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Introduction

One of the many problems central to paleoprimatology and paleoanthropology concerns the reconstruction of dietary behaviours and adaptations in fossil species. Such endeavours become particularly difficult when the fossil species has left no living descendents. It thus becomes vital to identify plausible living analogs for the purpose of inferring possible behaviours in the fossil species. Unfortunately, there are times when a proper living analog does not exist (for example, Gigantopithecus). The dietary habits of extinct and extant primate species provide additional insights into the socioecological nature of the species. Differing dietary adaptations are partially responsible for many of the behavioural and ecological differences that separate extant taxa, and by extension, must obviously affect the differentiation of fossil taxa. Aspects of diet, living or fossil, can be used to infer metabolic rate, body mass, ecological niche and ranging patterns, among other things. This paper, adopts a broad comparative approach in order to more accurately reconstruct the diet of one of paleoprimatology's greatest enigmas, the fossil Miocene ape, Gigantopithecus.

History of Discovery & Taxonomic Considerations

For thousands of years, Chinese chemists have been using "dragon's teeth" as medicinal

ingredients. In 1935 a Dutch paleontologist, G.H.R. von Koenigswald, discovered these massive molars within Chinese pharmacies. Following the discovery, von Koenigswald identified the molars as belonging to a new, giant ape species, which he called *Gigantopithecus blacki* (von Koenigswald 1952). Since its original discovery, additional *Gigantopithecus* fragments have been discovered, both in the field and in Chinese drugstores. To date, only teeth and mandibular pieces have been recognized among these fragments.

Despite the ever increasing sample of *Gigantopithecus* remains, its taxonomic position remains elusive. Numerous taxonomic and evolutionary statements have been forwarded concerning the genus *Gigantopithecus*. Among these, two major positions have been posited regarding the affinities of *Gigantopithecus*: *i*) as a unique pongid, and *ii*) as either an extinct side branch, or ancestral stock, of later Asian hominids. Those favouring the former position include Ti-Cheng (1962), Simons and Pilbeam (1965, 1972, 1978), Simons and Chopra (1969a, 1969b), Simons and Ettel (1970), Pilbeam (1970, 1972), Simons (1972, 1978), Corruccini (1975), and Delson and Andrews (1975). The latter position is held by Weidenreich (1945, 1946), von Koenigswald (1952), Dart (1960), Woo (1962), and Eckhardt (1972). Although divided, the literature now seemingly points towards a pongid relation (Klein 1999; Fleagle 1999). A note of caution is warranted: if diet underlies the behavioural and ecological differences that separate extant taxa, the reverse – that taxonomic differences may reflect differing dietary adaptations – may also hold true. If this is the case, determining the correct taxonomic position of *Gigantopithecus* may be required prior to any accurate dietary reconstruction. With this in mind, the comparative approach taken here assesses the dietary skeletal evidence of *Gigantopithecus* based on the underlying assumption that it does belong to a pongid (albeit a unique one), rather than a hominid, classification.

Dietary Considerations

Identifying the anatomical evidence for diet among modern primates contributes immensely to our understanding of fossil primate dietary habits. Following Ungar (2002), two lines of evidence can be used to infer the diets of extinct primates. First, adaptive evidence "concerns analyses of the sizes and shapes of jaws and teeth, and the thickness and structure of tooth enamel" (Ungar 2002:261). Second, material that pertains to the actual foods consumed by the individual represents nonadaptive evidence. This would include studies such as dental microwear, stable isotopes, and trace element analyses.

One of the first attempts to reconstruct the diet of *Gigantopithecus* occurred following the discovery of a giant ape's jaw bone in a cliffside cave, south of the Yangtze River in China. Within this cave, the skeletal remains of deer, boar, tapir, stegodon and rhinoceros were found in association with the *Gigantopithecus* remains (Wen-Chung 1957). These associated remains were all hoofed animals, and thus, could not have possibly climbed the 270-foot, near vertical, cliff to access the cave's mouth (Wen-Chung 1957). The only alternative, then, was that the giant ape carried these hoofed animals into the cave for food. Based on this evidence, and the surface of the newly discovered teeth, Wen-Chung (1957:836) concluded that, "it was obvious that the animal had a mixed diet of meat and vegetables, quite different from that of modern apes which live on fruit." This early reconstruction has been turned upside-down in light of relatively recent paleoenvironmental evidence which indicates that, "what are now cliffside caves were sinkholes in a limestone plateau when the giant apes flourished" (Simons and Ettel 1970:83).

Thus, it seems apparent that the dietary reconstruction of *Gigantopithecus* will not be as simplistic as previously thought. The traditional and most conservative view, based upon jaw and teeth morphology, postulates that *Gigantopithecus* probably foraged on hard, fibrous material (Conroy 1990). This view, like Wen-Chung's (1957) inference, may also be in jeopardy based on the numerous findings elicited from studies of adaptive and nonadaptive elements. The results of such studies shall be discussed below.

Dental Morphology

Since it is the enormous size of the *Gigantopithecus* teeth that have so captured the attention of the primatological world, it is not surprising that most adaptive studies have focused on this particular aspect. It has long been assumed that relative tooth size reflects functional specialization (Ungar 2002). Additionally, variations in relative tooth shape may reflect a means of adapting to changes in the internal

characteristics of foods, such as the strength and toughness (Teaford and Ungar 2000).

Gigantopithecus teeth are colossal, exceeding all known primate teeth in their dimensions. Even those of an adult male gorilla are dwarfed by comparison. Data taken from von Koenigswald (1952) indicate that the third lower molars range from 22.3 to 23.1 mm in length. Such dimensions place crown volume estimates at about six times larger than modern humans, and twice as large as adult male gorillas, when compared to the corresponding teeth of such individuals (Weidenreich 1944). Von Koenigswald (1952:311) also reports that, "in addition to the usual five main cusps, the tooth pattern includes virtually all the secondary cusps that might possibly occur in the molar of a higher primate." As in anthropoid apes, the second molar of the *Gigantopithecus* specimens are larger than the first molar. Additionally, the molars are distinctly longer than broad (Strauss Jr. 1957). In *Gigantopithecus bilaspurensis*, cheek tooth cusps show little relief and are flattened and plate-like rather than conical; occlusal surfaces are relatively broad and flat (Pilbeam 1970). *Gigantopithecus blacki*, while sharing similar characteristics, tends to have higher crowned and more cuspidate molars (Pilbeam 1970). It would seem that the molars of *Gigantopithecus* are extremely large, with high, blunt cusps separated by deep, narrow furrows (von Koenigswald 1952). It is also worth mentioning that the lower anterior premolar is relatively broad (as in *Homo sapiens*) rather than elongated (Fleagle 1999). In other words, the premolars have become "molarized" – that is, broad and flattened.

With such enormous molars, it would come as no surprise for this gigantism trend to continue into other teeth. However, relative to cheek tooth size, the incisors of *Gigantopithecus* are small and closely packed between the canines (Pilbeam 1970). Furthermore, the incisors appear to be almost peg-like, rather than chisel-like (Strauss, Jr. 1957).

The canine morphology of *Gigantopithecus* is also unique. Although the front premolar was clearly bicuspid, the trigonid was still quite developed, suggesting that the upper canine continued to shear against the anterior face of the lower premolars (Pilbeam 1970). However, recovered canines show little projection beyond the plane of the cheek teeth. In both sexes, it seems, the canines wore down rapidly at the tips, even at an early dental age

(Pilbeam 1970). Thus, a stout and broad morphology appears to characterize *Gigantopithecus* canines. Since the lower canines of *Gigantopithecus* are truncated more than sharpened, it is reasonable to infer that the maxillary canine was not large, and not similar in function compared to that of the gorilla (Frayer 1973). Frayer (1973:418) also reasoned that "since the mandibular canine was truncated during life, masticatory actions performed at the canine appear to be more involved with grinding, than with shearing and gripping functions." Thus, the canines seem to have been essentially grinding teeth additional to the premolars and molars. It should come as no surprise, then, that these morphological characteristics of the teeth of *Gigantopithecus* have led many to assume and predict a diet of hard, tough, and rigid food items that required heavy grinding and crushing.

Enamel Thickness

Attempts at dietary reconstructions have also examined the implications of enamel thickness. Two adaptive explanations for possessing thick enamel have been offered: either to prolong the use-life of teeth in an abrasive diet; or to minimize the risk of crown damage given high occlusal forces caused by a diet including very hard objects (Ungar 2002). In recent years, it has become common to describe *Gigantopithecus* molars as thick enameled (Fleagle 1999; Klein 1999). If such is true, and the assumptions underlying the adaptive function of thick enamel are true, possession of thick enamel buttresses the data from dental morphology, which together suggests a hard, abrasive diet, possibly consisting of nuts, seeds, and subterranean tubers.

Mandibular Morphology

Mandibular fragments are among the most common bony remains found on fossil primate sites. It is assumed that the architecture of this bone has been adapted to withstand the stresses and strains associated with oral food processing. If this is the case, its morphology probably reflects (at least indirectly) some aspects of diet.

The mandibular body of *Gigantopithecus* is extremely deep and highly robust. Powerful mastication is indicated by numerous features. The symphysis was long, deep and powerfully buttressed by large tori (Yinyun 1982). That the face was short is indicated by the M_3 origination position of the ascending ramus (Pilbeam 1970). Powerful mastication is also indicated by the

everted and buttressed mandibular gonial angles (Pilbeam 1970). Short, deep faces are adapted to powerful mastication (Klein 1999).

Dental orientation within the jaw is also of interest. The "*Theropithecus* complex" describes a unique orientation whereby grinding teeth dominate – and may include adapted premolars and canines (Pilbeam 1970). Here, large grinding cheek teeth and powerful masticatory muscles are vital, while incisors are relatively unimportant. Gelada baboons (*Theropithecus*), which subsist on small seeds and nuts – thus, grinding – represent a living member of the "*Theropithecus* complex." Surprisingly, if we review the aforementioned data on *Gigantopithecus* dentition, we see that it shares many characteristics that belong to the "*Theropithecus* complex." Such dental orientation within the mandible of *Gigantopithecus* may indicate a similar diet to the gelada baboon – nuts and seeds. A study by Groves (1970) also shows "*Theropithecus* complex"-like characteristics in the modern mountain gorilla, whose differences with the eastern and western lowland gorilla mimic those differences found between *Gigantopithecus* and its dryopithecine forbearers. Groves (1970) concludes that these similarities may provide a basis for inferring the *Gigantopithecus* diet from the mountain gorilla diet, which includes roots, bark, and similar hard-wearing, bulky items.

Dental Microwear

Associations between aspects of diet, tooth use, and microwear in living primates have been used to infer diets of fossil primates. Primates that often use their anterior teeth during ingestion have high densities and frequencies of microwear striations on their incisors (Teaford and Ungar 2002). High incidences of long narrow scratches on molars point towards folivores, where as frugivores tend to have more pits than scratches (Teaford and Ungar 2002).

Von Koenigswald's (1952:317) original assessment of the gross dental wear on *Gigantopithecus* molars, "suggests the kind of attrition found in man." It was later determined by Strauss (1957:685) that, "the occlusal surfaces of the teeth appear to have been worn down considerably, so that the crown patterns of the molars cannot be made out." Such a statement lends critical support to the idea of massive grinding and crushing as the primary mode of mastication in *Gigantopithecus*. These

early specimens were poor representatives; more recent finds provide a better basis for microwear analysis.

Daegling and Grine (1987) examined occlusal microwear in a sample of *Gigantopithecus blacki* teeth, and concluded that this species was unlikely to have been a hard-object specialist. In a recent study by Daegling and Grine (1994), occlusal microwear on the teeth of *Gigantopithecus* were compared with microwear on the molars of two extant bamboo specialists, *Hapalemur griseus* (the gentle lemur) and *Ailuropoda melanoleuca* (the giant panda). Bamboo feeding within the extant species does not produce a consistent pattern of microwear. Thus, because of these dissimilar patterns, dental microwear on *Gigantopithecus* provides little direct evidence for bamboo feeding. It does, however, appear unlikely that *Gigantopithecus* subsisted exclusively on this particular resource (Daegling and Grine 1994). Rather, the microwear patterns found on the molars of *Gigantopithecus* most closely resemble that of the predominantly frugivorous *Pan troglodytes*, the common chimpanzee (Daegling and Grine 1994). This would suggest a diet of a broad range of fruits and fibrous materials.

An alternative technique, based on the identification of opal phytoliths found bonded to the enamel surfaces of the teeth of fossil species, allows for the identification of individual plant remains eaten prior to death (Ciochon *et al.* 1990b). The phytoliths found on *Gigantopithecus* molars derive from two distinct taxonomic groups and from different plant organs: *i*) the vegetative parts of grasses, and *ii*) the fruits and seeds of dicotyledons, specifically of a species in the Moraceae, or a closely related, family (Ciochon *et al.* 1990b). The relative roles of grasses and fruits in the diet of *Gigantopithecus* are difficult to estimate. However, judging from the present frequency of dental phytoliths in *Gigantopithecus*, fruits may have constituted a significant portion of the diet (Ciochon *et al.* 1990b).

Locomotor Limitations

While these dental aspects provide invaluable clues to the diet of *Gigantopithecus*, one must not forget the limitations imposed by body size. Body size and stature estimates for *Gigantopithecus* have ranged greatly: 10 feet tall and 1200 pounds (Ciochon *et al.* 1990a), 9 feet tall and 600 pounds (Simons and Ettel 1970), a height of twelve or more feet (Wen-Chung 1957), and more recently, possessing a body mass of 300 kg (Fleagle 1999). Given its size,

Gigantopithecus must have been completely terrestrial. Recently, the long bones of *Gigantopithecus* have been determined to be 20-25% longer and more robust, on average, than those of living gorillas (Johnson, Jr. 1979). Even this increase in size would most likely restrict *Gigantopithecus* to a ground-dwelling locomotor repertoire. This restriction has numerous implications on the type of foodstuffs available to *Gigantopithecus*, and will be discussed in the next section.

Discussion

The preceding sections discussed the various lines of evidence that appear in the fossil record which indicate, either directly or indirectly, the diet of *Gigantopithecus*. An often overlooked variable in discussions of fossil diets is the influence of the environmental context in determining resource availability. Knowledge of the paleoenvironment during the existence of *Gigantopithecus* provides additional clues to its diet. Early paleoenvironment reconstructions, based mainly on associated fauna, indicated a grassland and open woodland terrain (Pilbeam 1970; White 1975). More recent reconstructions (Ciochon *et al.* 1990a; Jablonski *et al.* 2000) suggest subtropical-seasonal to tropical forest settings. Like the range of dietary reconstructions discussed earlier, paleoenvironmental settings also vary, depending on the source. This shift in reconstruction to a tropical forest setting is undoubtedly related to recent microwear and phytolith analyses.

Locomotion and resource acquisition are intimately linked, and are the direct consequences of environmental setting. With such enormous mass, the only plausible locomotor pattern for *Gigantopithecus* would involve some form of terrestrial, quadrupedal movement. This great size would, no doubt, eliminate any form of arboreality. Thus, foodstuffs in the diet of *Gigantopithecus* would be limited to low-lying (or often-falling) items. As a general rule, fruits require high light to grow, and thus, in tropical forests most fruits are found on terminal branches high-up in the canopy ceiling (Campbell 1996). Such positioning would obviously be problematic for a ground-dwelling species such as *Gigantopithecus*.

A number of explanations are possible. Perhaps body size reconstructions have been grossly over-estimated. Until post-cranial remains are recovered which permit more accurate body stature estimates, current reconstructions must be taken with a grain of salt. It is unlikely, however, that a post-cranial skeleton indicating arboreality would be associated with a dental and mandibular morphology of such extreme size. Thus, it appears that a consensus has been reached regarding the habitually terrestrial nature of *Gigantopithecus*. Assuming this, how then would fruit become a vital part of the diet, as was posited by the phytolith analysis of Ciochon *et al.* (1990b)? First, perhaps some species of the Moraceae family represent low-lying fruits. Second, overly ripe fruit may fall to the ground, upon which *Gigantopithecus* could subsist. However, the chances of enough fruit, left to over-ripen by other frugivores, to sustain *Gigantopithecus* is slim. Similarly, it is also unlikely that *Gigantopithecus* could have subsisted on fruit dropped by clumsy arboreal frugivores. Lastly, perhaps the indication of heavy frugivory suggested by phytolith frequencies is erroneous. For instance, only four teeth, among thousands now discovered, were selected for inclusion in the phytolith study. Such selective sampling introduces a large amount of bias. Schwartz (1991) concurs, and notes that a great deal is being drawn from the analysis of four teeth, only two of which were found to be harbouring phytoliths, with the greatest concentration on only one. Clearly, larger samples of teeth need to be similarly analyzed. Furthermore, phytolith accumulation properties need additional investigation. Perhaps the phytoliths associated with various species accumulate at differing rates and concentrations; or perhaps, the phytoliths only represent the last, or most recent, foods consumed by the individual prior to death, and not necessarily the most commonly eaten item.

The importance of Ciochon *et al.*'s (1990b) phytolith study must not be entirely dismissed. As argued by Daegling and Grine (1994), bamboo feeding may be a possible dietary adaptation for *Gigantopithecus*. Supporting evidence for such a scenario may be found in Ciochon *et al.*'s (1990b) analysis. In addition to phytoliths belonging to the Moraceae family, phytoliths of vegetative grasses were also recovered. The recovery of such phytoliths may be of some importance in that the bamboo family is a vegetative grass. As stated earlier, additional phytolith analysis need to be conducted.

A cautionary note is also warranted for the dental microwear analyses of diet of *Gigantopithecus*. Microwear features do not

necessarily reflect specific food items *per se*, but rather the mechanical properties of those foodstuffs, or the constituents of those foodstuffs. Thus, the varying degrees of mechanical properties of food items will produce varying degrees of microwear on the dentition of a specimen. This may create somewhat of a "dental paradox", in that the microwear found on dentition may not reflect the most common, or distinctive, dietary foodstuff of that species, but merely the most abrasive item within the dietary range of that individual (Plavcan *et al.* 2002).

As discussed earlier, one of the most frequently cited enamel correlations is between the consumption of hard, and abrasive, food items, and thick molar enamel. However, thick enamel by itself does not necessarily provide protection against hard objects, which commonly cause fractures in the enamel layer (Ungar 2002). To prevent fracturing, the best protection is "prism or crystallite decussation or interweaving" within the enamel structure (Teaford and Ungar 2000:13508). Thus, it may be the structure, and not the thickness of enamel, that provides clues to the abrasive and rigid nature of dietary foodstuffs. If this is the case, the thick enamel layers on *Gigantopithecus* teeth may not provide evidence for a diet that consists of hard, tough objects. To date, analyses of *Gigantopithecus* enamel structure have not been conducted, and thus, statements and inferences about such properties cannot be made.

It should also be noted that the enormous molar size found in *Gigantopithecus* may fall victim to the aforementioned "dental paradox." During its existence, the environmental setting of *Gigantopithecus* habitats experienced increasing aridity and seasonality (Jablonski *et al.* 2000). These climatic fluctuations may have created shortages of preferred food items. The large molars and increased occlusal surface may have evolved as a coping strategy during periods of stress in which dietary habits were forced to switch to tough, fibrous, and hard food items. In this way, the enormous gross morphology of *Gigantopithecus* dentition is an adaptation for critical feeding, and not a reflection of the most common dietary foodstuffs.

Conclusions

Reconstructing behaviour in any fossil species requires an equilibrium between the enthusiastic inference of how organisms lived in the past, and the skepticism necessary to understand the boundary between supported hypothesis and unsupported speculation (Plavcan *et al.* 2002). Reconstructions of the behaviour of fossil species are limited to the evidence available in the fossil record. This includes adaptive (dental morphology, mandibular form, and enamel structure) and nonadaptive (dental microwear, gross tooth wear, stable isotope, and trace element analyses) lines of evidence.

Though the current nonadaptive evidence regarding the diet of *Gigantopithecus* is somewhat controversial, the adaptive evidence does provide some important clues. The mandibles are deep – top to bottom – and are extremely thick. The molars are low-crowned and flat, with very thick enamel caps. The canine teeth are not sharp and pointed – as is the case in other apes – but are more similar to premolars in morphology, while the incisors are small, peg-like, and closely packed. The features of the teeth, combined with the massive, robust jaws, lead to the conclusion that *Gigantopithecus* was adapted to the consumption of tough, fibrous foods through the extensive use of crushing and grinding. However, as discussed previously, this conclusion should be met with the same amount of skepticism as that given to other dietary reconstructions, namely those of Ciochon *et al.* (1990b) and Daegling and Grine (1994).

Taken cumulatively, primary foodstuffs relating to the reconstructed diet of *Gigantopithecus* have included nuts, seeds, tubers, and other hard objects, grasses, bamboo, and fruit. Various skeletal elements point towards differing sets of food items. It can only be concluded that the most distinctive characteristic of the diet of *Gigantopithecus* is the enormous range and variability of that diet. Since *Gigantopithecus* represents an ape unlike any other in primate history, it should come as no surprise that its diet should reflect its enigmatic persona. As such, it probably exploited numerous resources, including all those mentioned here. In terms of dietary foodstuffs, the range of resources exploited by *Gigantopithecus* most closely resembles that of anatomically modern *Homo sapiens* (i.e. an opportunistic omnivore). This extensive range in diet, along with a gigantic stature, are just two of the many characteristics that make *Gigantopithecus* an enigmatic ape.

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