asian hominid.

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