THE TEMPOROMANDIBULAR JOINT IN ANTHROPOID PRIMATES

FUNCTIONAL, ALLOMETRIC, AND PHYLOGENETIC INFLUENCES

by

Claire Elizabeth Terhune

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has been approved

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Graduate Supervisor Committee:

William H. Kimbel, Chair
Gary T. Schwartz
Mark A. Spencer

ACCEPTED BY THE GRADUATE COLLEGE

ABSTRACT

The temporomandibular joint (TMJ) is a morphologically and functionally complex component of the skull. Temporomandibular joint shape varies considerably across mammals and within primates, and some aspects of the TMJ have been linked to differences in feeding behavior. However, a broad comparative context describing TMJ variation across primates is lacking. This dissertation therefore evaluated TMJ shape variation in the context of biomechanical hypotheses regarding TMJ function, and in light of phylogenetic and body size variation across anthropoid primates.

Three-dimensional geometric morphometrics were used to quantify TMJ shape across a broad sample of 48 anthropoid primates, and more narrowly among small groups of closely related taxa with documented dietary differences. Linear measurements of the TMJ (e.g., glenoid length) were subsequently calculated and compared among taxa. Results of the dietary analyses indicate that taxa with more resistant diets tend to have larger joint surface areas, as well as mediolaterally wider and anteroposteriorly shorter TMJs. Strong correlations were found between glenoid length and measures of gape, suggesting that one way increased gape is achieved is through increased translation at the TMJ. Analyses of scaling in the TMJ found that many variables scaled with positive allometry against cranial and body size, although differences in scaling patterns among platyrrhines, cercopithecoids, and hominoids were identified. In the phylogenetic analysis, genetic and morphological phylogenies were compared and not found to be particularly congruent. This congruence varied across clades, however, and in many instances dietary and body size variation were correlated with morphology, suggesting that TMJ morphology is adaptive. These data highlight the myriad ways in which multiple factors may influence TMJ shape, which may or may not be congruent with known genetic relationships among taxa.

Although the TMJ is only a small portion of the skeleton, the morphology of this joint can provide valuable information with which to infer or reconstruct the biology of primate taxa. Ultimately, these data will help to provide a framework for future analyses of primate, and particularly fossil hominin, TMJ variation, and more generally to contribute to the growing body of literature regarding form and function in the primate masticatory apparatus.

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CHAPTER 1: INTRODUCTION

Variation in cranial shape can indicate phylogenetic, dietary, or locomotor patterns, as well as changes in cognition. The ability to tease apart these influences over cranial shape is critical to the accurate interpretation of fossil remains, and the reconstruction of the biology of fossil taxa. One portion of the skull that can provide important insight into the biology of living and extinct species is the masticatory apparatus. In mammals, this complex is uniquely characterized by a mandible made up of a single bone (or of two bones if it not fused at the mandibular symphysis) which articulates with the cranium at the temporomandibular joints (TMJ). Masticatory variation has been examined extensively across many orders of mammals (e.g., Davis, 1955, 1961; Maynard Smith and Savage, 1959; Crompton and Parker, 1978; Woods and Howland, 1979; Greaves, 1980; Weijs and Dantuma, 1981; Janis, 1983; Reduker, 1983; Gorniak, 1985; Radinsky, 1985; Riley, 1985; Smith and Redford, 1990; Dumont, 1997; Perez-Barbeia and Gordon, 1999; Dumont and Herrel, 2003; Sacco and Van Valkenburgh, 2004; Nogueira et al., 2005), and has been a particular focus of interest in primates (e.g., DuBrul, 1974, 1977; Hylander and Bays, 1978; 1979; Hylander, 1979a,1979b, 1985, 2006; Bouvier 1986a,b; Ravosa, 1990, 1996, Daegling, 1992; Jablonski, 1993; Anapol and Lee, 1994; Anton, 1994; 1996, 1999, 2000; Wood 1994; Pan et al., 1995; Spencer, 1995, 1998, 1999; Daegling and McGraw, 2001, 2007, 2008; Williams et al., 2002; Vinyard et al., 2003; Burrows and Smith, 2005; Singleton, 2005; Wright, 2005; Constantino, 2007).

One aspect of the masticatory apparatus that varies considerably across mammals is the TMJ. In carnivores, range of motion at the joint is limited by multiple processes that wrap around the mandibular condyle, whereas in other groups such as ungulates and primates, the joint is open, allowing for increased mediolateral (ML) and anteroposterior (AP) excursion of the mandible during mastication (e.g., Maynard Smith and Savage, 1959; DuBrul, 1974; Crompton, 1989; Herring, 2003). Temporomandibular joint form has also been documented to vary within humans (Sullivan, 1917; Weidenreich, 1943; Angel, 1948; Van Gerven et al., 1978; Carlson and

Van Gerven, 1977; Hinton and Carlson, 1979; Hinton, 1983; Kozam, 1985; Spencer and Demes, 1993; Harvati, 2001, 2003; Lockwood et al., 2002; Terhune et al., 2007), and across primates as a whole (Weidenreich, 1943; Ashton and Zuckerman, 1954; Bouvier, 1986a,b; Wall, 1995; Vinyard, 1999; Lockwood et al., 2002; Kimbel et al., 2004), and some of these analyses have directly linked this variation to functional differences among taxa (e.g., Bouvier, 1986a,b; Wall, 1995, 1999; Vinyard, 1999; Vinyard et al., 2003). The goal of the current research was to evaluate this variation in the context of biomechanical hypotheses regarding TMJ function, and in light of phylogenetic and body size variation across anthropoid primates. Ultimately, these data will help to provide a framework for future analyses of primate, and particularly fossil hominin, TMJ variation, and more generally to contribute to the growing body of literature regarding form and function in the primate masticatory apparatus. In the following sections I will outline previous analyses of morphological variation in the TMJ, discuss the functional significance of this region and the use of the TMJ in phylogenetic analyses, and evaluate scaling in the masticatory apparatus.

MORPHOLOGICAL VARIATION IN THE TMJ

One of the first researchers to document variation in the modern human temporomandibular joint was Sullivan (1917). Sullivan was particularly interested in glenoid fossa variation, as one of his colleagues had, two years earlier, suggested that Eskimo possess a very shallow glenoid fossa as a consequence of their mastication of very tough foods. Sullivan (1917) therefore questioned whether this morphology was a “racial characteristic” or was environmentally determined. After noting a great deal of variation in glenoid depth in Eskimo and other human populations, Sullivan concluded that this feature must be functionally modified, suggesting that “such a structure [the articular eminence] would be depressed by pressure.” (Sullivan, 1917:22). Notable analyses of glenoid variation following Sullivan include those of

Weidenreich (1943) and Angel (1948), with the former author's observations of human TMJ form embedded in his detailed comparative analysis of the temporal bones of the *Sinanthropus* fossil specimens. Drawing on descriptions by previous researchers as well as his own observations and measurements, Weidenreich (1943) described the distinctiveness of the modern human mandibular fossa in relation to the great apes and *Sinanthropus*, and attributed this unique morphology to expansion of the brain, rather than a consequence of differences in diet. In contrast, Angel (1948), in his examination of TMJ variation and differences in glenoid fossa depth and articular eminence slope, concluded that, while genetics may play a large role in determining the shape of the glenoid fossa, external factors such as mastication were also important.

Differences in TMJ shape among modern human populations have been further documented since these early studies (Van Gerven et al., 1978; Carlson and Van Gerven, 1977; Hinton and Carlson, 1979; Hinton, 1983; Kozam, 1985; Spencer and Demes, 1993; Harvati, 2001, 2003; Lockwood et al., 2002; Terhune et al., 2007). Rather than discussing the morphological features that vary among populations, however, a number of these researchers have simply stated that variation within this morphology exists (Harvati, 2001, 2003; Lockwood et al., 2002; Terhune et al, 2007). Those authors who have quantified morphological differences have documented temporal changes in TMJ morphology (Hinton and Carlson, 1979) as well as changes in TMJ shape associated with craniofacial (Hinton, 1983) and orthodontic (Kozam, 1985) variation.

Although a number of analyses have evaluated variation in the masticatory apparatus (e.g., Hylander, 1979b; Bouvier 1986a,b; Ravosa, 1990; Anapol and Lee, 1994; Wood 1994; Pan et al., 1995; Spencer, 1999; Williams et al., 2002; Vinyard et al., 2003; Wright, 2005; Burrows and Smith, 2005; Singleton, 2005) and basicranium (e.g., Strait; 1999, 2001; Lieberman et al., 2000a; McCarthy, 2001) of non-hominoid primates, details of TMJ morphology in primates other than the great apes and humans are few and far between. Among non-human primates, few comprehensive analyses have focused specifically on variation in the TMJ, and the majority of work that has been done has almost exclusively included the great apes. As a result, there are many data regarding how the TMJ differs among the great apes, especially in comparison to generalized human TMJ morphology. In general, the ape mandibular fossa is very shallow, with a weak articular eminence. This ‘open’ morphology contrasts sharply with that observed in humans, where the glenoid is considered very ‘deep’ (Weidenreich, 1943; Ashton and Zuckerman, 1954; Kimbel, 1986; Lockwood et al., 2002; Kimbel et al., 2004). Details of this morphology are discussed in more detail in Chapter 2.

THE FUNCTIONAL SIGNIFICANCE OF THE TMJ

Considerable debate regarding the role of the TMJ during mastication has taken place in the literature, with some researchers hypothesizing that the TMJ is not loaded and that the mandible serves only as a link between the bite force and muscle resultant force (the “link” hypothesis) (Robinson, 1946; Scott, 1955; Steinhardt, 1958; Gingerich, 1971; Tattersall, 1973). Other researchers argue that the TMJ is load bearing and the function of the mandible can be modeled as a class three lever (the “lever” hypothesis) (Hylander, 1975, 1979a, 1991, 2006; Hylander and Crompton, 1980; Hylander and Johnson, 1985; Hylander et al., 1992; Hylander et al., 2005).

Early observations of the TMJ by Robinson (1946) led him to conclude that the TMJ was unable to withstand stress because the bone of the roof of the mandibular fossa was paper thin, and because synovial tissue, nerves, and blood vessels were located within the articular disc. These observations, as well as the absence of epiphyses at this joint, suggested to several authors that this region was non-stress bearing (Robinson, 1946; Scott, 1955; Steinhardt, 1958). Tattersall (1973) further proposed the idea that the morphology of the TMJ was inadequate to withstand any forces generated during mastication, by suggesting that 1) the thin condylar neck would be unable to dissipate any stresses generated within the joint, and 2) the fibrocartilage within the joint is more adapted to sliding rather than compression.

As discussed in detail by Hylander (1975), these conclusions are flawed for several reasons. First, while the bone at the roof of the mandibular fossa is indeed thin, this portion of the glenoid is not actually the stress-bearing portion- it is instead the articular eminence, which is composed of thick cancellous bone with a dense cortical plate (Moss, 1960; Sicher, 1950) that articulates with the mandibular condyle and is well suited to bearing joint reaction forces. Similarly, that the TMJ incorporates synovial tissues as well as nerves and blood vessels is also not of significance in this debate, as the center and anterior of the articular disc (i.e., that portion lying between the mandibular condyle and the glenoid) is avascular and lacks both nerves and a synovial layer (Hylander, 1975). The proposition that the fibrocartilagenous articular disc itself is not adapted to withstand stress was addressed by Leeson and Leeson (1970) and Ham (1969), who concluded that fibrocartilage is equally capable of withstanding stresses, and may actually be more adapted to tensile and shearing forces than hyaline cartilage (as suggested by Moss, 1959, 1960). Furthermore, the fact that fibrocartilage rather than hyaline cartilage, exists in this joint at all, as well as the lack of epiphyses at the TMJ, can be explained by the unique evolutionary history and intramembranous ossification of these elements (Moffett, 1966; Barbenel, 1972; Nobel, 1973; DuBrul, 1974; Himalstein, 1978; Taylor, 1986). Hylander (1975) addressed the suggestion by Tattersall (1973) that the neck of the mandibular condyle was insufficient to withstand stresses at the TMJ by demonstrating that the distribution of cortical bone within the neck was optimally deployed to resist tensile stresses during incisal biting. Finally, additional refutation of this tenet of the link hypothesis has come from theoretical modeling of forces within the masticatory apparatus (Barbenel, 1972, 1974; Faulkner et al., 1987), and the direct measurement of joint reaction forces in the TMJ via experimental studies (Hylander, 1979a;

Smith, 1978; Brehnan and Boyd, 1979; Brehnan et al., 1981; Boyd et al., 1982, 1990), which have shown that the TMJ is in fact load-bearing.

That the TMJ is indeed a load bearing joint has been further supported by analyses of joint remodeling by Bouvier and Hylander (1982, 1984) and more recently by Ravosa and colleagues (2007, 2008). These studies, which evaluated condylar dimensions in lab animals that were fed diets with different material properties, have indicated that the mandibular condyle experiences substantial levels of remodeling as a result of masticatory function. Groups that were habitually fed more resistant diets were found to have relatively larger condylar dimensions and thicker articular discs than subjects that were fed less resistant diets. These findings suggest that the TMJ continuously remodels in response to changes in joint loading during the life of an individual.

These data therefore suggest that the form of the TMJ varies as a consequence of joint loading, and further indicate the likelihood that TMJ shape varies across species as a consequence of functional demands of the masticatory apparatus. In other words, specific TMJ forms are better adapted to particular loading regimes than others. This premise has been demonstrated for the masticatory apparatus as a whole (e.g., Spencer, 1995; Taylor, 2002; Wright, 2005; Constantino, 2007) but fewer studies have focused on the morphology of the TMJ as it relates to dietary variation. However, more recent work by Wall (1995, 1999) and Vinyard (Vinyard, 1999; Vinyard et al., 2003) has examined the morphological correlates of particular movements at the TMJ. Wall (1995, 1999) evaluated the shape of the TMJ in *Ateles*, *Macaca*, *Papio*, and *Pan* and identified a suite of features that were significantly correlated with the amount of sagittal sliding that takes place at the TMJ during mastication. Similarly, Vinyard (Vinyard, 1999; Vinyard et al., 2003) found that some of the variation in TMJ form in extant strepsirrhines and Eocene primates can be linked to estimates of joint reaction forces, and that some aspects of TMJ shape are correlated with gape in tree-gouging primates. In the great apes, Taylor (2005) also assessed variation in the mandibular condyle, and found that *Gorilla* morphology was better adapted to the utilization of tougher food objects (e.g., leaves) than *Pan*.

This previous research has therefore established that the TMJ is a load-bearing structure, the morphology of which is likely to be shaped as a consequence of masticatory function. It largely remains unclear, however, the extent to which this morphology varies among closely related species with different diets, and particularly whether variation in this morphology is likely to be adaptive.

Identifying adaptive morphologies

What does it mean to say that a particular feature is adaptive? What is an adaptation? Although the answer to this question continues to be debated in the literature (e.g., Bock and von Wahlert, 1965; Clutton-Brock and Harvey, 1979; Bock, 1980; Gould and Vrba, 1982; Mayr, 1982; Harvey and Pagel, 1991; Reeve and Sherman, 1993), adaptation can be broadly defined in two ways. The most common definition is similar to what one might consider to be the non-scientific meaning of the term: a feature is an adaptation if it was shaped by natural selection for the function it is currently performing. This definition regards an adaptation as static, and refers to the current fitness or immediate utility of that feature, regardless of how it originally arose (Bock and von Wahlert, 1965; Gould and Vrba, 1982; Harvey and Pagel, 1991). In contrast, adaptation may also be defined in an historical perspective, as a feature that arose as a result of selection for a particular function, but need not necessarily be the function it currently performs (Harvey and Pagel, 1991). These two definitions outline the difference between a historical and non-historical approach for identifying adaptations, which will be discussed in more detail below. Regardless of its origin, however, in both of these definitions, an adaptation refers to a feature that confers some sort of advantage to its possessor.

Attempts to identify adaptations are centered on the concept that, where taxa live in similar environments, they are likely to evolve similar characters through the process of natural selection. These studies have relied heavily on the comparative method, a means by which questions regarding common patterns of evolutionary change can be addressed (Harvey and Pagel, 1991). In essence, the comparative method is a search for evolutionary regularities or phenomena from which a particular conclusion regarding adaptation can be drawn, and potentially applied to extinct forms. This particular methodology has been used extensively in evolutionary biology, and was the primary foundation upon which Darwin built his theory of natural selection (Darwin, 1859). In essence, the comparative method searches for correlations among characters or between characters and environments. However, an observed correlation can only suggest a particular adaptive scenario, not prove its validity (Harvey and Pagel, 1991). The finding of a correlation therefore necessitates further study of the form-function relationship.

As outlined by Bock and von Wahlert (1965), the form-function complex consists of the appearance of specific features (=form) and the action (or multiple actions) of those features (=function), that together have a specific “biological role” in the life history of an organism. This biological role, as argued by Bock and von Wahlert (1965), is closely linked to, but not necessarily inferable from, the form-function complex, except through observation of the organism in its natural environment. The extent to which this form-function complex then can be linked to a specific biological role depends on whether the organism in question can be directly observed carrying out this biological role. As a result, comparative morphometric analyses such as the one presented here are a search for correspondence between a specific form and a predicted function, but cannot confirm the biological role of a particular form-function complex. The study of form-function relationships is inherently tied to understanding adaptation, and in many cases, the finding that a specific form-function complex is used in a specific biological role allows for the inference that the complex in question is an adaptation.

It is also important to be able to place adaptations in an historical context. In the strictest definition of adaptation, adaptive characters are those that arose historically in response to a specific selective agent (Harvey and Pagel, 1991). However, characters that are of current utility may not necessarily be indicative of the origin of the trait; in other words, such a trait would be considered an exaptation (Gould and Vrba, 1982). Furthermore, understanding the evolutionary relationships among the taxa of interest is important for inferring adaptation, since some adaptations may be shared as a result of common ancestry whereas others may be independently derived. There are two different approaches to studying adaptation, one of which makes use of phylogenetic information to examine the rates and directions of evolutionary change within a particular clade. Harvey and Pagel (1991) define this as the directional approach. In contrast, non-directional analyses examine covariation among different phylogenetic groups. This approach (which is the one used in the analyses presented here) considers those features that are independently derived in distinct lineages to be of the most interest, since they should indicate similar selective pressures that have resulted in the same morphologies, or in other words, features that have evolved convergently. However, this approach has little power to identify the original selective pressure under which a particular feature evolved, and can only describe the current utility of the feature of interest (Harvey and Pagel, 1991).

Harvey Pagel (1991) proposed three steps in the identification of an adaptation. First, one must observe phenotypic variation among taxa. Given this variation, the second step is to propose an adapative explanation for the variation. Finally, the proposed explanation must be tested by predicting particular environmental or constitutional correlates of the variation and, where possible, compare ancestral and derived states of the feature. Kay and Cartmill (1977) further identified several criteria for supporting a comparative hypothesis between a morphological trait and an ecological or behavioral trait (as summarized by Anthony and Kay, 1993):

1) There must be a functional relationship between the morphology and the behavior in question.
2) The hypothesis cannot be based on a unique co-occurrence of the two traits in question.
3) All observed forms that possess the morphological trait must also possess the behavioral trait. The relationship must hold true for all taxa in which it can be observed.

There have been critiques of the adaptationist program, however, the most notable of which was outlined by Gould and Lewontin (1979). These critiques primarily center around the adaptationist view that all features of an organism must be the result of some selective process. Alternatively, Gould and Lewontin (1979) outline the numerous ways in which traits of no particular adaptive significance may arise, including genetic drift, allometry, pleiotropy, and others. Instead, these authors advocate that it is more useful to view the entire *Bauplan* of an organism since multiple constraints within an organism (developmental, mechanical, phylogenetic) will likely mediate the effects of natural selection. It is therefore important to consider alternative explanations in any analysis of adaptation, since some observed correlations may not be easily interpretable in an adaptive context. Furthermore there may be multiple morphological solutions to a single adaptive demand (Harvey and Pagel, 1991; Anthony and Kay, 1993).

Critical function

What are the selective pressures that are likely to have shaped the morphology of the masticatory apparatus and the TMJ? One major consideration is that of food processing behavior (or generally, diet). Characterization of the diets of primate species has most frequently been based on the trichotomous system proposed by Kay (1973), which separated taxa into frugivores, folivores, and insectivores. This approach has been particularly useful for analyses of tooth crown morphology, as particular crown shapes are likely to be more or less efficient at processing these foods (e.g., Kay, 1973, 1975, Rosenberger and Kinzey, 1976; Anapol and Lee, 1992; Rosenberger, 1992; Anthony and Kay, 1993). For example, frugivores tend to have relatively smaller teeth with less relief to the tooth crown, whereas folivores tend to have larger teeth in relation to their body size, which have well developed shearing crests (Kay, 1975). These correlations have also been applied to fossil species in attempts to identify their dietary regimes (Kay, 1977; Kay and Cartmill, 1977; Kay, 1985). There are some limitations to this method of categorizing diet, however. Most critically, food items that fall into one category may not all share the same mechanical properties, and therefore they are unlikely to present the same mechanical challenges during food processing (Rosenberger and Kinzey, 1976; Rosenberger, 1992). Items that fall in the category of fruit are particularly prone to variation in material properties (e.g., fruit pulp vs. seeds).

As a result, more recent categorizations of primate diets have incorporates aspects of food material property (i.e., Rosenberger and Kinzey, 1976; Kinzey and Norconk, 1990; Rosenberger, 1992; Lucas et al., 2001; Elgart-Berry, 2004; Lucas, 2004; Williams et al., 2005; Marshall and Wrangham, 2007; Taylor et al., 2009). Rosenberger and Kinzey (1976:293) first identified this need by stating “selection for a particular molar form can often be related to some ‘critical function’” and they linked this critical function most closely with the physical properties of food items. As elaborated upon by Rosenberger (1992), the terms advocated by Kay (1973) do not accurately reflect the mechanical demands of the food items being processed, particularly in regard to frugivory, where different portions of fruits (e.g., sclerocarp, pulp, seeds, shells, nuts, skins, etc.) can have radically different material properties. Thus, a critical function such as harvesting or masticating hard food objects such as seeds may directly select for a specific morphology, whereas noncritical functions such as crushing soft fruits would not provide a strong selective pressure for a particular masticatory shape (Rosenberger, 1992). Rosenberger (1992) therefore argues that the selective pressure driving adaptive change in the masticatory apparatus is the material property of foods, and that a critical function therefore arises to enable an organism to harvest or process a food item of a particular material property which is crucial for their continued survival. This critical function could be a food item that is utilized year round, or alternatively could be a resource that is utilized only during a short time period but which is important for that organism to access when other resources are not available (Rosenberger, 1992; Marshall and Wrangham, 2007; Lambert, 2009; Marshall et al., 2009). This latter concept is referred to as a fallback food. As defined by Marshall and Wrangham (2007) fallback foods are most commonly considered to be foods of poor nutritional quality but high abundance that are eaten during periods when there is a lack of preferred food items available (Laden and Wrangham, 2005; Lambert et al., 2004; Ungar, 2004). In other words, fallback foods tend to be foods that are less preferred (either because they are of lower nutritional value and/or are more difficult to process) but are seasonally important (Marshall and Wrangham, 2007).

The significance of fallback foods for shaping masticatory adaptations has been a point of debate. How frequently does a primate need to utilize a particular resource for the mechanical processing of the resources to be selected for? Do observable traits represent adaptations to food items that are only occasionally exploited, and do the morphologies we observe have any relationship to preferred, rather than fallback, food items? How can we explain the avoidance of particular food items by taxa that appear adapted to utilize these very foods (e.g., Liem’s Paradox [Robinson and Wilson, 1998])? As initially outlined by Rosenberger and Kinzey (1976) and Rosenberger (1992), morphological adaptations should reflect the use of particularly important foods that may be mechanically more challenging, since adaptations for fallback foods are not likely to preclude the use of preferred food items that require little specialization to process (Robinson and Wilson, 1998; Marshall and Wrangham, 2007).

What does this mean for the analysis presented here? The species analyzed as part of the comparative groups examined (the composition of which is discussed in Chapter 4) all either differ from other closely related species in their consistent reliance on food items that are more resistant (e.g., *Theropithecus*, *Alouatta*), or more commonly, have been documented to exploit food items that are more mechanically challenging during times of food scarcity (e.g., *Cebus apella*, *Macaca fuscata*/ *sylvanus*, *Gorilla*). As a result, the comparative approach employed here allows for the comparison of taxa with different masticatory adaptations for a critical function (whether related to fallback foods or not), to other closely related taxa. If a link is found between TMJ morphology and the hypothesized function of the masticatory apparatus, as predicted by the existing data regarding dietary variation among primate taxa, the data can therefore suggest that the TMJ is adapted to specific masticatory functions. This will be elaborated upon in the project description below and in further chapters.

TMJ SHAPE IN RELATION TO PHYLOGENTIC AND ALLOMETRIC VARIATION

Not only is a consideration of how variation in TMJ shapes corresponds to phylogenetic variation important for identifying adaptation in the TMJ, the extent to which TMJ morphology covaries with phylogeny may indicate whether this region is useful for recovering relationships among fossil taxa. Allometry may also drive variation in TMJ shape, such that features of the TMJ vary as a function of size, rather than because of some functional or phylogenetic difference (although these factors are not mutually exclusive). This section will outline how these two avenues of research have been employed in analyses of TMJ variation, and how they may inform the current study.

Phylogenetic signals in the cranial base

An alternative approach to examining variation in TMJ morphology has focused on the utility of the temporal bone (including the glenoid fossa) in phylogenetic analyses. Characters on and around the TMJ are frequently used in taxonomic and phylogenetic analyses of living and fossil primates (e.g., Kimbel, 1986; Strait et al., 1997; Martinez and Arsuaga, 1997; Harvati, 2001; Kimbel et al., 2004; Lockwood et al., 2002, 2004; Harvati and Weaver, 2006a,b; Smith et al., 2007; Terhune et al., 2007; Gilbert, 2008; HF Smith, 2009; von Crammon-Taubadel, 2009). The use of this region has a long history in physical anthropology (Weidenreich, 1943; Tobias, 1967; Olson, 1981; Kimbel, 1986; Strait et al., 1997; Martinez and Arsuaga, 1997; Lockwood et al., 2002, 2004; Kimbel et al., 2004). This heavy reliance on the temporal bone is primarily because this region (and the basicranium as a whole) is thought to more directly reflect genetic variation than variation that might be caused by environmental factors (Olson, 1981; Strait et al., 1997; Lieberman et al., 2000; Harvati, 2001; Wood and Lieberman, 2001; Harvati and Weaver, 2006a,b), because of its early development, enchondral ossification, and relationship to the developing brain (Houghton, 1996; Scheuer and Black, 2000; White, 2000). Recent analyses focusing on the temporal bone have supported this assumption, and indicate that the complex morphology of the temporal bone strongly reflects phylogenetic variation in great apes and relationships among human populations (Lockwood et al., 2004; Harvati and Weaver, 2006a,b; Smith et al., 2007; HF Smith, 2009; von Crammon-Taubadel, 2009). Additional work needs to be done to assess whether this relationship is consistent across primate clades.

It is unclear what components of the temporal bone are driving the observed phylogenetic signal, since the temporal bone itself is functionally and developmentally complex. The temporal bone lies at the confluence of a number of different functional complexes in the skull. Portions of the temporal bone are associated with the mastication, hearing, posture, balance, and formation of the braincase. As a result, any of these functional complexes may constrain other aspects of temporal bone morphology. Ontogenetically, the temporal bone forms from four separate parts: the petromastoid, squamous, tympanic, and the styloid process (Scheuer and Black, 2000). The bulk of the glenoid is composed of squamous temporal, with the exception of the posterior portion, which is formed by the tympanic, a separate developmental component to which the joint capsule attaches (Hylander, 1991; Mérida-Velasco et al., 1999). During prenatal development, the most critical period for TMJ morphogenesis is between 7 and 11 weeks, with intramembranous ossification of the squamous part of the temporal beginning at approximately 8 weeks, the same time at which the articular disc starts to appear (Mérida-Velasco et al., 1999; Radlanski et al., 1999). Notably, though, it is not until this time (9 to 11 weeks) that movement begins at the TMJ. Given these data, most authors agree that the major components of the TMJ are in place by week 12, with the morphological relationships between these portions similar to those observed in adults (Symons, 1952; Baume, 1962; Baume and Holz, 1972; Öğütcen-Toller and Juniper, 1994 as reviewed in Mérida-Velasco et al., 1999).

The prenatal development and ossification of the TMJ continues until birth, with major changes in morphology involving increasing convexity of the glenoid fossa and an overall increase in size (Radlanski et al., 1999; Öğütcen-Toller and Juniper, 1994). In comparison, the bony labyrinth, auditory ossicles, and tympanic ring reach their adult proportions by fetal midterm (~20 weeks) with no subsequent increase in size (Scheuer and Black, 2000). Thus, at birth, the petrous portion is well ossified, and the structures of the middle ear and the squamous portion are obvious, as is the small mastoid region. Postnatal development of the TMJ is associated with continued ossification of the components of the TMJ, and growth of the articular eminence and postglenoid process, with subsequent deepening of the glenoid fossa (Keith, 1982; Wright and Moffett, 1974; Nickel et al., 1988a; Itoh et al., 1995; Katsavrias and Dibbets, 2001, 2002; Katsavrias, 2002). This complex and early development of the components of the temporal bone have therefore led a number of authors to suggest that the morphology of the temporal bone (including the glenoid fossa) is less likely to be influenced by epigenetic factors, and is therefore more likely to display a phylogenetic signal.

It is unclear to what extent the morphology of the TMJ will reflect the results of the previous analyses of the temporal bone as a whole. There are two alternative expectations for how TMJ shape may covary with neutral genetic variation. First, results of analyses of TMJ shape may be consistent with previous studies that have analyzed the entire temporal bone, suggesting that this morphology does contain a phylogenetic signal. Alternatively, because of this region's importance in the masticatory apparatus, the components of the temporal bone associated with the TMJ may be more variable, and therefore poorly reflect phylogenetic history.

Size and scaling in the masticatory apparatus

To what extent do body or cranial size variation influence the shape of the TMJ? Previous analyses of scaling in the masticatory apparatus have found that features of the masticatory apparatus tend to scale with positive allometry (Smith et al., 1983; Hylander, 1985; Bouvier, 1986a,b; Ravosa, 1996, 2000; Vinyard, 1999). These authors have interpreted this scaling relationship to indicate functional differences among different sized primates. Hylander (1985), who identified a series of positively allometric relationships between aspects of mandibular morphology when scaled against mandibular length in cercopithecines, concluded that perhaps larger cercopithecines also engage in more repetitive chewing cycles due to their more mechanically resistant diets, which therefore necessitates larger mandibular dimensions. Comparisons of mandibular scaling patterns in the frugivorous cercopithecines and the more folivorous colobines have also been explained in the context of biomechanical differences as a consequence of diet (Ravosa, 1996). Positive allometry of mandibular dimensions in living and fossil apes has been identified by Ravosa (2000), again suggesting a size-related increase in dietary toughness. Analyses of TMJ shape have largely supported this signal of positive allometry. Smith et al. (1983) examined condylar shape across anthropoid primates and found that condylar length, width, and area scaled with slight positive allometry relative to body size. In strepsirrhines, Vinyard (1999) also found that glenoid and condylar width and area scaled with positive allometry (although condyle and glenoid length scaled with isometry). In contrast, Bouvier (1986a,b) evaluated scaling of mandibular and condylar dimensions in both Old and New World monkeys and found that, when scaled against either mandibular length or body size, most of these dimensions scaled with isometry. However Bouvier (1986a,b) did identify a number of different scaling patterns between platyrrhines and cercopithecoids, and within cercopithecoids, that she interpreted in light of biomechanical differences in these groups.

Scaling of the masticatory musculature has also been of particular interest in recent years. Cachel (1984) initially analyzed masticatory muscle mass scaling in relation to body size across primates and found that these variables scaled with isometry. Similarly, in her analysis of masticatory muscle variation in macaques, Anton (1999, 2000) found that masseter and medial pterygoid physiological cross sectional area (PCSA) scaled with isometry in relation to body size. More recently, Anapol et al. (2008) found that PCSA scaled with positive allometry in both prosimians and catarrhines, although a similar analysis within prosimians conducted by Perry and Wall (2008) concluded that muscle cross-sectional area scales primarily with isometry or only slight positive allometry. These data are therefore unclear on the extent to which the masticatory muscles reflect geometric isometry or positive allometry.

What can we infer from these previous analyses? The above outlined analyses would seem to suggest that the bony morphology of the masticatory apparatus scales primarily with positive allometry, and to some extent the masticatory musculature does as well. There are gaps in these analyses, however. Many of these studies have been restricted to a single clade (Hylander, 1985; Ravosa, 1996, 2000; Vinyard, 1999; Bouvier, 1986a,b; but see Smith et al., 1983) or have examined relatively small samples, particularly in analyses of muscle parameters

(Anapol et al., 2008; Cachel, 1984; Perry and Wall, 2008). There are also considerable methodological differences among these studies, particularly in regard to which size variable aspects of masticatory morphology should be examined regressed against (Hylander, 1985; Smith, 1993), and the regression equations that should be used (RJ Smith, 1993, 2009). Furthermore, only a few studies have explicitly examined features of the TMJ (Smith et al., 1983; Bouvier, 1986a,b; Vinyard, 1999), only one of which included the cranial component of the TMJ, the glenoid fossa (Vinyard, 1999). It is therefore unclear how the components of the TMJ should scale in relation to body or cranial size. Given these previous findings, and the hypothesis of a size-related increase in dietary toughness (Hylander, 1985; Sailer et al., 1985; Ravosa, 1996, 2000) which would result in increased stresses at the TMJ, it could be therefore be predicted that features of the TMJ should scale with positive allometry.

PROJECT DESIGN

The above review outlines a number of outstanding questions regarding morphological variation in TMJ shape. Attempts to fill these gaps in our current understanding of the biology of the TMJ can further enhance our understanding of the functional and phylogenetic significance of this region in both living and extinct primate taxa. These three areas of interest are by no means the only possible influences over TMJ morphology, but they represent the three main ways in which previous authors have assessed variation in TMJ shape, and therefore represent a logical starting point for a comprehensive look at morphological variation in the TMJ.

For this study, these outstanding questions can be summarized by three main research questions that will be addressed in the course of this dissertation:

1. Can the morphology of the TMJ be used to infer functional differences among primate taxa?
2. What role does allometric variation play in governing TMJ shape?

3. To what extent does variation in TMJ morphology reflect phylogenetic differences among primate taxa?

Each of these research questions will be addressed by testing a series of predictions formulated on the basis of previous work. These predictions are outlined in detail in subsequent chapters. It is important to note that none of these research questions are mutually exclusive. All of these factors – masticatory function, allometry, and phylogeny – are likely to influence TMJ shape to varying degrees. Furthermore, different combinations of factors may influence the shape of the TMJ within different groups of primates; as such, each of these analyses were conducted at multiple taxonomic levels (e.g., all taxa, platyrrhines only, hominoids only, etc.). It is the goal of this dissertation, therefore, to investigate each of these influences, as well as the correlations that may be present among the factors themselves, to develop a comprehensive picture of how and why TMJ shape varies across anthropoid primates.

These predictions were tested using three-dimensional landmark data of the skull and geometric morphometrics, a powerful quantitative method that allows shape differences among individuals and groups to be summarized and compared. This methodology is particularly useful for quantification of the TMJ, the complexity of which has hindered previous analyses. Use of these methods allows for the identification of previously unquantified differences in TMJ morphology among primate taxa. The results of this research will therefore provide important insight into the utility of this region for testing hypotheses regarding phylogeny and function, the results of which can then be applied to understanding variation in fossil primates. Specifically, variation in the shape of the TMJ in great ape and fossil hominin taxa has been discussed frequently in regard to understanding evolutionary relationships, particularly because the temporal bone is frequently preserved in the fossil record. In particular, the basicrania of the robust australopith (i.e., *Paranthropus*) species and *Homo* are similar in many aspects of morphology, including the mandibular fossa (DuBrul, 1974, 1977; Dean and Wood, 1981, 1982;

Kimbel et al., 1984, 2004). These similarities are considered convergent because of the more primitive morphology present in the presumed ancestor of the robust australopith clade, *A. aethiopicus*. However, while several studies have focused on the implications of this similar morphology for reconstructing phylogenetic relationships (Kimbel et al., 1984; Skelton and McHenry, 1992; Strait, 2001; Kimbel et al., 2004), and possible functional implications of this morphology have been suggested (DuBrul, 1974, 1977), few rigorous tests of the functional or structural implications of this convergence have been conducted. Application of the data collected and analyzed as part of this dissertation for this and other questions regarding fossil hominin morphology will be discussed in the concluding chapter.

The TMJ is only a small portion of the skeleton, yet this single joint can provide information regarding a number of topics that are important for accurately reconstructing the biology of fossil species. Understanding how and why TMJ shape varies is particularly critical for analyses of fossil hominin cranial remains, since this region is frequently discussed in taxonomic and phylogenetic analyses of fossil hominins. As a result, the construction of a framework for understanding TMJ shape variation is crucial, and it is this task that the proposed research will undertake.

STRUCTURE OF THE DISSERTATION

This dissertation is organized around the three research questions presented in this chapter. First in Chapter 2, I provide the necessary background information for understanding the morphology of the TMJ and its role in the function of the masticatory apparatus. Chapter 3 outlines the samples used and the methods by which the data were collected. The remaining chapters provide the results of the investigations into each of the three research questions, in the order they are listed above. Results of the functional analyses are presented in Chapter 4, followed by an evaluation of scaling in the TMJ in Chapter 5. The last data chapter (Chapter 6) further evaluates TMJ shape variation in phylogenetic perspective. In the closing chapter (Chapter 7), I critically evaluate the results of my analyses, and examine the extent to which each of these three major factors contributes to morphological variation in the TMJ, particularly in the context of outstanding hypotheses regarding TMJ shape in fossil hominin taxa.

CHAPTER 2: BACKGROUND

To provide a background for the research presented in this dissertation, in this chapter I first review the hard and soft tissue anatomy of the TMJ; these descriptions focus on TMJ anatomy in humans since the bulk of the existing literature is clinical in nature. Known variations in TMJ morphology and departures from human TMJ shape are also discussed. Next, a review of masticatory biomechanics focuses on the generation of forces and range of motion at the TMJ. This biomechanical framework provides a basis for more detailed discussions of previous analyses regarding TMJ function and the corresponding expectations that will be tested in this study, which are presented in Chapter 4.

ANATOMY

The TMJ is a true synovial joint, and consists of two discrete units: the glenoid fossa of the temporal bone, and the mandibular condyle of the mandible. A pad of dense fibrous tissue, the articular disc, separates these two components, dividing the articular space into upper and lower joint spaces (Hylander, 1991, 2006). Motion at this joint is complex; gliding (or translatory) movements are primarily confined to the upper joint compartment and rotary or hinge movements to the lower. As a result, the TMJ is frequently referred to as a hinge joint with a moveable socket (Sicher, 1951; Hylander, 1991).

Although multiple terms have been coined to refer to different portions of TMJ anatomy, the terminology used here follows Hylander (1991, 2006), and unless otherwise noted, the bulk of the descriptive discussion of TMJ anatomy is drawn from Sicher (1951), Walker (1978), Hylander (1991, 2006), and Aiello and Dean (1990).

Hard tissue anatomy

The most prominent feature of the temporal bone’s glenoid region is the articular eminence (Fig. 2-1), a transverse bar of dense bone that forms the anterior boundary of the concave articular fossa. This fossa is the main articulation for the mandibular condyle (via the articular disc), and during occlusion the head of the condyle directly abuts the posterior slope of the articular eminence, rather than lying in the depth of the fossa (Hylander, 2006). The articular eminence in humans is a raised bar that is convex anteroposteriorly (AP) and slightly concave mediolaterally (ML). In most other primates, the articular eminence is relatively flat and undefined, resulting in a gradually sloping anterior border to the articular fossa. Medially, the articular eminence gives rise to the entoglenoid process, which curves slightly posteriorly and projects posteroinferiorly in humans. In apes, and many other primate taxa, this process is greatly enlarged and projects inferiorly, prohibiting medial migration of the mandibular condyle during translatory movements when the mandibular condyle is positioned at the apex of the articular eminence (Aiello and Dean, 1990).

The anterior slope of the articular eminence, from the apex of the articular eminence to the most anterior border of the joint capsule, is the preglenoid plane (Fig. 2-1). This plane is relatively small in humans compared to other primates (particularly *Pan* and *Gorilla*), and its anterior boundary is often indistinct. At the lateral edge of the articular eminence, where it joins the posterior root of the zygomatic arch, is a small rugose projection of bone called the articular tubercle. Although this term is frequently used to refer to the articular eminence (Weidenreich, 1943; Rightmire, 1993), these two structures are distinct, since the articular tubercle is non-articulating, and serves as an attachment point for the temporomandibular ligament.

Posterior to the articular fossa is a small ridge of bone that in humans is frequently enlarged into the postglenoid process (Fig. 2-1). This feature, in conjunction with the vertically oriented tympanic plate, forms the posterior border of the fossa in modern humans. This process

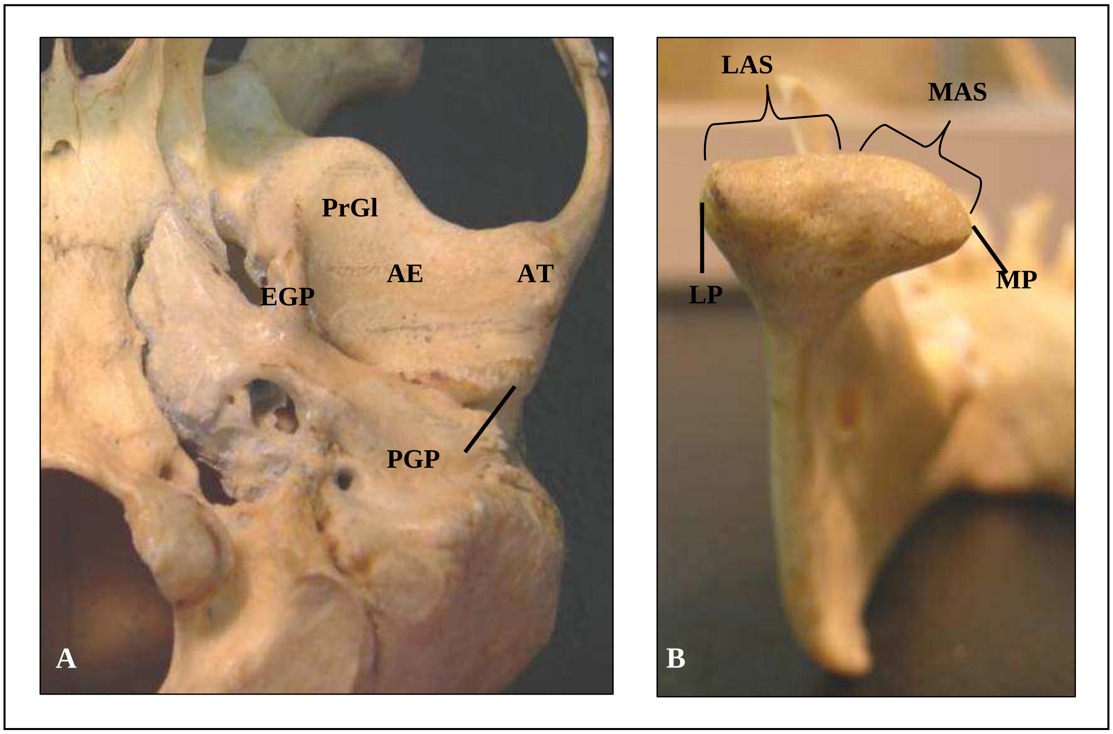


Fig. 2-1. Photographs of the mandibular fossa (A) and mandibular condyle (B) in *Pan*. AE= articular eminence, PGP= postglenoid process, EGP= entoglenoid process, PrGl= preglenoid plane, AT= articular tubercle, LAS= lateral articular surface, LP= lateral pole, MAS= medial articular surface, MP= medial pole. Photographs not to scale.

is often higher and thicker at its lateral end, forming a triangular outline in lateral view. The postglenoid process is variable in size in modern humans, but is markedly larger and significantly more projecting in non-human primates. Sicher (1951) noted that the presence of the postglenoid process is important, as it would limit any posterior displacement of the condyle, which would therefore not impinge upon the tympanic bone. However, such displacement of the mandibular condyle and its impingement of the tympanic in humans remains to be demonstrated (Hylander, 1991, 2006).

In comparison to the glenoid, the morphology of the mandibular condyle is relatively simple (Fig. 2-1). In most primates, the mandibular condyle, when viewed superiorly, is cylindrically shaped, with its mediolateral width approximately twice its anteroposterior length (Hylander, 2006). The condyle is situated perpendicular to the long axis of the body of the mandible, but because of the flare of the ascending ramus, the long axes of the articular condyles are offset from one another, crossing approximately at the anterior margin of the foramen magnum (Hylander, 2006). The condyle is offset medially in relation to the ascending ramus of the mandible, and both the medial and lateral poles of the condyle are slightly roughened due to the attachment of the temporomandibular ligament (laterally) and articular disc (both medially and laterally).

The articular surface of the condyle is strongly convex in both lateral and anterior view, with the anteroposterior curvature of the condyle much stronger than the mediolateral curvature. This convexity corresponds to the marked mediolateral concavity of the articular eminence often observed in modern humans. In superior view, the condyle can be divided into three articular areas: anterior, superior, and posterior. These surfaces are varyingly emphasized in different primate taxa (Wall, 1995) and are important during movement of the condyle. Additionally, when viewed anteriorly the condyle can be described as “tentlike” (Hylander, 2006) in shape, with distinct medial and lateral slopes; the medial slope is often particularly pronounced in many taxa, including humans, as it articulates with the medial wall of the articular fossa and the entoglenoid process.

Soft tissue anatomy

In contrast to other synovial joints in which hyaline cartilage lines the articular surfaces, the TMJ instead incorporates dense, avascular fibrous connective tissue. The presence of this type of tissue in the TMJ is a result of its type of ossification. Rather than ossifying from a cartilaginous anlage as in enchondrally formed bones (which incorporate hyaline cartilage to line joint surfaces), the components of the TMJ ossify intramembranously (i.e., dermal bone), and the periosteum surrounding these elements is co-opted early in development to form the major articular tissues of the TMJ (Nobel, 1973; Hylander, 2006).

The articular disc (Fig. 2-2) is an important component of the TMJ that facilitates movement in the superior and inferior joint compartments, and also gives rise to the articular capsule. The disc is oval in shape, with its greatest diameter oriented mediolaterally. The peripheral portions of the disc are considerably thicker than the central and intermediate zones. Anteriorly, the disc is bound to the anterior portion of the joint capsule, and posteriorly it splits into a double layer of connective tissue, the superiormost portion of which attaches to the postglenoid process and squamotympanic fissure, with the inferior portion attaching to the posterior portion of the condylar neck. Medially and laterally, the disc is not connected to the articular capsule, but is instead bound tightly to the medial and lateral edges of the articular component of the mandibular condyle.

In addition to fusing with the articular disc, the articular (or synovial) capsule attaches to the rim of the temporal bone’s articular surface. Anteriorly, the capsule attaches along the anterior surface of the articular eminence, posteriorly to the postglenoid process and squamotympanic fissure, medially to the entoglenoid process/articular eminence, and laterally to the articular

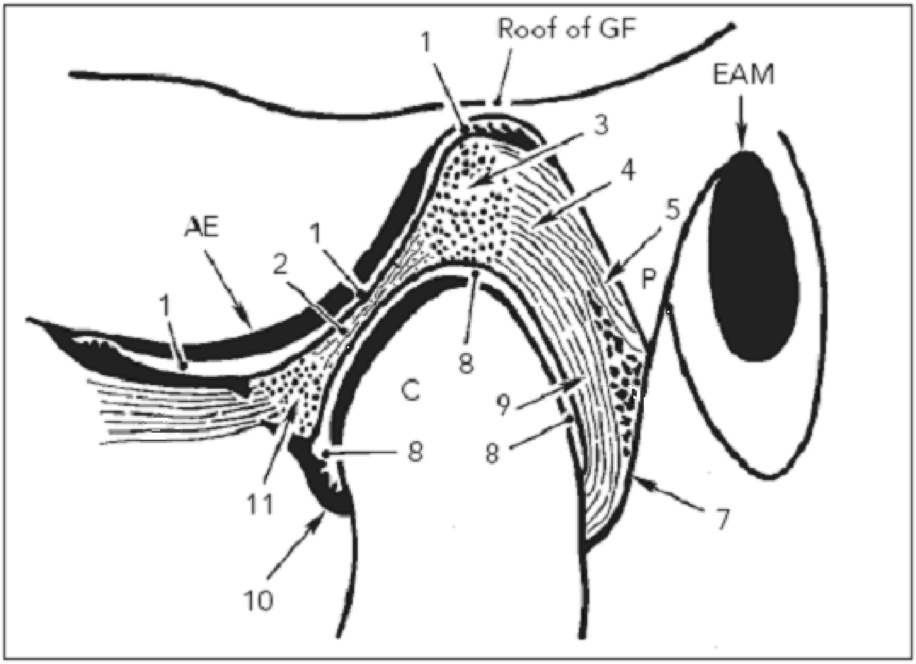


Fig. 2-2. Parasagittal section of the TMJ showing the articular tissues. Abbreviations are as in Figure 1. Components of the articular tissues include (1) upper joint compartment; (2) intermediate zone; (3) posterior band of articular disc; (4) bilaminar zone; (5) upper portion of bilaminar zone; (7) posterior portion of joint capsule; (8) lower joint compartment; (9) lower portion of bilaminar zone; (10) anterior portion of joint capsule; (11) anterior band of articular disc (Modified from Hylander, 2006).

tubercle. The entire capsule is fused inferiorly to the articular disc and head of the mandibular condyle. Whereas the articular capsule is relatively thin anteromedially, posteriorly, and medially, this fibrous tissue is markedly thickened laterally and anterolaterally and is referred to as the temporomandibular ligament (TML) (Hylander, 1991). The morphology of this ligament has been debated in the literature (DuBrul, 1988; Savelle, 1988; Hylander, 1991), with disagreement as to how frequently the articular capsule thickens to form a true TML. The consensus, however, is that the TML (at least in humans) is more frequently present than not, and that this structure is divided into two layers: a wide, fan-shaped superficial portion that runs anteroposteriorly and inferiorly, and a narrow deep portion that runs horizontally (Hylander, 1991). The organization of the fibers constituting the TML helps resist lateral displacement of the condyle, as well as forward excursion (resisted by the posterior fibers) and backward excursion (resisted by the anterior fibers).

Variation in TMJ morphology

Among the many species of non-human primates, few analyses have focused comprehensively on variation observed within the TMJ. Of these, the majority have focused almost exclusively on the great apes, likely because of their close relationship to hominins. As a result, there are many data regarding TMJ variation among the great apes, especially in comparison to human TMJ morphology. In general, the ape mandibular fossa is very shallow, with a poorly formed articular eminence. This ‘open’ morphology contrasts sharply with that observed in humans, where the glenoid fossa is considered very ‘deep,’ primarily as a consequence of the vertical reorientation of the tympanic (with the coincident merging of the tympanic and greatly reduced postglenoid process), the steep preglenoid plane, and highly angled posterior slope of the articular eminence (Weidenreich, 1943; Ashton and Zuckerman, 1954; Kimbel, 1986; Lockwood et al., 2002; Kimbel et al., 2004). The dimensions of the glenoid fossa differ among the apes and between apes and humans. The glenoids of *Pongo* and *Gorilla* can be characterized as relatively short AP and wide ML, while chimps have a relatively AP longer and ML narrower glenoid. In comparison, the human glenoid fossa is anteroposteriorly compressed, making it generally wider than it is long, but is still both absolutely and relatively smaller than the fossae of apes (Ashton and Zuckerman, 1954; Lockwood et al., 2002).

Other particularly notable differences in morphology include variations in the size of the preglenoid plane, entoglenoid process position and projection, and the overall position of the TMJ in relation to the lateral wall of the braincase (Lockwood et al., 2002). In all of the apes, the preglenoid plane is larger than in modern humans, with *Pan* possessing the largest preglenoid plane. This difference is especially significant, as it may help to explain the appearance of an AP compressed glenoid fossa in humans (i.e., the glenoid fossa seems AP compressed because of its reduced preglenoid plane), as well as the long narrow conformation of the glenoid in *Pan* (in which the preglenoid plane is enlarged and acts to elongate the glenoid fossa anteroposteriorly). Variation in the morphology of the entoglenoid process is also noteworthy; in the apes, the entoglenoid is absolutely much larger than it is in humans and is directed inferiorly from the medial edge of the articular eminence (DuBrul, 1974; Aiello and Dean, 1990; Lockwood et al., 2002). In humans, the entoglenoid is reduced in size and angles inferiorly and posteriorly. This distinct morphology can been explained as a consequence of the ‘twisting’ of the articular eminence about its transverse axis, which causes the lateral portion of the articular eminence to face inferiorly, while the medial portion faces primarily posteriorly (Kimbel, 1986; Aiello and Dean, 1990; Lockwood et al., 2002; Kimbel et al., 2004).

There are also marked differences in the mediolateral positioning of the glenoid fossa in the great apes and humans. In the great apes, the glenoid fossa has frequently been characterized as medially positioned in relation to the lateral wall of the cranial vault. However, the large degree of pneumatization of the temporal squama in the apes (and particularly *Pan*) means that the glenoid is actually more laterally positioned, in contrast to the more medially placed fossa of humans (Sherwood 1995; Sherwood et al., 2002). In addition, Sherwood (1995) noted that pneumatization of the temporal squama also affects the size of the postglenoid process in the apes. Sherwood (1995) characterized the postglenoid processes of *Pongo, Gorilla,* and *Pan* as variable in size, stating that "to classify the postglenoids as 'large' for this mixed group (*Pan* + *Gorilla*) is misleading. *Pongo* tends to show a sizable postglenoid and, interestingly, this often shows no signs of pneumatization" (Sherwood, 1995:90). However, in comparison to the human postglenoid process, there is little doubt that the great ape postglenoid is considerably larger, despite apparent variation within and among ape species (Ashton and Zuckerman, 1954; Kimbel, 1986; Sherwood, 1995; Lockwood et al., 2002). The highly variable postglenoid process of megaladapid strepsirrhines was also evaluated by Wall (1997), who proposed that the expanded posterior articular surface of the mandibular condyle in this group articulates with the postglenoid process during browsing.

The shape and orientation of the tympanic element is also distinctive in humans in comparison to other primates. In the great apes, the large postglenoid process is coupled with a horizontally oriented tympanic element, from which the postglenoid is spatially distinct. The tympanic element itself appears as a rounded tube, particularly in chimpanzees; *Gorilla* and *Pongo* have relatively more inferiorly projecting and vertically oriented tympanic elements, but these elements are still more tubular than the platelike form the tympanic assumes in humans (Kimbel et al., 2004). In this position, it is the postglenoid process, rather than the tympanic, that forms the posterior border of the mandibular fossa in all primates except humans. In contrast, the morphology of this region in humans is characterized by a tympanic element that directly abuts (and often merges with) the small postglenoid process, and the tympanic element is very platelike in form and vertically oriented so that it functions as the posterior border of the deep mandibular fossa (Weidenreich, 1943; Kimbel, 1986; Lockwood et al., 2002; Kimbel et al., 2004).

FUNCTIONAL ANATOMY

The TMJ is a mechanically complex joint that has been the subject of much investigation and debate in the scientific literature. Numerous biomechanical models have been proposed to explain the function of the masticatory apparatus, and many experimental analyses have been conducted to test these hypotheses. This section provides a brief overview of the primary models of the biomechanics of the masticatory apparatus and TMJ, including a review of the movements of the mandible, the muscles of mastication, and masticatory muscle activity, followed by a discussion of reaction forces in the masticatory apparatus and, in particular, at the TMJ.

Free movements of the mandible

There are two basic movements of the mandible: translation and rotation. Translatory movements primarily take place in the upper joint compartment, while rotary movements primarily occur in the lower compartment. Free movements of the mandible, which include depression and elevation (i.e., opening and closing), protrusion and retrusion, and lateral shifting, combine translation and rotation and these two movements therefore rarely occur independently. During opening and closing actions, both translatory and rotatory movements occur, although experimental analyses suggest that rotation may account for 75% of movement during jaw opening (Ferrario et al., 2005). As the mouth is opened, translation begins in the upper joint compartment and the condyle moves anteriorly and inferiorly along the slope of the articular eminence in conjunction with the articular disc. Coincidently, the condyle begins to rotate against the disc in the lower joint compartment. Protrusion and retrusion are simply the forward and backward shifting of the mandible, which are primarily (but not exclusively) translatory (Travers et al., 2000; Buschang et al., 2001). These movements mostly take place in the upper joint compartment, and are therefore limited by the TMJ joint capsule and the bony morphology of the mandibular fossa itself (Hylander, 2006).

Lateral deviation can occur at the TMJ, where the mandible rotates around a dorsoventrally oriented axis. This movement results from the unilateral translation of the balancing-side (non-biting) condyle anteriorly along the articular eminence (Harper, 1990; Piehslinger et al., 1994). The condyle on the opposite side (the resting or working condyle) does not translate as much as the balancing-side condyle, and there is slight rotation at this joint (Miyawaki et al., 2000). Additionally, during the opening stroke of mastication involving lateral deviation, the entire mandible is shifted transversely toward the working-side; this movement is referred to as the "Bennett shift" (Miyawaki et al., 2001; Hylander, 2006).

The morphology of the TMJ is a result of the trade-off between stability and mobility. For instance, the TMJ in carnivores, particularly some groups of canids, is shaped in such a way as to make the joint extremely stable, and therefore less mobile. In these groups, this stability is accomplished via the enlargement of the postglenoid and preglenoid processes, which wrap around the mandibular condyle, prohibiting mandibular translation (DuBrul, 1974). This increased stability is required to minimize the risk of TMJ dislocation associated with the use of the masticatory apparatus in capturing and subduing struggling prey (Maynard Smith and Savage, 1959).

As reviewed above, the primate TMJ is a relatively open joint with increased mobility, which is characterized by large amounts of anteroposterior translation. This ability, however, is not unique to primates, as it is also found in many omnivores and herbivores (Aiello and Dean, 1990; Wall, 1995). That primates possess this ability suggests increased mobility in this joint, which in turn results in more mobility of the mandible during mastication (Hylander, 2006). However, even this increase in mandibular mobility cannot adequately explain the full range of AP translation, an observation that has engendered discussion of the significance of AP translation, with two primary hypotheses proposed. The first, the airway impingement hypothesis (Smith, 1984), suggests that translation at the TMJ occurs as a consequence of raising the TMJ above the occlusal plane, which increases the depth of the mandible and therefore increases the likelihood that the mandible could impinge upon the airway during opening if only rotation occurs at the TMJ. Translation therefore occurs to move the mandible forward at the TMJ during opening, thus reducing the chances that the airway will be impaired. As discussed by Hylander (2006), two problems exist with this hypothesis: 1) it does not explain why AP translation occurs in those mammals with TMJs at or near the occlusal plane; and 2) there is no convincing evidence in humans that the airway would be obstructed if translation did not take place when opening the mouth. Alternatively, Hylander (1978, 2006) and Carlson (1977) have proposed a second explanation for translation at the TMJ: the sarcomere-length hypothesis. This hypothesis states that AP condylar translation is a mechanism to improve the mechanics of the masseter-medial pterygoid complex by minimizing the sarcomere length changes in these muscles during wide gapes. In other words, by translating the mandibular condyle forward and/or down onto the articular eminence, the masseter and medial pterygoid are stretched less than would be the case if the mandible were a simple hinge joint. As the force output of muscle fibers is inversely proportional to the amount they are stretched, this decreased stretch during translation allows for increased force output at a wide variety of gapes.

Although Hylander’s (2006) objections to the air-way impingement hypothesis are convincing, Wall (1995, 1999) found a positive correlation between the amount of gape and sagittal sliding (i.e., movement of the condyle in the sagittal plane whether due to rotation or translation). This finding suggests that the relative amount of gape is indeed linked to translatory movements of the mandible, and therefore translation in the mammalian TMJ cannot solely be explained via maximization of force output as suggested by Hylander (1978, 2006) and Carlson (1977).

Movements of the mandible during mastication

Masticatory movements are divided into two different types that incorporate elements of the free movements discussed above: incision (cutting with the anterior teeth) and mastication (grinding with the posterior teeth). Incision consists of three parts: opening, closing, and the power stroke, the first two of which can be almost directly equated to the free mandibular opening and closing movements. In these movements, the depressors of the mandible act to translate and rotate the mandibular condyles forward onto the articular eminence; the extent of this opening movement is governed by the size of the food object (Hylander, 2006). Next, the mandible swings anteriorly and superiorly via the actions of the elevators. As the incisors contact the food object, the power stroke begins, at which time force is applied to the food object as the jaw continues to close. During these movements, opening of the mandible is generally bilateral (i.e., movements occurring at the left and right TMJ are approximately equal). Correspondingly, the joint reaction force is approximately the same at each TMJ (Hylander, 2006).

Movements of the mandible during mastication include the opening, closing, and power strokes; together these three movements constitute a single chewing cycle. Multiple chewing cycles, often interspersed with multiple swallows makes up a chewing sequence (Hylander, 2006; Vinyard et al., 2008). However, in contrast to the movements occurring during incision, the actions of opening and closing of the jaw in mastication are very different from opening and closing of the free mandible. This difference is primarily a consequence of the lateral deviation of the mandible during opening, where the midline is shifted to the nonchewing or balancing-side and then back again to the working-side during closing (Byrd et al., 1978; Miyawaki et al., 2001; Hylander, 2006). During unilateral mastication, the working-side condyle does not move far from its starting position (at rest on the posterior slope of the articular eminence) with only slight rotation and lateral movement of the condyle, whereas the balancing-side condyle shifts downward and medially along the articular eminence (Komiyama et al., 2003; Miyawaki et al., 2000, 2001).

Masticatory musculature

The muscles governing movement at the TMJ are referred to as the muscles of mastication. Traditionally, this term refers to five paired muscles, the temporalis, the masseter, the medial and lateral pterygoids, and the digastric (Fig. 2-3 and 2-4). Four of these five muscles are most active during jaw closing, whereas the remaining muscle, the digastric (along with gravity), acts to depress the mandible during jaw opening. As with the preceding sections, terminology follows Hylander (1991, 2006), and the bulk of the descriptive detail for this discussion, unless otherwise noted, is drawn from Sicher (1951), Walker (1978), Hylander (1991, 2006), and Aiello and Dean (1990).

The masseter muscle is located on the lateral side of the skull, and originates superiorly from the zygomatic arch and inserts inferiorly on the ascending ramus of the mandible. This muscle can be divided into two portions, the superficial masseter and the deep masseter, and although these muscles can be divided posteriorly, anteriorly they are indistinguishable. The superficial masseter, which makes up the bulk of the muscle as a whole, arises along the lower border of the zygomatic arch via strong tendinous fibers. This attachment extends as far anteriorly as the zygomatic process of the maxilla, and may extend as far posteriorly as the zygomaticotemporal suture. These fibers are directed inferiorly and slightly posterior to attach along the lower one third of the ascending ramus of the mandible.

The deep masseter also arises from the lower border of the zygomatic arch but is located further posteriorly, extending as far as the articular eminence or zygomatic process root. On the

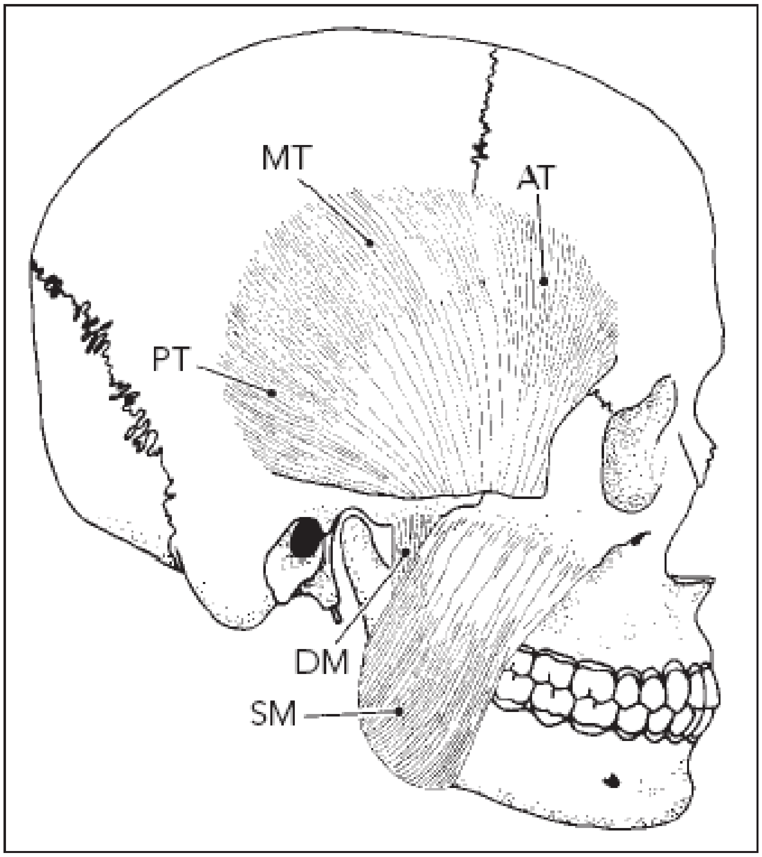


Fig. 2-3. Human cranium showing the temporalis and masseter muscles. (PT) posterior temporal; (MT) middle temporal; (AT) anterior temporal; (DM) deep masseter; (SM) superficial masseter (From Hylander, 2006).

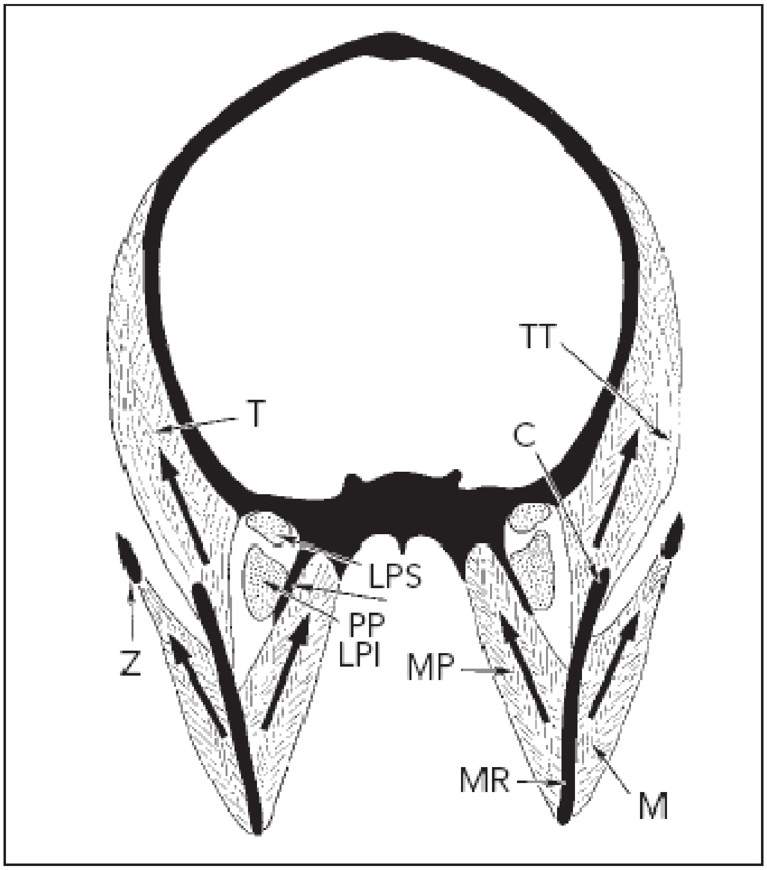


Fig. 2-4. Coronal section through a human skull showing the muscles of mastication. Direction of muscle forces are indicated by the heavy arrows. (T) temporalis; (TT) central tendon of temporalis muscle; (Z) zygomatic arch; (C) coronoid process; (LPS) lateral pterygoid, superior head; (PP) pterygoid process (lateral); (LPI) lateral pterygoid, inferior head; (MP) medial pterygoid; (MR) mandibular ramus; (M) masseter. (From Hylander, 2006).

mandible, the deep masseter inserts above the superficial portion, along the upper part of the ascending ramus. The two portions of the masseter act together as powerful elevators of the mandible, although these muscles are active at slightly different times during movements of the mandible (Van Eijden et al., 1993). The line of action of the deep masseter is primarily vertical, whereas the superficial masseter exerts a force that is directed slightly anteriorly. There is also a lateral component of the force exerted by these muscles, since the zygomatic arch flares more laterally than does the ascending ramus of the mandible.

A third portion of the masseter is sometimes also distinguishable, particularly in non-human primates. This portion of the masseter is referred to as the zygomaticomandibularis muscle, and is often considered part of the deep masseter. The fibers of the zygomaticomandibularis muscle are fused with the superficial fibers of the anterior temporalis muscle and run from the inner border of the zygomatic arch to the base of the coronoid process (Aiello and Dean, 1990).

The temporalis is a fan-shaped muscle that originates along the lateral surface of the cranium and runs inferiorly and anteriorly to insert on the coronoid process of the mandible. The origin of this muscle leaves two elevated bony markings, the inferior and superior temporal lines, which run along the frontal, sphenoid, parietal and temporal bones. These two lines are formed by the attachment of the temporalis fascia (a tough layer of investing tissue surrounding the exterior of the temporalis) and the central tendon of the temporalis muscle, respectively (Aiello and Dean, 1990). The main action of this muscle, like the masseter, is to elevate the mandible. Furthermore, like the masseter, the temporalis can be divided into several portions. These portions, however, are less discrete than those of the masseter, and are primarily differentiated on the basis of their fiber orientation and lines of action. Within the fan-shaped structure of the temporalis, there are roughly three groups of fibers: the anterior fibers, which constitute the bulk of the muscle and run almost vertically; the posterior fibers, which are oriented almost horizontally and bend around the posterior root of the zygomatic arch before becoming vertical and attaching to the coronoid process, and the middle fibers, which become increasingly oblique posteriorly. Because of this arrangement of muscle fibers, the temporalis can exert varying degrees and directions of force, depending on which fibers are active at any given time (Blanksma and van Eijden, 1990; van Eijden et al., 1996, 1997). For instance, action of the vertically oriented anterior fibers acts simply to exert an upward force on the mandible. In contrast, differential use of the posterior fibers, for which the line of action is primarily posterior, would serve to retrude or retract the mandible. Further division of the temporalis was proposed by Lovejoy and Ferrini (1974), who identified seven biomechanically distinct portions of this muscle during dissections of rhesus macaque masticatory musculature. Subsequent EMG studies by van Eijden and colleagues (e.g., Blanksma and van Eijden, 1990; van Eijden et al., 1996, 1997) have identified at least six regions of the temporalis, the activity of which varies as a result of the bite force. This increased segmentation could influence patterns of mechanical action of the mandible, as these different portions each possess varying lines of action and cross-sectional areas.

The pterygoid muscles are situated medial to the temporalis and masseter muscles and attach along the medial side of the mandible and to the pterygoid plates of the sphenoid. Of these two muscles, the medial pterygoid is the largest, and is often referred to as the anatomical counterpart of the masseter, because it exerts a medially directed force on the mandible that opposes the slightly laterally directed force of the masseter. The medial pterygoid originates medially primarily within the pterygoid fossa of the sphenoid, and runs inferiorly, posteriorly, and laterally to insert along the medial surface of the mandibular angle. As with the temporalis and masseter, the medial pterygoid also acts as an elevator of the mandible. Additionally, the orientation of its fibers allows for a medial component of the exerted force.

The lateral pterygoid is located just lateral and superior to the medial pterygoid. This muscle can also be divided into two portions, the superior and inferior heads, which originate separately (superior: inferior surface of the greater wing of the sphenoid; inferior: lateral aspect of the lateral pterygoid plate) but are indistinguishable at their insertion, a small depression along the antero-medial surface of the neck of the mandibular condyle (termed the pterygoid fovea). A small portion of the superior head also attaches to the TMJ capsule and disc, and has been suggested to have a ligamentous attachment to the malleus (Öğütcen-Toller and Juniper, 1994; Öğütcen-Toller and Keskin, 2000). The two portions of the lateral pterygoid have slightly different actions. The inferior head, which runs slightly superiorly and posteriorly from the cranium to the mandible, acts primarily to open and protrude the mandible. In contrast, the fibers of the superior head run inferiorly and posteriorly, and act to elevate the mandible. Unilateral action of either head, however, acts to shift the midline of the mandible to the opposite side (lateral excursion).

The digastric, while not as large as the four muscles discussed above, is also considered to be an important muscle of mastication. This muscle, which as its name implies has two distinct bellies, is a long, thin muscle with anterior and posterior bellies that are connected via a strong intermediate tendon. The posterior belly arises posteriorly from the medial side of the mastoid process in the digastric groove, and runs anteriorly and inferiorly to the hyoid, where the intermediate tendon is connected via a loop of fascia. The anterior belly then rises superiorly to attach at the digastric fossa, which is located along the midline lingual surface of the mandible. Although small, the digastric muscles act as the primary depressors of the mandible (with gravity providing most of the force required to depress the mandible and open the mouth). In addition, the digastric has also been suggested to assist in retrusion of the mandible. The anatomy of this muscle is especially variable, both within and between species. In particular, the anterior belly is most frequently altered, with fusion of the two parts of the anterior belly along the midline common. An especially notable variation in the morphology of the digastric is found in orangutans, which lack the anterior belly completely, with the posterior belly attaching via a thick round tendon to the angle of the mandible between the medial pterygoid and masseter (Aiello and Dean, 1990).

Finally, a number of other muscles that attach to the hyoid and run to the mandible and the styloid are also active during mastication. These include the mylohyoid (hyoid to lingual surface of mandibular corpus), geniohyoid (hyoid to midline lingual surface of mandible), stylohyoid (hyoid to styloid), and infrahyoid (hyoid to thyroid cartilage and manubrium). The geniohyoid and mylohyoid muscles together form the floor of the oral cavity, and both act to slightly raise the hyoid and the floor of the mouth, or when the hyoid is fixed, they can function to depress the mandible. In contrast, the stylohyoid and infrahyoid muscles play larger roles in governing the movements of the hyoid; the stylohyoid functions as a stabilizer, retractor, and elevator of the hyoid, while the infrahyoid acts to stabilize and lower the hyoid.

All of these masticatory muscles fire at different times during a chewing cycle. Although there is considerable variation across mammals in the firing patterns of these muscles during chewing, some researchers have suggested that there is a common, primitive firing pattern that can be found in many mammals, including some primates (Hiiiemae, 1978; Gorniak, 1985; Weijs, 1994; Langenbach and van Eijden, 2001). This pattern is characterized by three groups of muscles that fire together. The first is referred to as the vertically oriented group of symmetric closers (VSC), which includes the anterior and deep portions of the temporalis and zygomaticomandibularis muscles on both the working- and balancing- sides. These muscles are thought to fire first in the chewing cycle, with their peak activity occurring during the closing stroke. The second group is referred to as Triplet I, and includes the working-side posterior temporalis, balancing-side medial pterygoid, and balancing-side superficial masseter. Activity in these muscles peaks after the VSC group and near the start of the power stroke. Finally, muscles in Triplet II, which includes the balancing-side posterior temporalis, working-side medial pterygoid, and working-side superficial masseter, peak just after Triplet I and later during the power stroke (Hylander et al., 2005; Vinyard et al., 2005; Vinyard et al., 2008).

The relative proportion of the balancing- and working- side forces of these muscles have been shown to vary among taxa. In particular, the activity of the deep masseters varies among species and has not been consistently linked to either Triplet I or II (Vinyard et al., 2008). Activity of the balancing-side deep masseter has been associated with wishboning stresses at the mandibular symphysis (Hylander et al., 1987; Hylander and Johnson, 1994). In anthropoid primates, the balancing-side deep masseter is consistently recruited late in the power stroke, whereas no such pattern has been observed in nonanthropoid primates (Hylander et al., 2000, 2002). This finding led Hylander and colleagues (2000, 2002) to hypothesize that fusion of the mandibular symphysis in anthropoids is associated with wishboning stresses created when the balancing-side deep masseter is recruited in this way.

Forces within the masticatory apparatus

The masticatory apparatus has frequently been conceptualized as a class-three lever, primarily on the basis of work performed by Hylander and colleagues (Hylander, 1975a,b, 1979a,b, 1991, 2006; Hylander and Crompton, 1980; Hylander and Johnson, 1985; Hylander et al., 1992; Hylander et al., 2005). This model indicates that the TMJ is loaded during mastication, and that this load (the joint reaction force) resists the adducting force of the muscle resultant in conjunction with the bite force. In order to maintain static equilibrium, the magnitudes of these forces and their respective moment arms must then cancel one another out. These forces act to maintain static equilibrium, with the assumption that no motion is occurring (i.e., translatory and rotary forces cancel one another out) (Spencer, 1995). This system can be modeled in either two or three dimensions. Modeling the mandible two-dimensionally requires a number of assumptions and/or simplifications. First and foremost, all loads and reaction forces are projected into a single plane, and then are often analyzed in lateral projection. Such a model is simplistic, since it does not allow for the analysis of how joint reaction forces vary between the working- and balancing-side condyles. Neither does it consider how the balancing- and working-side muscle resultant forces vary, since joint reaction forces and muscle resultant forces along both the working- and balancing-sides are summed (Smith, 1978; Spencer, 1995; Hylander, 2006). Incorporation of these aspects of jaw biomechanics is particularly critical when the goal of the analysis is to understand the forces involved in unilateral mastication or biting (Hylander, 2006). This model is sufficient, however, for analyses of bilateral biting or incision, which would therefore load both condyles equally, making the force output of the balancing- and working-side musculature equal (Hylander, 2006). Calculation of joint reaction forces under this model indicate that, as the bite point moves posterior to the muscle resultant force, the joint reaction force becomes negative, or tensile (i.e., the condyle is pulled away from the articular eminence) and when the bite point is anterior to the muscle resultant force, the joint reaction force is positive, or compressive. Tensile loading can cause distraction and injury of the joint, and comparative analyses of the primate masticatory apparatus suggest the bite point is situated well anterior to the muscle resultant to avoid this type of loading (Spencer, 1999). Furthermore, the bite force increases curvilinearly as it approaches the TMJ, indicating that bite forces are greatest along the posterior dentition.

In contrast, viewing the mandible as a three-dimensional unit allows for a consideration of unequal joint reaction and muscle resultant forces on the working- and balancing-sides of the masticatory apparatus. The most frequently utilized three-dimensional model is the one developed by Greaves (1978), who proposed that forces within the masticatory apparatus were best understood by viewing the mandible occlusally, with force vectors mapped onto the mandible in the occlusal plane (Fig. 2-5). In this model, the force vectors are viewed anteriorly, and the working-side joint reaction force, the balancing-side joint reaction force, and the bite force form the corners of what Greaves (1978) refers to as the “triangle of support.” The three components of

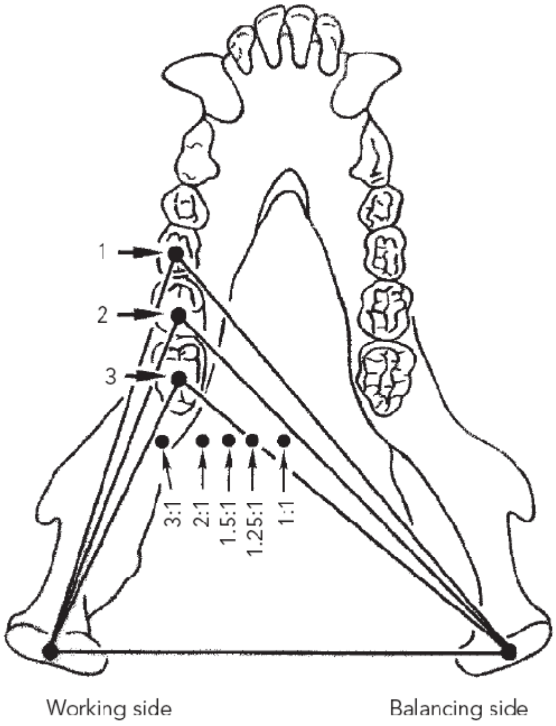


Fig. 2-5. Occlusal view of a macaque mandible showing three “triangles of support” as defined by Greaves (1978). Bite points are located along the first, second, and third molars, and the muscle resultant is indicated by the solid circles and ratios. Ratios indicate the pattern of muscle recruitment on the working- and balancing- sides; for instance, when the working- side muscle force is 2.0 times the balancing- side muscle force, the muscle resultant is located at 2:1. (From Hylander, 2006).

this triangle must therefore provide an equal amount of force to the muscle resultant in order to maintain static equilibrium. The magnitude of joint reaction force and how it is distributed between the working- and balancing-side condyles during incision or mastication is dependent upon the magnitude of the muscle resultant force but also on the position of the bite point. If the bite point is located on the anterior teeth, the bite force will be relatively low, and therefore most of the muscle resultant force must be resisted at the TMJs; since the muscle resultant is likely to lie close to the midline (e.g., mid-sagittal plane), forces in both TMJs should be approximately equal (Spencer, 1995; Hylander, 2006). As the bite point moves posteriorly, the bite force increases and TMJ reaction force decreases (Hylander, 1979a; Brehnan et al., 1981). Since the bite point is no longer in the midline, the side of the triangle of support connecting the balancing-side condyle and the bite point approaches the muscle resultant force (assuming that it still lies in the midline; i.e., the force produced by the working- and balancing-side musculature is equal). This shift results in the balancing-side reaction force resisting more of the muscle resultant force than the working-side. Further posterior movement of the bite point should result in the muscle resultant force lying outside of the triangle of support, which causes the mandible to rotate about the axis between the balancing-side condyle and the bite point, with the working-side condyle pulled away from the articular eminence, results in tensile forces in the TMJ (Greaves, 1978; Hylander, 1979a; Spencer, 1995).

Greaves (1978) argued that, since the TMJ is poorly suited to resist tensile forces, the optimal configuration of the masticatory apparatus is one in which the muscle resultant does not fall outside of the triangle of support. The primary mechanism by which this is accomplished is the shifting of the muscle resultant force away from the midline towards the working-side by the generation of unequal force in the working- and balancing-side masticatory musculature. Greaves (1978) acknowledged, however, that differential activity of the masticatory musculature could not necessarily always adequately shift the muscle resultant so that it remained within the triangle of support. For example, if the muscle resultant force vector was located anterior to the bite point, the triangle of support would lie entirely posterior to the muscle resultant, which would then cause the TMJ to be loaded in tension. Greaves therefore hypothesized that the molar dentition should be located immediately anterior to the muscle resultant force, in order to maximize bite force and minimize joint reaction forces. Experimental analyses of joint loading support Greaves' model; at various bite points along the tooth row, Hylander and colleagues (Hylander, 1979a, Hylander and Bays, 1978, 1979) observed that joint reaction forces were compressive when located anteriorly (along the premolars and M1-M2), whereas the condyle was either only slightly compressed, was not stressed, or was loaded in tension at more posterior bite points. Analyses by Hylander (1979a) and Hylander and Bays (1978, 1979) found that forces on the balancing-side condyle were, on average, greater than those recorded on the working-side. Spencer (1995, 1999) confirmed that, at least in anthropoid primates, the expectations of Greaves' (1978) "constrained lever model" (Spencer, 1995, 1999) are met, although the muscle resultant force was found to lie further posterior than was expected (i.e., not immediately posterior to the dentition). These results suggest that the form of the masticatory apparatus is relatively conserved in the taxa examined, so that unpredictable loading scenarios that may result in tensile forces at the TMJ can be avoided.

In their most basic incarnations, both the two- and three-dimensional models are simplified by assuming that 1) the mandible is a homogenous, rigid body, 2) all muscle vectors are added to create a single muscle resultant force, 3) the TMJ is level with the occlusal plane, and 4) the vectors of the muscle resultant, joint reaction, and bite forces are perpendicular to the reference plane (defined here as the axis between the bite point and the TMJ) (e.g., Gysi, 1921; Barbenel, 1972; Grant, 1973; Hylander, 1975b; Greaves, 1978; Smith, 1978; Baragar and Osborn, 1984, 1987; Spencer, 1995; Gallo et al., 1997; Wall and Hylander, 1999; Hylander, 2006). Of these assumptions, variations on the latter three are the easiest to incorporate into biomechanical models. With a TMJ positioned above the occlusal plane, as it is in most primates and many other mammals (which is contrary to the third assumption above), a single reference plane drawn between the occlusal plane (which encompasses all possible bite points) and the joint is no longer possible. Instead, multiple reference planes must be considered depending upon the position of the bite point in either the two- or three-dimensional models. In conjunction with the retention of a vertical muscle resultant force, this change reduces forces at both the bite point and at the TMJ. However, inclining the muscle resultant force anteriorly (therefore making it once again perpendicular to the reference plane) causes an increase in bite forces and a decrease in TMJ reaction forces (Spencer, 1995).

Incorporating forces that are not perpendicular to the reference plane (i.e., non-normal) is even more complicated than understanding the effects of raising the TMJ above the occlusal plane (Barbenel, 1972; Baragar and Osborn, 1987; Spencer, 1995). Assuming that the muscle resultant is perpendicular (or normal) to the reference plane automatically implies that the vectors of the joint reaction and bite forces are also normal. However, inclination of the muscle resultant requires that the non-normal components of this force be resisted by non-normal forces at the TMJ and/or the bite point (Throckmorton and Throckmorton, 1985; Throckmorton, 1985; Faulkner et al., 1987). While shifts in the positioning of the muscle resultant are accomplished via changes in the positioning or size of the masticatory muscles, non-normal forces in the TMJ or bite point must be generated primarily via hard tissue changes (i.e., inclination of the articular eminence, occlusal topography, etc.); whether the bite force or the joint reaction force contribute more in resisting the muscle resultant is likely dependent upon bony morphology of the TMJ or the dentition.

The instantaneous center of rotation (ICR) has been proposed to be either stationary within the mandibular condyle or changing during movement of the mandible (Grant, 1973; Hylander, 1975b; Baragar and Osborn, 1984). Most recent calculations of the ICR favor the latter of these two interpretations, suggesting that the ICR is most frequently found in the gonial region along the lower border of the mandible and that its path forms a U-shaped arch in lateral view during mouth opening (Grant, 1973; Gallo et al., 1997; Wall and Hylander, 1999). Several authors have argued that incorporating the ICR into analyses of TMJ biomechanics is critical, as the ICR influences the calculation of muscle moments. However, for the lever model of jaw biomechanics, it has been demonstrated that the analysis of the ICR does not influence estimates of reaction fores and muscle force vectors, as is needed in this model (Stern, 1974; Hylander, 1975b; Smith, 1978).

The conceptualization that different amounts of force may be acting on each of the TMJs simultaneously (i.e., one is loaded in compression while the other is in tension) may give the impression that forces are evenly distributed within a single condyle. Evidence to suggest otherwise, however, has been proposed primarily via studies of joint remodeling and dysfunction (Moffett et al., 1964; Richards and Brown, 1981; Hinton, 1981; Richards, 1987, 1988, 1990; Sheridan et al., 1991). Remodeling of the TMJ is continuous following the attainment of adult TMJ proportions. Histological examination of normal human TMJs by Moffett et al. (1964) showed that both progressive (where bone is added) and regressive (where bone is resorbed) remodeling can occur simultaneously in different portions of the same joint. More specifically, progressive remodeling was primarily identified on the medial portion of the articular eminence, and on the roof of the mandibular fossa. In contrast, regressive remodeling was mostly identified on the lateral part of the articular eminence. These findings suggest that different portions within the TMJ experience different patterns of loading. The biomechanical reasons for differential loading within the TMJ are not clear, although it has been suggested that these patterns are a result of twisting of the mandibular condyle during the power stroke of mastication and during isometric biting (Hylander, 1979b, 2006). Twisting results in eversion of the lower border of the mandible with coincident inversion of the coronoid process, which may cause the lateral border of the condyle to be pressed firmly against the lateral portion of the articular eminence. Increased stresses within the lateral component of the working-side TMJ may also be related to the mediolateral shifting of the condyle during unilateral mastication. Both of these explanations invoke higher compressive stresses along the lateral edge of the articular eminence, which is consistent with the finding by Moffett et al. (1964) that this portion of the articular eminence experiences a larger degree of regressive remodeling than the medial portion of the articular eminence. These forces may then explain the higher degree of degenerative pathologies identified in this region of the glenoid (Richards and Brown, 1981), as well as an increased incidence of perforations of the articular disk along its lateral edge (Oberg et al., 1971).

FACTORS INFLUENCING TMJ SHAPE

Given this model of TMJ function, three main factors that primarily influence TMJ morphology can be identified. First, the amount of muscle force required to process a food item will vary depending upon the material properties of the food (e.g., Lucas, 2004; Williams et al., 2005). Second, the location of the bite point will influence the amount of bite force versus joint reaction force, as well as the distribution of the joint reaction force across the balancing- side and working- side condyles (e.g., Hylander, 1979a; Hylander and Bays, 1979; Brehnan et al., 1981). Finally, behavioral and dietary demands associated with gape requirements will also influence the range of motion within the TMJ (e.g., Lucas, 1981, 1982; Wall, 1995, 1999; Vinyard et al., 2003; Hylander and Vinyard, 2006; Hylander et al., 2008).

Food material properties

The material property of a given food object is largely a function of that object’s elastic modulus and toughness. The elastic modulus refers to the rigidity or stiffness of an object (e.g., the ratio of stress to strain); food objects are defined along a continuum of elasticity, the endpoints of which can be referred to as rigid (difficult to deform) or soft (easily deformable). In contrast, toughness refers to the energy required to propagate cracks within a given material. The toughness of an object can then be identified as either tough (difficult to propagate cracks) or brittle (easy to propagate cracks). Thus, the elastic modulus describes the initial resistance of an object to crack propagation, and the relative toughness of the food object determines the amount of energy required to further break down the food item (Lucas, 2004; Williams et al., 2005). A further way in which food items may be characterized is hardness. Although not a material property in the same way as elastic modulus and toughness, hardness is defined as the resistance of an object to deforming under indentation (Lucas, 2004). On the basis of these material properties, primate diets primarily include three major combinations of these variables; hard/rigid and brittle, soft and brittle, and soft and tough (Lucas and Luke, 1984; Spencer, 1995; Williams et al., 2005). Hard/rigid and brittle foods such as seeds and nuts tend to resist fracture initiation, but once punctured, shatter easily. Soft and brittle foods, in contrast, are easily fractured and do not require much energy to further break down; examples of this type of food are fleshy fruit parts or soft-bodied insects. Finally, foods that are both soft and tough, such as leaves, require little energy to initially fracture, but are generally made of a fibrous material that reduces crack propagation, therefore increasing the amount of energy needed to fully break down the food item (Spencer, 1995; Lucas, 2004; Williams et al., 2005).

For the purposes of the discussion here, these categories are referred to simply as hard, soft, and tough food objects. Hard and tough food objects may be referred to collectively as resistant foods, as both require increased force production either via an increase in the magnitude or frequency of the force applied to the food object. For primates to adequately process more resistant food objects, higher magnitude and/or higher frequency bite forces must be produced by the masticatory apparatus, which, in turn, increases the total magnitude of the joint reaction force at the TMJ. Analyses of masticatory movements during the comminution of foods with different food material properties suggest that, as the food-object becomes more resistant (either because of toughness or hardness), lateral deviation of the mandible increases (Byrd et al., 1978; Anderson et al., 2002; Komiyama et al., 2003; Wall et al., 2006). Therefore, in addition to increased forces occurring at the TMJ, taxa that masticate hard and/or tough foods may have adaptations within the TMJ associated with this increased range of motion. In comparison to soft-object feeders, hard- and tough- object feeders should have TMJs that are designed to 1) withstand larger and/or minimize joint reaction forces, and 2) accommodate increased movement of the condyle.

Bite point location

The location of the bite point (i.e., on the anterior or the posterior teeth) plays a major role in the amount of force occurring at the TM joints. Theoretical and experimental analyses have shown that bite force increases as the bite point moves posteriorly and the TMJ reaction force concurrently decreases (Hylander, 1979a; Hylander and Bays, 1979; Brehnan et al., 1981). Thus, bite forces are lowest on the anterior teeth and highest on more posterior teeth, while the joint reaction force is higher during use of the anterior teeth than during mastication on the posterior teeth (Hylander, 1979a; Hylander and Bays, 1979; Brehnan et al., 1981). All other factors being equal, taxa that extensively use their anterior teeth should therefore need to withstand larger joint reaction forces than taxa that rarely use their anterior teeth. However, such a distinction is difficult to test, primarily due to the difficulty of finding taxa that represent a pure comparison between anterior versus posterior tooth use. For example, many taxa that use their anterior dentition to process resistant food objects may still produce increased forces along the posterior dentition during mastication of the same food objects. Alternatively, taxa that tend not to process food items on their anterior dentition tend to rely very heavily on repetitive mastication of food objects along their posterior dentition. However, it is unclear whether the force associated with increased use of the anterior teeth is more intensive than repetitive loading of the posterior teeth, and only a few analyses have addressed this topic (Smith et al., 1983; Bouvier, 1986a,b;

Taylor, 2006, 2009). As a result, although a series of expectations are laid out in Chapter 4 in regard to the relative influence of anterior versus posterior tooth use, the present study may serve to provide initial data regarding masticatory apparatus variation in relation to differential tooth use that may be explored in more detail in subsequent analyses, particularly in conjunction with addition experimental analyses of the forces associated with anterior or posterior dental use and food material property data.

Gape requirements

The shape of the TMJ is also likely to be related to the range of motion at the joint. In particular, gape requirements should necessitate specific morphological characters at the joint which may function to maximize the distance that the mouth can be opened. Large gapes in primates have been linked to the incision or mastication of large food objects, tree-gouging associated with exudate feeding, as well as social displays and canine length (Lucas, 1981, 1982; Ravosa, 1990; Wall, 1995, 1999; Spencer, 1999; Vinyard et al., 2003; Burrows and Smith, 2005; Hylander and Vinyard, 2006; Hylander et al., 2008). Gape can be increased in several ways. Linear gape (the distance between the upper and lower incisors at maximum jaw opening) can be increased by lengthening the mandible or decreasing the distance between the occlusal plane and the TMJ (Herring and Herring, 1974; Smith, 1984; Ravosa, 1990; Wall, 1995; Singleton, 2005). Minimizing muscular constraints on gape is also important; more posteriorly positioned masticatory muscles (particularly the masseter) are more advantageous for increased jaw gapes, whereas anteriorly positioned muscles act to decrease gape (but increase muscle force by decreasing the ratio between the bite force and muscle force moment arms) (Herring and Herring, 1974; Smith, 1984; Spencer, 1999). Since gape is essentially achieved by the mandible rotating around the skull, the amount and type of movement at the TMJ is also correlated with gape; accordingly, the amount of sagittal sliding in the TMJ has been shown by Wall (1995, 1999) to be positively correlated with gape. Consequently, in taxa with large gapes (whether for behavioral or dietary reasons), adaptations that allow for increased sagittal sliding in the TMJ should be observed (Wall, 1995, 1999; Hylander and Vinyard, 2006). In the TMJ, features that increase movement at the joint should be observed in those taxa that have relatively larger gape, and particularly those features that increase the anteroposterior movement at the joint (e.g., a relatively AP long glenoid and postglenoid plane, and larger articular area of the mandibular condyle).

SUMMARY

The bony and soft tissue components of the TMJ are variable within and among taxa. Yet most of what is known regarding variation in the shape of this joint is only applicable to humans. As a result, much work remains to quantify variation in this joint across primates as a whole. Furthermore, as part of the masticatory apparatus, the TMJ is a functionally complex joint that in primates is optimized for increased mobility, which may be associated with the wide array of food items ingested by members of this order. The loading regimes experienced in this joint are also highly variable, and dependent upon the position of the bite point and the recruitment of working- versus balancing- side muscles.

As outlined in the preceding chapter, much of the variation in TMJ morphology that has been observed across primate taxa has been linked to variation in masticatory demands associated with the use of different diets. In particular, this variation can potentially be linked to observed variation across taxa in the utilization of foods with different material properties, the use of the anterior vs. posterior dentition, and relative gape. These three aspects of variation in primate masticatory function tie in more generally to differences in the relative amount of joint reaction force and the range of motion allowed by the TMJ. The biomechanical framework presented here provides the basis upon which more detailed experimental and comparative research regarding

TMJ function has been founded (which will be presented in Chapter 4), and with which a series of predictions regarding the function of the specific components of the TMJ will be proposed and tested.

CHAPTER 3: MATERIALS AND METHODS

DATA COLLECTION METHODS

Geometric morphometrics

By far the predominant way in which TMJ form has previously been quantified has been through linear measurements describing the length and width of the joint (e.g., Weidenreich, 1943; Ashton and Zuckerman, 1954; Smith et al., 1983; Bouvier, 1986a,b; Wall, 1999, Taylor, 2005, 2006). Other analyses have employed the use of angular measurements or indices of curvature (e.g., Angel, 1948; Wall, 1995, 1999). Although many of these measurements are employed here, a great deal of shape variation is lost in these analyses, particularly in regard to the topography of the glenoid fossa. Fortunately, the increasing use of geometric morphometrics in physical anthropology (Lynch et al., 1996; O’Higgins and Jones 1998; Delson et al. 2001; Harvati, 2001, 2003; Hennessey and Stringer, 2002; Lockwood et al., 2002, 2004; Guy et al., 2003; Harvati et al., 2004; Slice, 2005; McNulty et al., 2006; Baab 2007; Constantino, 2008; Gunz et al., 2009; and many more) provides an alternative to traditional methodologies. Geometric morphometrics is a powerful quantitative method that allows shape differences among individuals and groups to be summarized and compared. The use of 3D coordinate data in conjunction with the analytical methodologies of geometric morphometrics can therefore evaluate aspects of TMJ shape that have previously been difficult to quantify and compare among taxa, with considerably less loss of shape information. Aspects of shape that would have previously been broken into specific measurements of components of the TMJ can be analyzed together as a single unit. Although not employed here because of the current lack of software infrastructure, three-dimensional semilandmarks describing the entire surface and/or outline of the joint surfaces will capture additional shape information and will be incorporated into future analyses.

Geometric morphometrics is defined as a collection of approaches for the multivariate statistical analysis of Cartesian coordinate data, usually limited to landmark point locations (Bookstein, 1991). Simply put, these methods allow for the analysis of complex shapes that would otherwise be virtually impossible to measure via traditional craniometric or morphometric methods. Superimposition methods allow for the decomposition of complex forms, such as the temporal bone, into size and shape (Zelditch et al., 2004). Shape in geometric morphometrics is defined as “all the geometric information that remains when location, scale, and rotational effects are filtered out from an object” (Kendall, 1977). Size of an object in geometric morphometric analyses is retained after superimposition as centroid size: the sum of squared Euclidean distances from each landmark to the centroid of the shape. Generalized Procrustes Analysis (GPA), the method of superimposition used here, minimizes differences between landmark configurations (Zelditch et al., 2004). This method works by centering, scaling, and rotating objects so that the sum of the squared distances between equivalent landmarks in a group of forms is minimized (Zelditch et al., 2004; Rohlf, 1990). Following GPA, landmark coordinates are represented as points in Kendall’s Shape space, where each point in this shape space represents the shape of a configuration of points in space, irrespective of size, position, and orientation (Slice et al., 1998). Procrustes residuals, the set of vectors connecting the landmarks in the final Procrustes rotated consensus configuration (Slice et al., 1998) then form the basis for all subsequent statistical analyses, which were conducted using Statistica (Release 8.1, Statsoft, Inc.). Geometric morphometric analyses were carried out using the program *Morphologika* (O’Higgins and Jones, 1998), and the program MorphoJ (Klingenberger, 2008).

Because of the very specific nature of the analyses conducted for each of the three main sections of this dissertation, the analytical methods used subsequent to the initial geometric morphometric analyses outlined above will be described in detail in each chapter.

Landmark data

A total of 81 geometrically homologous landmarks (e.g., landmarks representing the same geometric feature on all specimens) (Zelditch et al., 2004; Gunz et al., 2005) were digitized for this study (Table 3-1, Fig. 3-1) using a Microscribe G2X digitizer (Immersion Corp., San Jose, CA). These landmarks were chosen because they reflect aspects of variation in the masticatory apparatus and cranium, and many of these same landmarks have been used in previous analyses of these regions (e.g., Spencer, 1995; Lockwood et al., 2002, 2004). During data collection, landmarks were identified and marked using pencil or artist's putty prior to digitization. Each specimen was mounted upside down in a stable elevated ring and the mandible placed in occlusion so that all cranial and some mandibular landmarks could be obtained in a single series. Additional points were captured that were not accessible when the mandible is in occlusion (e.g., points on the mandibular condyle). Coordinate data were then used in a series of geometric morphometric analyses, primarily utilizing landmarks on the articular surfaces of the TMJ, relationships among which were then visualized using wireframe diagrams (Fig. 3-2).

The coordinate data were further used to calculate linear and angular measurements using the program MacMorph (Spencer and Spencer, 1993). These measurements included variables designed to quantify aspects of TMJ morphology (e.g., glenoid length and width), bony masticatory morphology (e.g., TMJ height, mandible length), variation in masticatory musculature (e.g., temporalis orientation), and overall cranial size (e.g., cranial length and height) (Table 3-2, Figure 3-3). Many of these variables were measured as distances or angles in relation to several standard references planes (Frankfurt Horizontal, midsagittal plane, and the occlusal plane). Additional indices describing the shape of the glenoid and condylar articular surfaces were also calculated using these measurements (e.g., glenoid shape index). These variables (not including dimensionless indices) were standardized for variation in size by dividing each variable by a geometric mean calculated from size measurements of calvarial size (bi-asterionic breadth, bi-porionic breadth, basioccipital length, cranial height, cranial length, and orbital width). This procedure follows the recommendation of Jungers et al. (1995), who evaluated a series of size-

TABLE 3-1. Landmark definitions. Asterisks denote landmarks excluded from the geometric morphometrics analyses.

Landmark Number	Landmark Description
	Skull Landmarks
1	Gnathion
2	Infradentale
3	Most inferior point on mental foramen
4	Point on lateral alveolar margin of mandibular canine*
5	Tip of mandibular canine*
6	Point on lateral alveolar margin of mandibular fourth premolar
7	Point on lateral alveolar margin of mandibular first molar
8	Point on lateral alveolar margin of mandibular second molar
9	Point on lateral alveolar margin of mandibular third molar*
10	Coronion*
11	Centroid of masseteric scar on mandible*
12	Centroid of medial pterygoid scar on medial surface of angle of ascending ramus*
13	Prosthion
14	Nasospinale
15	Sellion*
16	Nasion
17	Glabella
18	Bregma
19	Inion*
20	Opisthion*
21	Basion
22	Midpoint of spheno-occipital synchondrosis
23	Hormion
24	Intersection of median and transverse palatine sutures
25	Point on alveolar margin of maxillary canine*
26	Tip of maxillary canine*
27	Point on alveolar margin of maxillary fourth premolar
28	Point on alveolar margin of maxillary first molar
29	Point on alveolar margin of maxillary second molar
30	Point on alveolar margin of maxillary third molar*
31	Point just posterior to the alveolus of the last maxillary molar
32	Orbitale
33	Opposite side orbitale
34	Maxillofrontale
35	Frontomolare orbitale
36	Point where temporal line and coronal suture meet
37	Intersection of fronto-zygomatic suture and temporal line*
38	Jugale
39	Point on the superior border of the zygomatico-temporal suture
40	Point on inferior edge of zygomatic arch in coronal plane of zygomatico-temporal suture*

Landmark Number	Landmark Description
41	Most medial point on margin of temporal fossa in transverse plane*
42	Most posterior point on margin of temporal fossa in sagittal plane
43	Point on the ectocranial surface of the sphenoid at maximum postorbital constriction*
44	Deepest and most superior point in the pterygoid fossa*
45	Most anterior point on cranial masseteric scar
46	Midpoint of cranial masseteric scar*
47	Most posterior point on cranial masseteric scar*
48	Most lateral point on anterior basicranium at the spheno-occipital synchondrosis
49	Most lateral point on posterior basicranium/ most medial point on jugular fossa
50	Point at intersection of infratemporal crest and sphenotemporal suture
51	Most lateral point on foramen ovale
52	Apex of the petrous
53	Most inferolateral point on the carotid canal
54	Most anterosuperior point on the tympanic plate at the external auditory meatus*
55	Most inferior point on the tympanic plate/ tube in the coronal plane of porion
56	Porion
57	Opposite side porion
58	Most lateral point on jugular fossa*
59	Most lateral point on stylomastoid foramen*
60	Apex of mastoid process*
61	Point of inflection where the braincase curves laterally into the supraglenoid gutter, in the coronal plane of mandibular fossa*
62	Point on superolateral margin of zygomatic arch at the anteroposterior location of the postglenoid process*
63	Asterion
64	Most inferior point on entoglenoid process
65	Most inferior point on articular tubercle
66	Most inferior point on postglenoid process
67	Deepest point in mandibular fossa in sagittal plane of postglenoid process point
68	Most anterior point on the articular surface of the glenoid fossa
69	Most lateral point on the articular surface of the glenoid at the end of the long axis of the articular eminence
70	Most lateral point on the surface of the articular eminence
71	Most medial point on the surface of the articular eminence
72	Most medial point on the articular surface of the glenoid at the end of the long axis of the articular eminence
73	Midpoint of the crest of the articular eminence
74	Most anterior point on the articular surface of the glenoid along a line perpendicular to the long axis of the articular eminence
75	Point on the posterior edge of the articular eminence along a line perp to the long axis of the articular eminence

Landmark Number	Landmark Description
76	Most posterior point on articular surface of glenoid along line perp to long axis of the articular eminence*
	Condyle Landmarks
77	Most lateral point on the articular surface of the mandibular condyle
78	Most medial point on the articular surface of the mandibular condyle
79	Midpoint of line connecting the medial and lateral poles of the mandibular condyle
80	Most posterior point on the articular surface of the mandibular condyle at the midpoint of the mediolateral curve
81	Most anterior point on the mandibular condyle at the midpoint of the mediolateral curve

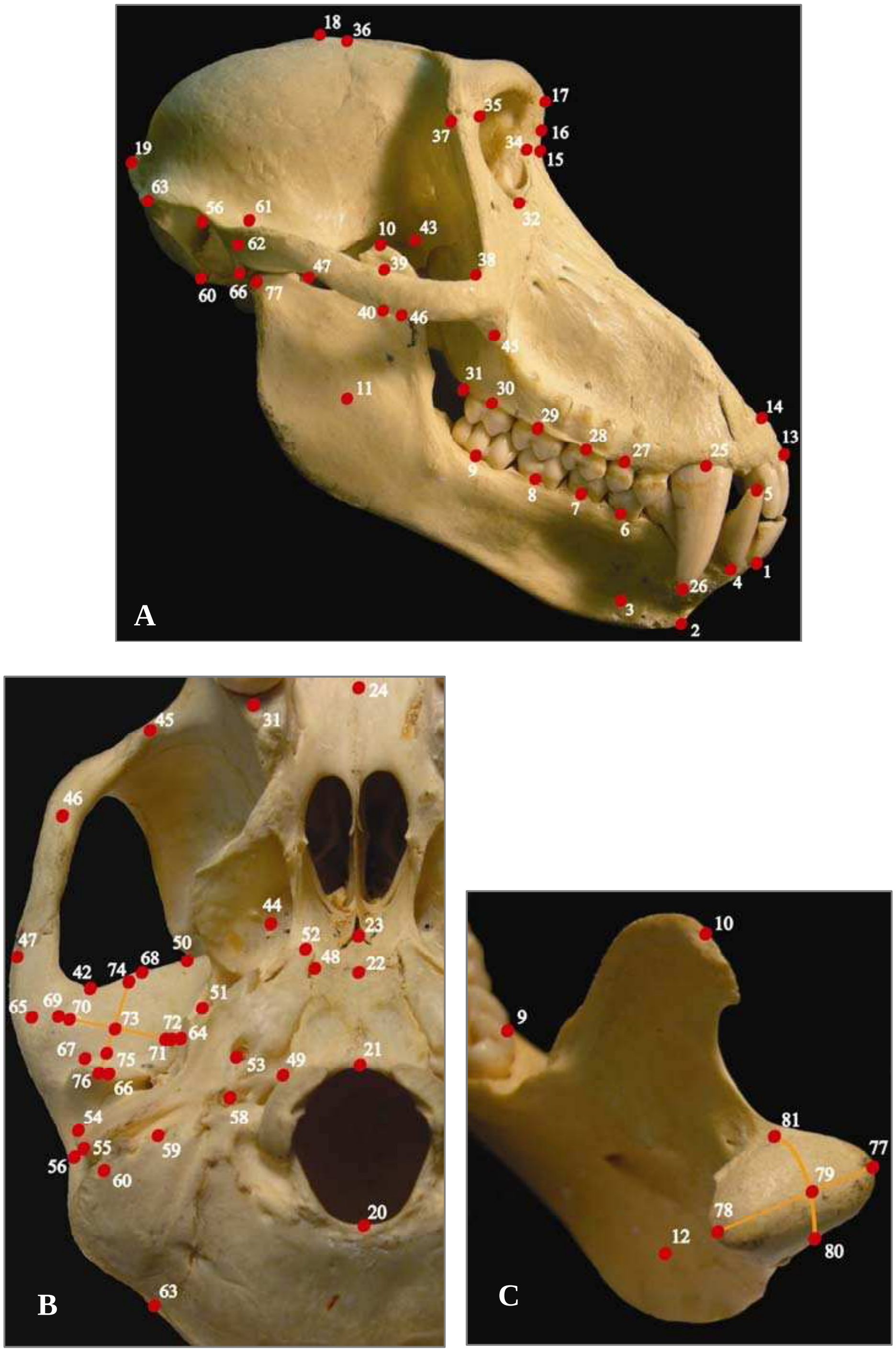


Fig. 3-1. Lateral (A), inferior (B), and mandibular condyle (C) views of a *Papio anubis* cranium illustrating the landmarks to be used in the proposed study. Orange lines illustrate the mediolateral and anteroposterior axes running through the cranial and mandibular components of the TMJ. Numbers correspond to landmarks described in Table 3-1. Photographs not to scale.

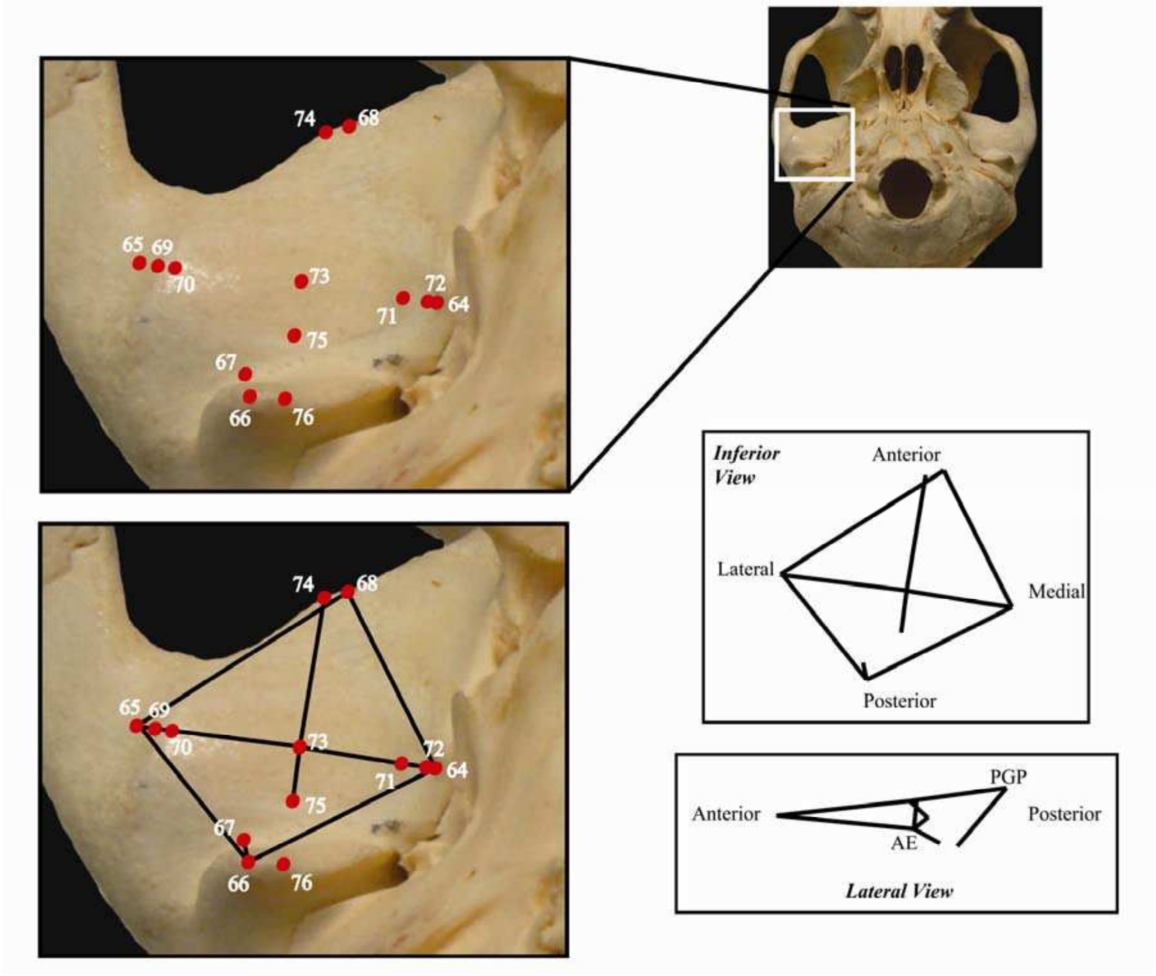


Fig. 3-2. Inferior views of a *P. anubis* glenoid showing landmarks and wireframe diagrams used in this study. Numbers correspond to landmarks listed in table 3-1 in chapter 3. Features indicated on the lateral view wireframe are the articular eminence (AE) and postglenoid process (PGP).

TABLE 3-2. Mandibular and cranial measurements extracted from the 3D landmark and surface data. ML= mediolateral, AP=anteroposterior. All distances were measured in millimeters and angles were calculated as degrees.

Measurement name	Measurement abbreviation	Landmarks or measurements used to calculate variable	Measurement type
Frankfurt Horizontal	FH	32-33-56	Reference Plane
Occlusal plane (on alveolar margin)	OP	13-27-29	Reference Plane
Sagittal plane	SP	13-18-21	Reference Plane
TMJ MEASUREMENTS			
Articular eminence inclination (against FH)	AEIncl-FH	73 to 75	Angle against FH
Articular eminence inclination (against OP)	AEIncl-OP	73 to 75	Angle against OP
Articular tubercle height (to FH)	ArtTubHtFH	65	Distance to FH
Entoglenoid height (to FH)	EntGlHtFH	64	Distance to FH
Glenoid AP curvature index	GlenAPIndex	Glenoid AP arc length/ chord length	Index
Glenoid ML curvature index	GlenMLIndex	Glenoid ML arc length/ chord length	Index
Glenoid area	GlenArea	n/a	Area
Glenoid length	GlenLg	66 to 68	Distance
Glenoid shape index	GlenShape	GlenWid / GlenLg	Index
Glenoid width	GlenWid	64 to 65	Distance
Postglenoid process height (to FH)	PGPHtFH	66	Distance to FH
Preglenoid plane length	PreglenLg	68 to 73	Distance
Condyle AP curvature index	CondAPIndex	Cond AP arc length/ chord length	Index
Condyle ML curvature index	CondMLIndex	Cond ML arc length/ chord length	Index
Condyle length	CondLg	80 to 81	Distance
Condyle width	CondWid	77 to 78	Distance

Measurement name	Measurement abbreviation	Landmarks or measurements used to calculate variable	Measurement type
Condyle shape index	CondShape	CondWid * CondLg	Index
Condyle area	CondArea	n/a	Area (ArcMap)
OVERALL SKULL MEASUREMENTS			
Asterionic breadth	AstBr	63	Distance to SP
Biporionic breadth	BiPorBr	56 to 57	Distance to SP
Cranial height	CranHt	18 to 21	Distance
Cranial length	CranLg	17 to 19	Distance
Face height	FaceHt	17 to 24	Distance
Face length	FaceLg	13 to 21	Distance
Orbital width	OrbWid	35	Distance to SP
MASTICATORY SYSTEM MEASUREMENTS			
Palate breadth	PalateBr	29	Distance to SP
Palate/ tooth row length	PalateLg	13 to 31	Distance in SP
Maxillary canine height	MaxCanLg	25 to 26	Distance
Mandibular canine height	MandCanLg	4 to 5	Distance
Mandible length	MandLg	13	Distance to line between L&R articular eminences in OP
TMJ height (above OP)	TMJHt	73	Distance to OP
MUSCLE MEASUREMENTS			
Temporalis angle	TempAng	10 to 43	Angle against OP
Masseter angle	MassAng	11 to 46	Angle against OP
Medial pterygoid angle	MedPtAng	12 to 44	Angle against OP

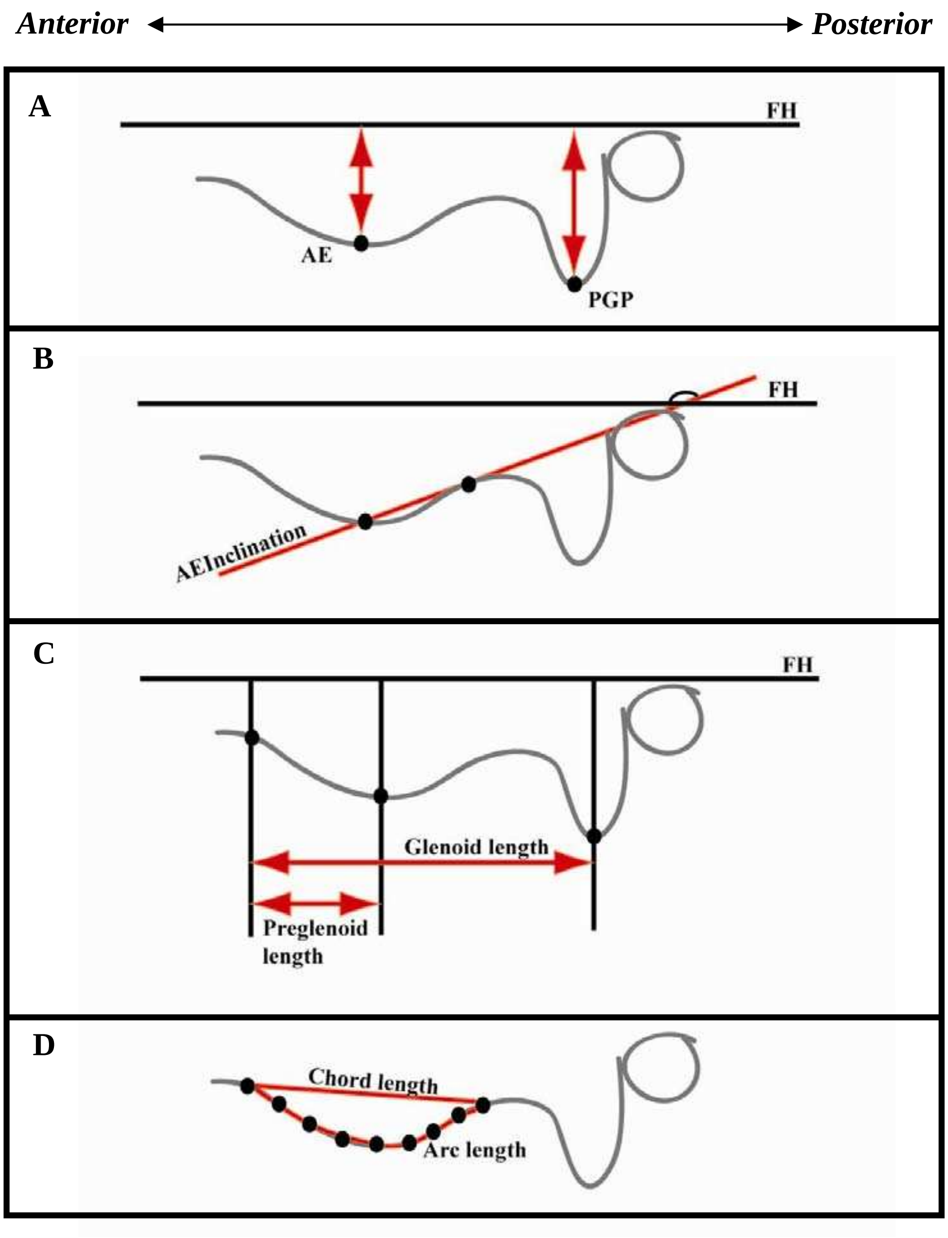


Fig. 3-3. Schematic cross-section through the glenoid cavity of the TMJ showing:. (A) measurements of articular tubercle and entoglenoid process projection (both represented by AE), and postglenoid process projection as measured from Frankfurt Horizontal (FH); (B) inclination of the articular eminence (AE) as measured by an angle between a line through the apex of the AE and the most posterior point on the AE and Frankfurt Horizontal; (C) measurements of glenoid length (most anterior point on the glenoid cavity to the postglenoid process) and preglenoid plane length (most anterior point on the glenoid cavity to the apex of the articular eminence; (D) measurement of curvature of the glenoid (illustrated here in the AP direction). Indices of curvature were calculated by summing the distance between points along the curve (arc length), and dividing that value by the length between the two end points of the curve (chord length).

adjustment methods and found that variables in the Mosimann family of shape ratios (including raw values divided by a geometric mean) were most effective for size-standardization.

Orientation of the temporalis, superficial masseter, and medial pterygoid muscles was quantified to assess correlations between muscle orientation and articular eminence inclination. This was done by estimating the centroid of the muscle scar for the origin and insertion of each of these muscles, and calculating a three-dimensional angle between a line connecting these centroids and the occlusal plane (Figure 3-4). The quantification of muscle orientation involves multiple assumptions regarding the position of the muscle force vector and the magnitude of muscle force produced during mastication. In particular, the method of quantification here assumes that all of the muscle fibers of a given muscle are firing equally and therefore the orientation of the muscle force vector corresponds to the centroid of the muscle scar. Experimental data suggest that this is unlikely to occur on a regular basis during mastication, however (Herring 1992; Blanksma and van Eijden, 1990; Blanksma et al., 1992; van Eijden et al., 1997; Spencer, 1998; Murray et al., 1999). Intrinsic aspects of muscle architecture such as fiber number, direction, and pinnation, location and number of intramuscular tendons, and sarcomere length have also been documented to vary among species of primates (e.g., Cachel, 1984; Lovejoy and Ferrini, 1987; Hannam and Wood, 1989; Koolstra et al., 1990; Anton, 1994, 1999, 2000; Taylor and Vinyard, 2004).

Surface data

Data describing the surfaces of the mandibular fossa and condyle were also collected. These data were obtained by collecting a dense cloud of XYZ coordinates along the articular surfaces of both the mandibular fossa and condyle using the Microscribe digitizer (e.g., Gunz et al., 2005) (Fig. 3-5). These point clouds were collected by running the stylus of the Microscribe

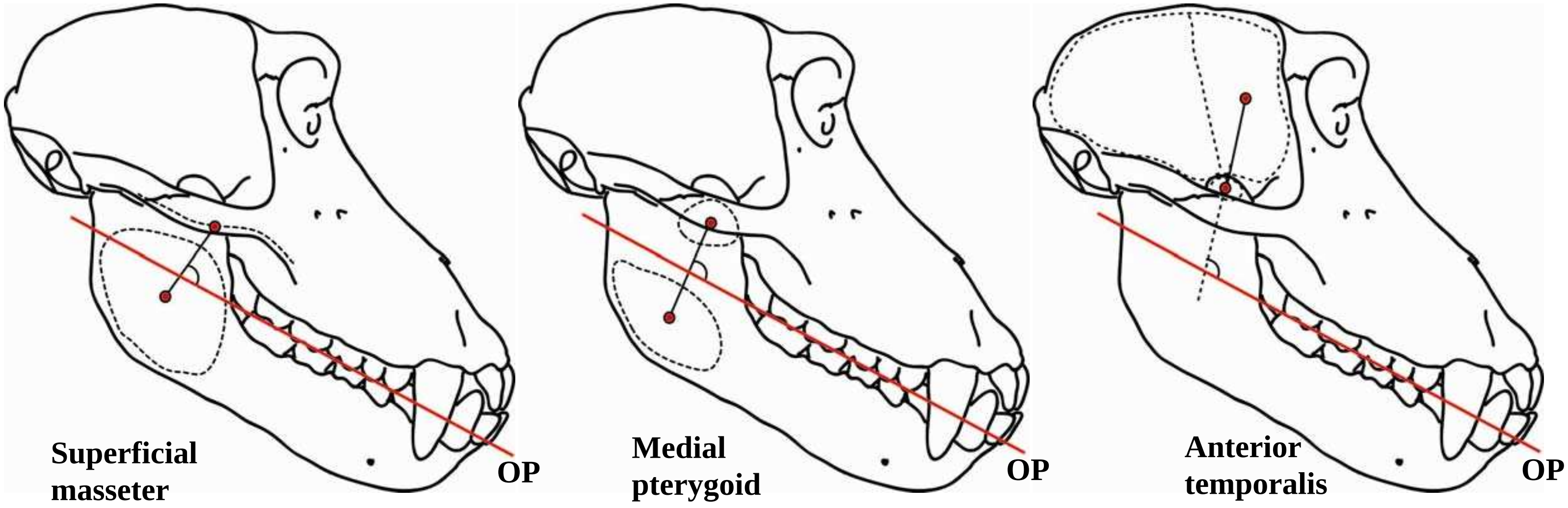


Fig. 3-4. Lateral views of a *Papio* cranium showing approximate areas of attachment (dashed lines) for the superficial masseter, medial pterygoid, and anterior temporalis muscles. Red dots indicate the centroids of these muscle attachments. Orientations of each of these muscles were measured as a three-dimensional angle between a line connecting the centroids of the origin and insertion and the occlusal plane (OP).

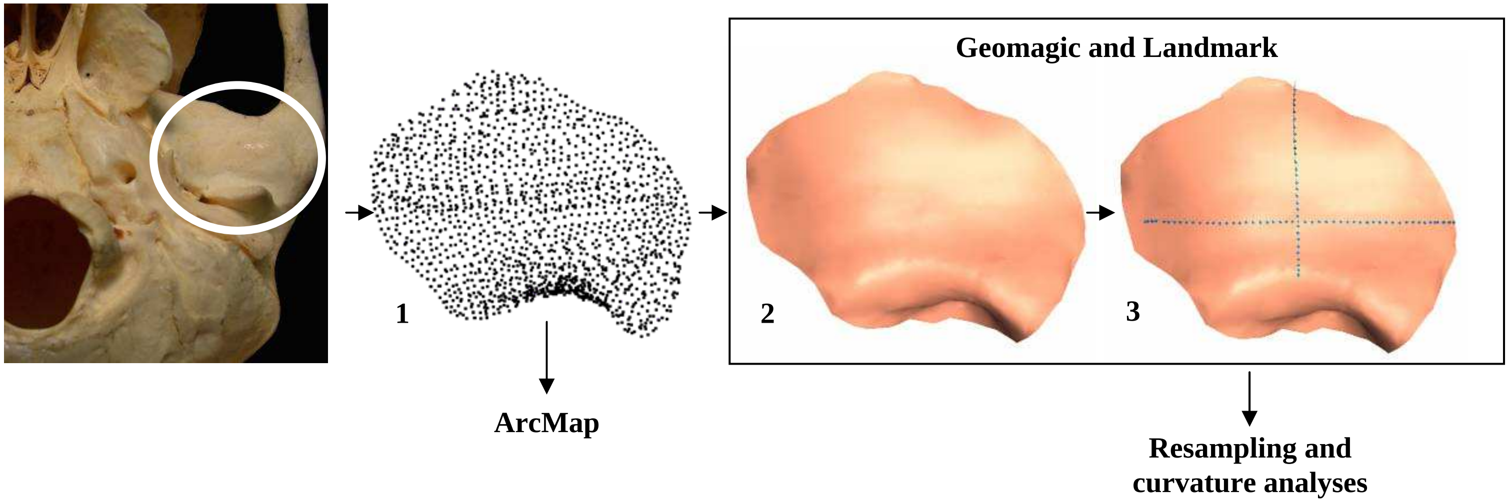


Fig. 3-5. Surface data collection. 1) Point cloud data are collected using the Microscribe digitizer and are exported into ArcMap for surface area quantification and into Geomagic and Landmark for surface rendering; 2) XYZ coordinates are used to create a surface rendering of the glenoid fossa; 3) mediolateral and anteroposterior curves are identified on the glenoid surface and exported for resampling and curvature analyses. Refer to the text for a description of how these curves were defined.

over the surface in question while points were continuously collected. The point cloud was visualized during the procedure using the program Rhino 3D (McNeel & Associates, 2008) to ensure that no areas of the articular surface were left unsampled. These point clouds were used to capture the articular surfaces of the mandibular fossa and condyle as delineated by the attachment of the joint capsule (which is generally visible as a smooth articular surface contrasting with the nonarticular surfaces of the surrounding bone).

Point cloud data were used in two ways (Fig. 3-5). Raw XYZ coordinates were imported into the program Rhino 3D, and a surface rendered by connecting the XYZ coordinates with a triangular mesh. Three-dimensional surface areas were then calculated, and the surfaces were used to delineate curves running mediolaterally and anteroposteriorly through the glenoid fossa and mandibular condyle using the program Landmark (IDAV version 3.0). The mediolateral curve was oriented along the apex of the articular eminence between the tip of the entoglenoid process and the most inferior point on the articular tubercle; this line may or may not be coincident with the coronal plane depending upon the orientation of the TMJ. The anteroposterior curve was defined as a curve running perpendicular to the ML curve, and located approximately at the midpoint of the ML curve. Once extracted, curves were resampled using the program Resample.exe (NYCEP Morphometrics Group). For example, curves were generated for each specimen in Landmark, with points digitized during data collection used to anchor the two ends of each curve (Table 3-1, landmarks 69, 72-75). These points were then exported and resampled so that the curve for each specimen included fifteen evenly spaced points. The arch length for each of these curves was then calculated and divided by the chord distance between points at either end of the curve, resulting in a curvature index for each of the four curves analyzed (glenoid AP curvature, glenoid ML curvature, condyle AP curvature, and condyle ML curvature).

STUDY SAMPLE

This study involved collecting three-dimensional (3D) coordinate data for 1023 specimens from 48 primate taxa (Table 3-3). The sample for most taxa includes between 20 and 24 specimens, with approximately equal numbers of males and females. Some taxa, however, were less well represented in the museum collections visited, and therefore are present in smaller numbers. Data were collected from specimens housed in five separate museums: the National Museum of Natural History at the Smithsonian Institution (Washington, DC), the American Museum of Natural History (New York, NY), the Field Museum (Chicago, IL), the Royal Museum for Central Africa (Tervuren, Belgium), and the Department of Primatology at the State Collection of Anthropology and Palaeoanatomy (Munich, Germany).

Only adult specimens with all permanent teeth erupted were included in the analysis, although no special effort was made to exclude specimens with unfused sphenoccipital synchondroses. Specimens displaying any pathological changes to the skull were excluded, and specimens with extensive dental attrition were generally avoided, although this was difficult for some taxa, particularly the hominoid and human samples.

Taxa were chosen to represent all major clades of anthropoid primates, as well as species with a range of body sizes and diets. Because species' estimates of body size cannot be accurately obtained from a relatively small sample of skeletal specimens, these data were collected from the literature (Smith and Jungers, 1997; Fleagle, 1999).

ERROR TESTING

To gauge intraobserver error, 43 specimens from a wide range of taxa and of varying body sizes were digitized two times on separate days, and these digitizations were statistically compared in several ways. Following methods outlined by von Crammon-Taubadel et al. (2007)

TABLE 3-3. Comparative taxa used in this study.

Species	Female	Male	Total	Museum
Alouatta belzebul	12	12	24	1
Alouatta palliata	12	12	24	1
Alouatta seniculus	12	12	24	1
Aotus trivirgatus	11	10	21	1
Ateles geoffroyi	12	12	24	1
Cacajao melanocephalus	11	11	22	1,2,3
Cebus albifrons	12	11	23	1
Cebus apella	11	12	23	1
Cebus capucinus	13	11	24	1
Cercocebus torquatus	4	5	9	1,3
Cercopithecus mitis	12	12	24	4
Cercopithecus nictitans	10	12	22	4
Chiropotes satanas	12	12	24	1,3
Colobus polykomos	12	12	24	4
Erythrocebus patas	7	12	19	1,2,4
Gorilla beringei	8	10	18	1,2,3,4
Gorilla gorilla	12	12	24	1,4
Homo sapiens (Aleutians)	11	10	21	1
Homo sapiens (Arikara)	10	10	20	1
Homo sapiens (Illinois Bluff)	10	10	20	1
Hylobates agilis	9	12	21	1,2
Hylobates klossi	10	8	18	1,2
Hylobates lar	10	12	22	1,3
Lagothrix lagothrica	11	12	23	1,2
Lophocebus albigena	12	12	24	1,4
Macaca fascicularis	12	12	24	1,5
Macaca fuscata	12	9	21	1,2,5
Macaca nemestrina	11	12	23	1,2,3,5
Macaca sylvanus	9	4	13	1,2,5
Macaca thibetana	3	7	10	1,2,3
Mandrillus sphinx	5	9	14	2,4,5
Miopithecus talapoin	5	9	14	1,3,4,5
Nasalis larvatus	12	12	24	1,5
Pan paniscus	12	10	22	4
Pan troglodytes schweinfurthii	12	12	24	1,2,4
Pan troglodytes troglodytes	7	9	16	1,2,4
Pan troglodytes verus	4	5	9	1,2
Papio anubis	9	12	21	1,4
Papio cynocephalus	9	12	21	1,4,5
Papio ursinus	3	11	14	1,2,4,5
Pithecia pithecia	11	12	23	1,2,3
Pongo abelii	9	10	19	1,5
Pongo pygmaeus	12	12	24	1,5
Procolobus badius	12	12	24	1,4
Procolobus verus	11	12	23	4

Species	Female	Male	Total	Museum
Saimiri sciurius	10	10	20	1
Semnopithecus entellus	12	11	23	1,3,5
Symphalangus syndactylus	10	12	22	1,2,5
Theropithecus gelada	3	10	13	1,2,3,5
Trachypithecus obscurus	10	10	20	1,3

1- National Museum of Natural History, Washington, DC, USA
2- American Museum of Natural History, New York, NY, USA
3- Field Museum, Chicago, IL, USA
4- Royal Museum for Central Africa, Tervuren, Belgium
5- Department of Primatology at the State Collection of Anthropology and Palaeoanatomy, Munich, Germany

all specimens were registered via generalized Procrustes analysis using three control points (basion, point on the lateral alveolar margin of maxillary M1, and the most inferior process on the postglenoid process). Linear distances were then calculated for each landmark between the original and repeated digitizations. For example, after GPA, the linear distance between landmark 1 for a given specimen and the same landmark for the redigitization of the same specimen was calculated. This was done for all landmarks, allowing the error for each landmark to be quantified and examined. For the skull, the average error between trials per landmark was 0.03 mm, with a minimum of 0.014 mm and a maximum of 0.11 mm, while the average error for the mandible was 0.04 mm, with a minimum of 0.01 mm and a maximum of 0.07 mm.

Procrustes distances were also calculated between repeated digitizations of the same specimen, between individuals in the same species, and between specimens of different species, following Lockwood et al., (2002). Figure 3-6 shows a box-plot of these distances. Two-sample t-tests were performed to assess whether these Procrustes distance measurements differed significantly between these three categories; all comparisons were significantly different at $p<0.00001$.

These low error rates indicate that landmarks could be precisely relocated during repeated digitizations of the same specimen, and error between trials of the same specimen was smaller than differences between individuals within the same species and between specimens of different species.

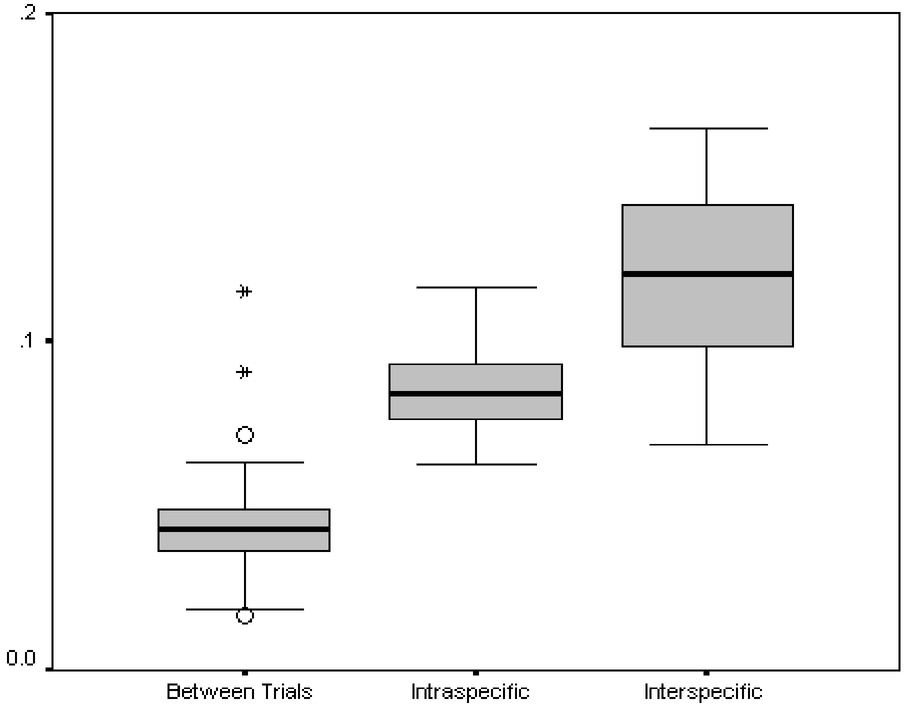


Fig. 3-6. Box plot showing the distributions of Procrustes distances between repeated digitizations of the same specimen (Between Trials), between specimens in same species (Intraspecific), and between different species (Interspecific). Darkened bars represent the median value for each group, while the boxes show the interquartiles range, from the 25th to the 75th percentile, and the whiskers extend to data within the 1.5 times the interquartile range. Outliers are designated by open circles and extremes are designated by asterisks.

CHAPTER 4: DIETARY CORRELATES OF TEMPOROMANDIBULAR JOINT SHAPE

INTRODUCTION

A number of analyses have assessed variation in the masticatory apparatus in conjunction with biomechanical demands, how different components of the masticatory apparatus may be altered to create more favorable arrangements of the moment arms of the muscle resultant, and bite forces and to accommodate bone strain in the masticatory apparatus (e.g., Hylander, 1977, 1984; 1985; Ward and Molnar, 1980; Bouvier, 1986a,b; Ravosa, 1990; Spencer and Demes, 1993; Spencer, 1995, 1999; Hylander and Johnson, 2002; Taylor, 2002, 2005, 2006; Wright, 2005; Constantino, 2007; Ross, 2008; Strait et al., 2008). For instance, one way to maximize bite force is to decrease the distance between the bite point and the muscle resultant; consequently, Spencer (1995) showed that, within a group of closely related taxa, harder and/or tougher object feeders have more anteriorly placed muscle resultants and more posteriorly placed bite points than taxa that tend to masticate softer food-objects. Several analyses have suggested that the elevation of the TMJ high above the occlusal plane is related to increased postcanine force production and an even distribution of occlusal loads along the posterior teeth (Aresden de Wolff-Exalto 1951 a, b; Herring and Herring, 1974; Ward and Molnar, 1980; Greaves, 1995; Spencer, 1995, 1999; Taylor, 2002, 2005). Taxa that masticate tougher and/or harder food-objects tend to have a higher TMJ in relation to taxa that eat softer foods.

Given these differences in the configuration of the masticatory apparatus among taxa with diets that differ in the mechanical demands on the masticatory system, it may be expected that components of the TMJ also vary as a consequence of masticatory function. It is the goal of this chapter to evaluate variation in anthropoid TMJ morphology in the context of functional and dietary differences among taxa.

As discussed in Chapter 2, the TMJ is morphologically and functionally complex, and is an integral part of the masticatory apparatus. Three main factors that are most likely to significantly influence variation in the TMJ were identified and discussed: food material properties, bite point location, and gape requirements. The following section reviews previous research regarding TMJ function and lays out specific predictions regarding how particular features of the TMJ will vary in association with these factors, drawing heavily on the functional background presented in Chapter 2. Subsequently, I outline three main research predictions associated with these factors that will be tested in this chapter.

Previous research on the TMJ

TMJ size and shape. Perhaps the most frequently explored aspect of TMJ variation has been the overall size of the two major components of this joint, the mandibular fossa and condyle. Differences in the structure of the glenoid in modern humans have been examined by a number of authors (Carlson and Van Gerven, 1977; Van Gerven et al., 1978; Hinton and Carlson, 1979; Hinton, 1983; Kozam, 1985), with particular attention paid to changes in TMJ morphology in the archaeological record (Hinton and Carlson, 1979; Hinton, 1983) and orthodontic variation (Kozam, 1985). Hinton and Carlson (1979) demonstrated that, over a span of 10,000 years in medieval Nubia, the TMJ decreased in size—which they associated with decreases in masticatory apparatus robusticity coincident with the shift from hunting and gathering to agriculture. Similarly, Hinton (1983) investigated the relationship between overall TMJ size, masticatory stress, and craniofacial size, finding that TMJ size varied predictably as a function of the intensity of masticatory stress. Hunter-gatherers (which presumably masticate the hardest or coarsest food items, although this may not necessarily have been the case) had the largest TMJs, while industrialized American Caucasians and 17th century British had the smallest TMJs (prehistoric agriculturalists were intermediate in size). These analyses are of particular interest because they suggest that diet is an important factor in driving morphological differences between human populations.

Size and shape variation of the mandibular condyle, in contrast to the glenoid, has been evaluated in more detail and this variation has been explicitly discussed in terms of functional differences between taxa. Smith et al. (1983) examined condylar variation across anthropoid primates, looking at the overall size of the condyle. Their analysis indicated that folivores tend to have smaller condyles than frugivores, and very large condylar areas were associated with hard object feeding (as seen in *Pongo pygmaeus* and *Cercocebus torquatus*). These findings are consistent with those of Hinton and Carlson (1979), who found that TMJ size varied predictably with intensity of masticatory function, and with the idea that taxa using their anterior teeth have higher joint reaction forces than taxa that use their posterior teeth (Hylander, 1979a; Hylander and Bays, 1979).

Bouvier (1986a,b) examined this relationship further. She broke the dimensions of the condyle down into mediolateral (ML) and anteroposterior widths (AP) and assessed variation in these dimensions in relation to increased use of the posterior or anterior dentition during mastication or food processing. Bouvier (1986a) found that cercopithecines had AP long condyles associated with increased use of the anterior dentition, while colobines had ML wide condyles associated with intensive use of the postcanine dentition as in processing large quantities of leaves. As outlined by Bouvier (1986a), this finding is consistent with previous biomechanical analyses by Hylander (1979) and Hylander and Bays (1979), which point to twisting of the mandibular ramus and differentially higher compressive loads on the lateral surface of the mandibular condyle, which result in ML wider condyles in taxa that intensively use their postcanine dentition. Taylor (2005) found that, in comparison to other *Gorilla* species and subspecies, the more folivorous *Gorilla beringei* had relatively wider condyles, as did *Gorilla* species in comparison to *Pan.* Comparable results were obtained by Taylor (2006) in her evaluation of masticatory variation in *Pongo pygmaeus* and *P. abelii*. Finally, in her cineradiographic studies of mandibular movement, Wall (1995, 1999) observed that a flattened mandibular condyle in *Pan* and *Ateles* was associated with increased sagittal sliding. Wall first quantified the amount of movement at the TMJ during masticatory behaviors and assessed the correlation between this measure of sagittal sliding and gape. Results of this analysis indicated that these two variables were highly positively correlated. Wall (1995, 1999) then also assessed the shape of the components of the TMJ in relation to sagittal sliding, and found that AP curvature of the condyle was highly negatively correlated with sagittal sliding, suggesting that a flatter condyle increases the congruence at the joint and facilitates sagittal sliding.

Given these previous analyses, it is predicted that:

1) where forces within the TMJ are high, both the glenoid and the mandibular condyle should have relatively larger surface areas to improve the load resistance capabilities of the TMJ by increasing the area over which force is applied;
2) taxa that use their anterior teeth extensively should have a relatively AP long TMJ in contrast to taxa that do not regularly use their anterior teeth. Conversely, where intensive unilateral mastication of food items is emphasized (i.e., in hard- and tough- object feeders), the TMJ should be wide mediolaterally to withstand increased stresses on the lateral portion of the glenoid and condyle; and
3) increased sagittal sliding associated with gape should be manifested by an elongation of the glenoid AP as well as anteroposterior flattening of the condyle.

Entoglenoid process and articular tubercle shape. The functional significance of the entoglenoid process, which borders the glenoid cavity medially, and the articular tubercle, which borders it laterally are unclear, since very few analyses have explored variation in entoglenoid process and articular tubercle morphology. In his 1974 functional comparison of gracile and robust australopiths, DuBrul proposed that the size and orientation of the entoglenoid was associated with mediolateral shifting of the condyle. In hominoids, the large, inferiorly projecting entoglenoid therefore assists in prohibiting medial dislocation of the condyle, whereas in humans, the entoglenoid is small and often posteriorly projecting, and more mediolateral movement of the condyle is allowed. Cineradiographic analyses performed by Wall (1995, 1999) confirmed that the mandibular condyle does contact the entoglenoid during opening and closing movements of the mandible. However, Wall observed that the condyle frequently translated anterior to the anterior border of the entoglenoid. This finding, in conjunction with the observation that the entoglenoid is small in many primate species led Wall (1995) to conclude that the entoglenoid is unlikely to function as a bony stop, at least when the condyle is translated anteriorly. Wall (1999) did, nevertheless, find an association between the shape of the entoglenoid and the shape of the mandibular condyle. In fact, in both *Ateles* and *Pan*, Wall observed that ML wide entoglenoid processes were correlated with curvature of the medial aspect of the mandibular condyle, and suggested that this correlation indicated increased congruence of the medial portion of the joint. Functionally, this congruency was considered to indicate that the entoglenoid acts to guide the mandibular condyle during sagittal sliding, and possibly to prevent excessive mediolateral movements.

The articular tubercle serves primarily as the bony attachment site for the temporomandibular ligament (TML), and therefore the size of the articular tubercle is likely a reflection of the size of the TML. Wall (1995) observed that this ligament was most fibrous in taxa that were seed predators, and suggested that a stronger TML may serve to increase the ability of the condyle to maintain contact with the articular eminence during relatively high loads. Osborn (1989) proposed that the TML is pulled taut during jaw opening, and that the mandible rotates around the lowest attachment of the TML; functionally, this situation is advantageous in that the TML acts to keep the mandibular condyle close to the articular eminence during jaw opening so there are no eccentric movements of the condyle during the power stroke and jaw closing. Maintaining contact between the mandibular and cranial components of the TMJ would be advantageous for decreasing tensile forces at the joint (the potential for which has been indicated in work by Greaves [1978], Hylander [1979] and Spencer [1995, 1999]) as accidental tensile loading of the condyle can cause severe injury to the temporomandibular joint capsule and its ligaments (Greaves, 1978; Spencer, 1995; 1998). Sun et al.'s (2002) analysis of the TMJ tissues of miniature pigs concluded that the primary function of the lateral joint capsule was to stabilize the TMJ when the condyle performs lateral movements, such as occur at both the working and balancing side condyles during lateral deviation. Increased lateral deviation as a result of increased food object resistance (Byrd et al., 1978; Anderson et al., 2002; Komiyama et al., 2003; Wall et al., 2006) would therefore be expected to be correlated with articular tubercle size.

Several predictions can be generated from these data:

1) in hard- and tough-object feeders the entoglenoid process will be large to prohibit medial movements of the working side condyle during mastication and to increase joint surface area and reduce stress at the joint;
2) where sagittal sliding has been shown to be high (e.g., taxa with large gapes), the entoglenoid should be large to guide the anterior-posterior movement of the condyle and to prohibit excessive mediolateral sliding; and
3) where lateral deviation has been shown to be high (e.g., during resistant object feeding), the articular tubercle should be larger than in soft-object feeders to prohibit both medial and lateral dislocation of the condyle and/or the articular disc. This should be particularly true in tough object feeders where repetitive masticatory movements result in very high levels of lateral deviation in a given chew cycle.

Preglenoid plane shape. The preglenoid plane is located anterior to the articular eminence; in humans, this plane is small in relation to the overall joint surface area, whereas the preglenoid plane in other primates can take up a substantial portion of the glenoid surface. As with many of the other components of the TMJ, variation in this structure is poorly understood. However, the preglenoid is the primary surface upon which the condyle translates, and as observed by Wall (1995) the posterior articular surface of the condyle was observed to articulate with the preglenoid plane (via the articular disc) during large gapes. Furthermore, Vinyard et al. (2003) observed that tree-gouging primates tend to have an anteroposteriorly elongated temporal articular surface. Thus, it can be predicted that the anteroposterior length of the preglenoid plane should be relatively large in taxa with large gapes; correspondingly, preglenoid plane length should be positively correlated with canine crown height and height of the TMJ above the occlusal plane, which are proxies for gape (Hylander and Vinyard, 2006; Hylander, 2008).

Articular eminence shape. Of the various components of the TMJ, variation in the shape of the articular eminence (AE) has been the most frequently analyzed. This is in part because it is considered one of the most functionally critical portions of the TMJ, as it is the primary articular surface upon which the mandibular condyle rotates and translates during movements of the mandible. In comparison to many primates, the articular eminence of humans is described as raised (or inclined) and bar-like in form. A number of functional reasons have been proposed to account for this morphology. Nickel et al. (1988a,b) suggested that the articular eminence forms as a response to joint loading; however, this hypothesis doesn’t explain why the articular eminence is not raised and bar-like in all primate taxa, since joint reaction forces are not exclusive to humans. Several analyses have shown that increased loading causes the cartilage cells located in the proliferative zones along the glenoid fossa and mandibular condyle to form mesenchymal precursor cells, which inhibit osteogenesis (Petrovic, 1972; Hall, 1979; Hinton, 1981); thus, increased loading at the TMJ, in contrast to many other joints, results in regressive remodeling of bone, rather than progressive remodeling.

Conversely, Osborn (1989, 1996) proposed that an inferiorly inclined articular eminence (where the face of the AE is directed posteriorly or postero-inferiorly) acted to maximize vertical bite force by resisting the translatory component of an anteriorly directed muscle resultant force and also to standardize the opening movement of the mandibular condyle, which is held against the eminence by the temporomandibular ligament (Osborn, 1989). Of these two proposed functions, the former, that the AE acts to resist translatory (or non-normal forces) at the TMJ, will be expanded and evaluated here.

In a simplified model of masticatory function, the TMJ is often assumed to be level with the bite point and occlusal plane (e.g., Hylander, 1975; Walker, 1978; Spencer, 1995). In such a configuration, and assuming that all of the forces in the model are normal , or perpendicular to the reference plane (e.g., a plane between the joint reaction force and bite force), there need not be a translatory component of the joint reaction force that must be resisted by the articular eminence in order to maintain static equilibrium. As a consequence, the articular eminence would be expected to be relatively flat, since all forces will be vertical (Fig. 4-1a). However, a TMJ level with the occlusal plane is observed in very few primate taxa (e.g., patas monkey, aye-aye), and in most primate species the TMJ is raised well above the occlusal plane. In such an instance, and assuming that the forces acting upon the joint remain normal, the slope of the articular eminence might be expected to covary with the height of the TMJ above the occlusal plane, simply to maintain the same spatial relationships of the components of the masticatory apparatus (Fig. 4-1b). Alternatively, in the absence of changes in TMJ height, changes in the orientation of the muscle resultant force that would produce a non-normal component of the JRF could necessitate changes in the orientation of the articular eminence (Fig. 4-1c). A correlation between orientation

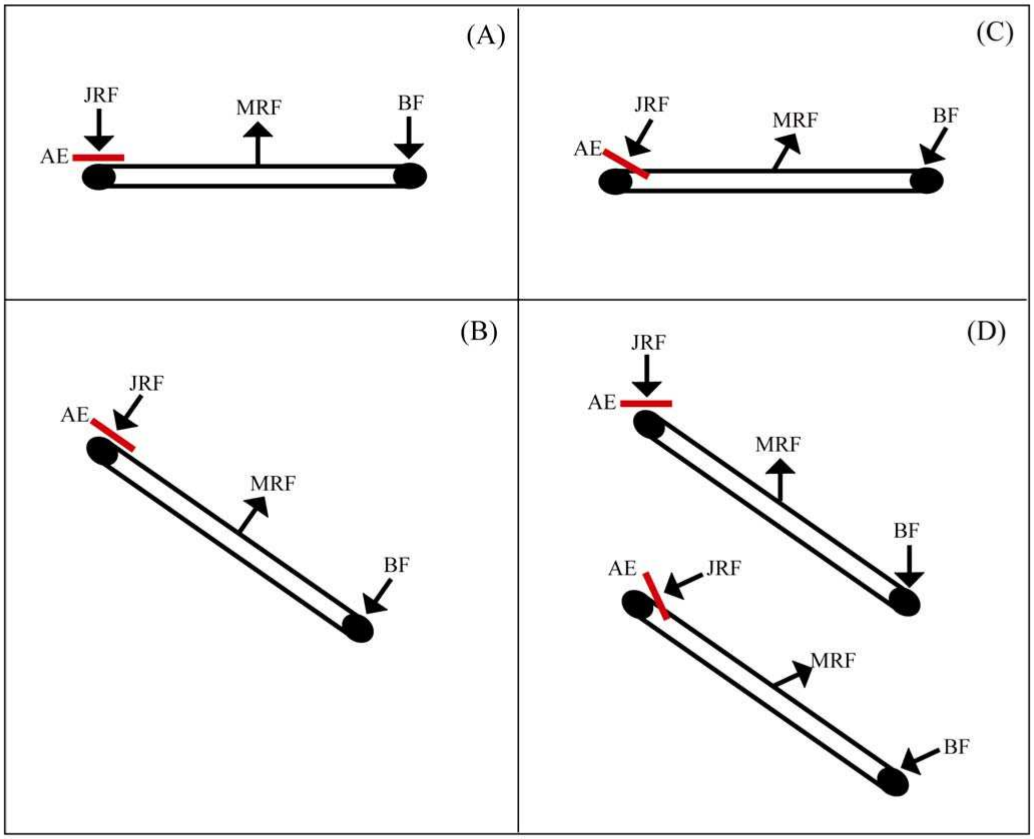


Fig. 4-1. Simplified two dimensional biomechanical models of the components of the masticatory apparatus showing the TMJ level with the occlusal plane and the force vectors normal to the reference plane (a), the TMJ raised above the occlusal plane and the force vectors normal (b), the TMJ level with the occlusal plane and the force vectors non-normal (c), and the TMJ raised above the occlusal plane and the muscle resultant force more vertically oriented (top) or anteriorly oriented (bottom). AE=articular eminence; JRF= joint reaction force; MRF=muscle resultant force; BF=bite force.

of the muscle resultant force and the orientation of the articular eminence would consequently be expected.

We can therefore identify two potential factors that may influence the slope of the AE: height of the TMJ above the occlusal plane and orientation of the muscle resultant. These two factors could also be expected to work in conjunction with one another (Fig. 4-1d), such that a TMJ raised well above the occlusal plane but with a primarily vertical muscle resultant force, should be expected to have a relatively flat articular eminence. Conversely, if the TMJ is raised above the occlusal plane and the muscle resultant force is significantly anteriorly oriented, the AE would be predicted to have an increased slope so that the joint reaction force is normalized and static equilibrium is maintained. Changes in the orientation of the AE in both of these scenarios would assist in counteracting the bulk of the non-normal forces at the TMJ rather than the bite point, and would therefore function to maximize the bite force during mastication (e.g., Osborn, 1996).

Given these data, it is predicted that:

1) in the absence of variation in the orientation of the muscle resultant force in relation to the reference plane, variation in the inclination of the articular eminence should be correlated with the height of the TMJ above the occlusal plane; and
2) inclination of the muscle resultant force should be correlated with the inclination of the articular eminence.

Postglenoid process shape. The postglenid process (PGP) has been suggested to limit the posterior displacement of the mandibular condyle within the fossa (Sicher, 1951), and also to articulate with the mandibular condyle during mastication, as indicated by the posterior and inferior extension of the articular surface of the condyle in some strepsirrhine primates (Wall, 1997). However, examinations of the anatomy of the postglenoid by Carlson et al. (1980), DuBrul (1980) and Wall (1995) indicate that the postglenoid is almost exclusively non-articular. Wall (1995) proposed that variation in the size of the postglenoid process is at least in part a function of the size of the postglenoid ligament, which is poorly formed in the great apes and absent in humans, and therefore corresponds to a small (or sometimes absent) postglenoid process (Wall, 1995). The posterior articular surface of the condyle, rather than articulating with the postglenoid, was suggested by Wall (1995, 1997) to articulate with the preglenoid plane during large gapes.

Although it is unclear given this lack of data what exactly the function of the postglenoid process is, quantification of this portion of TMJ anatomy will provide detailed information regarding the extent to which postglenoid morphology varies and whether this variation is biomechanically significant.

RESEARCH PREDICTIONS

These various predictions regarding specific aspects of the TMJ can be summarized in three main predictions related to the three main factors outlined in Chapter 2. These three issues tie in more generally to differences in the production of force (food material properties, anterior vs. posterior tooth use) and range of motion (food material properties, gape) at the TMJ. Differences in the amount of force applied at the joint should result in changes in the size of the condyle and the glenoid fossa, and with the size of the various processes present within the joint; larger processes should lend more stability to the joint by increasing the surface area for contact with the condyle, therefore improving the ability of the TMJ to accommodate increased loads. The range of motion within the joint is influenced by both food material properties and gape requirements. For instance, the mastication of more resistant foods is associated with larger degrees of lateral deviation, and larger gapes should be associated with relatively larger amounts of sagittal sliding; therefore, increased movement within the TMJ may be associated with the enlargement of structures that guide movement of the condyle, and also with differences in the shape of the articular surfaces of both the mandibular fossa and condyle.

These expectations can be summarized by three predictions that will be tested as part of this study. These predictions are listed below and summarized in Tables 4-1 and 4-2.

> Prediction 1: In comparison to closely related taxa that masticate soft food items, taxa that consume more resistant food objects will exhibit adaptations within their TMJs associated with increased joint reaction force and range of motion, such as increased joint surface area, and a larger entoglenoid process and articular tubercle.
>
> Prediction 2: In comparison to closely related taxa that rely less heavily on their anterior dentition for food processing and do not intensively and repetitively load their posterior teeth, the TMJs of taxa that intensively use their anterior teeth are expected to show adaptations to resist larger centrally or medially located joint reaction forces. Taxa that repetitively load their posterior teeth should show adaptations within their TMJs related to increased joint reaction forces on the lateral surface of the TMJ. These adaptations would be represented by changes in the relative mediolateral and anteroposterior dimensions of the joint and the size of the entoglenoid process and articular tubercle.
>
> Prediction 3: In comparison to closely related taxa with small gapes, taxa with relatively larger gapes (whether for dietary or behavioral reasons) should have adaptations in their TMJ related to increased range of motion (e.g., sagittal sliding), such as an anteroposteriorly longer TMJ, large preglenoid plane, and anteroposteriorly flat mandibular condyle.

TABLE 4-1. Predicted relationships between dietary variables to be assessed in the current study and force and range of motion at the TMJ.

	Food Material Property			Tooth Use		Gape	
	Soft	Hard	Tough	Anterior	Posterior	Low	High
Force	low	high	high	high	low	--	--
Lateral Deviation	less	most	more	low	high	--	--
Sagittal Sliding	--	--	--	--	--	low	high

TABLE 4-2. Predicted relationships between aspects of TMJ shape and force, lateral deviation, and sagittal sliding at the TMJ. ML= mediolateral, AP=anteroposterior.

	Force		Lateral Deviation		Sagittal Sliding	
	Low	High	Low	High	Low	High
Glenoid size	small	large	--	--	--	--
Glenoid shape	--	--	AP < ML	AP > ML	AP < ML	AP > ML
Entoglenoid	small	large	small	large	small	large
Articular tubercle	small	large	small	large	small	large
Preglenoid plane	--	--	--	--	small	large
Condyle size	small	large	--	--	--	--
Condyle shape	--	--	flat ML	curved ML	curved AP	flat AP

* Note that articular eminence shape and postglenoid process size are not included in this set of predictions, since there is little existing evidence to suggest that variation in either of these features is directly related to the amount of force, lateral deviation, or sagittal sliding at the TMJ.

DIETARY ECOLOGY OF COMPARATIVE GROUPS AND PREDICTED VARIATION

Analyses of TMJ shape were performed by including several sets of closely related taxa with different diets, which allowed multiple pairwise comparisons of TMJ morphology between closely related taxa in a single clade. These comparative groups of taxa are composed of between three and six species that are relatively closely related, but which utilize foods with different material properties and/or have been documented to rely on the use of their anterior or posterior dentition to differing degrees. These groups are defined relatively loosely; two of the six comparative groups examined here are restricted to a single genus (e.g., *Cebus* and *Macaca*), whereas the remaining groups include multiple species from as many as three genera. These comparative groups were drawn from all major groups of anthropoid primates, and include three groups of platyrrhines and three groups of catarrhines, generally at the level of subfamily: atelines, cebines, pitheciines, papionins, colobines, and hominids.

This pairwise approach is useful because it allows for the comparison of taxa with different diets, even though the specific parameters of their diet that differ may not have been quantified in such a way that lends itself to statistical analyses of the diets themselves. For instance, it has long been known that *Pan* and *Gorilla* differ substantially in their use of terrestrial herbaceous vegetation (THV) (e.g., Badrian and Malenky, 1984; Watts, 1984; Williamson et al., 1990; Tutin and Fernandez, 1993; Malenky and Wrangham, 1994; Nishihara, 1995; Elgart-Berry, 2004), but few data are available regarding the actual frequency at which these genera utilize this resource in comparison to one another. Thus, the general observation that *Gorilla* tends to rely more heavily on THV than does *Pan* is sufficient here because only the relative differences in masticatory morphology are being compared among the two genera (rather than their correlation with the dietary data).

By comparing closely related taxa in this way, differences in TMJ shape due to phylogeny (and for the most part size) are minimized. In other words, since closely related species are being compared, there is no need for the data to be corrected for phylogenetic codependence (e.g., independent contrasts, Felsenstein, 1985), because there are likely to be considerably fewer differences due to phylogenetic distance than if taxa from two families, superfamilies, or infraorders were being compared.

Finally, this approach is beneficial since many of the taxa examined here have been used by other researchers to quantify differences in masticatory morphology based on dietary variation (e.g., Daegling, 1992; Takahaski and Pan, 1994; Spencer, 1995; Antón, 1996; Daegling and McGraw, 2001; Taylor, 2002; Wright, 2005; Constantino, 2007); this will allow differences in TMJ shape to be discussed in the context of previously identified differences in masticatory shape.

The following section reviews the dietary ecology of the taxa included in the comparative groups, and will identify which of the taxa examined are soft/tough/hard object feeders (Table 4-3). Predicted variation for each group is discussed in the text below, and outlined in Table 4-4. Photographs of glenoid morphology in many of the species included in the comparative groups are provided in Appendix A.

Atelines

Three ateline species were studied: *Ateles geoffroyi*, *Lagothrix lagothrica*, and *Alouatta seniculus*. Like other New World primates, fruits make up a large portion of the diet for these three species, although to varying degrees. *At. geoffroyi* and *L. lagothrica* are the most frugivorous species in this sample, consuming between 74 and 87% fruit parts in their diets (Chapman, 1987, 1989; Peres, 1994; Di Fiore, 2004; Russo et al., 2005). Estimates of the percentage of leaves consumed by these species are variable, ranging between 6 and 17%, but suggest that roughly the same amount of foliage is included in each of their respective diets (Chapman, 1987, 1989; Peres, 1994; Di Fiore, 2004; Russo et al., 2005). These species differ,

TABLE 4-3. Comparative groups examined in the dietary analyses, divided by food material property category.

Comparative Group	Soft	Tough	Hard
Cebines	*Cebus capucinus* *Cebus albifrons*	--	*Cebus apella*
Pitheciines	--	*Pithecia pithecia*	*Chiropotes satanas* *Cacajao melanocephalus*
Atelines	*Ateles geoffroyi*	*Alouatta seniculus*	*Lagothrix lagothrica*
Macaques	*Macaca fascicularis* *Macaca nemestrina*	*Macaca thibetana*	*Macaca sylvanus* *Macaca fuscata*
Papionins	*Papio cynocephalus*	*Theropithecus gelada*	*Papio ursinus*
Hominids	*Pan troglodytes*	*Gorilla gorilla* *Gorilla beringei*	*Pongo pygmaeus* *Pongo abelii*

TABLE 4-4. Predicted variation in aspects of TMJ shape in each comparative group examined in the dietary analyses.

	Atelines	Cebines	Pitheciines
Articular Tubercle Ht	*Alouatta > Lagothrix > Ateles*	*C. apella > C. albifrons/ C. capucinus*	*Cacajao/ Chiropotes > Pithecia*
Entoglenoid Ht	*Alouatta > Lagothrix > Ateles*	*C. apella > C. albifrons/ C. capucinus*	*Cacajao/ Chiropotes > Pithecia*
Glenoid Length	*Alouatta > Lagothrix/ Ateles*	*C. apella > C. albifrons/ C. capucinus*	*Cacajao/ Chiropotes > Pithecia*
Glenoid Width	*Alouatta > Lagothrix > Ateles*	*C. apella > C. albifrons/ C. capucinus*	*Pithecia > Cacajao/ Chiropotes*
2D Glenoid Area	*Alouatta > Lagothrix > Ateles*	*C. apella > C. albifrons/ C. capucinus*	*Cacajao/ Chiropotes > Pithecia*
3D Glenoid Area	*Alouatta > Lagothrix > Ateles*	*C. apella > C. albifrons/ C. capucinus*	*Cacajao/ Chiropotes > Pithecia*
Preglenoid Length	*Alouatta > Lagothrix/ Ateles*	*C. apella > C. albifrons/ C. capucinus*	*Cacajao/ Chiropotes > Pithecia*
Glenoid Shape Index	*Lagothrix/ Ateles > Alouatta*	*C. albifrons/ C. capucinus > C. apella*	*Pithecia > Cacajao/ Chiropotes*
Condyle Width	*Alouatta > Lagothrix > Ateles*	*C. apella > C. albifrons/ C. capucinus*	*Pithecia > Cacajao/ Chiropotes*
Condyle Length	*Alouatta > Lagothrix/ Ateles*	*C. apella > C. albifrons/ C. capucinus*	*Cacajao/ Chiropotes > Pithecia*
2D Condyle Area	*Alouatta > Lagothrix > Ateles*	*C. apella > C. albifrons/ C. capucinus*	*Cacajao/ Chiropotes > Pithecia*
3D Condyle Area	*Alouatta > Lagothrix > Ateles*	*C. apella > C. albifrons/ C. capucinus*	*Cacajao/ Chiropotes > Pithecia*
Glenoid ML Index	*Alouatta > Lagothrix > Ateles*	*C. apella > C. albifrons/ C. capucinus*	*Cacajao/ Chiropotes > Pithecia*
Glenoid AP Index	*Lagothrix/ Ateles > Alouatta*	*C. albifrons/ C. capucinus > C. apella*	*Pithecia > Cacajao/ Chiropotes*
Condyle ML Index	*Alouatta > Lagothrix > Ateles*	*C. apella > C. albifrons/ C. capucinus*	*Cacajao/ Chiropotes > Pithecia*
Condyle AP Index	*Lagothrix/ Ateles > Alouatta*	*C. albifrons/ C. capucinus > C. apella*	*Pithecia > Cacajao/ Chiropotes*

TABLE 4-4.Continued.

	Macaques	Papionins
Articular Tubercle Ht	*M. thibetana/ M. sylvanus/ M. fuscata > M. fascicularis/ M. nemestrina*	*Theropithecus > Papio*
Entoglenoid Ht	*M. thibetana/ M. sylvanus/ M. fuscata > M. fascicularis/ M. nemestrina*	*Theropithecus > Papio*
Glenoid Length	*M. fascicularis/ M. nemestrina > M. sylvanus/ M. fuscata > M. thibetana*	*Papio > Theropithecus*
Glenoid Width	*M. thibetana > M. sylvanus/ M. fuscata > M. fascicularis/ M. nemestrina*	*Theropithecus > Papio*
2D Glenoid Area	*M. thibetana/ M. sylvanus/ M. fuscata > M. fascicularis/ M. nemestrina*	*Theropithecus > Papio*
3D Glenoid Area	*M. thibetana/ M. sylvanus/ M. fuscata > M. fascicularis/ M. nemestrina*	*Theropithecus > Papio*
Preglenoid Length	*M. fascicularis/ M. nemestrina > M. sylvanus/ M. fuscata > M. thibetana*	*Papio > Theropithecus*
Glenoid Shape Index	*M. thibetana > M. sylvanus/ M. fuscata > M. fascicularis/ M. nemestrina*	*Theropithecus > Papio*
Condyle Width	*M. thibetana > M. sylvanus/ M. fuscata > M. fascicularis/ M. nemestrina*	*Theropithecus > Papio*
Condyle Length	*M. fascicularis/ M. nemestrina > M. thibetana/ M. sylvanus/ M. fuscata*	*Papio > Theropithecus*
2D Condyle Area	*M. thibetana/ M. sylvanus/ M. fuscata > M. fascicularis/ M. nemestrina*	*Theropithecus > Papio*
3D Condyle Area	*M. thibetana/ M. sylvanus/ M. fuscata > M. fascicularis/ M. nemestrina*	*Theropithecus > Papio*
Glenoid ML Index	*M. thibetana/ M. sylvanus/ M. fuscata > M. fascicularis/ M. nemestrina*	*Theropithecus > Papio*
Glenoid AP Index	*M. thibetana/ M. sylvanus/ M. fuscata > M. fascicularis/ M. nemestrina*	*Theropithecus > Papio*
Condyle ML Index	*M. thibetana/ M. sylvanus/ M. fuscata > M. fascicularis/ M. nemestrina*	*Theropithecus > Papio*
Condyle AP Index	*M. thibetana/ M. sylvanus/ M. fuscata > M. fascicularis/ M. nemestrina*	*Theropithecus > Papio*

TABLE 4-4.Continued.

	Hominids	Gorilla	Pongo	Pan
Articular Tubercle Ht	*Gorilla > Pongo > Pan*	*G. beringei > G. gorilla*	*P. pygmaeus > P. abelii*	*P. paniscus > P. troglodytes*
Entoglenoid Ht	*Gorilla > Pongo > Pan*	*G. beringei > G. gorilla*	*P. pygmaeus > P. abelii*	*P. paniscus > P. troglodytes*
Glenoid Length	*Pan > Pongo > Gorilla*	*G. gorilla > G. beringei*	*P. abelii > P. pygmaeus*	*P. troglodytes > P. paniscus*
Glenoid Width	*Gorilla > Pongo > Pan*	*G. beringei > G. gorilla*	*P. pygmaeus > P. abelii*	*P. paniscus > P. troglodytes*
2D Glenoid Area	*Gorilla > Pongo > Pan*	*G. beringei > G. gorilla*	*P. pygmaeus > P. abelii*	*P. paniscus > P. troglodytes*
3D Glenoid Area	*Gorilla > Pongo > Pan*	*G. beringei > G. gorilla*	*P. pygmaeus > P. abelii*	*P. paniscus > P. troglodytes*
Preglenoid Length	*Pan > Pongo > Gorilla*	*G. gorilla > G. beringei*	*P. abelii > P. pygmaeus*	*P. troglodytes > P. paniscus*
Glenoid Shape Index	*Gorilla > Pongo > Pan*	*G. beringei > G. gorilla*	*P. pygmaeus > P. abelii*	*P. paniscus > P. troglodytes*
Condyle Width	*Gorilla > Pongo > Pan*	*G. beringei > G. gorilla*	*P. pygmaeus > P. abelii*	*P. paniscus > P. troglodytes*
Condyle Length	*Pan > Pongo > Gorilla*	*G. gorilla > G. beringei*	*P. abelii > P. pygmaeus*	*P. troglodytes > P. paniscus*
2D Condyle Area	*Gorilla > Pongo > Pan*	*G. beringei > G. gorilla*	*P. pygmaeus > P. abelii*	*P. paniscus > P. troglodytes*
3D Condyle Area	*Gorilla > Pongo > Pan*	*G. beringei > G. gorilla*	*P. pygmaeus > P. abelii*	*P. paniscus > P. troglodytes*
Glenoid ML Index	*Gorilla > Pongo > Pan*	*G. beringei > G. gorilla*	*P. pygmaeus > P. abelii*	*P. paniscus > P. troglodytes*
Glenoid AP Index	*Gorilla > Pongo > Pan*	*G. beringei > G. gorilla*	*P. pygmaeus > P. abelii*	*P. paniscus > P. troglodytes*
Condyle ML Index	*Gorilla > Pongo > Pan*	*G. beringei > G. gorilla*	*P. pygmaeus > P. abelii*	*P. paniscus > P. troglodytes*
Condyle AP Index	*Gorilla > Pongo > Pan*	*G. beringei > G. gorilla*	*P. pygmaeus > P. abelii*	*P. paniscus > P. troglodytes*

however, in their relative consumption of seeds and animal prey. Peres (1994) reported that *L. lagothrica* included a relatively large proportion of seeds in its diet, and that young seeds were exploited more frequently at certain times of the year, therefore indicating that this species (particularly the subspecies *L. lagothrica cana*) is a seasonal seed predator. In contrast, Russo et al. (2005) found that only 1% of the feeding observations on *At. geoffroyi* in Panama were for seed predation. Di Fiore (2004) reported that the diet of *L. lagothrica* contained a substantial component of animal parts (approximately 9.3% of all feeding observations) and that this species spent a large amount of time searching for insect prey. Previous studies have indicated that spider monkeys rarely deliberately forage for insects and that animal prey makes up a very small component of their diet (van Roosmalen, 1985; Symington, 1987; Chapman, 1988, 1990; van Roosmalen and Klein, 1988).

The diet of *Al. seniculus* sharply contrasts with that of *At. geoffroyi* and *L. lagothrica*. *Al. seniculus* consumes approximately 50% leaves, with a preference for young, rather than mature, leaves; the remainder of its diet is composed of fruit and flowers (Gaulin and Gaulin 1982; Julliot, 1996). The genus *Alouatta* is the most folivorous of all New World primates, but there is considerable variability within this group. Hladik and Hladik (1969) and Gaulin et al. (1980) suggest that over 50% (by weight) of all food consumed by *Al. palliata* is fruit. Julliot (1996) indicates that the frugivory of howler monkeys follows seasonal variation in fruit availability.

The majority of the comparative analyses of atelines have focused on molar occlusal morphology, which indicates a sharp distinction between the high shearing crests and expanded occlusal surfaces of *Alouatta* and the relatively smaller and lower occlusal relief of *Ateles*, with *Lagothrix* displaying an intermediate morphology (Kay, 1975; Rosenberger and Kinzey, 1976; Rosenberger and Strier, 1989; Anapol and Lee, 1994). Incisor morphology also differs among these taxa, with *Ateles* and *Lagothrix* having larger spatulate incisors, and *Alouatta* with considerably reduced incisor dimensions (Hylander, 1975a; Eaglen, 1984; Anapol and Lee, 1994). All of these differences are attributable to the dietary differences between the more frugivorous *Ateles* and *Lagothrix* and the folivorous *Alouatta*. Several analyses of craniofacial variation have also been conducted; Rosenberger and Strier (1989) identified a suite of features (e.g., high TMJ, more robust mandible, larger temporal foramen) in *Alouatta* and *Ateles* relative to *Lagothrix* that together indicate a more powerful masticatory apparatus in *Alouatta* in comparison to a relatively weaker masticatory system in *Ateles*. These visual observations were supported by quantification of the masticatory apparatus in these taxa by Spencer (1995).

An additional factor that must be considered is the highly derived nature of the vocal apparatus in *Alouatta*, and its variation within this genus. In comparison to other Atelines, *Alouatta* has a relatively smaller cranial capacity and a considerably less flexed cranial base, a unique characteristic that has been related to the greatly expanded hyoid apparatus used for producing the territorial calls characteristic of this genus (Fleagle, 1999). As documented by Hershkovitz (1949) and Hill (1962), there is a range of variation in size and shape of this structure, with the most expanded hyoid observed in *Al. seniculus*, and the least expanded in *Al. palliata*. At present it is unclear how this variation is reflected in cranial anatomy, although preliminary work by Halenar (2008) suggests that vocal variation is reflected in basicranial morphology, and potentially some aspects of TMJ shape. As a consequence, potential correlates between TMJ shape and vocal behaviors, particularly relative gape, will need to be examined in this analysis.

Given these observations, the TMJ morphology of these three taxa is predicted to be the most robust in *Alouatta*, slightly less so in *Lagothrix*, and the most generalized in *Ateles*. In particular, *Alouatta* should have relatively larger joint surface areas because of their heavy reliance on tough food objects. In other taxa this would suggest that the TMJ of *Alouatta* should also be relatively mediolaterally wider than it is anteroposteriorly, but given the vocal behaviors in this species, it is predicted that *Alouatta* should have significant anteroposteriorly longer joints.

Accordingly, *Alouatta* should also have the largest entoglenoid processes to guide movement of the condyle during jaw opening and closing. In contrast, *Lagothrix* and *Ateles* should have relatively smaller joint surface areas and processes, and also have relatively shorter joints in the anteroposterior dimension. Given the slightly heavier reliance of *Lagothrix* on seeds, it is also predicted that the morphology of *Lagothrix* will be intermediate between *Alouatta* and *Ateles*.

Cebines

Three taxa from the subfamily Cebinae were included in this study: *Cebus capucinus*, *C. albifrons*, and *C. apella*. This closely related group has a long history of field observation and study, and as a consequence a great deal of data are available regarding their dietary ecology. Although primarily frugivorous, all three of these taxa consume vertebrates, invertebrates, leaves, and flowers to some extent (Izawa and Mizuno, 1977; Izawa, 1979; Freese and Oppenheimer, 1981; Chapman and Fedigan, 1990; Janson and Boinski, 1992; Rose, 1994; Port-Carvalho et al 2004). In addition, all three species are known to use their anterior teeth during food processing and to incorporate seeds into their diet (Terborgh, 1986; Janson and Boinski, 1992). However, the diet of *C. apella* differs substantially from those of *C. albifrons* and *C. capucinus* in the relative amounts of resistant food objects exploited (Terborgh, 1983). In particular, *C. apella* spends a larger percentage of time feeding on *Astrocaryum* nuts, the hard outer husks of which require either manual preparation (e.g., cracking open using force) and/or dental preparation, often in the form of the use of the canines as a wrench to further propagate cracks (Izawa and Mizuno, 1977; Izawa, 1979; Terborgh, 1983; Janson and Boinski, 1992). Izawa and Mizuno (1977: 782) report that “after completely cracking the husk, the capuchin takes out some part of the hardened coco inside the husk with its teeth.”

Previous morphological analyses of cebine masticatory morphology are consistent with the finding that *C. apella* exploits much harder food objects than other species in its genus. In comparison to *C. capucinus*, Kinzey (1974) and Rosenberger and Kinzey (1976) identified the low crowned occlusal morphology of *C. apella* as better adapted to powerful grinding and crushing behaviors, and noted a suite of morphological characters that they linked with this occlusal morphology, including a higher TMJ, frequent development of a sagittal crest, a thick mandibular body, and wide zygomatic arches. Teaford (1985) found evidence for hard-object feeding in *C. apella* in molar microwear patterns; in relation to other *Cebus* species, microwear in *C. apella* shows more enamel pitting, a feature that is indicative of hard-object feeding. Spencer (1995) and Wright (2005) both examined variation in *Cebus* masticatory morphology in the context of Greaves's (1978) model, with somewhat mixed results. Spencer (1995) did not find any consistent differences in masticatory system configuration among the various species of *Cebus* and hypothesized instead that their differing abilities to utilize resistant food objects were related to a greater maximum force potential of the masticatory muscles in *C. apella*. In contrast, Wright (2005) found that the masticatory apparatus of *C. apella* was more advantageous for generating and dissipating higher masticatory forces than other *Cebus* species, with very anteriorly positioned masticatory muscles that act to increase bite forces along the anterior dentition. However, field data collected by Wright indicate that *C. apella* only occasionally ingests food items of exceptional toughness, and therefore the masticatory morphology of *C. apella* is advantageous for producing high but relatively infrequent bite forces. Constantino (2007) found that in four comparative groups, including cebines, resistant object feeders could be reliably distinguished from other closely related taxa using four primary traits: taller mandibular symphyses, corpora, and rami, and more orthognathic faces.

Given these data, it is predicted that *C. apella* will exhibit relatively larger joint surface areas as a consequence of larger reaction forces at the joint. In addition, the increased use of the anterior dentition by *C. apella* suggests that this species should have a relatively anteroposteriorly longer glenoid and mandibular condyle, which should allow this species to achieve the larger gapes necessary during food processing. This increased gape should also be accompanied by relatively large entoglenoid processes that act to guide the movement of the condyle.

Pitheciines

The comparative sample from the subfamily Pitheciinae includes three taxa: *Cacajao melanocephalus*, *Chiropotes satanas*, and *Pithecia pithecia*. All three of these species feed primarily on fruit, with approximately 90% or more of the food items in their diet being fruit (Buchannon et al., 1981; van Roosmalen et al, 1981, 1988; Kinzey, 1992; Ayres, 1989; Boubli, 1999). In addition, all three taxa rely heavily on seeds, particularly during times of resource stress (Ayres, 1989; Kinzey, 1992; Boubli, 1999). Together, these three taxa have been identified as "sclerocarp harvesters" (Kinzey, 1992). Kinzey (1992) noted that this type of foraging involves two distinct stages: initial removal of the hard outer husk of seeds with the anterior dentition, and mastication by the posterior dentition of the softer inner seed parts. The first part of this process requires the use of the pitheciine's large wedge-shaped canines and procumbent incisors to open tough food items (van Roosmalen et al., 1988; Ayres, 1989; Kinzey, 1992). Of these three taxa, *Pithecia* has been suggested to be the least specialized for seed predation, primarily on account of its more generalized masticatory morphology, lower molar relief, and less well-developed canines (Kinzey, 1992; Kinzey and Norconk, 1993). Spencer (1995) tested this hypothesis, and found that the mechanical advantage of the masticatory muscles in *Pithecia* was substantially lower than in *Chiropotes* and *Cacajao*, and that the masticatory system of *Pithecia* was much more generalized, with lower mechanical advantage found for biting on the anterior teeth, which is potentially associated with the greater proportion of leaves in its diet than is the case for the remaining two taxa.

These data suggest that *Cacajao* and *Chiropotes* should both have relatively larger joint surface areas as a consequence of their increased reliance on seed predation (and therefore presumably larger joint reaction forces). Both of these taxa may also be expected to have relatively anteroposteriorly longer joint surface areas because of their extensive use of the anterior dentition. In contrast, *Pithecia* should have relatively mediolaterally wider joints with a larger articular tubercle.

Macaques

Five species of macaques were examined in this comparative group, *Macaca fuscata*, *M. sylvanus*, *M. thibetana*, *M. nemestrina*, and *M. fascicularis*. Field data for the first three species suggest that they routinely masticate relatively more resistant food objects than either *M. nemestrina* or *M. fascicularis*.

Living at the highest latitude of any non-human primate species, *M. fuscata*, or the Japanese Macaque, must deal with pronounced fluctuations in food availability due to extreme seasonality (Tsuji et al., 2006). A number of studies suggest that this species' diet shifts considerably seasonally (Maruhashi, 1980; Hill, 1997; Tsuji et al., 2006). In spring and fall, *M. fuscata* relies most heavily on fruit, leaves, and flowers, whereas in the summer and winter months nuts are the primary food source, which is supplemented by buds and bark in winter (Maruhashi, 1980; Hill, 1997; Tsuji et al., 2006). Bark is relatively more fracture resistant than food consumed during the summer months, suggesting that the Japanese Macaque's ability to masticate this resistant food object may be important for its ability to survive winter (Constantino, 2007), making bark a critical resource or "fallback" food (Rosenberger and Kinzey, 1976).

Like *M. fuscata*, the Barbary macaque (*M. sylvanus*) also lives in areas with high seasonal variation in resource availability (Drucker, 1982; Deag, 1983; Menard and Vallet, 1997; Menard, 2002). This species is frequently considered a generalist feeder because its diet is highly flexible across seasons and habitats (Menard, 2002), and different food items can make up the major component of their diet depending on the season. Menard and Vallet (1997) compared two populations of *M. sylvanus* and found that observations for leaf eating made up 49% of the feeding time in the cedar-oak forest population of Djurdjura, Algeria, and seeds made up 32% of the diet of Barbary macaques living in the oak forest of Akfadou, Algeria. Marked seasonal variation was also present, with a folivorous phase documented in winter and early spring, a gramnivorous phase in fall with an increased consumption of herbaceous seeds and/or acorns, and an insectivorous phase in early spring (Menard and Vallet, 1997; Menard, 2002). Increasing human pressure may also impact the diet of the Barbary macaque; Menard (2002) documented an increase in bark stripping in the Middle Atlas region, which she attributed to modifications of the forest system by increased human pressure.

Fewer data are available regarding the dietary ecology of *M. thibetana*. Zhao et al. (1991) report that the majority of this species' unprovisioned diet includes bamboo shoots and fruits in autumn and mature leaves and bark for the remainder of the year. These authors suggest that this unique diet may explain why this species has the largest body size of all macaques (Zhao and Deng, 1988; Zhao et al., 1991).

The remaining two species in this comparative sample, *M. fascicularis* and *M. nemestrina*, have diets with considerably higher percentages of fruits than the macaque species already discussed (Wheatley, 1976, 1980; Crockett and Wilson, 1980; Lucas and Corlett, 1991). Both taxa live in Southeast Asia, with much of their ranges overlapping (Rowe, 1996). Their diets are very similar, and consist mostly of fruits; however, Crockett and Wilson (1980) suggested that *M. nemestrina* is able to masticate larger food items as a consequence of their larger size, whereas *M. fascicularis* can access food items on smaller branches that are inaccessible to *M. nemestrina*.

Several studies have evaluated and compared the masticatory morphology of macaque species in the context of dietary differences among taxa. Takahashi and Pan (1994) found that the pattern of mandibular morphology in *M. thibetana* was consistent with Zhao et al.'s (1991) observations that this species is considerably more folivorous than other macaque species. In particular, Takahashi and Pan found that *M. thibetana* had relatively wider mandibular condyles and thick mandibular corpora. Subsequently, Anton (1996) suggested that *M. fuscata* has a vertically deeper and anteroposteriorly shorter face, a broader mandibular corpus, and more anteriorly placed masseter than in *M. nemestrina* and *M. fascicularis*; all three of these characters suggest that *M. fuscata* can more effectively dissipate large occlusal forces than *M. nemestrina* and *M. fascicularis*, as was expected from field observations of their feeding habits. Constantino (2007) performed a geometric morphometric analysis of cranial and masticatory shape in *M. sylvanus*, *M. fuscata*, *M. nemestrina*, *M. fascicularis*, and *M. mulatta*. Constantino found that the two resistant-object feeders in the sample (*M. sylvanus* and *fuscata*) had similar masticatory morphologies that were consistent with expectations of Greaves (1978) and Spencer's (1995) constrained lever model, suggesting that these two taxa are indeed adapted for the consumption of fracture-resistant food objects.

These data indicate that *M. sylvanus*, *M. fuscata*, and *M. thibetana* consume relatively more resistant food objects than either *M. fascicularis* or *M. nemestrina*. As a result, it is predicted that these three resistant taxa will have relatively larger joint surface areas than *M. fascicularis* or *M. nemestrina*. In addition, the resistant taxa will have relatively larger entoglenoid processes to guide movement of the condyle and to further increase joint surface area for the dissipation of joint reaction forces. It is also predicted that the resistant object feeders should have relatively shorter (AP) and wider (ML) joints than the non-resistant object feeders, as a consequence of their increased reliance on the posterior dentition. This pattern should be the most extreme in *M. thibetana*, which relies heavily on tough objects such as leaves.

Papionins

Members of the papionin clade have often been characterized as having a diverse diet. This is particularly true of the genus *Papio*, which, depending upon the species definition in use, may contain a single highly variable species or as many as five distinct species (Jolly, 1993). All of these taxa (whether considered separate species or multiple subspecies of *P. hamadryas*) exploit a wide variety of food items, including leaves, flowers, fruit, bark, exudates, birds' eggs, vertebrate prey, roots, underground storage organs, herbs, grasses, and sedges (Moreno-Black and Maples, 1977; Hamilton et al., 1978; Whiten et al., 1991; Byrne et al., 1993; Pochron, 2000; Hill and Dunbar, 2002; Swedell, 2002). In this study, the morphology of three *Papio* species, *P. anubis*, *P. cynocephalus*, and *P. ursinus* will be compared to that of *Theropithecus gelada*. These three species (or subspecies, if preferred) of *Papio* were chosen for comparison because they represent a range of body sizes (Fleagle, 1999) and inhabit a variety of habitats that allows them to exploit similar food items with varying mechanical properties.

Like *Papio*, the gelada baboon (*Theropithecus gelada*) also eats a wide variety of foods (including fruit, seeds, flowers, insects, and leaves), but in contrast to *Papio*, *Theropithecus* focuses heavily on grasses. Dunbar (1977) and Iwamoto (1979, 1993) report that over 90% of the gelada's time spent foraging is on grass, including grass leaves, seeds, roots and flower parts (Dunbar, 1977; Iwamoto, 1993). Furthermore, between the wet and dry seasons, geladas focus primarily on seeds (Dunbar, 1977), and during the dry season rhizomes form the bulk of their diet (Iwamoto, 1993). These data suggest that *Theropithecus* consumes considerably more fracture-resistant food items than *Papio*, and spends a greater proportion of their waking time feeding, likely because of the low nutrient quality of their food items (Dunbar, 1977).

Together, these data indicate that the masticatory apparatus of *Theropithecus* should be better adapted to dissipating higher magnitude and/or higher frequency forces than *Papio*. Several analyses have tested this hypothesis. Jablonski (1981, 1993) first quantified the masticatory apparatus of *Theropithecus*, and compared it to those of several species of *Papio* and *Macaca*. Jablonski (1993) found that *T. gelada* is highly specialized for chewing grass parts, as evidenced by relatively longer moment arms of the masseter and temporalis muscles (e.g., more anteriorly positioned musculature and a shorter mandibular length), a higher TMJ, and generally enlarged masticatory muscles. Spencer (1995) and Constantino (2007) further evaluated the masticatory apparatus of *Theropithecus* in the context of the constrained lever model. Spencer (1995) found that the observed differences in masticatory shape were consistent with an increased area over which force is dispersed on the postcanine dentition in *Theropithecus* in comparison to *Papio*. Constantino (2007) found marked differences in the shape of the masticatory apparatus between these two genera, with *Theropithecus* distinguished by a taller mandibular symphysis, corpus, and ramus, and a more orthognathic face; all of these features suggest that *Theropithecus* is adapted for processing more fracture-resistant food objects than *Papio*.

These observations of the dietary ecology of *Theropithecus* and *Papio* indicate that the TMJ morphology of *Theropithecus* should be considerably more adapted to the mastication of resistant food objects than *Papio*. This should be exemplified by larger joint surface areas and joint processes, and a relatively ML wider joint in *Theropithecus* than in *Papio*.

Hominids

The hominid comparative sample examined here includes species from all three genera of living great apes: *Pan troglodytes, P. paniscus, Gorilla gorilla*, *G. beringei*, *Pongo pygmaeus*, and *P. abelii*. Each of these genera includes two species that have been documented to differ in the amount of resistant food objects incorporated into their diets. Field studies of the dietary ecology of the common chimpanzee (*P. troglodytes*) and the bonobo (*P. paniscus*) suggest that bonobos have a greater reliance on piths and leaves of terrestrial herbaceous vegetation (THV) than do chimpanzees (Badrian and Malenky, 1984). Further work by Malenky and Wrangham (1994) confirmed this initial observation using fecal analyses, and indicated that, while chimps consume more THV during times of fruit scarcity, bonobos ingest similar levels of THV year round, regardless of fruit availability.

Similar differences in diet have been documented between lowland (*G. gorilla*) and highland (*G. beringei*) gorillas. Populations of lowland gorillas have been documented to consume relatively large quantities of fruit (approximately 63.2%), and thus fruits are their preferred food; however, THV consumption was noted year round, and particularly in times of low fruit availability (Williamson et al., 1990; Tutin and Fernandez, 1993; Nishihara, 1995). In contrast, the diet of *G. beringei* consists almost entirely of terrestrial vegetation, including leaves, stems, vines, and shrubs at ground level, with flowers, pith, bark, and roots making up a small component of their diet (Watts, 1984). Furthermore, Elgart-Berry (2004) measured the fracture toughness of foods consumed by *G. beringei* and found that tree barks were the toughest food items eaten, followed by piths, stems, and woody fungi, although the top five ranked food items were low to moderately tough.

Species in the remaining genus include the Bornean (*P. pygmaeus*) and Sumatran (*P. abelii*) orangutans. Bornean orangs were found by MacKinnon (1977) to eat a wide variety of foods, but preferred fruit. Fruit was highly seasonal, however, and in times of fruit abundance they accounted for over 90% of the feeding observations, versus only 10% of feeding observations when fruit was scarce. Galdikas (1988) observed that fruit accounted for 61% of all foraging time (over four years) for Bornean orangs. *P. pygmaeus* also ate many other food items, including buds, flowers, leaves (usually young), bark, sap, vines, insects, fungi, honey, and others. Bark, small vines, insects, and young leaves, were further characterized as fallback foods that were relied upon during times of fruit scarcity (Galdikas, 1988). For instance, bark accounted for 11% of all documented foraging time, although the orangs went for long periods before heavily exploiting this resource. Notably, bark accounted for 47% of foraging time for a single wet month, in which it was the predominant food type. Sumatran orangs have been documented to consume similar quantities of fruit (Rodman, 1988; Knott, 1998; Fox et al., 2004; Wich et al., 2006). However, fewer fluctuations in fruit availability in Sumatra allow *P. abelii* to rely on fruit throughout the year, and therefore bark and other plant parts make up a very small percentage of their diet (2.7% vs. 9.3-14.2% for *P. pygmaeus*). Notably, however, *P. abelii* incorporates a much larger percentage of insects into their diet (8.8-13.4% vs. 0.8-4.3% for *P. pygmaeus*).

In addition to the documented dietary differences among the species in each genus, the dietary ecology of each of these genera varies considerably, and these differences have formed the basis of a number of comparative analyses of masticatory morphology. A series of studies conducted by Taylor (2002, 2005, 2006) examined the mandibular morphology of *Pan*, *Gorilla*, and *Pongo* in light of the above discussed dietary differences. Taylor (2002) compared the mandibular shape of *Gorilla* and *Pan*, as well as the species within both of these genera, with the expectation that the more folivorous species (*G. beringei* and *P. paniscus*, respectively) would differ from other members of their genus as a consequence of their more mechanically demanding diets. Furthermore, Taylor expected that *Gorilla* would differ from *Pan* in the same ways as the more folivorous species in each genus. Taylor's results indicate that the taxa with the more mechanically resistant diets were significantly different, with relatively wider mandibular corpora and symphyses, larger area for the masseter muscle, and a higher mandibular ramus and condyle. However, Taylor's data failed to find a statistically significant difference between the mandibular morphology of *P. troglodytes* and *P. paniscus*. Taylor (2005) extended these analyses to the temporomandibular joint with similar results: *G. beringei* was significantly different in shape from *G. gorilla*, no significant difference was found between *P. paniscus* and *P. troglodytes*, and *Gorilla* differed significantly from *Pan*. In the more folivorous taxa, the TMJ was placed higher above the occlusal plane, and the mandibular condyles were significantly wider; these features allow for a more even distribution of occlusal forces along the posterior teeth, and increased ability to resist compressive loads along the lateral aspect of the condyle, respectively, both of which are associated with increased folivory.

Following on these analyses of the African apes, Taylor (2006) examined mandibular shape in *Pongo*, finding that several populations of the more folivorous *P. pygmaeus* had a relatively deeper mandibular corpus, deeper and wider mandibular symphysis, and a larger condylar area than the more frugivorous *P. abelii*, suggesting that *P. pygmaeus* is better suited to resisting larger and/or more frequent masticatory loads than *P. abelii*. Similarly, Constantino (2007) examined the overall masticatory morphology of the African apes, and found that *G. beringei* had a relatively taller mandibular symphysis, corpus, and ramus, and a more orthognathic face compared to *G. gorilla* and *Pan*. However, although *P. paniscus* was included in the sample, the morphology in this species did not vary from *P. troglodytes* in the same way that *G. beringei* varied from *G. gorilla*, suggesting that the masticatory morphology of *P. paniscus* may not be adapted for masticating more resistant food objects. Furthermore, Constantino (2007) later incorporated *P. pygmaeus* into the analysis with the African apes, with the expectation that *Pongo* would better adapted to masticating resistant food objects due to field observations that orangs regularly masticate very hard fruits and seeds (Galdikas, 1988; Lucas et al., 1994; Conklin-Brittain et al., 2001). Although *Pongo* differed from *Pan* in the same way as *Gorilla*, no significant difference was found between *Pongo* and *Gorilla*.

These data suggest that there should be a number of differences among hominid taxa if TMJ morphology is associated with dietary differences. At the generic level, *Gorilla* and *Pongo* should have relatively larger joint surface areas and joint processes than *Pan*, and it is expected that *Pongo* should be intermediate between *Gorilla* and *Pan* because of the very heavy and more continuous utilization of resistant food objects in *Gorilla* (as opposed to the more seasonal use of these resources in *Pongo*). Furthermore, *Gorilla* should have the widest (ML) TMJs, while *Pan* is expected to have considerably narrower (ML) and longer (AP) joint dimensions; *Pongo* is predicted to be intermediate between *Gorilla* and *Pan* in these variables. Two species were also examined in each of these genera, one of which exploits more resistant food objects than the other. In *Pan*, *P. paniscus* is predicted to exhibit features associated with a more resistant diet when compared to *P. troglodytes*; thus, *P. paniscus* should have a larger joint surface area and joint processes, as well as a mediolaterally wider joint. In *Gorilla*, the same differences should be observed between *G. beringei* and *G. gorilla*, with the former utilizing resistant food objects more habitually than the latter. Finally, in Pongo, *P. pygmaeus* has been shown to rely more heavily on resistant food objects during times of food scarcity than *P. abelii*, and therefore *P. pygmaeus* should have a relatively larger joint area and processes, and likely should have a relatively ML wider and AP compressed joint than *P. abelii*.

MATERIALS AND METHODS

Data used in this analysis included three-dimensional (3D) coordinate data for 48 anthropoid taxa, as previously described in Chapter 3. The coordinate data were used to calculate linear and angular measurements describing TMJ size and aspects of TMJ shape in the programs MacMorph (Spencer and Spencer, 1993) and Rhino 3D (McNeel & Associates, 2008). Variables measured included glenoid and condyle length (in the AP dimension), glenoid and condyle width (in the ML dimension), two-dimensional (2D) and 3D glenoid and condylar area, preglenoid plane length, entoglenoid and postglenoid process height, articular tubercle height, and articular eminence inclination (refer to Chapter 3 for more detailed descriptions of these variables). Three dimensional coordinates describing AP and ML curvature of the glenoid and condyle were also used to calculate curvature indices (arc/ chord length). Geometric morphometric (GM) analyses were performed using the twelve landmarks describing glenoid fossa shape (as outlined in Chapter 3).

Several complimentary analyses were performed to assess how the shape of the TMJ was related to masticatory function. First, GM methods were used to visually evaluate variation in glenoid fossa shape among taxa in the six comparative groups discussed above. Landmark data were first standardized using Generalized Procrustes Analysis (GPA), and a principal components analysis (PCA) was then performed to assess how the sample varied in morphospace. Wireframe diagrams were used to examine how landmark configurations differed among taxa. Wireframe diagrams in all figures are as illustrated in Figure 3-2. Results of these analyses were then further evaluated by performing a two-tailed Kruskal-Wallis test with multiple (post-hoc) comparisons for each linear measurement calculated from the landmark data. Alternatively, where only two genera were compared (e.g., *Papio* vs. *Theropithecus*) a Mann-Whitney U test was performed. All variables were standardized for variation in size by dividing each variable by a geometric mean calculated from measurements of calvarial size (bi-asterionic breadth, bi-porionic breadth, basioccipital length, cranial height, cranial length, and orbital width). All pairwise comparisons were performed using individual specimens, rather than species means, and in most comparative groups, analyses were confined to the female sample so as to minimize the effects of sexual dimorphism. However, in one instance (Papionins) the sample size for *Theropithecus* females was too small to achieve statistical significance (n=3), and the male sample was analyzed instead. The GM analyses were performed in the program Morphologika, and the Kruskal-Wallis and Mann-Whitney U tests were calculated using the program Statistica (Release 8.1, Statsoft, Inc.).

Correlation analyses were then performed to test for correlations between articular eminence orientation, muscle resultant orientation, and TMJ height, and between measures of gape, glenoid length, and AP condylar curvature (details of these measurements are outlined in Chapter 3). For each of these sets of data, Pearson product-moment correlations (r) and p-values were calculated using species means, which were separated by sex. In addition, as the data points are not considered to be phylogenetically independent, independent contrasts analysis (Felsenstein, 1985) was used to correct for covariance due to phylogeny (refer to Chapter 6 for a review of this method).

Criteria for hypothesis testing

It is expected that the results of these analyses will vary across taxa. As stated by Anthony and Kay (1993) and outlined in the introductory chapter, there may be multiple solutions to a particular functional demand. Here, I am only testing one way in which this morphology is expected to vary in association with masticatory function, but this does not mean that the same end is not being achieved in different ways in other comparative groups. However, for the purpose of hypothesis testing, it is expected that the majority of the comparative groups examined should show the predicted trend in a particular feature or suite of features in order for that prediction to be upheld. At the beginning of this chapter I outlined three main predictions of the overarching research question regarding the relationship between masticatory function and TMJ morphology. These predictions were in regard to material food properties, use of the anterior vs. posterior dentition, and gape requirements. It is these main predictions that I will return to in my discussion of the validity of my research question later in this chapter.

RESULTS

Comparative groups

Atelines. Results of the GM analyses for the atelines indicated marked differences in TMJ shape among taxa. *Alouatta* was separated from *Lagothrix* and *Ateles* along PC 1 (30.3% of sample variation) (Fig. 4-2). This separation may be a result of size differences among these taxa, since this axis was significantly correlated with centroid size ($r^2 = 0.539$, $p<0.001$). Variation in shape along this axis was primarily associated with the relative size of the PGP, which is considerably larger in *Alouatta*, but also with the AP length of the glenoid. A separate GM analysis including the condylar configurations, however, did not appear to separate these taxa.

Results of the Kruskal-Wallis test (Table 4-5; refer to Appendix B for box plots illustrating these variables) indicate that most comparisons among these three taxa are statistically

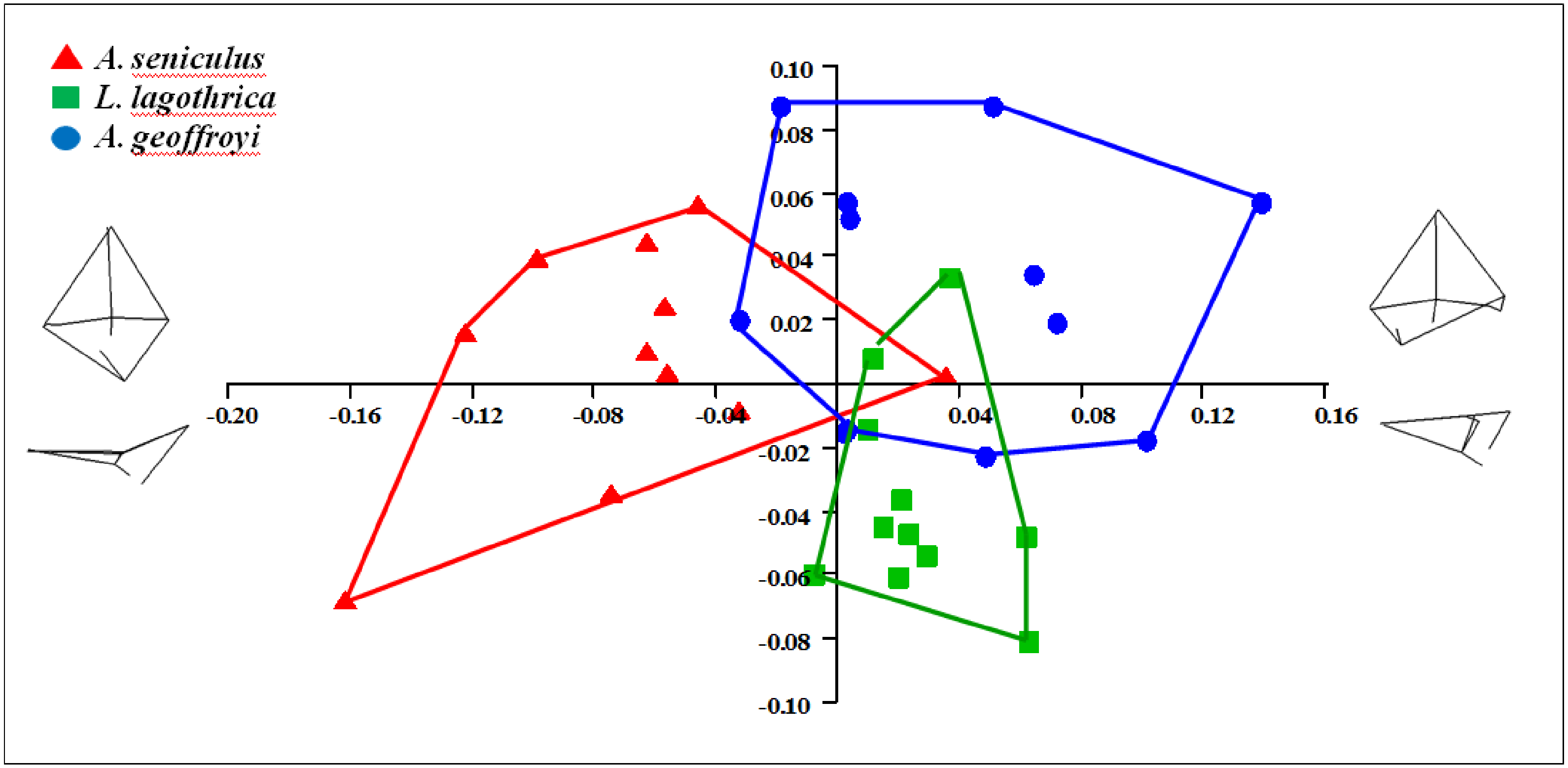


Fig. 4-2. Bivariate plot of PC 1 (x-axis) and PC 2 (y-axis) from the PC analysis of the glenoid configurations in the Atelinae females. Wireframe diagrams illustrate the shape variation from the resistant to soft-object feeders in the sample.

TABLE 4-5. Results of the Kruskal-Wallis test for the Atelinae (females only). Values represent the meansof each variable by taxon (reported either as angles or dimensionless indices), the H-value and p-value for each variable, and significantly different pairs of taxa, as indicated by a Tukey post-hoc test for significance between groups. Critical alpha was set at 0.05/18 = 0.0028, with statistically significant results highlighted in grey. Bolded but unhighlighted values indicate marginally significant (0.05> p > 0.0028) H-values.

	Mean						
Variable	*Ateles*	*Lagothrix*	*Alouatta*	H	p-value	Significant Pairs	As predicted?
AE Inclination	22.929	20.445	26.935	5.45	0.066	n/a	n/a
Articular Tubercle Ht	0.129	0.182	0.225	**28.98**	**<0.0001**	*Alouatta > Ateles/ Lagothrix*	Yes
Entoglenoid Ht	0.159	0.173	0.253	**23.67**	**<0.0001**	*Alouatta > Ateles/ Lagothrix*	Yes
Glenoid Length	0.364	0.394	0.493	**24.0**	**<0.0001**	*Alouatta > Ateles/ Lagothrix*	Yes
Glenoid Width	0.323	0.347	0.402	**23.84**	**<0.0001**	*Alouatta > Ateles/ Lagothrix*	Yes
2D Glenoid Area	3.706	4.146	5.874	**23.38**	**<0.0001**	*Alouatta > Ateles/ Lagothrix*	Yes
3D Glenoid Area	5.082	5.283	7.265	**21.41**	**<0.0001**	*Alouatta > Ateles/ Lagothrix*	Yes
Postglenoid Length	0.200	0.235	0.328	**25.42**	**<0.0001**	*Alouatta > Ateles/ Lagothrix*	n/a
Preglenoid Length	0.220	0.242	0.274	**21.54**	**<0.0001**	*Alouatta > Ateles/ Lagothrix*	Yes
Glenoid Shape Index	0.887	0.882	0.818	**8.98**	**0.011**	*Alouatta/ Lagothrix > Ateles*	No
Condyle Width	0.247	0.276	0.316	**21.01**	**<0.0001**	*Alouatta > Ateles/ Lagothrix*	Yes
Condyle Length	0.105	0.122	0.124	**15.43**	**0.0004**	*Alouatta/ Lagothrix > Ateles*	Yes
2D Condyle Area	0.813	1.020	1.161	**20.30**	**<0.0001**	*Alouatta/ Lagothrix > Ateles*	Yes
3D Condyle Area	1.758	2.096	2.701	**25.11**	**<0.0001**	*Alouatta > Ateles/ Lagothrix*	Yes
Glenoid ML Index	1.149	1.119	1.062	**17.57**	**0.0002**	*Ateles/ Lagothrix > Alouatta*	No
Glenoid AP Index	1.015	1.014	1.018	1.95	0.378	n/a	n/a
Condyle ML Index	1.134	1.156	1.088	**11.43**	**0.0033**	*Ateles > Alouatta*	No
Condyle AP Index	1.191	1.200	1.170	1.83	0.400	n/a	n/a

significant, with *Alouatta* having larger mean values in comparison to *Ateles* and *Lagothrix*. Notably, glenoid and preglenoid plane length are significantly larger in *Al. seniculus,* potentially as a result of the wider relative gapes that may be expected in this species due to their vocal behaviors (refer to discussion in Chapter 4). These findings are consistent with the predictions outlined above for this group, which indicated that the dimensions of the TMJ would be relatively larger in *Alouatta* than in other atelines. In most of these comparisons, the values for *Ateles* and *Lagothrix* were not statistically significantly different, although examination of the box plots indicates that the mean values for each variable tended to be slightly higher in *Lagothrix*. This indicates that the morphology observed in this genus is somewhat intermediate between *Alouatta* and *Ateles*, as was predicted based on their dietary ecology.

Cebines. The PC analysis for the cebine glenoid configuration separates *C. apella* from *C. capucinus* and *C. albifrons* along PC 1 (27.2% of variation) and PC 2 (15.2% of variation) (Fig. 4-3). The wireframe diagrams indicate that *C. apella* differs from the other species in the AP length and ML width of the glenoid, and in the relative size of the PGP. *C. apella* also separated from *C. albifrons*/ *capucinus* in condylar morphology (Fig. 4-4), with a relatively AP shorter condyle that is less ML convex. No consistent pattern of differences in shape between *C. albifrons* and *C. capucinus* was observed in the sample.

In contrast to the GM analyses, however, the Kruskal-Wallis test (Table 4-6, Appendix B) indicated that most comparisons among these taxa were not statistically significant, and those that were significant were not in the expected direction (e.g., that *C. apella* would have larger joint dimensions than *C. albifrons* or *C. capucinus*). These significant comparisons showed that *C. apella* has a relatively smaller articular tubercle, entoglenoid process, and less ML curved glenoid and condyle than *C. albifrons* or *C. capucinus*. However, area measurements of the glenoid and condyle suggest that *C. apella* does have a slightly larger joint surface area, and also

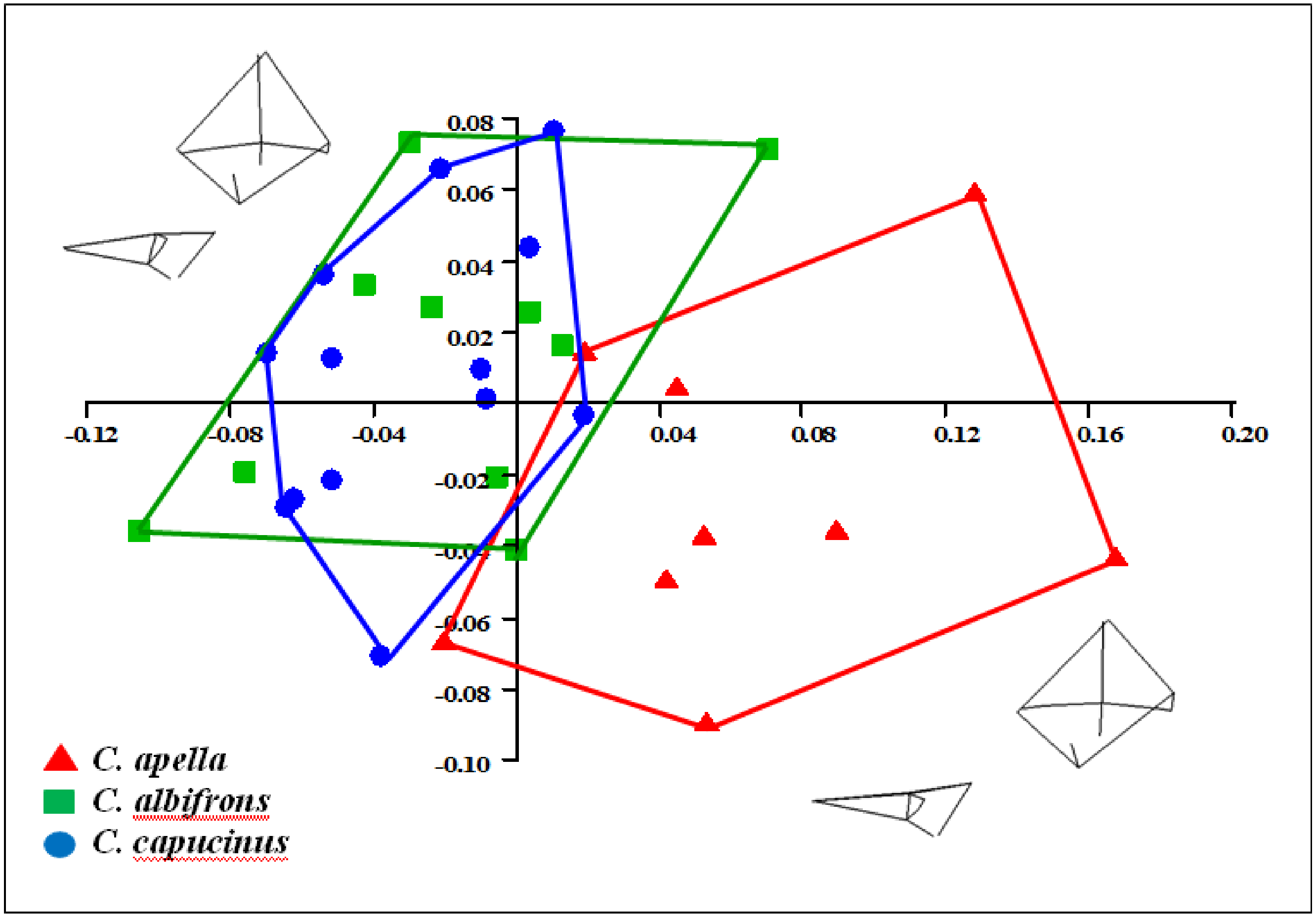


Fig. 4-3. Bivariate plot of PC 1 (x-axis) and PC 2 (y-axis) from the PC analysis of the glenoid configurations in the Cebinae females. Wireframe diagrams illustrate the shape variation from the resistant to soft-object feeders in the sample.

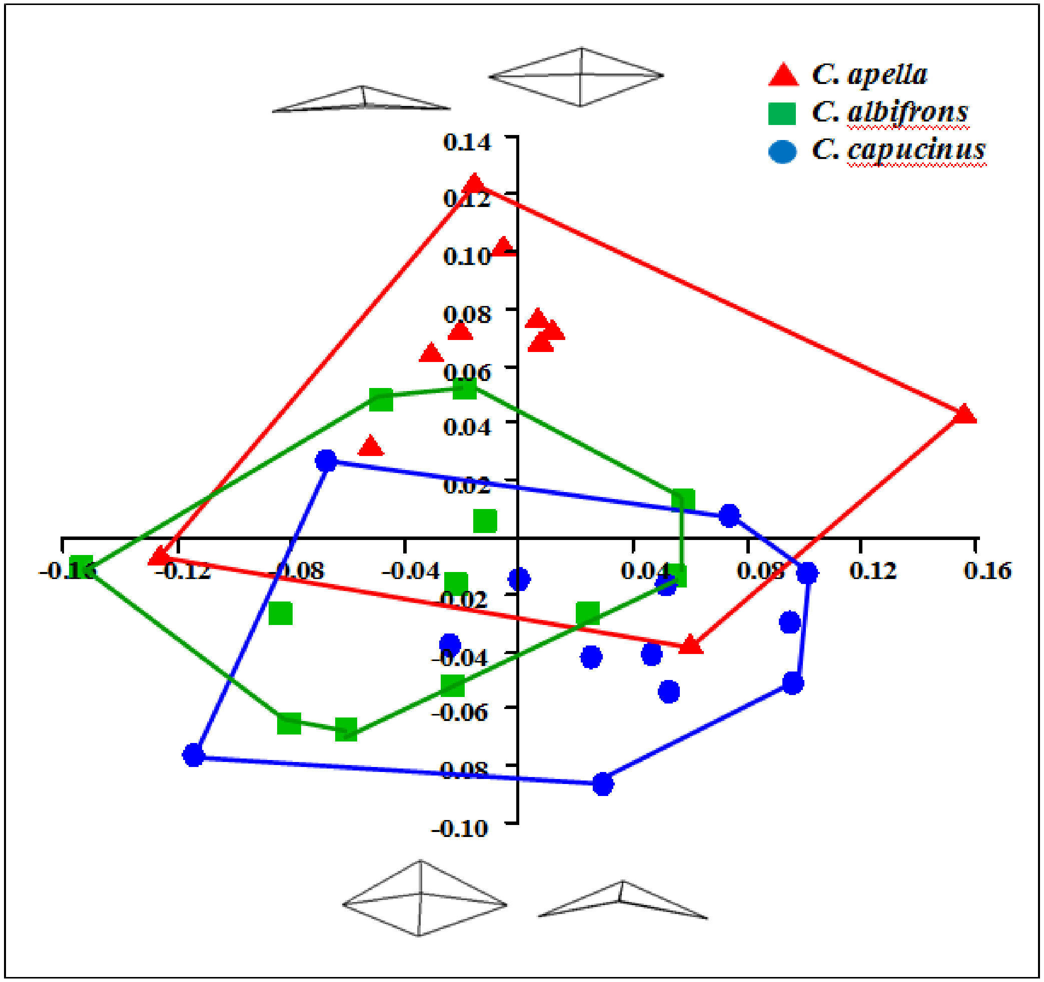


Fig. 4-4. Bivariate plot of PC 1 (x-axis) and PC 2 (y-axis) from the PC analysis of the condylar configurations in the Cebinae females. Wireframe diagrams illustrate the shape variation from the resistant to soft-object feeders in the sample.

TABLE 4-6. Results of the Kruskal-Wallis test for the Cebinae (females only). Values represent the meansof each variable by taxon (reported either as angles or dimensionless indices), the H-value and p-value for each variable, and significantly different pairs of taxa, as indicated by a Tukey post-hoc test for significance between groups. Critical alpha was set at 0.05/18 = 0.0028, with statistically significant results highlighted in grey. Bolded but unhighlighted values indicate marginally significant (0.05> p > 0.0028) H-values.

	Mean						
Variable	*C. capucinus*	*C. albifrons*	*C. apella*	H	p-value	Significant Pairs	As predicted?
AE Inclination	22.042	21.002	26.389	5.32	0.070	n/a	n/a
Articular Tubercle Ht	0.125	0.134	0.092	**16.64**	**0.0002**	*C. albifrons/ C. capucinus > C. apella*	No
Entoglenoid Ht	0.129	0.122	0.104	**11.77**	**0.0028**	*C. capucinus > C. apella*	No
Glenoid Length	0.331	0.322	0.341	4.10	0.129	n/a	n/a
Glenoid Width	0.322	0.318	0.342	**6.31**	**0.043**	none	n/a
2D Glenoid Area	2.996	2.750	3.130	**8.37**	**0.015**	*C. apella > C. albifrons*	Yes
3D Glenoid Area	4.071	3.526	4.184	**13.46**	**0.001**	*C. apella > C. albifrons/ C. capucinus*	Yes
Postglenoid Length	0.148	0.153	0.141	0.51	0.777	n/a	n/a
Preglenoid Length	0.193	0.186	0.192	1.29	0.524	n/a	n/a
Glenoid Shape Index	0.973	0.991	1.007	2.16	0.340	n/a	n/a
Condyle Width	0.257	0.240	0.274	**10.16**	**0.006**	*C. apella > C. albifrons*	Yes
Condyle Length	0.101	0.095	0.101	3.77	0.152	n/a	n/a
2D Condyle Area	0.737	0.614	0.747	**8.19**	**0.017**	*C. apella > C. albifrons*	Yes
3D Condyle Area	1.638	1.415	1.651	5.99	0.050	n/a	n/a
Glenoid ML Index	1.094	1.104	1.061	**12.99**	**0.002**	*C. albifrons > C. apella*	No
Glenoid AP Index	1.021	1.020	1.025	2.20	0.333	n/a	n/a
Condyle ML Index	1.134	1.123	1.086	**11.95**	**0.0025**	*C. albifrons > C. apella*	No
Condyle AP Index	1.225	1.217	1.222	0.31	0.856	n/a	n/a

a greater condylar width than is found in *C. albifrons* (and to some extent, *C. capucinus*). These findings are only partly consistent with the predictions outlined based on these species' dietary ecology. In particular, the wide condyle and relatively small articular tubercle and entoglenoid processes, as well as a lack of difference in AP dimensions of the joint indicate that the morphology of the TMJ in *C. apella* is not particularly specialized for relatively wider gapes than in *C. albifrons* or *C. capucinus*, as was predicted based on the observed use of the anterior dentition in this species.

Pitheciines. For both glenoid and condylar morphology, PC analysis of the 3D landmarks failed to significantly distinguish among *C. melanocephalus*, *Ch. satanas*, and *P. pithecia* (Fig. 4-5 and 4-6). However, the Kruskal-Wallis test (Table 4-7, Appendix B) did identify several significant differences in TMJ shape among these three species, all of which indicated that *Ch. satanas* and/or *C. melanocephalus* have relatively larger joint surface areas and dimensions than *P. pithecia*. These findings are largely consistent with the above outlined predictions (e.g., that *Pithecia* would have relatively smaller joint dimensions than *Cacajao* or *Chiropotes*). The only exception is in the width of the TMJ; because of their increased reliance on foliage, *Pithecia* was predicted to have a relatively wider joint than *Cacajao* or *Chiropotes*, in fact the reverse was found. *Cacajao* and *Chiropotes* did tend to have relatively longer glenoids (AP) than *Pithecia*, however, which was consistent with the predictions outlined above based on these taxa's use of their anterior dentition during food processing.

Macaques. The GM analysis for the macaques indicated separation among taxa that masticate relatively more resistant (*M. fuscata*, *M. sylvanus*, and *M. thibetana*) foods and those that utilize softer foods (*M. nemestrina* and *M. fascicularis*), as was predicted (Fig. 4-7). Although there was a small sample size for *M. thibetana*, these specimens loaded more negatively along PC 1 (19.4%

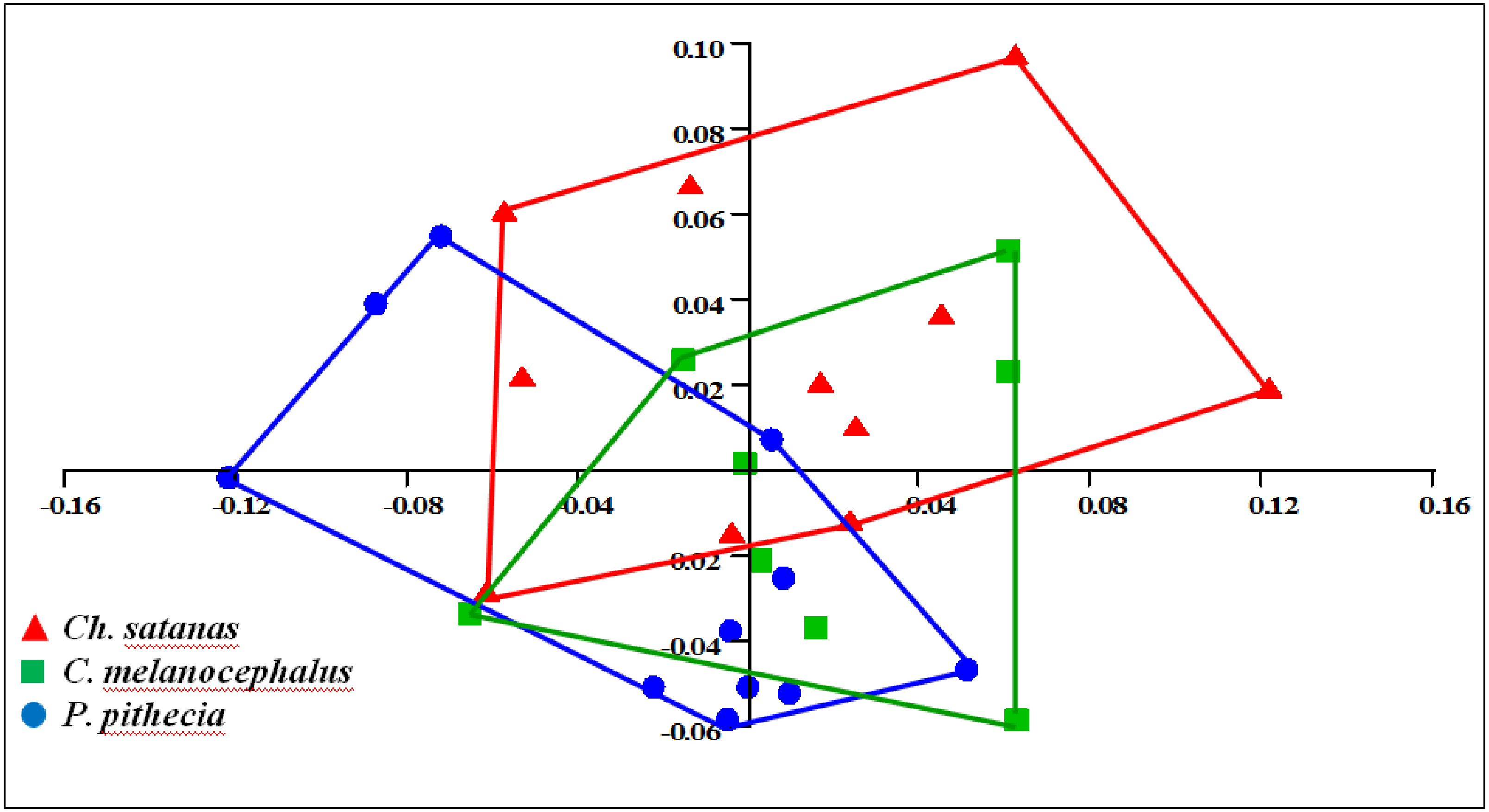


Fig. 4-5. Bivariate plot of PC 1 (x-axis) and PC 2 (y-axis) from the PC analysis of the glenoid configurations in the Pitheciinae females.

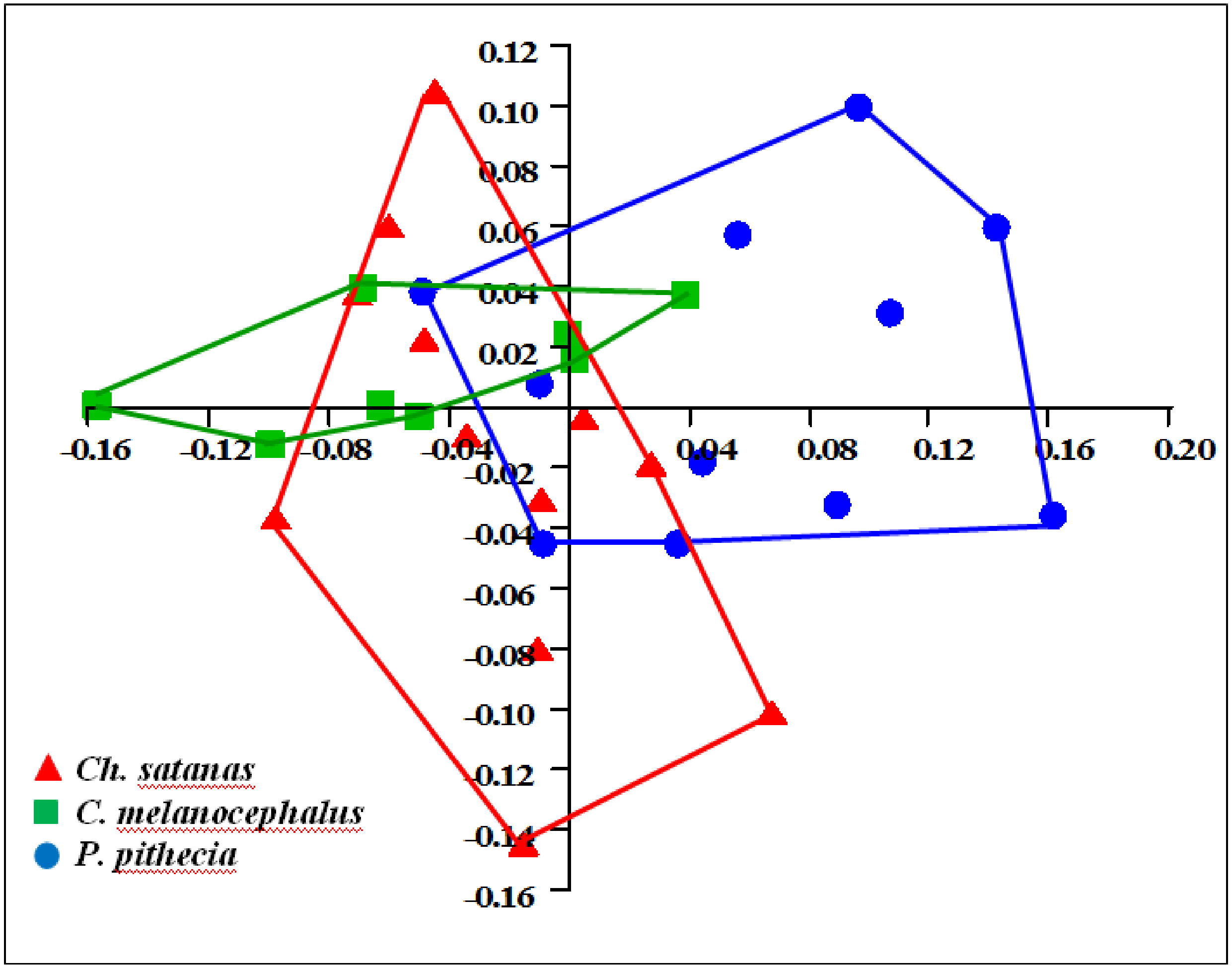


Fig. 4-6. Bivariate plot of PC 1 (x-axis) and PC 2 (y-axis) from the PC analysis of the condylar configurations in the Pitheciinae females.

TABLE 4-7. Results of the Kruskal-Wallis test for the Pitheciinae (females only). Values represent the meansof each variable by taxon (reported either as angles or dimensionless indices), the H-value and p-value for each variable, and significantly different pairs of taxa, as indicated by a Tukey post-hoc test for significance between groups. Critical alpha was set at 0.05/18 = 0.0028, with statistically significant results highlighted in grey. Bolded but unhighlighted values indicate marginally significant (0.05> p > 0.0028) H-values.

	Means						
Variable	*P. pithecia*	*C. melan.*	*Ch. satanas*	H	p-value	Significant Pairs	As predicted?
AE Inclination	22.664	16.153	17.263	**6.29**	**0.043**	none	n/a
Articular Tubercle Ht	0.120	0.104	0.126	5.39	0.067	n/a	n/a
Entoglenoid Ht	0.136	0.125	0.147	**7.39**	**0.025**	*Ch. satanas* > *C. melanocephalus*	No
Glenoid Length	0.361	0.381	0.401	**10.95**	**0.004**	*Ch. satanas* > *P. pithecia*	Yes
Glenoid Width	0.342	0.374	0.368	**8.23**	**0.016**	*C. melanocephalus* > *P. pithecia*	No
2D Glenoid Area	2.755	3.757	3.719	**19.52**	**0.0001**	*Ch. satanas* / *C. melanocephalus* > *P. pithecia*	Yes
3D Glenoid Area	3.651	4.954	4.607	**16.09**	**0.0003**	*Ch. satanas* / *C. melanocephalus* > *P. pithecia*	Yes
Postglenoid Length	0.168	0.154	0.194	**14.5**	**0.001**	*Ch. satanas* > *P. pithecia*	n/a
Preglenoid Length	0.217	0.224	0.229	1.49	0.476	n/a	n/a
Glenoid Shape Index	0.950	0.986	0.921	3.22	0.200	n/a	n/a
Condyle Width	0.273	0.282	0.283	1.87	0.393	n/a	n/a
Condyle Length	0.110	0.116	0.126	4.59	0.101	n/a	n/a
2D Condyle Area	0.704	0.863	0.908	**8.15**	**0.017**	*Ch. satanas* / *C. melanocephalus* > *P. pithecia*	Yes
3D Condyle Area	1.252	1.951	1.960	**12.02**	**0.003**	*Ch. satanas* / *C. melanocephalus* > *P. pithecia*	Yes
Glenoid ML Index	1.115	1.087	1.111	2.13	0.344	n/a	n/a
Glenoid AP Index	1.017	1.012	1.016	4.20	0.122	n/a	n/a
Condyle ML Index	1.132	1.109	1.158	4.06	0.131	n/a	n/a
Condyle AP Index	1.214	1.166	1.217	2.62	0.270	n/a	n/a

of variation) than most other specimens, and PC 2 (15% of variation) separated *M. sylvanus* and *M. fuscata* (which loaded negatively) from *M. nemestrina* and *M. fascicularis* (which loaded positively). Centroid size was not correlated with PC 1, but was found to be correlated with shape variation along PC 2 (r^2= 0.1, p=0.037), although this correlation was not very high. The wireframe diagrams indicate that variation along these axes is primarily associated with size of the PGP, inclination of the AE, and relative AP and ML dimensions of the glenoid. Taxa that eat more resistant foods (*M. fuscata*, *M. sylvanus*, and *M. thibetana*) tend to have a ML wider and AP shorter joint, with a more inclined AE, whereas the reverse is true for the taxa that eat relatively softer food items (*M. fascicularis*, *M. nemestrina*). In contrast, analysis of the condylar configurations did not successfully separate taxa in shape space.

The Kruskal-Wallis test found that most variables differed significantly among the taxa examined (Table 4-8, Appendix B). Glenoid and condylar area measurements were significantly greater in *M. thibetana*, *M. fuscata*, and *M. sylvanus*, especially in comparison to *M. fascicularis* (values for *M. nemestrina* were relatively higher than *M. fascicularis*). Similarly, condylar and glenoid width were also significantly larger in taxa that regularly masticate resistant-food objects in comparison to *M. fascicularis* and *M. nemestrina*. These findings are therefore consistent with the predictions based on dietary ecology of these species. The remaining measurements that differed significantly among taxa, however, did not appear to be patterned on the basis of dietary differences (e.g., entoglenoid height, postglenoid height, and glenoid AP curvature).

Papionins. Based on their dietary ecology, it was predicted that *Theropithecus* would show adaptations in the TMJ related to more resistant object feeding than *Papio*. Although the sample size for *Theropithecus* was very small, specimens of *T. gelada* separated from *Papio* along PC 1 (27.2% of variation) when glenoid morphology was examined (Fig. 4-8). There was still a large amount of overlap among taxa, however. Variation along this axis was associated with relative

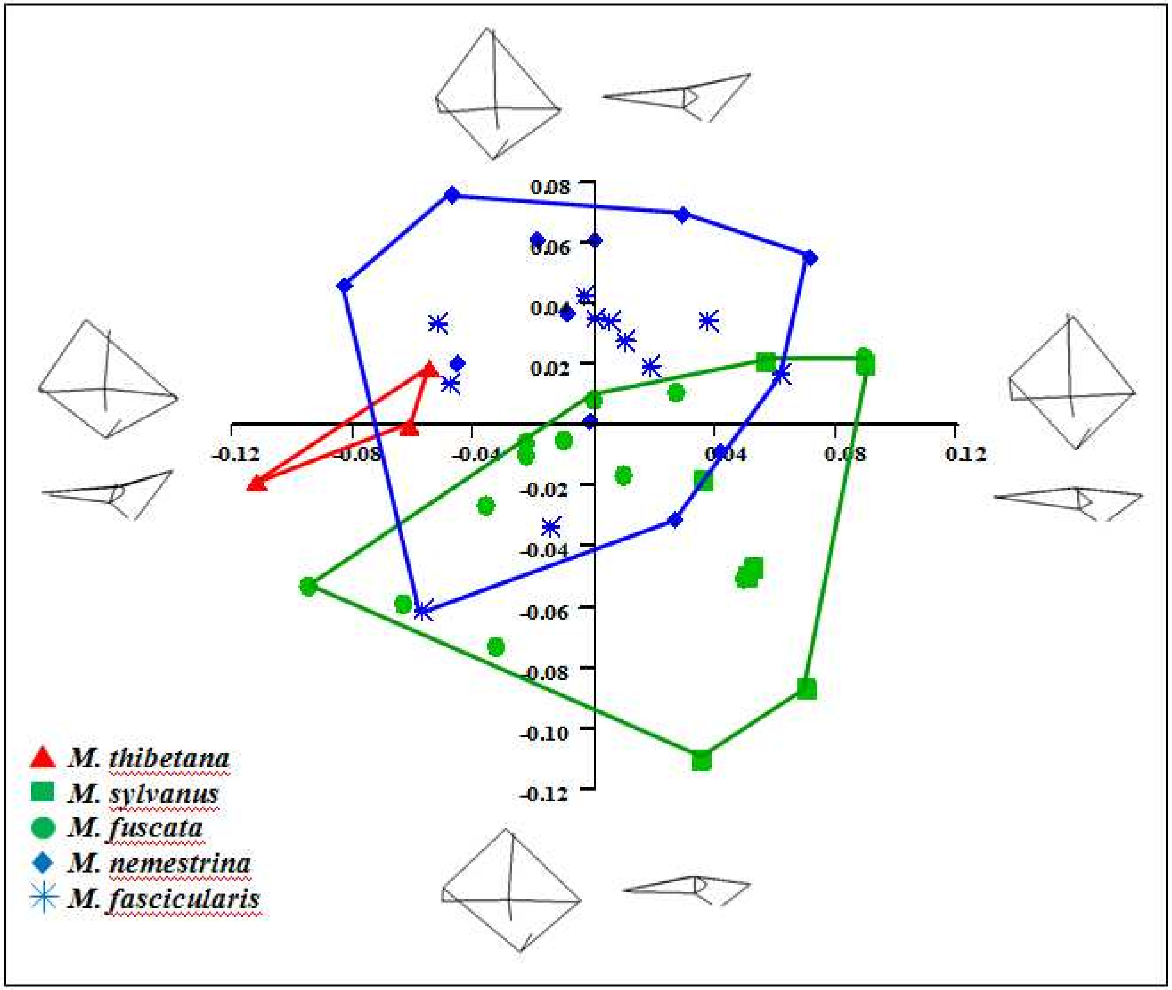


Fig. 4-7. Bivariate plot of PC 1 (x-axis) and PC 2 (y-axis) from the PC analysis of the glenoid configurations in the *Macaca* females. Wireframe diagrams illustrate shape variation along the PC axes.

TABLE 4-8. Results of the Kruskal-Wallis test for Macaca *(females only). Values represent the meansof each variable by taxon (reported either as angles or dimensionless indices), the H-value and p-value for each variable, and significantly different pairs of taxa, as indicated by a Tukey post-hoc test for significance between groups. Critical alpha was set at 0.05/18 = 0.0028, with statistically significant results highlighted in grey. Bolded but unhighlighted values indicate marginally significant (0.05> p > 0.0028) H-values.*

Variable	Means					H	p-value	Significant Pairs	As predicted?
	M. fasc.	*M. nem.*	*M. fusc.*	*M. sylv.*	*M. thib.*				
AE Inclination	19.763	21.912	30.243	19.499	21.793	**11.20**	**0.024**	*M. fuscata > M. sylvanus*	n/a
Articular Tubercle Ht	0.170	0.184	0.133	0.175	0.152	**15.42**	**0.004**	*M. sylvanus/ nemestrina > M. fuscata*	No
Entoglenoid Ht	0.168	0.195	0.159	0.185	0.150	**17.74**	**0.001**	*M. nemestrina > M. fuscata/ thibetana*	No
Glenoid Length	0.350	0.361	0.373	0.380	0.363	6.16	0.187	n/a	n/a
Glenoid Width	0.318	0.321	0.352	0.362	0.381	**30.33**	**<0.0001**	*M. fuscata/ sylvanus/ thibetana > M. fascicularis/ nemestrina*	Yes
2D Glenoid Area	3.532	4.398	5.031	5.160	5.444	**29.0**	**<0.0001**	*M. fuscata/ sylvanus/ thibetana > M. fascicularis*	Yes
3D Glenoid Area	4.551	5.483	6.230	6.054	6.112	**30.0**	**<0.0001**	*M. fuscata/ sylvanus/ thibetana > M. fascicularis*	Yes
Postglenoid Length	0.212	0.246	0.186	0.194	0.203	**17.24**	**0.002**	*M. nemestrina > M. fuscata/ sylvanus*	n/a
Preglenoid Length	0.194	0.195	0.205	0.216	0.215	7.42	0.115	n/a	n/a
Glenoid Shape Index	0.909	0.893	0.949	0.959	1.047	9.36	0.053	n/a	n/a
Condyle Width	0.262	0.255	0.279	0.283	0.312	**16.52**	**0.002**	*M. thibetana > M. fascicularis/ nemestrina*	Yes
Condyle Length	0.102	0.103	0.109	0.114	0.113	**10.9**	**0.028**	none	n/a
2D Condyle Area	0.862	1.003	1.175	1.216	1.388	**21.18**	**0.0003**	*M. fuscata/ sylvanus/ thibetana > M. fascicularis*	Yes
3D Condyle Area	1.891	2.271	2.368	2.466	2.852	**18.48**	**0.001**	*M. fuscata/ sylvanus/ thibetana > M. fascicularis*	Yes
Glenoid ML Index	1.053	1.052	1.058	1.038	1.033	7.23	0.124	n/a	n/a
Glenoid AP Index	1.025	1.029	1.054	1.023	1.036	**16.19**	**0.0028**	*M. fuscata > M. nemestrina/ sylvanus/ fascicularis*	No
Condyle ML Index	1.091	1.087	1.096	1.080	1.057	3.85	0.427	n/a	n/a
Condyle AP Index	1.217	1.213	1.228	1.221	1.187	1.21	0.876	n/a	n/a

size of the PGP, AP length and ML width of the glenoid, and inclination of the AE. Results of the Mann-Whitney U test for differences between *Theropithecus* and *Papio* indicated significant differences between these two genera in several variables (Table 4-9, Appendix B). *Theropithecus* had relatively larger entoglenoid and postglenoid processes, a longer preglenoid plane, a wider condyle, and a more inclined AE. These findings are only partly consistent with the predicted variation in this group, since no significant differences were found in joint surface area, as was expected given the heavy reliance on grass parts by *Theropithecus*.

Hominids. The GM analysis of glenoid morphology in the hominid sample separated the three genera included in the analysis (Fig. 4-9). The first axis (30.3% of variation) separated *Gorilla* from *Pan*/ *Pongo*. Variation along this axis is primarily associated with ML width and AP length of the glenoid, as well as general relief of the joint. At the negative end of this PC axis, *Pan* has a relatively AP long glenoid that is very flat, while at the positive end of the axis, *Gorilla* has a very AP compressed glenoid that is ML wide and has considerably more topographic relief. Axis two (15% of variation) separates *Pan* and *Pongo*, and shape variation along this axis is a result of variation in the anterior border of the glenoid articular surface and angulation of the PGP; in *Pan*, the most anterior point on the preglenoid plane tends to be more laterally positioned, as does the postglenoid process, whereas in *Pongo* this morphology is reversed with both the anterior border of the glenoid and postglenoid placed more medially. Both of these axes are significantly correlated with centroid size (PC 1: $r^2 = 0.359$, $p<0.001$; PC 2: $r^2 = 0.194$, $p<0.001$), indicating that at least some of this variation is associated with allometry.

The condylar landmarks also discriminate well among these three genera (Fig. 4-10); most of the separation is along PC 1, with *Gorilla* loading more positively and *Pan* and *Pongo* more negatively. Condylar variation along this axis ranges from very AP short, ML wide, and ML curved in *Gorilla*, to a relatively more AP long and much less ML curved condyle in *Pongo*.

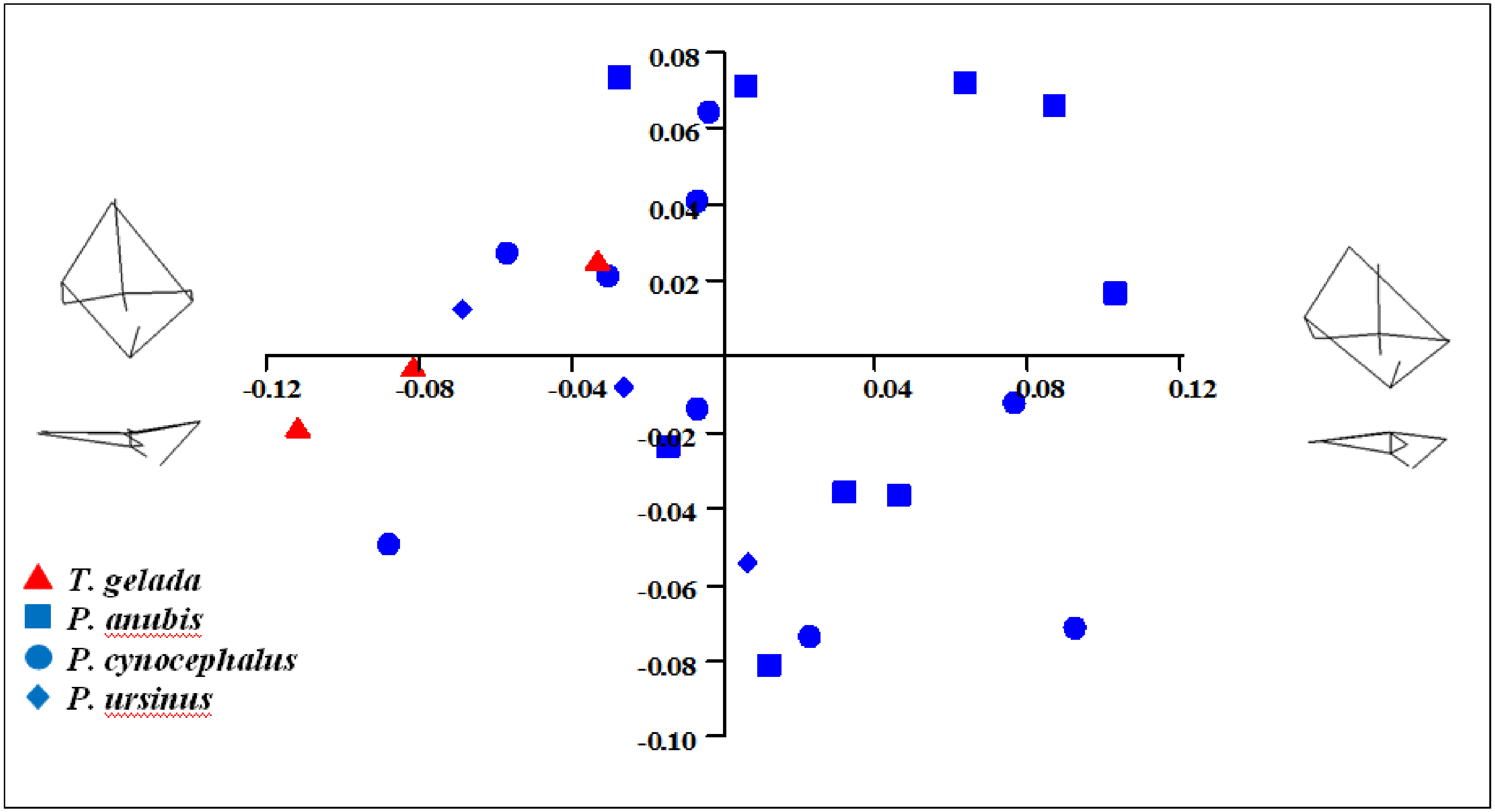


Fig. 4-8. Bivariate plot of PC 1 (x-axis) and PC 2 (y-axis) from the PC analysis of the glenoid configurations in the *Papio* and *Theropithecus* females. Wireframe diagrams illustrate the shape variation along PC 1.

TABLE 4-9. Results of the Mann-Whitney U-test comparing Papio *and* Theropithecus *(males only). Values represent the meansof each variable by taxon (reported either as angles or dimensionless indices) followed by the U-value and p-value for each variable. Critical alpha was set at 0.05/18 = 0.0028, with statistically significant results highlighted in grey. Bolded but unhighlighted values indicate marginally significant (0.05> p > 0.0028) U-values.*

	Means					As predicted?
	Papio	*Theropithecus*	U	p-level	Significant Pairs	
AE Inclination	22.767	31.938	**56**	**0.004**	*Theropithecus > Papio*	n/a
Articular Tubercle Ht	0.223	0.237	115	0.257	n/a	n/a
Entoglenoid Ht	0.233	0.268	**53**	**0.0028**	*Theropithecus > Papio*	Yes
Glenoid Length	0.397	0.416	88	0.052	n/a	n/a
Glenoid Width	0.367	0.388	98	0.101	n/a	n/a
2D Glenoid Area	7.750	7.876	145	0.811	n/a	n/a
3D Glenoid Area	8.771	9.331	107	0.293	n/a	n/a
Postglenoid Length	0.241	0.302	**24**	**0.0001**	*Theropithecus > Papio*	n/a
Preglenoid Length	0.234	0.259	**63**	**0.007**	*Theropithecus > Papio*	No
Glenoid Shape Index	0.926	0.934	152	0.976	n/a	n/a
Condyle Width	0.265	0.298	**82**	**0.034**	*Theropithecus > Papio*	Yes
Condyle Length	0.107	0.118	96	0.089	n/a	n/a
2D Condyle Area	1.569	1.727	124	0.387	n/a	n/a
3D Condyle Area	3.921	4.259	103	0.345	n/a	n/a
Glenoid ML Index	1.027	1.020	95	0.182	n/a	n/a
Glenoid AP Index	1.021	1.042	**32**	**0.001**	*Theropithecus > Papio*	Yes
Condyle ML Index	1.062	1.045	**57**	**0.036**	*Papio > Theropithecus*	No
Condyle AP Index	1.233	1.265	74	0.148	n/a	n/a

The results of the Kruskal-Wallis test indicate significant differences among these taxa for almost all variables (Table 4-10, Appendix B). Most of the significant comparisons indicate that *Gorilla* and *Pongo* had relatively greater mean values than *Pan*. Notably, articular tubercle height, glenoid length, and postglenoid process length were not statistically significant after Bonferroni correction, whereas preglenoid plane length was marginally significantly different, with the multiple comparisons test indicating that *Gorilla* had a significantly smaller preglenoid plane than either *Pongo* or *Pan*.

Mann-Whitney U tests were performed to compare species within each of these genera (Table 4-11). In *Gorilla*, only two significant differences were identified after Bonferroni correction of the p-values; glenoid and condylar width were both significantly greater in *G. beringei* than in *G. gorilla*; this finding is consistent with predictions based on these species' dietary ecology. Similarly, two significant differences separated the species of *Pongo* (glenoid shape index and glenoid ML curvature), with each of these dimensions significantly larger in *P. abelii* than in *P. pygmaeus*. These findings indicate a relatively AP longer glenoid with a larger entoglenoid process in *P. abelii*, which would be consistent with larger gapes and less reliance on the posterior dentition for food processing in this species. Finally, multiple significant differences were found between *P. troglodytes* and *P. paniscus,* although many of these differences did not show the directionality of change that was expected (e.g., that *P. paniscus* would have relatively larger joint dimensions than *P. troglodytes*). In other words, for seven out of nine of the significant comparisons, *P. paniscus* had smaller mean values than *P. troglodytes*. These variables included glenoid and condylar length, glenoid and condylar area, and preglenoid plane length. In contrast, *P. troglodytes* only had significantly smaller mean values for the glenoid shape index (indicating a relatively wider glenoid in *P. troglodytes* than *P. paniscus*) and glenoid AP curvature (e.g., AE inclination).

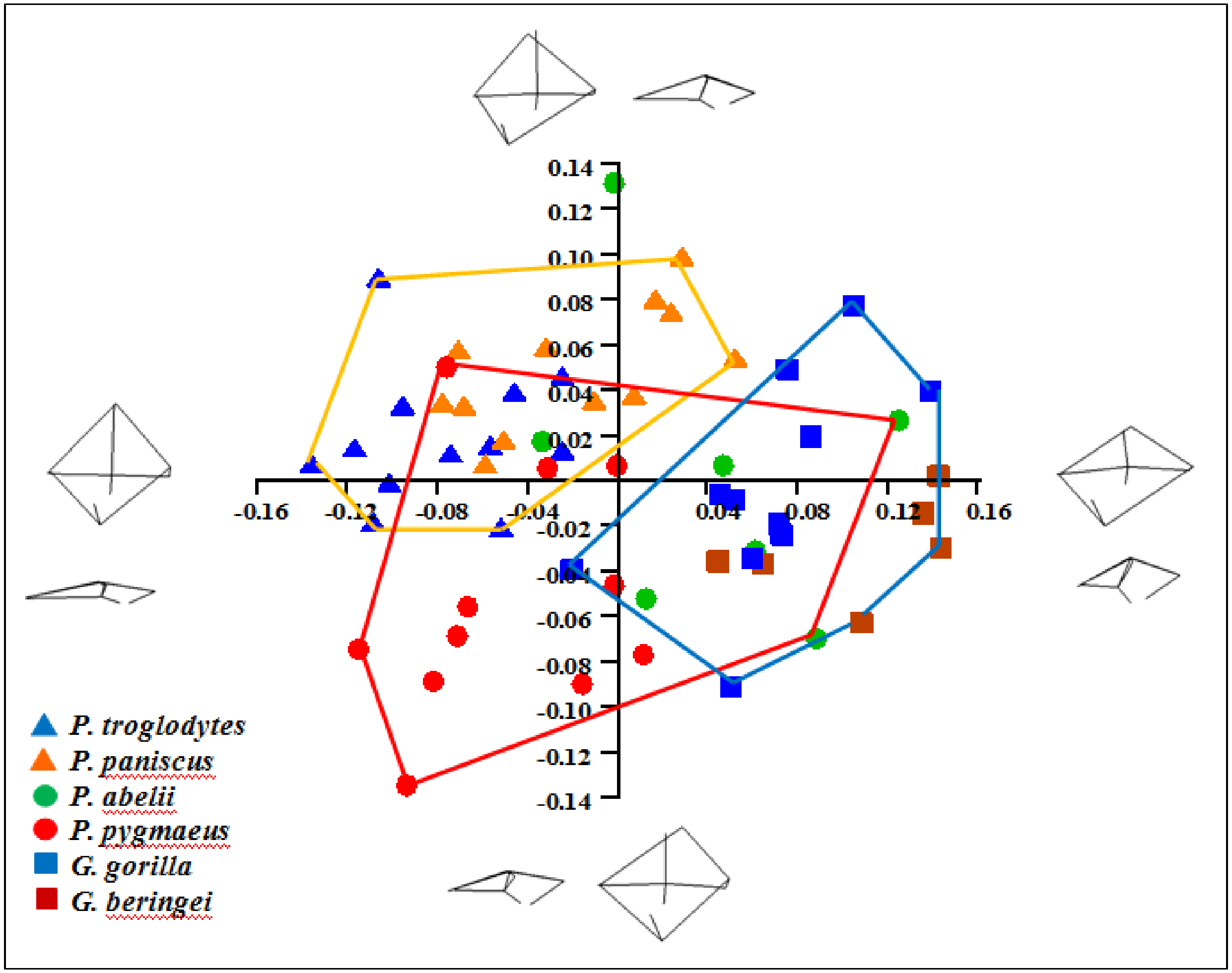


Fig. 4-9. Bivariate plot of PC 1 (x-axis) and PC 2 (y-axis) from the PC analysis of the glenoid configurations in the Hominidae females. Wireframe diagrams illustrate shape variation along the first two PCs.

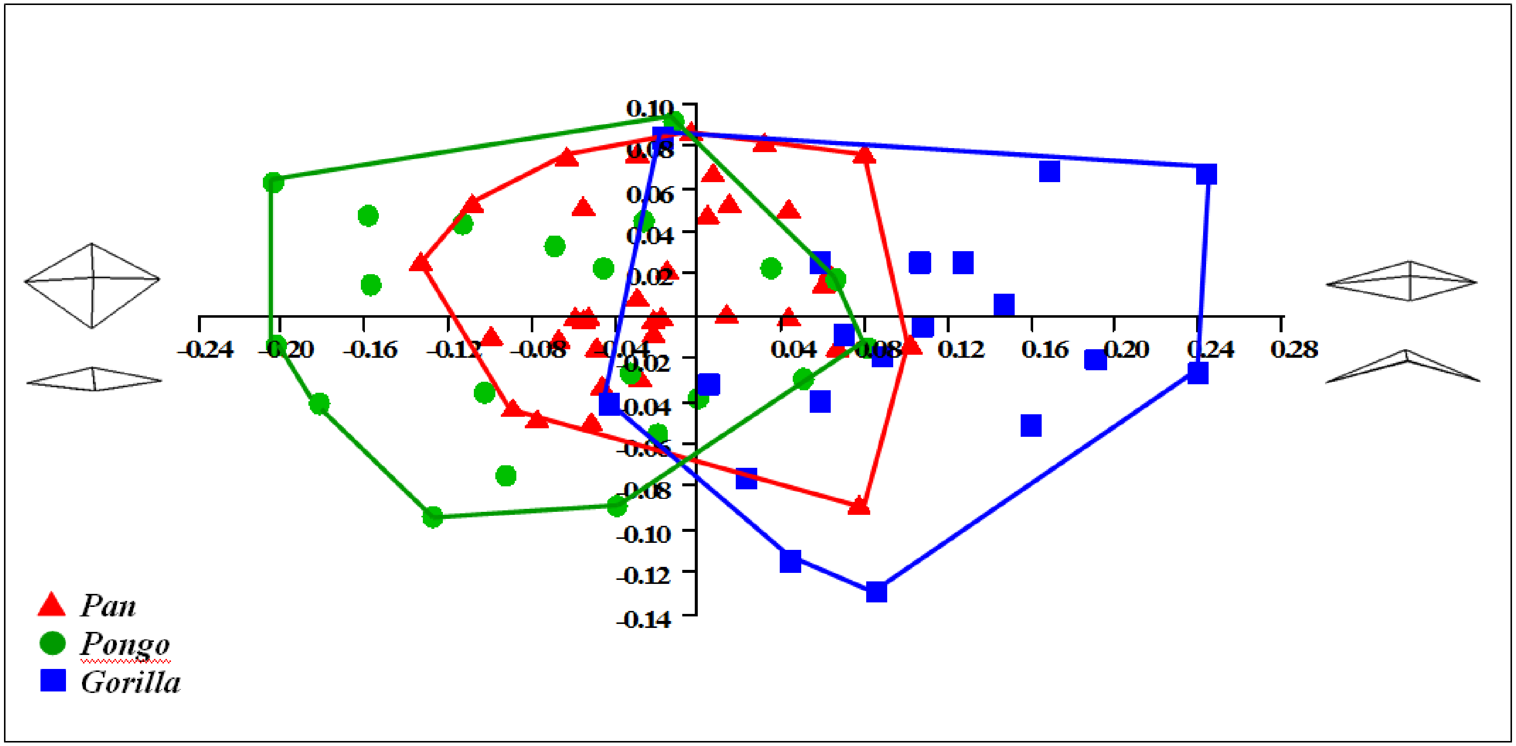


Fig. 4-10. Bivariate plot of PC 1 (x-axis) and PC 2 (y-axis) from the PC analysis of the condylar configurations in the Hominidae females. Wireframe diagrams illustrate shape variation along PC 1.

TABLE 4-10. Results of the Kruskal-Wallis test for the Hominidae (females only). Values represent the meansof each variable by taxon (reported either as angles or dimensionless indices), the H-value and p-value for each variable, and significantly different pairs of taxa, as indicated by a Tukey post-hoc test for significance between groups. Critical alpha was set at 0.05/18 = 0.0028, with statistically significant results highlighted in grey. Bolded but unhighlighted values indicate marginally significant (0.05> p > 0.0028) H-values.

	Means						
Variables	*Pan*	*Pongo*	*Gorilla*	H	p-value	Significant Pairs	As predicted?
AE Inclination	22.095	26.17	38.348	**28.57**	**<0.0001**	*Gorilla > Pan/ Pongo*	n/a
Articular Tubercle Ht	0.178	0.198	0.186	**6.86**	**0.032**	*Pongo > Pan*	Yes
Entoglenoid Ht	0.258	0.297	0.299	**13.23**	**0.001**	*Gorilla/ Pongo > Pan*	Yes
Glenoid Length	0.383	0.386	0.412	4.59	0.101	n/a	n/a
Glenoid Width	0.377	0.441	0.445	**38.26**	**<0.0001**	*Gorilla/ Pongo > Pan*	Yes
2D Glenoid Area	7.847	9.954	12.649	**42.45**	**<0.0001**	*Gorilla > Pongo > Pan*	Yes
3D Glenoid Area	8.772	12.15	15.919	**42.99**	**<0.0001**	*Gorilla > Pongo > Pan*	Yes
Postglenoid Length	0.183	0.202	0.205	**8.72**	**0.013**	*Gorilla/ Pongo > Pan*	n/a
Preglenoid Length	0.206	0.200	0.179	**11.64**	**0.003**	*Pongo/ Pan > Gorilla*	Yes
Glenoid Shape Index	0.991	1.155	1.081	**18.96**	**0.0001**	*Gorilla/ Pongo > Pan*	Yes
Condyle Width	0.313	0.348	0.358	**19.17**	**0.0001**	*Gorilla/ Pongo > Pan*	Yes
Condyle Length	0.129	0.145	0.132	**15.03**	**0.001**	*Pongo > Gorilla/ Pan*	No
2D Condyle Area	2.201	2.960	3.273	**27.95**	**<0.0001**	*Gorilla/ Pongo > Pan*	Yes
3D Condyle Area	4.613	6.488	6.638	**27.05**	**<0.0001**	*Gorilla/ Pongo > Pan*	Yes
Glenoid ML Index	1.089	1.053	1.150	**30.79**	**<0.0001**	*Gorilla > Pan > Pongo*	Yes
Glenoid AP Index	1.034	1.058	1.092	**29.91**	**<0.0001**	*Gorilla > Pongo > Pan*	Yes
Condyle ML Index	1.113	1.092	1.160	**22.87**	**<0.0001**	*Gorilla > Pan/ Pongo*	Yes
Condyle AP Index	1.199	1.256	1.282	**16.84**	**0.0002**	*Gorilla/ Pongo > Pan*	Yes

TABLE 4-11. Results of the Mann-Whitney U-test comparing the subspecies of the three great ape genera analyzed (females only). Values represent the meansof each variable by taxon (reported either as angles or dimensionless indices) followed by the U-value and p-value for each variable. Critical alpha was set at 0.05/18 = 0.0028, with statistically significant results highlighted in grey. Bolded but unhighlighted values indicate marginally significant (0.05> p > 0.0028) U-values.

	Means		*G. gorilla* vs. *G. beringei*			As predicted?
Variable	*G. gorilla*	*G. beringei*	U	p-value	Direction of Change	
AE Inclination	38.130	38.649	35	0.457	n/a	n/a
Articular Tubercle Ht	0.191	0.180	34	0.409	n/a	n/a
Entoglenoid Ht	0.306	0.289	31	0.283	n/a	n/a
Glenoid Length	0.402	0.425	29	0.216	n/a	n/a
Glenoid Width	0.419	0.480	**6**	**0.002**	*G. beringei* > *G. gorilla*	Yes
2D Glenoid Area	11.541	14.171	**13**	**0.010**	*G. beringei* > *G. gorilla*	Yes
3D Glenoid Area	14.838	17.406	**14**	**0.013**	*G. beringei* > *G. gorilla*	Yes
Postglenoid Length	0.214	0.193	**12**	**0.008**	*G. gorilla* > *G. beringei*	n/a
Preglenoid Length	0.178	0.181	35	0.457	n/a	n/a
Glenoid Shape Index	1.044	1.132	**15**	**0.017**	*G. beringei* > *G. gorilla*	Yes
Condyle Width	0.337	0.391	**3**	**0.001**	*G. beringei* > *G. gorilla*	Yes
Condyle Length	0.127	0.140	19	0.077	n/a	n/a
2D Condyle Area	2.940	3.797	**10**	**0.010**	*G. beringei* > *G. gorilla*	Yes
3D Condyle Area	5.896	7.805	**9**	**0.008**	*G. beringei* > *G. gorilla*	Yes
Glenoid ML Index	1.146	1.156	36	0.722	n/a	n/a
Glenoid AP Index	1.078	1.109	25	0.183	n/a	n/a
Condyle ML Index	1.172	1.140	26	0.258	n/a	n/a
Condyle AP Index	1.280	1.284	36	0.821	n/a	n/a

TABLE 4-11. Continued.

	Means		*P. abelii* vs. *P. pygmaeus*			As predicted?
Variable	*P. abelii*	*P. pygmaeus*	U	p-value	Direction of change	
AE Inclination	30.591	22.547	**26**	**0.074**	*P. abelii* > *P. pygmaeus*	n/a
Articular Tubercle Ht	0.195	0.201	46	0.790	n/a	n/a
Entoglenoid Ht	0.334	0.266	**4**	**0.001**	*P. abelii* > *P. pygmaeus*	No
Glenoid Length	0.361	0.407	**16**	**0.011**	*P. pygmaeus* > *P. abelii*	No
Glenoid Width	0.453	0.431	30	0.138	n/a	n/a
2D Glenoid Area	9.592	10.249	34	0.239	n/a	n/a
3D Glenoid Area	11.527	12.490	23	0.315	n/a	n/a
Postglenoid Length	0.187	0.214	34	0.239	n/a	n/a
Preglenoid Length	0.180	0.216	**15**	**0.009**	*P. pygmaeus* > *P. abelii*	No
Glenoid Shape Index	1.268	1.063	**8**	**0.002**	*P. abelii* > *P. pygmaeus*	No
Condyle Width	0.358	0.339	29	0.119	n/a	n/a
Condyle Length	0.146	0.145	48	0.909	n/a	n/a
2D Condyle Area	3.068	2.871	39	0.425	n/a	n/a
3D Condyle Area	6.249	6.684	33	0.210	n/a	n/a
Glenoid ML Index	1.082	1.037	**9**	**0.016**	*P. abelii* > *P. pygmaeus*	No
Glenoid AP Index	1.068	1.052	14	0.056	n/a	n/a
Condyle ML Index	1.101	1.085	32	0.288	n/a	n/a
Condyle AP Index	1.259	1.255	39	0.624	n/a	n/a

TABLE 4-11. Continued.

	Means		*P. paniscus* vs. *P. troglodytes*		Direction of change	As predicted?
Variable	*P. paniscus*	*P. troglodytes*	U	p-value		
AE Inclination	26.236	17.955	**23**	**0.005**	*P. paniscus* > *P. troglodytes*	n/a
Articular Tubercle Ht	0.175	0.181	67	0.773	n/a	n/a
Entoglenoid Ht	0.248	0.268	57	0.386	n/a	n/a
Glenoid Length	0.352	0.413	**0**	**0.00003**	*P. troglodytes* >*P. paniscus*	Yes
Glenoid Width	0.371	0.382	47	0.149	n/a	n/a
2D Glenoid Area	6.744	8.949	**0**	**0.00003**	*P. troglodytes* >*P. paniscus*	No
3D Glenoid Area	7.747	9.797	**0**	**0.00007**	*P. troglodytes* >*P. paniscus*	No
Postglenoid Length	0.176	0.189	49	0.184	n/a	n/a
Preglenoid Length	0.186	0.226	**5**	**0.0001**	*P. troglodytes* >*P. paniscus*	Yes
Glenoid Shape Index	1.057	0.925	**6**	**0.0001**	*P. paniscus* > *P. troglodytes*	Yes
Condyle Width	0.298	0.329	**26**	**0.014**	*P. troglodytes* >*P. paniscus*	No
Condyle Length	0.122	0.137	**16**	**0.002**	*P. troglodytes* >*P. paniscus*	Yes
2D Condyle Area	1.878	2.554	**5**	**0.0002**	*P. troglodytes* >*P. paniscus*	No
3D Condyle Area	4.104	5.123	**13**	**0.002**	*P. troglodytes* >*P. paniscus*	No
Glenoid ML Index	1.074	1.106	**27**	**0.049**	*P. troglodytes* >*P. paniscus*	No
Glenoid AP Index	1.045	1.021	**10**	**0.002**	*P. paniscus* > *P. troglodytes*	Yes
Condyle ML Index	1.103	1.124	32	0.174	n/a	n/a
Condyle AP Index	1.222	1.176	**16**	**0.010**	*P. paniscus* > *P. troglodytes*	Yes

Summary. In all, the analyses of the comparative groups indicate that there are some general patterns of differences among taxa with diets made up of different food material properties (Table 4-12). In most of the comparative groups the resistant object taxa tended to have relatively larger joint surface areas, as well as relatively ML wider joints; this finding is consistent with predictions based on the biomechanical data. Entoglenoid size also tended to be larger in taxa that masticated more resistant food objects, although this was not the case for cebines or *Pongo*, where the more resistant feeders actually were found to have relatively small entoglenoid processes. In addition, taxa that have been observed to have relatively large gapes (whether for behavioral or functional reasons) also tended to have relatively elongated joints anteroposteriorly (e.g., *Alouatta*, *Cacajao*, *Chiropotes*, *Pongo*, *Pan*). The most significant differences in glenoid fossa shape were observed among the atelines and hominids, whereas fewer significant differences were observed in the cebines, pitheciines, and papionins.

Correlation analysis

Articular eminence inclination. Very few significant correlations between articular eminence inclination and angulation of the muscles of mastication were identified (Table 4-13). After Bonferroni correction, the only significant correlation found for the raw data was a negative relationship between AE inclination and temporalis angle in females (r= -0.384, p= 0.007). However, this correlation disappeared when independent contrasts were used in the analysis. Articular eminence inclination is strongly correlated with TMJ height (e.g., the articular eminence becomes more inferoposteriorly oriented as the TMJ increases in height above the occlusal plane), although more significantly so when AE inclination is measured as an angle against the occlusal plane than when measured against Frankfurt Horizontal. This correlation decreased, but was still significant, after independent contrasts were used in the analysis.

TABLE 4-12. Summary table illustrating the results of the Kruskal-Wallis and Mann-Whitney U tests. Yes= results were consistent with predicted variation, No= results were not consistent with predicted variation, NS= comparison was not significant (p>0.05).

	Atelines	Cebines	Pitheciines	*Macaca*	Papionins	Hominids	*Gorilla*	*Pongo*	*Pan*	*#Yes*	*#No*
AE Inclination	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Articular Tubercle Ht	Yes	No	NS	No	NS	Yes	NS	NS	NS	2	2
Entoglenoid Ht	Yes	No	No	No	Yes	Yes	NS	No	NS	3	4
Glenoid Length	Yes	NS	Yes	NS	NS	NS	NS	No	Yes	3	1
Glenoid Width	Yes	NS	No	Yes	NS	Yes	Yes	NS	NS	4	1
2D Glenoid Area	Yes	Yes	Yes	Yes	NS	Yes	Yes	NS	No	6	1
3D Glenoid Area	Yes	Yes	Yes	Yes	NS	Yes	Yes	NS	No	6	1
Postglenoid Length	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Preglenoid Length	Yes	NS	NS	NS	No	Yes	NS	No	Yes	3	2
Glenoid Shape Index	No	NS	NS	NS	NS	Yes	Yes	No	Yes	3	2
Condyle Width	Yes	Yes	NS	Yes	Yes	Yes	Yes	NS	No	6	1
Condyle Length	Yes	NS	NS	NS	NS	No	NS	NS	Yes	2	1
2D Condyle Area	Yes	Yes	Yes	Yes	NS	Yes	Yes	NS	No	6	1
3D Condyle Area	Yes	NS	Yes	Yes	NS	Yes	Yes	NS	No	5	1
Glenoid ML Index	No	No	NS	NS	NS	Yes	NS	No	No	1	4
Glenoid AP Index	NS	NS	NS	No	Yes	Yes	NS	NS	Yes	3	1
Condyle ML Index	No	No	NS	NS	No	Yes	NS	NS	NS	1	3
Condyle AP Index	NS	NS	NS	NS	NS	Yes	NS	NS	Yes	2	0

TABLE 4-13. Results of the correlation analyses, showing the Pearson product-moment correlation (r) and p-value for the original and contrast data, separated by sex. Critical alpha was set at 0.05/ 4= 0.0125, with significant results highlighted in grey.

		Original data				Contrast data			
		females		males		females		males	
		r	p-value	r	p-value	r	p-value	r	p-value
AEIncl (FH) vs.	MassAngle	0.226	0.123	0.268	0.066	0.122	0.420	0.032	0.818
	MPAngle	-0.011	0.941	0.143	0.332	0.063	0.663	0.089	0.542
	TempAngle	-0.193	0.188	-0.129	0.383	0.176	0.238	0.000	0.893
	TMJHt	**0.520**	**<0.001**	0.301	0.038	0.272	0.065	0.055	0.706
AEIncl (OP) vs.	MassAngle	-0.038	0.796	-0.072	0.625	0.126	0.396	0.071	0.629
	MPAngle	**-0.292**	**0.044**	-0.195	0.185	0.063	0.685	0.110	0.465
	TempAngle	**-0.384**	**0.007**	**-0.290**	**0.046**	0.281	0.055	0.270	0.067
	TMJHt	**0.828**	**<0.001**	**0.789**	**<0.001**	**0.663**	**<0.001**	**0.571**	**<0.001**
GlenLg vs.	MandCanine	0.201	0.171	0.019	0.901	0.268	0.068	**0.565**	**<0.001**
	MaxCanine	0.131	0.373	0.037	0.805	0.217	0.145	**0.469**	**0.001**
	TMJHt	**0.688**	**<0.001**	**0.756**	**<0.001**	**0.511**	**<0.001**	**0.54**	**<0.001**
	TMJHt*	**0.7375**	**<0.001**	**0.884**	**<0.001**	**0.7392**	**<0.001**	**0.7993**	**<0.001**
PreGlenLg vs.	MandCanine	**0.379**	**0.008**	0.209	0.154	0.276	0.060	**0.549**	**<0.001**
	MaxCanine	**0.380**	**0.008**	**0.354**	**0.014**	**0.345**	**0.017**	**0.532**	**<0.001**
	TMJHt	0.199	0.1754	**0.407**	**0.004**	**0.176**	**0.003**	**0.31**	**<0.001**
	TMJHt*	**0.3493**	**0.016**	**0.6512**	**<0.001**	**0.4584**	**0.001**	**0.6176**	**<0.001**
CondAP Curve vs.	MandCanine	-0.260	0.078	-0.076	0.615	-0.170	0.259	-0.321	0.031
	MaxCanine	-0.209	0.159	-0.013	0.932	-0.071	0.643	-0.277	0.065
	TMJHt	0.099	0.507	-0.184	0.220	0.167	0.271	-0.084	0.597

*Second values for TMJHt are partial correlations controlling for maxillary canine length

AP Condyle curvature. No significant (or even marginally significant) correlations were found between AP condylar curvature and aspects of gape (e.g., TMJ height and canine length), either before or after independent contrasts (Table 4-13).

Glenoid length. Several significant correlations between glenoid and preglenoid plane length and the proxies for gape were found (Table 4-13). There were strong correlations between canine crown height and glenoid/ preglenoid plane length in males, but only after phylogenetic covariance was taken into account using independent contrasts. In comparison, after independent contrasts were included no significant correlations were found between canine length and aspects of glenoid morphology in females. TMJ height above the occlusal plane was found to be significantly correlated with glenoid/ preglenoid plane length, and in this case, correlations for both males and females were significant after independent contrasts. Correlations between TMJ height and glenoid/ preglenoid plane length were also examined while holding canine crown height constant; TMJ height was strongly correlated with both of these aspects of glenoid morphology. In all of these analyses, r-values for glenoid length tended to be larger than for preglenoid plane length, particularly in females.

DISCUSSION

The goal of this chapter was to test for associations between TMJ shape variation and the mechanical demands of the masticatory apparatus. First, I will review the results of these analyses for each variable describing TMJ shape (summarized in Table 4-12), which will then be used to evaluate the three main predictions outlined at the beginning of this chapter.

Predictions for the components of the TMJ

TMJ size and shape. The size and relative dimensions of the glenoid and condylar articular surfaces were predicted to differ among taxa that masticate more resistant food-objects and/or use their anterior or posterior teeth during food processing or mastication. Resistant-object feeders were expected to have relatively larger joint surface areas in order to improve the load resistance capabilities of the TMJ, and in almost all of the comparative groups examined, this was the case. Of the nine comparisons performed (e.g., the six comparative groups and comparisons between species in *Gorilla*, *Pongo*, and *Pan*), glenoid and condylar area were significantly larger in taxa that masticated more resistant food objects, except for the comparisons between *Papio* and *Theropithecus* and between the species of *Pongo*, in which no significant difference was observed. Notably, TMJ surface area was significantly <u>smaller</u> in *P. paniscus* when compared to *P. troglodytes*, a difference which was in the opposite direction from expected given *P. paniscus*' increased reliance on terrestrial herbaceous vegetation in comparison to *P. troglodytes* (Badrian and Malenky, 1984; Malenky and Stiles, 1991; Malenky and Wrangham, 1994). However, reports of dietary differences between *P. paniscus* and *P. troglodytes* are conflicting. The initial studies reporting increased THV consumption in *P. paniscus* (Badrian and Malenky, 1984; Malenky and Stiles, 1991) have come under increasing scrutiny, with some authors suggesting that this distinction may not hold true at all study sites (Chapman et al., 1996) or that these dietary differences are not significant enough to explain variation in masticatory morphology (Taylor, 2002, 2005; Deane, 2009). Given this uncertainty regarding the food material property data for the diets of these two species, it is difficult to determine whether the structural properties of these food items differ enough to impact variation in TMJ shape. The data presented here, however, would seem to suggest that *P. paniscus* experiences decreased forces at the TMJ (as evidenced by significantly smaller glenoid and condylar surface area) and also potentially that *P. paniscus* relies less heavily on incisal preparation of food objects (as evidenced by a significantly AP shorter TMJ). Additional field studies of feeding behavior and food material properties in chimpanzees and bonobos are required to test this hypothesis.

Taxa were also predicted to differ significantly in the relative AP and ML dimensions of the joint surfaces, depending upon the use of the anterior or posterior teeth. Taxa that repetitively masticate low quality food items (e.g., leaves) on their posterior teeth were expected to have relatively ML wider joints than taxa that use their anterior teeth to process food items (which should have very AP long joints as a consequence of intensive AP loading in the absence of lateral deviation or twisting of the mandible) (Smith et al., 1983; Bouvier, 1986a,b). Mixed support was found for this prediction. *Cebus apella* has been documented to process food items using its anterior dentition (in this case, the canines or first premolars), and it was therefore expected that this species should have relatively AP longer TMJs than *C. capucinus* or *C. albifrons*; however, no significant differences were found for variables describing TMJ width or length among these taxa. Similar results were found for *Papio*/*Theropithecus* and *Pongo*. The only comparison that did perform as expected was the comparison between *P. paniscus* and *P. trologlodytes*, with *P. paniscus* having a relatively AP shorter joint than *P. troglodytes*, as might be expected if this taxon does indeed rely more heavily on mastication of THV on the postcanine dentition than incisal preparation of food items as has been suggested. However, taxa that repetitively load their posterior dentition overwhelmingly had relatively wider glenoid and condylar articular surfaces (except again, *P. paniscus*) than other closely related species (Table 4-12).

Previous analyses by Wall (1995, 1999) and Vinyard et al. (2003) suggest that increased gape can be obtained by increased sagittal sliding at the TMJ, which is itself a function of the anteroposterior flattening of the mandibular condyle, and also the AP length of the glenoid articular surface. It was therefore predicted that there should be a positive correlation between measures of gape and AP curvature of the condyle (e.g., as measures of gape increase when AP curvature of the condyle approaches one), as well as AP length of the glenoid and the preglenoid plane, and that taxa with relatively larger gapes should have AP longer glenoids and/or preglenoid planes than other closely related taxa with smaller gapes. Correlation analyses indicated no relationship between AP curvature of the mandibular condyle and canine crown height or TMJ height, which were used as proxies for relative gape. These findings cast doubt on the relationship suggested by Wall (1995, 1999) between condylar curvature and the amount of sagittal sliding at the TMJ. Anteroposterior length of the glenoid and preglenoid plane, however, were found to be significantly correlated with gape, and particularly the height of the TMJ above the occlusal plane. These results are consistent with findings by Vinyard et al. (2003), who found that these measures of gape were also significantly larger in tree-gouging primates than non-tree gouging taxa, and implies that one way in which primate taxa achieve larger gapes is to increase the amount of AP translation (rather than rotation) of the condyle occurring at the TMJ during jaw opening. Furthermore, taxa that were expected to have relatively larger gapes for behavioral reasons (e.g., *Alouatta*) did have significantly longer glenoids and preglenoid planes than closely related taxa without these behavioral specializations.

Entoglenoid process and articular tubercle shape. The relative size of the entoglenoid process and articular tubercle were expected to vary as a function of joint reaction forces and range of motion at the TMJ. For both features, it was predicted that their relative size would increase with increasing joint reaction force (so as to increase joint surface area of the joint) and with increasing range of motion (to guide movement of the condyle and counteract tensile forces at the joint). Thus, in resistant-object feeders, the entoglenoid process and articular tubercle should be relatively larger than in taxa that masticate softer food-objects. The results were mixed. Resistant-object feeders did indeed have relatively larger articular tubercles and/or entoglenoid processes in the atelines, papionins, and hominids, but the other comparative groups showed either no significant differences among taxa (*Gorilla* and *Pan*), or, in several cases, resistant-object feeders had relatively smaller processes than other taxa (*Cebus* and *Pongo*).

It is worth noting that *C. apella* and *P. pygmaeus*, the more resistant-food-object eaters of their respective comparative groups, have both been identified to process food items extensively on their anterior teeth that are then masticated on their posterior teeth. As discussed in the section on dietary ecology above, extensive use of the anterior dentition for preparation of *Astrocaryum* nuts has been documented in *C. apella*, often with the use of the canines as a wrench to propagate cracks (Izawa and Mizuno, 1977; Izawa, 1979; Terborgh, 1983; Janson and Boinski, 1992). Similarly, during times of fruit scarcity *P. pygmaeus* has been observed to feed extensively on bark, often gnawing directly on the trunk or using incisors to strip bark from the ends of twigs using their canines to split bark (Rodman, 1988; Leighton, 1993). Such behaviors provide an interesting parallel between these two groups, and may suggest that their similarly small entoglenoid processes (at least in comparison to closely related taxa) may function to accommodate increased ML movement of the condyle during use of the canines as a wedge. Conversely, where resistant-object feeders tend to rely more heavily on the posterior dentition for repetitive mastication of lower quality food items (e.g., *Alouatta*, *Gorilla*) these two processes may play a larger role in guiding the movements of the mandibular condyle, acting to decrease the range of motion at the TMJ.

Articular eminence shape. The model of articular eminence function presented here posits that articular eminence form is optimized to minimize translatory forces at the TMJ, thereby maximizing vertical bite force. This could be accomplished in two non-mutually exclusive ways: 1) maintaining the same spatial relationships with other components of the masticatory apparatus by covarying with the height of the TMJ above the occlusal plane and 2) covarying with the orientation of the masticatory musculature so as to counteract non-normal forces produced by the muscle resultant force.

Partial support for this model was provided by the results found here. Articular eminence form was found to be particularly strongly correlated with the height of the TMJ above the occlusal plane. This finding suggests that the maintenance of spatial relationships among the various components of the masticatory apparatus, and particularly maintaining the relationship between the inclination of the AE and the reference plane is important for masticatory function and the maximization of bite force.

In contrast, substantially less support was found for the prediction that AE inclination covaries with muscle orientation. This result suggests two possible interpretations. First, this portion of the model may be invalid; although the correlations found between TMJ height and AE inclination suggest that the articular eminence may function to resist translation at the TMJ, lack of a correlation between muscle orientation and AE inclination may indicate that orientation of the muscle resultant is not a reliable enough indicator of the direction of the joint reaction force. In other words, variation in the extent to which particular portions of each of the masticatory muscles function during chewing (e.g., Vinyard et al., 2008) could result in so much variation in the orientation and position of the muscle resultant force that a straight forward correlation between AE inclination and the orientation of the muscle resultant force is unlikely.

Second, the lack of widespread correlations between muscle resultant orientation and AE inclination could be due to problems with the calculation of muscle resultant angulation. In this study, 3D angles between the three muscles of mastication (the medial pterygoid, masseter, and temporalis) and the occlusal plane were calculated and their individual correlations with AE inclination calculated. There are several potential problems with this approach. First, 3D angles may not be the most appropriate measure of muscle orientation, and these results could differ with the use of 2D angles. A more significant problem, however, lies with the general issue of estimating muscle angulation from skeletal material. For this analysis, the orientation of the three muscles examined were estimated based on methods developed and used by Spencer (1995). But as he acknowledges, these estimates are far from perfect in that they make a number of assumptions regarding the mean position of the muscle force vector (based on the centroid of the muscle scar) and for determining the distribution of a muscle over the entire area of its attachment (which is particularly difficult for the temporalis muscle). The magnitude and orientation of the force vector may differ considerably depending upon which muscles are recruited during mastication, as well as which portions of those muscles are recruited; this method therefore estimates only the mean force assuming that all fibers of the muscle (as well as all muscles) are firing equally. This is, however, highly unlikely to occur on a regular basis during mastication of food objects. Furthermore, although there is little documentation in this regard, there are many factors regarding intrinsic muscle architecture that can vary among individuals and among species, including fiber direction and muscle pinnation, location and number of intramuscular tendons, sarcomere length, and muscle attachment area (e.g., Cachel, 1984; Lovejoy and Ferrini, 1987; Hannam and Wood, 1989; Koolstra et al., 1990; Anton, 1994, 1999, 2000; Taylor and Vinyard, 2004).

Postglenoid process shape. No specific predictions were made regarding postglenoid process height, given the lack of data regarding the function of this feature. Unfortunately, the data here do not seem any more enlightening than previous analyses. The pattern of differences for the postglenoid process in resistant-object feeders is relatively mixed among the comparative groups. In several groups, resistant-object feeders tend to have larger PGPs than taxa that eat softer food items, whereas other comparisons were not statistically significant, or in the case of *G. beringei*, show a decrease in PGP size in comparison to *G. gorilla*. Future analyses of postglenoid process variation and function should perhaps therefore focus on assessing the extent to which PGP size varies with other features of the masticatory apparatus, and further experimental analyses of TMJ function may be required to elucidate the role of the PGP.

Comparisons to previous analyses

Atelines. The data presented for the atelines are consistent with previous analyses of masticatory morphology variation in this group. Previous research by Kay (1975), Rosenberger and Kinzey (1976), Rosenberger and Strier (1989), and Spencer (1995) found strong differences in occlusal and mandibular morphology in *Alouatta* in comparison to *Ateles* and *Lagothrix* that suggest a more powerful masticatory apparatus in this genus. Similarly, the data presented here indicate that *Alouatta* has a relatively larger joint surface area and enlarged processes surrounding the glenoid fossa, which would support the conclusion that the TMJ of *Alouatta* must accommodate higher joint reaction forces as a consequence of higher intensity and/or higher frequency occlusal loads. Another major consideration in this clade is the vocal behaviors engaged in by *Alouatta*, which could theoretically be associated with relatively higher gapes in this taxon. The results found here for *Alouatta* are also consistent with this prediction, since this species has a very AP elongated TMJ which would function to increase sagittal sliding, and therefore gape, at the joint. This will be discussed in further detail in subsequent chapters.

Cebines. The masticatory morphology of *C. apella* has perhaps been one of the most frequently studied of any of the resistant object feeders examined here. Previous analyses of occlusal morphology (Kinzey, 1974; Rosenberger and Kinzey, 1976), microwear patterns (Teaford, 1985), and masticatory apparatus configuration (Wright, 2005; Constantino, 2007) have all suggested that of the *Cebus* species examined, *C. apella* is adapted for generating higher masticatory forces. While the PC analysis presented here generally separated *C. apella* from the two other *Cebus* species, the results of the Kruskal-Wallis test indicated only a few significant differences in TMJ shape between *C. apella* and *C. capucinus*/ *albifrons*. Variables that were significantly different and that were in the predicted direction of change included glenoid area and condylar width (which was marginally significant). These results are therefore slightly more consistent with previous findings by Spencer (1995), who did not find any consistent differences in masticatory configuration among the species of *Cebus*, although they do suggest an increased ability to accommodate higher forces at the TMJ. It is unclear why these studies would differ, but it may be that soft tissue changes (e.g., muscle architecture or position), rather than hard tissue morphology, may be the driving factors that allow this taxon to generate higher masticatory forces than other closely related species.

Pitheciines. Relatively few analyses have evaluated the masticatory morphology of the pitheciines (Spencer, 1995; Norconk et al., 2009), but previous studies found that *Cacajao* and *Chiropotes* both display adaptations of the mandible and masticatory musculature that suggest an increased mechanical advantage in comparison to *Pithecia*. Although the PC analysis performed here did not strongly separate the glenoid fossa or condylar morphology of these three genera, the Kruskal-Wallis test did indicate significant differences in glenoid and condylar area, and marginally significant differences in glenoid length and width between *Pithecia* and *Chiropotes*/ *Cacajao*. These results are consistent with previous findings, and therefore suggest that *Pithecia* is less specialized for seed predation than other pitheciine genera. The disparity in these two analyses indicate that the difference in glenoid shape identified by the Kruskal-Wallis test is too subtle to be detected in the 3D analyses, or that perhaps the sample sizes were not large enough to adequately distinguish among these taxa.

Macaques. The data presented here point to strong differences in TMJ shape between *Macaca* species that routinely masticate resistant food objects (*M. thibetana*, *M. sylvanus*, and *M. fuscata*) and those that do not (*M. fascicularis* and *M. nemestrina*). These taxa differed in a number of features of the TMJ, particularly glenoid and condylar width and area, with the resistant-object feeders having significantly wider and larger joint surfaces than taxa that eat relatively softer foods. These results are consistent with several previous studies by Takahaski and Pan (1994), Anton (1996), and Constantino (2007), who previously indicated that the masticatory apparatus in the resistant-object taxa examined here were significantly more robust than other *Macaca* species, and therefore adapted to the consumption of resistant-food objects.

Papionins. Surprisingly few differences in TMJ shape were found between *Theropithecus* and *Papio*, although these taxa did differ significantly in entoglenoid and postglenoid process height, and relative curvature/ inclination of the articular eminence. This result is in contrast to previous analyses of masticatory configuration in these two genera that indicate an increased biomechanical advantage in *Theropithecus* for the mastication of grass parts (Jablonski, 1981, 1993; Spencer, 1995; Constantino, 2007). Notably, however, *Papio* has a very long mandible and tends to rely heavily on the anterior dentition for incisal processing. This masticatory configuration may result in very high TMJ loads (e.g., Hylander, 1979a; Hylander and Bays, 1979; Brehnan et al., 1981), that may rival those of *Theropithecus*, and therefore this lack of differentiation in TMJ dimensions is not necessarily indicative of a lack of difference in masticatory function.

Hominids. The results for the hominids were somewhat mixed. When specimens from all three genera were compared, taxa separated strongly in shape space and almost all of the variables were statistically significantly different among the genera. These results suggest substantial differences in glenoid and condylar shape across hominid species that are correlated with the use of resistant-food objects, and these findings are consistent with previous analyses of overall masticatory shape by Taylor (2002, 2005, 2006) and Constantino (2007).

When species within each of the three great ape genera were compared, however, substantially fewer differences in TMJ shape were found. In *Gorilla*, glenoid and condylar width (and to some extent glenoid and condylar surface area) were significantly larger in *G. beringei*. These differences were consistent with predicted differences among these two taxa, as *G. beringei* routinely masticates more resistant food objects than *G. gorilla*. In *Pongo* and *Pan*, there were no consistent differences in TMJ shape that were predicted based on previous research. As discussed above, the results of the comparison between *P. troglodytes* and *P. paniscus* were particularly unexpected, with *P. paniscus* having significantly smaller joint dimensions than *P. troglodytes*, a result which was opposite the predicted direction of change given previous reports of the diets of these two species.

Research predictions

The patterns of variation in TMJ shape identified here are complex and somewhat variable among the comparative groups examined (refer to Table 4-12). However, these data provide support for many of the predictions laid out at the beginning of this chapter, and indicate general support for the three main research predictions tested here regarding the influence of food material properties, anterior versus posterior tooth use, and relative gape. As predicted, joint surface area tends to be significantly greater in taxa that masticate more resistant food-objects. In fact, the features of the TMJ that were most consistently statistically significantly different among taxa, and varied in the predicted direction, were measures of joint surface area. Similarly the entoglenoid process tends to be larger in taxa that repetitively masticate resistant food objects, such as leaves (e.g., *Alouatta*, *Gorilla*). However, data for two species that tend to heavily use their anterior dentition for food processing (*P. pygmaeus* and *C. apella*), indicated that these species have smaller entoglenoid processes than expected. This may indicate that the entoglenoid process may be more strongly related to range of motion at the TMJ, rather than loading. Overall, these findings suggest that Prediction 1- that taxa that consume more resistant food objects exhibit adaptations in their TMJs associated with increased joint reaction force and range of motion- should not be rejected.

Results of the analyses regarding the role of anterior versus posterior tooth use are somewhat more difficult to interpret, however. The comparative groups examined here present a mixture of taxa that use their posterior teeth extensively for the repetitive mastication of food objects, as well as some taxa that use their anterior teeth for initial food processing, but still likely need to generate high magnitude bite forces on their posterior dentition. This distinction is particularly important because the significance of high bite-force magnitudes versus high bite-force frequencies is poorly understood (e.g., Yamashita, 2003; Taylor, 2006; Daegling and McGraw, 2007). For example, the magnitude of a single chew may be higher for biting on the incisors in comparison to the molars (as shown by Hylander et al., 1979a; Brehnan et al., 1981), but what about repetitive processing (e.g., increased frequency of forces) on the posterior teeth? Is the magnitude or frequency of forces more significant for influencing TMJ form? As concluded by Daegling and McGraw (2007), more data on the use of the anterior versus posterior dentition (in their case, for mangabeys), coupled with detailed data regarding food material properties, are needed to adequately test models regarding the relative influence of anterior or posterior tooth use during resistant object feeding. Despite this lack of data, the analysis presented here was designed to provide a starting point for further analyses of TMJ shape, which hopefully will be able to be coupled with enhanced data regarding food material properties.

In addition to the difficulties with identifying adequate taxa for comparison, the lack of statistically significant differences in AP length of the joint in taxa that do and do not use their anterior teeth for food processing could represent a trade-off between relative gape and increased bite forces. One way in which large gapes can be achieved is by a relatively posterior position and/or amount of stretch of the jaw adductor musculature, and particularly the masseter (e.g., Herring and Herring, 1974). However, this posterior migration of the masticatory musculature is achieved at the expense of the bite force; a more posteriorly positioned muscle resultant force acts to decrease the muscle resultant to bite force moment arm ratio, which results in a decreased bite force magnitude (e.g., Greaves, 1978; Spencer, 1995, 1999). As a result, taxa such as *C. apella* or *P. pygmaeus*, may sacrifice increased gapes (despite the utility of increased gapes for use of the anterior teeth during food processing) in favor of the generation of relatively large bite forces along their posterior dentitions.

Based on previous research, it was predicted here that taxa that rely on the anterior dentition for food processing would have relatively AP longer joint dimensions and somewhat smaller entoglenoid process and articular tubercle. In contrast, taxa that repetitively masticate tough food objects on their posterior dentition should have ML wide joints with a large entoglenoid process and articular tubercle. These results of the analyses presented here are mixed. There was no observable pattern in articular tubercle size among the groups examined, and therefore the function of this feature during mastication remains unclear. As mentioned above, entoglenoid process size tended to vary more as a consequence of range of motion at the TMJ. In taxa that repetitively masticate tough food objects on the posterior dentition, the entoglenoid processes tended to be large, while taxa that use their anterior dentition for food processing, the entoglenoid was small. These data are consistent with the predicted function of the entoglenoid as a feature that helps to guide or restrict movement of the condyle. The relative dimensions of the TMJ were also found to vary consistently with use of the anterior vs. posterior dentition. Width of the TMJ in particular varied as was predicted, and was consistently larger in taxa that use their posterior teeth heavily. These data therefore suggest that rejection of this prediction is not warranted at this time, although further research may be necessary to fully link the function of these features with variation in anterior vs. posterior tooth use. Experimental data may be particularly useful in this regard.

Strong support was found for the final prediction, that taxa with relatively larger gapes should have adaptations in their TMJ related to increased range of motion (e.g., sagittal sliding). Significant correlations were found between measures of TMJ length such as glenoid length and preglenoid plane length and several measures that were used as proxies for gape, including canine crown height and TMJ height. Canine height was found to be significantly correlated with these aspects of TMJ shape in male primates (especially after the data were corrected for phylogenetic codependence via independent contrasts); this finding is consistent with recent work conducted by Hylander (Hylander and Vinyard, 2006; Hylander, 2008) suggesting that canine height is significantly correlated with linear gape, and that gape is significantly larger in male primates. The data presented here found that height of the TMJ above the occlusal plane was significantly correlated with length of the glenoid and preglenoid plane, perhaps suggesting that, as the TMJ increases in height above the occlusal plane, more translation is needed at the TMJ to maintain the same amount of linear gape at the incisors. These data therefore indicate that this prediction should not be rejected.

CONCLUSIONS

The data presented here suggest that there is a correlation between the mechanical demands of particular diets and some aspects of the morphology of the TMJ. Analyses of 3D TMJ shape variation in each comparative group indicate that, for the most part, species with different diets can be distinguished on the basis of their TMJ morphology. Furthermore, in five out of six comparative groups, taxa with more mechanically demanding diets separated from taxa with less demanding diets in morphospace, suggesting an association between diet and the form of the TMJ. Aspects of TMJ shape that varied most consistently among taxa that masticate foods with different material properties were joint surface area, mandibular condyle width, and height of the entoglenoid process. Some of the strongest correlations were found between AP length of the glenoid and preglenoid plane and measures of gape, perhaps indicating that one way increased gapes can be achieved is through increased translation at the TMJ (as opposed to increased rotation at the joint).

The pattern of change for the variables describing TMJ shape differed for each of the comparative groups, however, and there were some notable differences in the variation of specific components of the TMJ among taxa with different diets. These results may imply that while some features can be reliably associated with increased force production and range of motion in the masticatory apparatus, other features are less strongly correlated with masticatory function. Further analyses, particularly regarding the articular eminence and postglenoid process, will be needed to fully understand the functions of these specific features.

In sum, these data indicate that TMJ shape is influenced by the function of the masticatory apparatus, particularly as related to food material properties and relative gape. These findings correspond well to previous analyses of other aspects of the masticatory apparatus in many of the same taxa examined here. Together, these data can provide important insight into the adaptive response of the masticatory apparatus in anthropoid primates.

CHAPTER 5: SCALING RELATIONSHIPS IN THE ANTHROPOID TEMPOROMANDIBULAR JOINT

INTRODUCTION

Knowledge of scaling differences in the masticatory apparatus among groups of primate taxa is informative in interpretations of both phylogenetic and biomechanical variation. For example, previous analyses of scaling within the mandible (Smith et al., 1983; Bouvier, 1986a,b; Ravosa, 2000) have shown that, where scaling relationships for particular taxa deviate from isometry, there is a concurrent change in the use of foods of varying mechanical properties. In taxa that masticate tougher foods (e.g., colobines) the mandible is significantly shorter (anteroposteriorly) than in taxa of similar body size that tend to eat less mechanically demanding foods (e.g., frugivorous cercopithecines). Therefore in a regression analysis of mandibular length on body size which incorporates both colobines and cercopithecines, colobines tend to fall below the regression line, and cercopithecines above it (Bouvier, 1986a).

These scaling relationships can be explored in two ways. The “criterion of subtraction” approach (Gould, 1966, 1975a; Shea, 1985a,b) posits that departure of a taxon from a common pattern of scaling may suggest a novel shape change indicative of adaptation to a particular selective pressure. The use of this approach, in conjunction with knowledge regarding biomechanical differences or changes in craniofacial configuration in particular taxa, therefore allows for the identification of unique changes in shape which may be functionally or structurally important.

Alternatively, assessing the rates at which particular aspects of shape change in relation to size can also be particularly informative in a biomechanical context. This approach emphasizes the slope of the regression line between two particular variables as the result of interest, rather than just departures from the line, and describes the relationship between these two variables as either positive or negative allometry (Schmidt-Nielsen, 1984).

Significant debate exists regarding what measure of size the variables of interest should be scaled against. Smith (1993) defined two types of allometric analyses: body size allometry and biomechanical allometry. Body size allometry is concerned with the investigation of relationships between body size (as the explanatory variable) and a specific feature. This type of analysis is generally exploratory in nature and is “concerned with an underlying relationship that may be powerful, predictive, and founded on physical principles, but not well understood” (Smith, 1993:180). As a consequence, specific hypotheses for scaling relationships among variables are generally not formulated prior to analysis in this type of allometric analysis.

In contrast, biomechanical allometry is concerned with the study of patterns of relationships between two variables as size changes (Smith, 1993). In this type of analysis, the question of interest is not how variables change in size, but whether a relationship is maintained between two variables as size changes. Such analyses usually predict a specific slope given a biomechanical model relating two variables, neither of which represents overall size of the organism (Smith, 1993). Hylander (1985) appropriately pointed out that the utility of body mass as the independent variable in analyses investigating the effects of size may be limited, particularly where the variables being analyzed are those that reflect the ability of the facial bones to resist stress, since the relationship between such variables is unlikely to be direct. Subsequent scaling analyses by Hylander and others have therefore focused on the use of variables such as mandibular length, which approximates the moment arm associated with bending moments along the mandible (e.g., Hylander, 1985; Bouvier, 1986a,b; Ravosa, 1990, 1996, 2000; Vinyard, 1999; Taylor, 2002, 2005).

Given the wide range of body sizes in this sample, and more generally across primates, it is important to consider how the structure of the skeleton changes across a range of body sizes (Schmidt-Nielsen, 1984). Indeed, a substantial portion of the observed variation in shape within the masticatory apparatus and TMJ has been linked to changes in body size (e.g., Freedman, 1962; Cachel, 1984; Bouvier, 1986a,b; Antón, 1999; Ravosa, 2000; Daegling, 2001; Singleton, 2005). As outlined in Chapter 1, analyses of mandibular scaling relationships across primate size classes indicate that there is a positively allometric relationship between mandibular dimensions and body/cranial size which also corresponds to a size-related increase in dietary toughness and/or hardness (Hylander, 1985; Bouvier, 1986a,b; Ravosa, 1996, 2000).

What does this mean for the TMJ? These previous analyses suggest that the bony morphology of the masticatory apparatus scales with positive allometry, and that to some extent, the masticatory musculature may as well. Methodological differences in these analyses make direct comparisons difficult. Moreover, many of these studies are restricted to particular clades (Hylander, 1985; Bouvier, 1986a,b; Ravosa, 1996, 2000; Vinyard, 1999; but see Smith et al., 1983), or are methodologically distinct in their use of which size variable aspects of the masticatory apparatus should be scaled against (Hylander, 1985; Smith, 1993) or the regression equations used (RJ Smith, 1993, 2009). To date, four analyses have specifically addressed how aspects of the TMJ scale in relation to size (Smith et al., 1983; Bouvier 1986a,b, Vinyard, 1999), and of these, the majority have examined only the mandibular condyle, rather than the cranial component of the TMJ (but see Vinyard, 1999). Smith et al. (1983) examined condylar shape across anthropoid primates and found that the dimensions of the condyle (length, width, area) scale with slight positive allometry relative to body size. In contrast, Bouvier's (1986a,b) analyses of condylar scaling in Old and New World monkeys found that the same dimensions were largely isometric in relation to body size. More recently, Vinyard (1999) examined the scaling patterns of mandibular condyle and glenoid length, width, and area in strepsirrhines, and found that most dimensions scaled with positive allometry when regressed against mandible length and cranial size (although condyle and glenoid length scaled with isometry). These results of these studies are therefore mixed, and it is unclear whether features of the TMJ scale with positive allometry or isometry, either in relation to body size or mandible length. However, these studies, coupled with the hypothesized size-related increases in dietary resistance (i.e., small primates eat less resistant foods than larger primates) (Kay, 1975; Hylander, 1985; Sailer et al., 1985; Ravosa, 1996, 2000) suggest that many aspects of TMJ size are likely to scale with positive allometry against body or cranial size. It is this general hypothesis that is tested in this chapter.

In addition to evaluating the general patterns of scaling in the TMJ, scaling can also be used to further test the dietary hypotheses outlined in Chapter 4. If indeed the TMJ varies as a consequence of functional differences among taxa, then these differences should be evident in the way in which aspects of TMJ shape scale with size. For example, as indicated above, previous analyses of mandibular scaling across anthropoid primates have indicated a positively allometric relationship between body size and mandibular dimensions (Hylander, 1985; Ravosa, 1996, 2000), and this relationship was interpreted to reflect a size-related increase in dietary hardness and/or toughness (Kay, 1975; Hylander, 1985; Sailer et al., 1985). In other words, smaller primate species tend to eat relatively softer foods than larger species, which suggests that the magnitudes of forces generated and dissipated during mastication are relatively larger in large-bodied taxa compared to small-bodied species. Alternatively, it has been suggested that daily ingested food volume scales with positive allometry (Ross et al., 2009), which would result in larger-bodied primates spending relatively more time feeding and chewing than smaller taxa. As a result, it could be expected that dimensions of the TMJ (as a whole) will show the same pattern of scaling as previous analyses of mandibular dimensions (e.g., Hylander, 1985; Ravosa, 1996, 2000), if indeed dietary resistance and/or magnitude of feeding increases at a greater rate than body size.

Similarly, as body size increases, the percentage of foods that are relatively large in relation to body size should decrease (Singleton, 2005). In other words, large gapes may be advantageous in taxa with relatively small body sizes so that large-diameter food items can be more easily processed and/or masticated. Since fewer food objects should present a mechanical challenge on the basis of food diameter for larger bodied primates, relatively large gapes may not be maintained in taxa with increased body sizes. Accordingly, it would be expected that gape scales with negative allometry when regressed against body size.

These data suggest two hypotheses that can be tested by this study:

H1: If the magnitude and/or frequency of joint reaction forces increase with body size, the size of the TMJ and its processes should scale with positive allometry.

H2: If relative food-object size decreases with body size, then larger bodied primates should have smaller gapes. Accordingly, in the absence of differences in canine size, aspects of TMJ morphology related to gape should show negative allometry with body size.

MATERIALS AND METHODS

Samples used for this study included 3D coordinate data for 48 anthropoid taxa, as described in Chapter 3. These coordinate data were used to calculate linear and angular measurements describing TMJ size and shape in the program MacMorph (Spencer and Spencer, 1993), and were also used in further geometric morphometric analyses, the goals of which were to qualitatively describe size related shape changes in the joint. As a result, two separate groups of analyses were performed, first for the univariate data, and then on the 3D coordinate data.

Univariate analyses

Twelve variables describing TMJ size (Table 5-1) were regressed against several measures of overall size, including body mass (Table 5-2; data from Smith and Jungers, 1997 and Fleagle, 1999), and a geometric mean of six variables describing the size of the calvarium (bi-asterionic breadth, bi-porionic breadth, basioccipital length, cranial height, cranial length, and orbital width). This variable is referred to more generally throughout the text as the cranial

TABLE 5-1. Measurements included in the univariate scaling analysis. Refer to table 3-2 in chapter 3 for definitions of how each variable was calculated.

Variable Name	Abbreviation
Articular tubercle (to FH)	ArtTubHt
Entoglenoid height (to FH)	EntGlHt
Glenoid length	GlenLg
Glenoid width	GlenWid
Glenoid area (2D)	GlenArea
Three-dimensional glenoid area	3DGlenArea
Postglenoid process height (to FH)	PGPHt
Preglenoid plane length	PreglenLg
Condyle length	CondLg
Condyle width	CondWid
Condyle area (2D)	CondArea
Three-dimensional condyle area	3DCondArea

TABLE 5-2. Body mass measurements used in the univariate scaling analyses.

Species	Body Mass (g)		Species	Body Mass (g)	
	F	M		F	M
Alouatta belzebul	5520	7270	*Macaca fuscata*	8030	11000
Ateles geoffroyi	7290	7780	*Macaca nemestrina*	6500	11200
Alouatta palliata	5350	7150	*Macaca sylvanus*	11000	16000
Alouatta seniculus	5210	6690	*Macaca thibetana*	9500	12200
Lagothrix lagotricha	7020	7280	*Cercocebus torquatus*	6230	11000
Cebus albifrons	2290	3180	*Lophocebus albigena*	6020	8250
Cebus apella	2520	3650	*Papio anubis*	13300	25100
Cebus capucinus	2540	3680	*Papio cynocephalus*	12300	21800
Chiropotes satanas	2580	2900	*Papio ursinus*	14800	29800
Cacajao melanocephalus	2710	3160	*Theropithecus gelada*	11700	19000
Pithecia pithecia	1580	1940	*Mandrillus sphinx*	12900	31600
Saimiri sciureus	668	779	*Hylobates agilis*	5820	5880
Aotus trivirgatus	736	813	*Hylobates klossii*	5920	5670
Colobus polykomos	8300	9900	*Hylobates lar*	5340	5900
Presbytis obscurus	6260	7900	*Symphalangus syndactylus*	10700	11900
Semnopithecus entellus	9890	13000	*Pan paniscus*	33200	45000
Procolobus verus	4200	4700	*Pan t. schweinfurthii*	33700	42700
Nasalis larvatus	9820	20400	*Pan t. troglodytes*	45800	59700
Procolobus badius	8210	8360	*Pan t. verus*	44600	46300
Cercopithecus mitis	4250	7930	*Gorilla beringei*	97500	162500
Cercopithecus nictitans	4260	6670	*Gorilla gorilla*	71500	170400
Miopithecus talapoin	1120	1380	*Pongo abelii*	35800	78500
Erythrocebus patas	5770	10600	*Pongo pygmaeus*	35600	77900
Macaca fascicularis	3590	5360	*Homo sapiens**	54425	62200

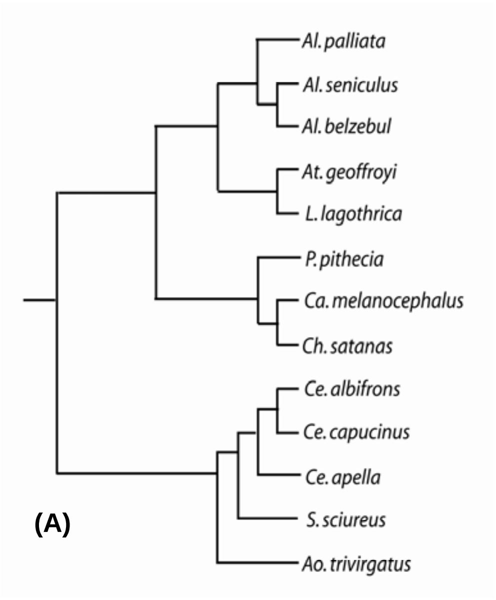
**Values for* H. sapiens *are averages of multiple populations listed in Smith and Jungers, 1997* geometric mean. Data points included in the analyses were means (by sex) for each species. The data were analyzed separately for males and females, as well as by taxonomic group (platyrrhines vs. cercopithecoids vs. hominoids). Analyses were also performed with humans removed from the sample, to assess their impact on the regression equations. This was done because the human sample differs considerably from the rest of the primates analyzed in cranial size relative to body or masticatory apparatus size, and was therefore likely to be a considerable outlier. All data were log-transformed prior to analysis. Regressions were calculated using the freely available program SMATR (Falster et al., 2006). For all analyses, alpha was set at 0.05 and was further adjusted for multiple comparisons using the Bonferroni method (Bonferroni, 1936), where alpha is divided by the number of tests (which in most cases here was twelve).

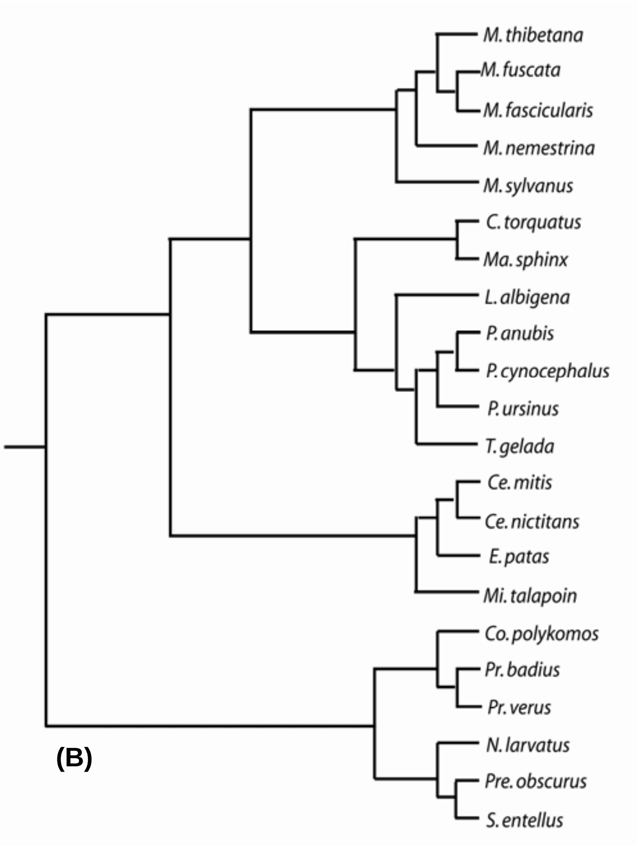
There has been considerable debate regarding the most appropriate regression method to be used in scaling analyses such as this. Although ordinary least squares (LS) regression is the more traditional approach, reduced major axis (RMA) regressions are also frequently used in scaling analyses because this type of regression is more appropriately used when the causality between the variables of interest is unknown and both variables are likely to contain error (Rayner, 1985; Sokal and Rohlf, 1995), as is likely the case here. RJ Smith (1993, 2009) argues strongly that RMA is the most methodologically appropriate choice to use in analyses where the slope of the regression line will be used to understand patterns of shape change in relation to size. RJ Smith (2009) makes this argument for several reasons. First, the patterns of error assumed by each of these methods differs considerably; in LS the X variable is assumed to have been measured without error, while in RMA regression both X and Y variables are assumed to incorporate error. Second, and more importantly according to RJ Smith (2009), is that LS regressions are asymmetric, while RMA regressions are symmetric. In other words, in RMA, the outcome of the regression analysis is not dependent upon which variable is placed on the X axis. Because of this, no causality of the relationship is unintentionally inferred with the use of RMA.

For these reasons, RMA is the most methodologically appropriate regression technique for this study, and is therefore used here instead of LS regression.

Because of the phylogenetic relationships among the taxa used for this analysis, many of the data points analyzed are unlikely to be independent of one another. To correct for this codependence, phylogenetically independent contrasts (PIC) were used (Felsenstein, 1985; Nunn and Barton, 2001). This method requires the construction of a phylogenetic tree (Fig. 5-1), which is then used to estimate nodal values throughout the phylogeny which represent comparisons between sister taxa. These contrasts can then be used as the basis for further regression or correlation analyses in place of the original data. The phylogeny used in this analysis was adapted from Purvis (1995) with supplemental data from Disotell (1996), Morales and Melnick (1998), Canavez et al. (1999), Page et al. (1999), Tosi et al. (2000, 2005), Page and Goodman (2001), Cortes-Ortiz et al. (2003), Newman et al. (2004), Takacs et al. (2005), Xing et al. (2005), Opazo et al. (2006), Whittaker et al. (2007), and Ting et al. (2008). All branch lengths used in the phylogeny were set equal to one another, as divergence dates are poorly known or missing for most of the nodes in the phylogeny. Contrasts were calculated using PHYLIP (version 3.68, Felsenstein, 2008). Regression analyses were subsequently re-run using the contrast data and compared to the raw data. In most cases, the corrected data (i.e., results of analyses run using the contrasts rather than the raw data) were considered more reliable because the datapoints were phylogenetically independent.

The expected slope of isometry for geometric similarity between the cranial geometric mean and linear variables was 1.0, between the cranial geometric mean and area measurements was 2.0, between body mass and a linear measurement was 0.33 and between body mass and area measurements was 0.66. Variables examined for the first biomechanical scaling hypothesis were expected to scale with positive allometry against body size; accordingly, when regressed against the cranial geometric mean, the linear variables were expected to have a slope of greater than





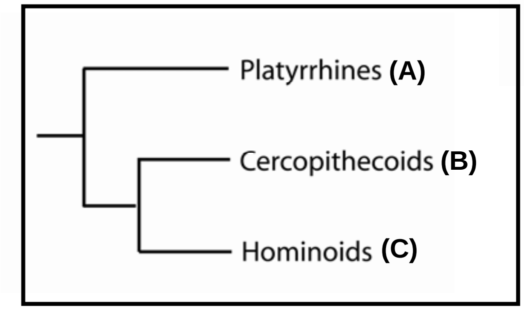
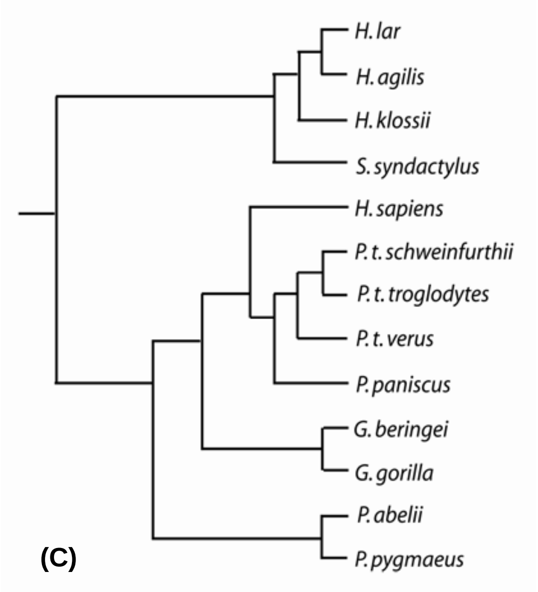


Fig. 5-1. Phylogenetic trees used in the independent contrasts analyses showing detail of evolutionary relationships for platyrrhines (A), cercopithecoids (B), and hominoids (C). Branch lengths for all taxa were set equal to one another.



0.33, and the area measurements were expected to have a slope of greater than 0.66. When regressed against the cranial geometric mean, the linear and area measurements were expected to have slopes of greater than 1.0 and 2.0, respectively. Where negative isometry was expected (hypothesis 2), the variables were predicted to have slopes of less than 0.33 and 1.0 when regressed against body mass and the cranial geometric mean, respectively. These predictions are for the sample as a whole and for lower taxonomic levels as well (e.g., superfamily).

Geometric morphometric analyses

Following registration of the 3D coordinate data using Generalized Procrustes Analysis (GPA), a principal components analysis (PCA) was performed to summarize and evaluate variation in the 3D datasets. The resulting principal component (PC) axes are interpreted as shape changes around a mean form, or consensus configuration, and the distribution of taxa along these axes then summarizes information regarding shape variation within the sample (Slice et al., 1998; Zelditch et al., 2004). Variation along each axis can be visualized using wireframe diagrams and thin-plate spline analysis (TPSA), which uses a Cartesian transformation grid to visualize changes in the relative placement of landmarks among landmark configurations (Thompson, 1917; Bookstein, 1991). Although GPA scales all specimens to the same unit centroid size, size related shape changes (i.e., allometry) are not eliminated; as a consequence, the extent to which shape covaries with size was evaluated by regressing the PC scores for each axis on centroid size using least squares regression. In this analysis, only the first five PC axes were examined for allometry; together these PCs represented between 85 and 95% of the total variation in the sample. All data points analyzed were average configurations by sex for each species, and as with the univariate analyses, separate regressions were run for males and females, and the overall dataset was further divided by family and separate regressions performed. In addition, the lack of phylogenetic independence of the PC scores among closely related taxa was subsequently corrected for using

PIC, as discussed above for the univariate data. All regression analyses were then re-run in SMATR using the contrasts for each PC axis as the dependent variables. Finally, shape variation along axes that covaried with centroid size was described for each taxonomic group using wireframe diagrams and TPSA. All geometric morphometric data were analyzed using the program *Morphologika* (O'Higgins and Jones, 1998). Landmarks used in the geometric morphometric analyses and their corresponding wireframe diagrams are illustrated in Figure 3-2.

RESULTS

Univariate data

Results of the regressions for the univariate data for both cranial and body size (Tables 5-3 through 5-14) indicate that the TMJ scales primarily with positive allometry, both across the entire sample and in lower taxonomic groups. The majority of the statistically significant relationships among variables were positively allometric or isometric, with only a couple of negatively allometric scaling relationships identified. However, the regression results varied depending on the size measure used. Fewer positively allometric relationships were identified when body mass was used as the independent variable than when TMJ size was scaled against the cranial geometric mean. This inconsistency can be explained by the strong negatively allometric scaling relationship between body mass and the cranial geometric mean. These two variables were strongly correlated ($r^2 = 0.963$, $p<0.001$), but the slope was considerably lower (slope=0.249 [+/- 0.014]) than would be expected if these two size measures scaled with isometry (slope of isometry= 0.33).

After independent contrasts were calculated for the univariate data, the regressions were rerun (refer to Tables 5-3 through 5-10). In general, the patterns observed for the original data remained after phylogenetic correction of the data, although fewer correlations were statistically

TABLE 5-3. Results of the scaling analyses for the TMJ variables on cranial geometric mean for all taxa (including humans) (n=48). Data include the reduced major axis (RMA) slopes and their corresponding confidence intervals and significant r-squared values. Critical alpha was set at 0.05/12= 0.0042. Highlighted cells indicate positively allometric relationships.

ALL TAXA	Original Data					Independent Contrasts				
Females	Slope	Low CI	Hi CI	R-sq	p-value	Slope	Low CI	Hi CI	R-sq	p-value
ArtTubHt	1.59	1.37	1.84	0.75	<0.001	1.88	1.50	2.35	0.44	<0.001
EntGlHt	1.96	1.73	2.22	0.82	<0.001	2.16	1.77	2.64	0.54	<0.001
GlenLg	1.22	1.10	1.36	0.87	<0.001	1.40	1.22	1.61	0.78	<0.001
GlenWid	1.34	1.22	1.47	0.90	<0.001	1.54	1.33	1.78	0.76	<0.001
GlenArea	2.54	2.31	2.80	0.90	<0.001	2.90	2.53	3.33	0.79	<0.001
3DGlenArea	2.47	2.22	2.75	0.87	<0.001	2.95	2.54	3.44	0.75	<0.001
PGPHt	1.40	1.14	1.72	0.52	<0.001	2.10	1.64	2.68	0.31	<0.001
PreglenLg	1.07	0.94	1.24	0.78	<0.001	1.32	1.10	1.57	0.65	<0.001
CondWid	1.42	1.28	1.56	0.89	<0.001	1.64	1.41	1.91	0.74	<0.001
CondLg	1.37	1.24	1.50	0.90	<0.001	1.53	1.32	1.77	0.75	<0.001
CondArea	2.78	2.52	3.05	0.90	<0.001	3.15	2.72	3.66	0.76	<0.001
3DCondArea	2.62	2.38	2.89	0.90	<0.001	2.97	2.54	3.47	0.74	<0.001
Males										
ArtTubHt	1.66	1.42	1.94	0.72	<0.001	2.13	1.73	2.63	0.51	<0.001
EntGlHt	2.02	1.79	2.29	0.83	<0.001	2.31	1.93	2.75	0.65	<0.001
GlenLg	1.26	1.13	1.41	0.86	<0.001	1.48	1.29	1.70	0.79	<0.001
GlenWid	1.37	1.24	1.50	0.89	<0.001	1.61	1.41	1.84	0.81	<0.001
GlenArea	2.61	2.37	2.89	0.89	<0.001	3.06	2.69	3.48	0.82	<0.001
3DGlenArea	2.53	2.26	2.83	0.86	<0.001	3.04	2.65	3.47	0.81	<0.001
PGPHt	1.55	1.28	1.88	0.57	<0.001	2.26	1.82	2.80	0.49	<0.001
PreglenLg	1.13	0.98	1.30	0.78	<0.001	1.42	1.21	1.67	0.70	<0.001
CondWid	1.44	1.32	1.57	0.91	<0.001	1.66	1.46	1.89	0.81	<0.001
CondLg	1.43	1.30	1.56	0.91	<0.001	1.60	1.41	1.83	0.81	<0.001
CondArea	2.86	2.62	3.12	0.92	<0.001	3.25	2.86	3.69	0.82	<0.001
3DCondArea	2.60	2.35	2.88	0.89	<0.001	2.92	2.54	3.35	0.80	<0.001

TABLE 5-4. Results of the scaling analyses for the TMJ variables on cranial geometric mean for platyrrhines only (n=13). Data include the reduced major axis (RMA) slopes and their corresponding confidence intervals and significant r-squared values. Critical alpha was set at 0.05/12= 0.0042. Highlighted cells indicate positively allometric relationships.

Platyrrhines	Original Data					Independent Contrasts				
Females	Slope	Low CI	Hi CI	R-sq	p-value	Slope	Low CI	Hi CI	R-sq	p-value
ArtTubHt	2.32	1.48	3.64	0.51	0.006	1.27	0.66	2.45	0.01	0.796
EntGlHt	2.81	1.90	4.15	0.64	0.001	1.89	1.21	2.95	0.57	0.004
GlenLg	1.82	1.28	2.58	0.71	<0.001	1.41	0.97	2.06	0.70	0.001
GlenWid	1.46	1.06	2.00	0.77	<0.001	1.24	0.87	1.77	0.73	<0.001
GlenArea	3.27	2.34	4.55	0.74	<0.001	2.64	1.83	3.80	0.72	<0.001
3DGlenArea	3.33	1.91	5.81	0.40	0.038	2.49	1.41	4.40	0.46	0.032
PGPHt	2.57	1.65	4.01	0.52	0.005	1.68	0.98	2.87	0.37	0.037
PreglenLg	1.71	1.22	2.41	0.73	<0.001	1.29	0.90	1.85	0.73	<0.001
CondWid	1.51	1.09	2.09	0.75	<0.001	1.36	0.94	1.97	0.71	0.001
CondLg	1.52	1.10	2.10	0.76	<0.001	1.34	0.92	1.96	0.70	0.001
CondArea	3.02	2.20	4.15	0.76	<0.001	2.68	1.85	3.87	0.71	0.001
3DCondArea	3.29	1.91	5.69	0.42	0.032	2.82	1.58	5.01	0.44	0.035
Males										
ArtTubHt	2.42	1.66	3.52	0.66	0.001	1.76	0.93	3.33	0.06	0.443
EntGlHt	2.97	2.13	4.14	0.74	<0.001	2.18	1.42	3.34	0.61	0.003
GlenLg	1.95	1.42	2.67	0.77	<0.001	1.56	1.04	2.33	0.65	0.001
GlenWid	1.53	1.16	2.02	0.82	<0.001	1.34	0.96	1.89	0.76	<0.001
GlenArea	3.47	2.58	4.67	0.80	<0.001	2.88	1.99	4.17	0.71	0.001
3DGlenArea	3.77	2.34	6.08	0.57	0.008	2.96	1.71	5.13	0.50	0.022
PGPHt	2.65	1.82	3.88	0.66	0.001	2.00	1.22	3.28	0.46	0.015
PreglenLg	1.82	1.33	2.48	0.77	<0.001	1.48	0.98	2.23	0.64	0.002
CondWid	1.64	1.29	2.09	0.87	<0.001	1.53	1.15	2.03	0.84	<0.001
CondLg	1.68	1.31	2.15	0.86	<0.001	1.54	1.16	2.04	0.84	<0.001
CondArea	3.31	2.61	4.20	0.87	<0.001	3.05	2.33	3.99	0.85	<0.001
3DCondArea	3.83	2.42	6.07	0.60	0.005	3.40	2.03	5.69	0.57	0.012

TABLE 5-5. Results of the scaling analyses for the TMJ variables on cranial geometric mean for cercopithecoids only (n=22). Data include the reduced major axis (RMA) slopes and their corresponding confidence intervals and significant r-squared values. Critical alpha was set at 0.05/12= 0.0042. Highlighted cells indicate positively allometric relationships.

Cercopithecoids	Original Data					Independent Contrasts				
Females	Slope	Low CI	Hi CI	R-sq	p-value	Slope	Low CI	Hi CI	R-sq	p-value
ArtTubHt	2.41	1.90	3.06	0.73	<0.001	2.30	1.71	3.10	0.60	<0.001
EntGlHt	2.41	2.01	2.89	0.85	<0.001	2.12	1.68	2.67	0.76	<0.001
GlenLg	1.57	1.40	1.76	0.94	<0.001	1.54	1.33	1.79	0.90	<0.001
GlenWid	1.73	1.47	2.04	0.87	<0.001	1.73	1.41	2.13	0.81	<0.001
GlenArea	3.27	2.87	3.71	0.92	<0.001	3.23	2.73	3.82	0.88	<0.001
3DGlenArea	3.38	2.96	3.87	0.92	<0.001	3.33	2.75	4.04	0.84	<0.001
PGPHt	2.07	1.66	2.58	0.77	<0.001	2.42	1.82	3.21	0.64	<0.001
PreglenLg	1.60	1.36	1.89	0.88	<0.001	1.57	1.31	1.88	0.86	<0.001
CondWid	1.95	1.65	2.31	0.87	<0.001	1.93	1.56	2.38	0.80	<0.001
CondLg	1.82	1.58	2.10	0.91	<0.001	1.75	1.43	2.13	0.83	<0.001
CondArea	3.75	3.23	4.37	0.89	<0.001	3.66	2.99	4.47	0.82	<0.001
3DCondArea	3.21	2.83	3.63	0.93	<0.001	3.11	2.59	3.74	0.85	<0.001
Males										
ArtTubHt	2.53	2.00	3.19	0.75	<0.001	2.65	2.01	3.49	0.66	<0.001
EntGlHt	2.59	2.17	3.09	0.86	<0.001	2.43	1.98	2.99	0.82	<0.001
GlenLg	1.54	1.38	1.71	0.95	<0.001	1.51	1.33	1.72	0.93	<0.001
GlenWid	1.70	1.46	1.97	0.90	<0.001	1.77	1.52	2.08	0.89	<0.001
GlenArea	3.20	2.86	3.58	0.94	<0.001	3.25	2.86	3.69	0.93	<0.001
3DGlenArea	3.30	2.92	3.73	0.93	<0.001	3.25	2.84	3.71	0.92	<0.001
PGPHt	2.23	1.81	2.75	0.80	<0.001	2.61	2.05	3.31	0.75	<0.001
PreglenLg	1.57	1.35	1.82	0.90	<0.001	1.54	1.32	1.81	0.89	<0.001
CondWid	1.70	1.43	2.03	0.86	<0.001	1.78	1.46	2.16	0.84	<0.001
CondLg	1.71	1.46	2.01	0.88	<0.001	1.68	1.38	2.05	0.83	<0.001
CondArea	3.40	2.89	3.99	0.88	<0.001	3.44	2.85	4.16	0.84	<0.001
3DCondArea	3.05	2.70	3.45	0.93	<0.001	2.92	2.47	3.45	0.88	<0.001

TABLE 5-6. Results of the scaling analyses for the TMJ variables on cranial geometric mean for hominoids only (including humans) (n=13). Data include the reduced major axis (RMA) slopes and their corresponding confidence intervals and significant r-squared values. Critical alpha was set at 0.05/12= 0.0042. Highlighted cells indicate positively allometric relationships.

Hominoids	Original Data					Independent Contrasts				
Females	Slope	Low CI	Hi CI	R-sq	p-value	Slope	Low CI	Hi CI	R-sq	p-value
ArtTubHt	1.46	1.02	2.09	0.69	<0.001	1.55	0.86	2.80	0.22	0.127
EntGlHt	1.86	1.25	2.76	0.62	0.001	2.29	1.24	4.23	0.14	0.231
GlenLg	1.21	0.96	1.54	0.87	<0.001	1.25	0.80	1.95	0.57	0.004
GlenWid	1.58	1.25	1.99	0.88	<0.001	1.56	1.04	2.35	0.64	0.002
GlenArea	2.78	2.22	3.48	0.88	<0.001	2.75	1.82	4.16	0.64	0.002
3DGlenArea	2.81	2.28	3.48	0.90	<0.001	2.81	1.95	4.04	0.72	<0.001
PGPHt	1.55	0.92	2.61	0.32	0.044	2.35	1.22	4.52	0.01	0.773
PreglenLg	0.91	0.62	1.33	0.65	0.001	1.08	0.59	1.98	0.17	0.187
CondWid	1.66	1.33	2.09	0.88	<0.001	1.71	1.12	2.61	0.62	0.002
CondLg	1.59	1.26	2.00	0.88	<0.001	1.56	1.02	2.39	0.61	0.003
CondArea	3.24	2.59	4.07	0.88	<0.001	3.25	2.14	4.95	0.62	0.002
3DCondArea	2.99	2.38	3.75	0.88	<0.001	3.01	2.00	4.52	0.65	0.002
Males										
ArtTubHt	1.46	1.05	2.04	0.74	<0.001	1.46	0.86	2.49	0.38	0.034
EntGlHt	1.94	1.39	2.71	0.74	<0.001	2.21	1.28	3.82	0.33	0.049
GlenLg	1.30	1.04	1.63	0.88	<0.001	1.32	0.89	1.97	0.67	0.001
GlenWid	1.60	1.29	1.98	0.90	<0.001	1.57	1.09	2.27	0.72	0.001
GlenArea	2.90	2.34	3.60	0.89	<0.001	2.87	1.97	4.17	0.70	0.001
3DGlenArea	2.90	2.37	3.54	0.91	<0.001	2.87	2.08	3.94	0.79	<0.001
PGPHt	1.64	1.04	2.58	0.50	0.007	2.35	1.28	4.32	0.15	0.210
PreglenLg	1.05	0.75	1.47	0.73	<0.001	1.23	0.72	2.10	0.36	0.040
CondWid	1.64	1.35	2.00	0.91	<0.001	1.63	1.15	2.33	0.74	<0.001
CondLg	1.63	1.33	2.00	0.90	<0.001	1.59	1.11	2.29	0.72	<0.001
CondArea	3.27	2.68	4.00	0.91	<0.001	3.21	2.25	4.59	0.73	<0.001
3DCondArea	2.99	2.48	3.61	0.92	<0.001	2.83	2.07	3.87	0.80	<0.001

TABLE 5-7. Results of the scaling analyses for the TMJ variables on body mass for all taxa (including humans) (n=48). Data include the reduced major axis (RMA) slopes and their corresponding confidence intervals and significant r-squared values. Critical alpha was set at 0.05/12= 0.0042. Highlighted cells indicate positively allometric relationships and values in italics indicate negatively allometric relationships.

ALL TAXA	Original Data					Independent Contrasts				
Females	Slope	Low CI	Hi CI	R-sq	p-value	Slope	Low CI	Hi CI	R-sq	p-value
ArtTubHt	0.43	0.37	0.49	0.76	<0.001	0.47	0.38	0.58	0.51	<0.001
EntGlHt	0.53	0.47	0.59	0.83	<0.001	0.54	0.45	0.65	0.60	<0.001
GlenLg	0.33	0.30	0.36	0.92	<0.001	0.35	0.31	0.39	0.85	<0.001
GlenWid	0.36	0.33	0.39	0.92	<0.001	0.38	0.34	0.43	0.84	<0.001
GlenArea	0.68	0.63	0.74	0.93	<0.001	0.73	0.65	0.81	0.87	<0.001
3DGlenArea	0.68	0.62	0.75	0.90	<0.001	0.73	0.65	0.83	0.83	<0.001
PGPHt	0.38	0.31	0.45	0.61	<0.001	0.52	0.42	0.66	0.42	<0.001
PreglenLg	***0.29***	0.26	0.32	0.84	<0.001	0.33	0.28	0.38	0.75	<0.001
CondWid	0.38	0.35	0.42	0.91	<0.001	0.41	0.36	0.47	0.82	<0.001
CondLg	0.37	0.33	0.40	0.90	<0.001	0.38	0.33	0.44	0.80	<0.001
CondArea	0.75	0.68	0.82	0.91	<0.001	0.79	0.69	0.90	0.82	<0.001
3DCondArea	0.72	0.66	0.79	0.90	<0.001	0.74	0.64	0.85	0.79	<0.001
Males										
ArtTubHt	0.42	0.37	0.49	0.77	<0.001	0.52	0.43	0.62	0.63	<0.001
EntGlHt	0.51	0.46	0.57	0.86	<0.001	0.56	0.48	0.65	0.75	<0.001
GlenLg	0.32	0.29	0.35	0.90	<0.001	0.36	0.32	0.40	0.86	<0.001
GlenWid	0.35	0.32	0.38	0.93	<0.001	0.39	0.35	0.44	0.86	<0.001
GlenArea	0.66	0.61	0.72	0.93	<0.001	0.74	0.67	0.82	0.88	<0.001
3DGlenArea	0.65	0.59	0.72	0.90	<0.001	0.74	0.66	0.83	0.87	<0.001
PGPHt	0.39	0.33	0.47	0.66	<0.001	0.55	0.45	0.66	0.62	<0.001
PreglenLg	0.29	0.25	0.33	0.82	<0.001	0.34	0.30	0.40	0.78	<0.001
CondWid	0.37	0.34	0.40	0.93	<0.001	0.40	0.36	0.46	0.82	<0.001
CondLg	0.36	0.33	0.39	0.92	<0.001	0.39	0.34	0.44	0.82	<0.001
CondArea	0.73	0.67	0.79	0.93	<0.001	0.79	0.70	0.89	0.83	<0.001
3DCondArea	0.67	0.62	0.73	0.92	<0.001	0.71	0.63	0.80	0.84	<0.001

TABLE 5-8. Results of the scaling analyses for the TMJ variables on body mass for platyrrhines only (n=13). Data include the reduced major axis (RMA) slopes and their corresponding confidence intervals and significant r-squared values. Critical alpha was set at 0.05/12= 0.0042. Highlighted cells indicate positively allometric relationships and values in italics indicate negatively allometric relationships.

Platyrrhines	Original Data					Independent Contrasts				
Females	Slope	Low CI	Hi CI	R-sq	p-value	Slope	Low CI	Hi CI	R-sq	p-value
ArtTubHt	0.52	0.37	0.74	0.70	<0.001	0.46	0.26	0.79	0.16	0.055
EntGlHt	0.63	0.48	0.83	0.83	<0.001	0.52	0.35	0.75	0.69	0.001
GlenLg	0.41	0.32	0.52	0.88	<0.001	0.38	0.29	0.51	0.83	<0.001
GlenWid	0.33	0.26	0.41	0.88	<0.001	0.34	0.25	0.45	0.83	<0.001
GlenArea	0.73	0.59	0.92	0.88	<0.001	0.72	0.54	0.95	0.84	<0.001
3DGlenArea	0.69	0.47	1.02	0.72	0.001	0.70	0.43	1.13	0.63	0.006
PGPHt	0.58	0.42	0.80	0.76	<0.001	0.46	0.29	0.72	0.55	0.006
PreglenLg	0.38	0.31	0.47	0.90	<0.001	0.35	0.27	0.46	0.86	<0.001
CondWid	0.34	0.27	0.43	0.87	<0.001	0.37	0.27	0.50	0.81	<0.001
CondLg	0.34	0.28	0.42	0.90	<0.001	0.37	0.27	0.49	0.82	<0.001
CondArea	0.68	0.55	0.84	0.89	<0.001	0.73	0.55	0.97	0.83	<0.001
3DCondArea	0.69	0.45	1.04	0.68	0.002	0.79	0.49	1.30	0.61	0.008
Males										
ArtTubHt	0.57	0.42	0.78	0.78	<0.001	0.54	0.32	0.90	0.42	0.022
EntGlHt	0.70	0.54	0.92	0.84	<0.001	0.60	0.42	0.86	0.73	<0.001
GlenLg	0.46	0.36	0.59	0.85	<0.001	0.43	0.31	0.60	0.78	<0.001
GlenWid	0.36	0.29	0.46	0.88	<0.001	0.37	0.28	0.49	0.83	<0.001
GlenArea	0.82	0.65	1.05	0.87	<0.001	0.79	0.59	1.07	0.81	<0.001
3DGlenArea	0.91	0.61	1.38	0.69	0.0020	0.92	0.56	1.52	0.59	0.009
PGPHt	0.63	0.46	0.87	0.76	<0.001	0.55	0.36	0.85	0.60	0.003
PreglenLg	0.43	0.34	0.55	0.86	<0.001	0.41	0.29	0.57	0.77	<0.001
CondWid	0.39	0.31	0.49	0.88	<0.001	0.42	0.32	0.56	0.83	<0.001
CondLg	0.40	0.32	0.50	0.87	<0.001	0.42	0.32	0.56	0.83	<0.001
CondArea	0.78	0.63	0.98	0.88	<0.001	0.84	0.64	1.11	0.85	<0.001
3DCondArea	0.93	0.61	1.40	0.68	0.0020	1.06	0.65	1.72	0.62	0.007

TABLE 5-9. Results of the scaling analyses for the TMJ variables on body mass for cercopithecoids only (n=22). Data include the reduced major axis (RMA) slopes and their corresponding confidence intervals and significant r-squared values. Critical alpha was set at 0.05/12= 0.0042. Highlighted cells indicate positively allometric relationships and values in italics indicate negatively allometric relationships.

Cercopithecoids	Original Data					Independent Contrasts				
Females	Slope	Low CI	Hi CI	R-sq	p-value	Slope	Low CI	Hi CI	R-sq	p-value
ArtTubHt	0.60	0.43	0.84	0.47	<0.001	0.50	0.36	0.68	0.55	<0.001
EntGlHt	0.61	0.45	0.82	0.58	<0.001	0.46	0.35	0.60	0.69	<0.001
GlenLg	0.39	0.33	0.48	0.83	<0.001	0.33	0.28	0.39	0.89	<0.001
GlenWid	0.43	0.37	0.51	0.88	<0.001	0.37	0.31	0.45	0.86	<0.001
GlenArea	0.82	0.70	0.97	0.88	<0.001	0.70	0.60	0.81	0.90	<0.001
3DGlenArea	0.85	0.71	1.02	0.85	<0.001	0.72	0.60	0.86	0.86	<0.001
PGPHt	0.52	0.40	0.68	0.68	<0.001	0.52	0.39	0.70	0.62	<0.001
PreglenLg	0.40	0.32	0.50	0.78	<0.001	0.34	0.28	0.40	0.87	<0.001
CondWid	0.49	0.41	0.59	0.84	<0.001	0.42	0.34	0.50	0.84	<0.001
CondLg	0.46	0.37	0.56	0.79	<0.001	0.38	0.31	0.46	0.84	<0.001
CondArea	0.94	0.78	1.15	0.82	<0.001	0.79	0.65	0.95	0.85	<0.001
3DCondArea	0.81	0.66	0.98	0.82	<0.001	0.67	0.56	0.80	0.86	<0.001
Males										
ArtTubHt	0.61	0.46	0.80	0.64	<0.001	0.59	0.45	0.77	0.68	<0.001
EntGlHt	0.62	0.49	0.79	0.72	<0.001	0.54	0.43	0.68	0.78	<0.001
GlenLg	0.37	0.31	0.44	0.87	<0.001	0.34	0.29	0.39	0.89	<0.001
GlenWid	0.41	0.34	0.48	0.87	<0.001	0.40	0.33	0.48	0.84	<0.001
GlenArea	0.77	0.66	0.89	0.89	<0.001	0.73	0.62	0.85	0.88	<0.001
3DGlenArea	0.79	0.68	0.92	0.89	<0.001	0.72	0.62	0.84	0.90	<0.001
PGPHt	0.54	0.43	0.67	0.77	<0.001	0.58	0.46	0.74	0.76	<0.001
PreglenLg	0.38	0.31	0.46	0.80	<0.001	0.34	0.28	0.42	0.84	<0.001
CondWid	0.41	0.33	0.50	0.81	<0.001	0.40	0.31	0.50	0.76	<0.001
CondLg	0.41	0.33	0.51	0.79	<0.001	0.38	0.30	0.47	0.77	<0.001
CondArea	0.81	0.67	1.00	0.81	<0.001	0.77	0.61	0.96	0.78	<0.001
3DCondArea	0.73	0.61	0.88	0.85	<0.001	0.65	0.55	0.78	0.86	<0.001

TABLE 5-10. Results of the scaling analyses for the TMJ variables on body mass for hominoids only (including humans) (n=13). Data include the reduced major axis (RMA) slopes and their corresponding confidence intervals and significant r-squared values. Critical alpha was set at 0.05/12= 0.0042. Highlighted cells indicate positively allometric relationships and values in italics indicate negatively allometric relationships.

Hominoids	Original Data					Independent Contrasts				
Females	Slope	Low CI	Hi CI	R-sq	p-value	Slope	Low CI	Hi CI	R-sq	p-value
ArtTubHt	0.40	0.29	0.56	0.74	<0.001	0.45	0.25	0.81	0.24	0.107
EntGlHt	0.51	0.35	0.73	0.69	<0.001	0.67	0.37	1.21	0.21	0.137
GlenLg	0.33	0.28	0.40	0.92	<0.001	0.36	0.24	0.54	0.66	0.001
GlenWid	0.43	0.36	0.52	0.91	<0.001	0.46	0.32	0.65	0.73	<0.001
GlenArea	0.76	0.63	0.91	0.93	<0.001	0.80	0.56	1.15	0.73	<0.001
3DGlenArea	0.77	0.65	0.91	0.93	<0.001	0.82	0.60	1.12	0.79	<0.001
PGPHt	0.42	0.26	0.69	0.40	0.02	0.69	0.36	1.31	0.03	0.574
PreglenLg	0.25	0.17	0.35	0.70	<0.001	0.31	0.18	0.57	0.23	0.116
CondWid	0.46	0.37	0.55	0.91	<0.001	0.50	0.34	0.74	0.68	0.001
CondLg	0.43	0.35	0.54	0.89	<0.001	0.45	0.30	0.69	0.62	0.002
CondArea	0.89	0.72	1.09	0.91	<0.001	0.95	0.63	1.42	0.66	0.001
3DCondArea	0.82	0.66	1.01	0.90	<0.001	0.88	0.59	1.31	0.66	0.001
Males										
ArtTubHt	0.36	0.28	0.47	0.84	<0.001	0.41	0.26	0.65	0.54	0.007
EntGlHt	0.48	0.37	0.63	0.84	<0.001	0.61	0.39	0.98	0.54	0.006
GlenLg	0.32	0.28	0.38	0.94	<0.001	0.37	0.27	0.51	0.79	<0.001
GlenWid	0.40	0.35	0.46	0.96	<0.001	0.44	0.32	0.59	0.82	<0.001
GlenArea	0.72	0.62	0.83	0.95	<0.001	0.80	0.59	1.07	0.82	<0.001
3DGlenArea	0.72	0.63	0.82	0.96	<0.001	0.80	0.62	1.03	0.87	<0.001
PGPHt	0.41	0.27	0.61	0.62	<0.001	0.65	0.37	1.14	0.30	0.064
PreglenLg	0.26	0.19	0.35	0.80	<0.001	0.34	0.21	0.56	0.48	0.012
CondWid	0.41	0.36	0.47	0.96	<0.001	0.45	0.34	0.62	0.81	<0.001
CondLg	0.41	0.35	0.47	0.95	<0.001	0.44	0.33	0.60	0.81	<0.001
CondArea	0.81	0.71	0.93	0.96	<0.001	0.89	0.66	1.21	0.82	<0.001
3DCondArea	0.74	0.66	0.84	0.97	<0.001	0.79	0.61	1.02	0.87	<0.001

TABLE 5-11. Results of the scaling analyses for the TMJ variables on cranial geometric mean for all taxa (excluding humans) (n=47). Data include the reduced major axis (RMA) slopes and their corresponding confidence intervals and significant r-squared values. Critical alpha was set at 0.05/12= 0.0042. Highlighted cells indicate positively allometric relationships.

ALL TAXA	Original Data					Independent Contrasts				
Females	Slope	Low CI	Hi CI	R-sq	p-value	Slope	Low CI	Hi CI	R-sq	p-value
ArtTubHt	1.67	1.47	1.90	0.81	<0.001	1.86	1.53	2.26	0.58	<0.001
EntGlHt	2.07	1.88	2.28	0.90	<0.001	2.08	1.80	2.41	0.77	<0.001
GlenLg	1.28	1.16	1.41	0.90	<0.001	1.43	1.27	1.61	0.85	<0.001
GlenWid	1.39	1.28	1.52	0.92	<0.001	1.57	1.39	1.78	0.83	<0.001
GlenArea	2.65	2.44	2.89	0.92	<0.001	2.96	2.65	3.31	0.87	<0.001
3DGlenArea	2.58	2.33	2.86	0.89	<0.001	3.06	2.68	3.50	0.82	<0.001
PGPHt	1.45	1.23	1.70	0.71	<0.001	1.88	1.55	2.28	0.60	<0.001
PreglenLg	1.13	1.00	1.28	0.84	<0.001	1.32	1.15	1.51	0.79	<0.001
CondWid	1.47	1.35	1.62	0.91	<0.001	1.68	1.47	1.91	0.81	<0.001
CondLg	1.42	1.31	1.55	0.92	<0.001	1.56	1.37	1.77	0.83	<0.001
CondArea	2.89	2.65	3.15	0.92	<0.001	3.22	2.84	3.65	0.83	<0.001
3DCondArea	2.74	2.51	2.99	0.92	<0.001	3.07	2.69	3.50	0.82	<0.001
Males										
ArtTubHt	1.74	1.51	2.00	0.78	<0.001	2.14	1.77	2.59	0.60	<0.001
EntGlHt	2.12	1.92	2.34	0.89	<0.001	2.28	1.99	2.60	0.81	<0.001
GlenLg	1.32	1.19	1.45	0.89	<0.001	1.50	1.35	1.68	0.87	<0.001
GlenWid	1.42	1.30	1.55	0.92	<0.001	1.64	1.47	1.82	0.88	<0.001
GlenArea	2.72	2.49	2.97	0.92	<0.001	3.11	2.81	3.44	0.89	<0.001
3DGlenArea	2.64	2.38	2.93	0.89	<0.001	3.13	2.80	3.50	0.87	<0.001
PGPHt	1.61	1.37	1.89	0.71	<0.001	2.17	1.83	2.58	0.68	<0.001
PreglenLg	1.19	1.05	1.34	0.84	<0.001	1.43	1.25	1.62	0.81	<0.001
CondWid	1.49	1.38	1.61	0.93	<0.001	1.69	1.52	1.88	0.88	<0.001
CondLg	1.48	1.37	1.60	0.93	<0.001	1.63	1.46	1.81	0.88	<0.001
CondArea	2.97	2.75	3.20	0.94	<0.001	3.31	2.98	3.66	0.88	<0.001
3DCondArea	2.71	2.47	2.97	0.91	<0.001	3.00	2.67	3.37	0.86	<0.001

TABLE 5-12. Results of the scaling analyses for the TMJ variables on cranial geometric mean for hominoids (excluding humans) (n=12). Data include the reduced major axis (RMA) slopes and their corresponding confidence intervals and significant r-squared values. Critical alpha was set at 0.05/12= 0.0042. Highlighted cells indicate positively allometric relationships.

Hominoids	Original Data					Independent Contrasts				
Females	Slope	Low CI	Hi CI	R-sq	p-value	Slope	Low CI	Hi CI	R-sq	p-value
ArtTubHt	1.50	1.33	1.70	0.96	<0.001	1.53	1.23	1.91	0.92	<0.001
EntGlHt	1.88	1.61	2.20	0.95	<0.001	2.18	1.56	3.05	0.80	<0.001
GlenLg	1.29	1.14	1.45	0.97	<0.001	1.42	1.06	1.91	0.85	<0.001
GlenWid	1.67	1.45	1.92	0.96	<0.001	1.79	1.41	2.25	0.90	<0.001
GlenArea	2.94	2.62	3.29	0.97	<0.001	3.14	2.53	3.91	0.92	<0.001
3DGlenArea	2.97	2.58	3.42	0.96	<0.001	3.21	2.52	4.09	0.90	<0.001
PGPHt	1.35	1.10	1.66	0.91	<0.001	1.74	1.16	2.60	0.70	0.001
PreglenLg	0.94	0.75	1.18	0.89	<0.001	1.13	0.71	1.80	0.59	0.006
CondWid	1.76	1.54	2.02	0.96	<0.001	1.95	1.50	2.55	0.87	<0.001
CondLg	1.68	1.46	1.93	0.96	<0.001	1.78	1.37	2.32	0.87	<0.001
CondArea	3.43	3.01	3.92	0.97	<0.001	3.72	2.88	4.80	0.88	<0.001
3DCondArea	3.16	2.72	3.67	0.95	<0.001	3.44	2.63	4.50	0.87	<0.001
Males										
ArtTubHt	1.51	1.26	1.80	0.93	<0.001	1.54	1.14	2.08	0.84	<0.001
EntGlHt	1.98	1.76	2.23	0.97	<0.001	2.25	1.80	2.81	0.91	<0.001
GlenLg	1.36	1.23	1.52	0.98	<0.001	1.48	1.20	1.84	0.92	<0.001
GlenWid	1.68	1.50	1.87	0.98	<0.001	1.76	1.46	2.12	0.94	<0.001
GlenArea	3.03	2.74	3.36	0.98	<0.001	3.21	2.69	3.84	0.94	<0.001
3DGlenArea	3.03	2.68	3.43	0.97	<0.001	3.20	2.65	3.87	0.94	<0.001
PGPHt	1.58	1.23	2.03	0.87	<0.001	2.20	1.52	3.17	0.75	0.001
PreglenLg	1.08	0.88	1.32	0.92	<0.001	1.32	0.91	1.91	0.75	0.001
CondWid	1.72	1.56	1.89	0.98	<0.001	1.83	1.52	2.21	0.94	<0.001
CondLg	1.71	1.55	1.88	0.98	<0.001	1.78	1.50	2.12	0.95	<0.001
CondArea	3.42	3.12	3.76	0.98	<0.001	3.60	3.04	4.27	0.95	<0.001
3DCondArea	3.13	2.82	3.47	0.98	<0.001	3.16	2.71	3.70	0.96	<0.001

TABLE 5-13. Results of the scaling analyses for the TMJ variables on body mass for all taxa (excluding humans) (n=47). Data include the reduced major axis (RMA) slopes and their corresponding confidence intervals and significant r-squared values. Critical alpha was set at 0.05/12= 0.0042. Highlighted cells indicate positively allometric relationships and values in italics indicate negatively allometric relationships.

ALL TAXA	Original Data					Independent Contrasts				
Females	Slope	Low CI	Hi CI	R-sq	p-value	Slope	Low CI	Hi CI	R-sq	p-value
ArtTubHt	0.44	0.38	0.50	0.80	<0.001	0.46	0.37	0.55	0.58	<0.001
EntGlHt	0.55	0.49	0.61	0.88	<0.001	0.51	0.44	0.60	0.74	<0.001
GlenLg	0.34	0.31	0.36	0.93	<0.001	0.35	0.32	0.39	0.88	<0.001
GlenWid	0.37	0.34	0.40	0.93	<0.001	0.39	0.35	0.43	0.87	<0.001
GlenArea	0.70	0.65	0.75	0.94	<0.001	0.73	0.66	0.80	0.90	<0.001
3DGlenArea	0.70	0.63	0.77	0.90	<0.001	0.74	0.65	0.84	0.85	<0.001
PGPHt	0.38	0.33	0.44	0.77	<0.001	0.46	0.38	0.56	0.63	<0.001
PreglenLg	0.30	0.27	0.33	0.88	<0.001	0.32	0.29	0.37	0.83	<0.001
CondWid	0.39	0.36	0.42	0.91	<0.001	0.41	0.36	0.47	0.84	<0.001
CondLg	0.37	0.34	0.41	0.91	<0.001	0.38	0.34	0.43	0.83	<0.001
CondArea	0.76	0.70	0.83	0.91	<0.001	0.79	0.70	0.89	0.84	<0.001
3DCondArea	0.74	0.67	0.81	0.91	<0.001	0.74	0.65	0.85	0.81	<0.001
Males										
ArtTubHt	0.43	0.38	0.49	0.80	<0.001	0.51	0.43	0.61	0.66	<0.001
EntGlHt	0.52	0.47	0.58	0.89	<0.001	0.54	0.47	0.62	0.81	<0.001
GlenLg	0.33	0.30	0.36	0.91	<0.001	0.36	0.32	0.40	0.88	<0.001
GlenWid	0.35	0.33	0.38	0.93	<0.001	0.39	0.35	0.43	0.87	<0.001
GlenArea	0.67	0.62	0.73	0.93	<0.001	0.74	0.67	0.82	0.89	<0.001
3DGlenArea	0.66	0.60	0.73	0.90	<0.001	0.74	0.66	0.83	0.87	<0.001
PGPHt	0.40	0.34	0.46	0.75	<0.001	0.52	0.44	0.61	0.70	<0.001
PreglenLg	0.29	0.26	0.33	0.85	<0.001	0.34	0.30	0.39	0.81	<0.001
CondWid	0.37	0.34	0.40	0.93	<0.001	0.40	0.36	0.46	0.83	<0.001
CondLg	0.37	0.34	0.40	0.92	<0.001	0.39	0.34	0.44	0.83	<0.001
CondArea	0.74	0.68	0.80	0.93	<0.001	0.79	0.70	0.89	0.84	<0.001
3DCondArea	0.68	0.62	0.74	0.92	<0.001	0.71	0.63	0.80	0.85	<0.001

TABLE 5-14. Results of the scaling analyses for the TMJ variables on body mass for hominoids (excluding humans) (n=12). Data include the reduced major axis (RMA) slopes and their corresponding confidence intervals and significant r-squared values. Critical alpha was set at 0.05/12= 0.0042. Highlighted cells indicate positively allometric relationships and values in italics indicate negatively allometric relationships.

Hominoids	Original Data					Independent Contrasts				
Females	Slope	Low CI	Hi CI	R-sq	p-value	Slope	Low CI	Hi CI	R-sq	p-value
ArtTubHt	0.40	0.33	0.48	0.93	<0.001	0.41	0.27	0.63	0.66	0.003
EntGlHt	0.50	0.41	0.61	0.92	<0.001	0.59	0.38	0.90	0.66	0.002
GlenLg	0.34	0.30	0.39	0.96	<0.001	0.38	0.27	0.54	0.79	<0.001
GlenWid	0.44	0.38	0.52	0.95	<0.001	0.48	0.36	0.64	0.85	<0.001
GlenArea	0.78	0.68	0.89	0.97	<0.001	0.85	0.64	1.12	0.86	<0.001
3DGlenArea	0.79	0.68	0.91	0.96	<0.001	0.86	0.65	1.16	0.85	<0.001
PGPHt	0.36	0.28	0.46	0.88	<0.001	0.47	0.28	0.78	0.51	0.014
PreglenLg	***0.25***	0.19	0.32	0.86	<0.001	0.30	0.18	0.51	0.51	0.014
CondWid	0.47	0.40	0.55	0.95	<0.001	0.53	0.37	0.74	0.79	<0.001
CondLg	0.44	0.37	0.54	0.93	<0.001	0.48	0.33	0.70	0.73	0.001
CondArea	0.91	0.77	1.08	0.94	<0.001	1.00	0.70	1.43	0.77	<0.001
3DCondArea	0.84	0.69	1.01	0.93	<0.001	0.93	0.64	1.34	0.75	0.001
Males										
ArtTubHt	0.36	0.30	0.44	0.92	<0.001	0.39	0.28	0.56	0.77	<0.001
EntGlHt	0.48	0.41	0.55	0.96	<0.001	0.57	0.44	0.75	0.87	<0.001
GlenLg	0.33	0.29	0.37	0.97	<0.001	0.38	0.28	0.50	0.85	<0.001
GlenWid	0.40	0.36	0.45	0.97	<0.001	0.45	0.34	0.59	0.87	<0.001
GlenArea	0.73	0.65	0.82	0.97	<0.001	0.82	0.63	1.07	0.87	<0.001
3DGlenArea	0.73	0.64	0.82	0.97	<0.001	0.82	0.63	1.06	0.88	<0.001
PGPHt	0.38	0.29	0.49	0.85	<0.001	0.56	0.37	0.85	0.67	0.002
PreglenLg	0.26	0.20	0.33	0.89	<0.001	0.34	0.22	0.52	0.66	0.002
CondWid	0.41	0.36	0.47	0.97	<0.001	0.47	0.35	0.63	0.85	<0.001
CondLg	0.41	0.36	0.46	0.97	<0.001	0.45	0.35	0.60	0.86	<0.001
CondArea	0.82	0.73	0.93	0.97	<0.001	0.92	0.70	1.22	0.86	<0.001
3DCondArea	0.75	0.67	0.84	0.97	<0.001	0.81	0.63	1.04	0.89	<0.001

significant, and as a result fewer positively allometric relationships and no negatively allometric relationships were found.

All analyses were run both for the entire sample, and for the individual subfamilies (platyrrhines, cercopithecoids, and hominoids) within the sample. When all taxa were considered in the analysis, most variables scaled with positive allometry, particularly against the cranial geometric mean (Tables 5-3, 5-7, 5-11, and 5-13). This was true for both males and females, regardless of whether humans were included in the analysis, and after independent contrasts were calculated. Separate examination of the platyrrhines indicated considerably fewer positively allometric relationships, particularly when independent contrasts were used instead of the raw data (Tables 5-4 and 5-8). Only entoglenoid height scaled consistently with positive allometry in males and females, against both the cranial geometric mean and body mass, and after independent contrasts. Results of the analyses for the cercopithecoids varied strongly depending upon which variable the measures of TMJ shape were scaled against. When variables were regressed against the cranial geometric mean, all aspects of the TMJ shape scaled with positive allometry, both before and after independent contrasts (Table 5-5). However, when variables were regressed against body mass (5-9), only articular tubercle height, entoglenoid height, and postglenoid process height were found to scale with positive allometry (after independent contrasts). A similar pattern was found in hominoids when humans were included in the sample (Tables 5-6 and 5-10). When scaled against the cranial geometric mean, glenoid width and area, as well as condyle length, width, and area were positively allometric after independent contrasts. Only one variable (condyle width) scaled with positive allometry when regressed against body mass, however (Table 5-10).

Exclusion of the human sample from the dataset (Tables 5-11 through 5-14) yielded broadly similar results to the analyses that included humans, particularly when the entire sample was examined. However, for the hominoid only analyses, humans represented enough of an outlier in most regressions that their removal increased the r-squared values and levels of significance for all analyses, allowing some previously borderline values to be identified as positively allometric (or negatively allometric in the case of the preglenoid plane regressions against body mass). There were particularly more positively allometric relationships for hominoids when humans were excluded and independent contrasts were used.

The extent to which specific features of the TMJ scaled with allometry or isometry depended upon the taxonomic group examined. Articular tubercle, entoglenoid process, and postglenoid process height all tended to scale with positive allometry in platyrrhines and cercopithecoids. However, this was less so in hominoids, where these variables scaled with isometry when humans were included, but with positive allometry with humans excluded. Similarly, glenoid length tended to scale with positive allometry in cercopithecoids and platyrrhines (particularly when the raw data were analyzed), but not in hominoids. Instead, glenoid length generally scaled with isometry in hominoids, although when humans were removed glenoid length scaled with positive allometry against the cranial geometric mean. This result is likely a consequence of the inclusion of the preglenoid plane in the overall measurement of glenoid length; preglenoid plane length scaled with isometry or slight positive allometry in platyrrhines and cercopithecoids, but scaled with either negative allometry or isometry in hominoids (both in analyses with and without humans).

Geometric morphometric data

Regressions of glenoid shape on centroid size. Regression of the first five PC axes on centroid size found a strong correlation between glenoid shape and PC 1 for platyrrhines and hominoids, but not cercopithecoids (Table 5-15). Centroid size was instead a significant explanatory variable for variation along PC 3 in this group. Examination of the scatterplots of PCs 1 through 3 versus

TABLE 5-15. Results for the regression of PC scores against centroid size for the glenoid. Critical alpha was set at 0.05/4= 0.0125. Highlighted cells indicate significant relationships.

		Original Data				Contrasts			
		Females		Males		Females		Males	
		R-sq	p-value	R-sq	p-value	R-sq	p-value	R-sq	p-value
PC 1	All Taxa	0.422	<0.001	0.352	<0.001	0.130	0.013	0.070	0.073
	Platyrrhine	0.497	0.007	0.680	0.001	0.123	0.265	0.297	0.067
	Cercopithecoid	0.107	0.137	0.008	0.699	0.011	0.651	0.154	0.079
	Hominoid	0.804	<0.001	0.803	<0.001	0.489	0.011	0.341	0.046
PC 2	All Taxa	0.108	0.022	0.102	0.027	0.020	0.339	0.116	0.019
	Platyrrhine	0.234	0.094	0.043	0.498	0.127	0.256	0.080	0.373
	Cercopithecoid	0.139	0.088	0.002	0.849	0.058	0.291	0.177	0.057
	Hominoid	0.004	0.842	0.038	0.521	0.094	0.333	0.064	0.426
PC 3	All Taxa	0.004	0.685	0.038	0.185	0.032	0.230	0.013	0.445
	Platyrrhine	0.026	0.602	0.021	0.637	0.073	0.394	0.005	0.828
	Cercopithecoid	0.314	0.007	0.548	<0.001	0.200	0.042	0.407	0.002
	Hominoid	0.011	0.730	0.000	0.998	0.000	0.979	0.151	0.212
PC 4	All Taxa	0.009	0.526	0.075	0.060	0.000	0.918	0.011	0.495
	Platyrrhine	0.004	0.840	0.005	0.816	0.176	0.174	0.016	0.698
	Cercopithecoid	0.003	0.822	0.019	0.540	0.027	0.479	0.177	0.057
	Hominoid	0.030	0.571	0.114	0.259	0.087	0.351	0.031	0.581
PC 5	All Taxa	0.006	0.595	0.187	0.002	0.045	0.154	0.269	<0.001
	Platyrrhine	0.010	0.743	0.005	0.824	0.162	0.194	0.024	0.634
	Cercopithecoid	0.000	0.974	0.000	0.996	0.015	0.597	0.037	0.402
	Hominoid	0.011	0.735	0.002	0.880	0.035	0.562	0.001	0.932

centroid size indicates that this result may be due to the fact that *Miopithecus talapoin* (a species which is considerably smaller in body size than all of the other cercopithecoids examined) is a strong outlier along PC 1; however, removal of *M. talapoin* does not change the pattern of the significance among these PC axes and centroid size.

Hominoids showed the highest correlations with centroid size along PC 1, with r-squared vales of 0.804 and 0.803 for females and males, respectively. To some extent, these significant correlations disappeared when independent contrasts were used in place of the original PC scores, although female hominoids still showed a significant correlation between centroid size and PC 1 (r^2=0.489, p=0.011), while centroid size for male cercopithecoids remained correlated with PC 3 (r^2=0.407, p=0.002). This decrease in the number of correlations after independent contrasts indicates at least moderate levels of phylogenetic codependence in the sample.

Size-related shape changes in the TMJ. Using wireframe diagrams, how shape changes in relation to size (or the allometric scaling) of the glenoid was examined (Figs. 5-2 through 5-5). Size related shape changes in the entire sample (Fig. 5-2) ranged from small taxa with anteroposteriorly long glenoids with less glenoid relief (although relatively large postglenoid processes) to large bodied taxa with mediolaterally wide joints with considerably more topographic relief to the joint.

In platyrrhines (Fig. 5-3), smaller-bodied taxa (e.g., *Saimiri*, *Aotus)* tended to have anteroposteriorly shorter and mediolaterally wider glenoid fossae, with a relatively small postglenoid process and large entoglenoid process and articular tubercle. In contrast, larger bodied platyrrhines, such as *Ateles*, *Lagothrix*, and particularly *Alouatta*, tended to have anteroposteriorly long and mediolaterally narrow glenoids, with a large postglenoid process and small entoglenoid process and articular tubercle. Little difference was observed in articular eminence inclination relative to Frankfurt Horizontal among small and large bodied taxa.

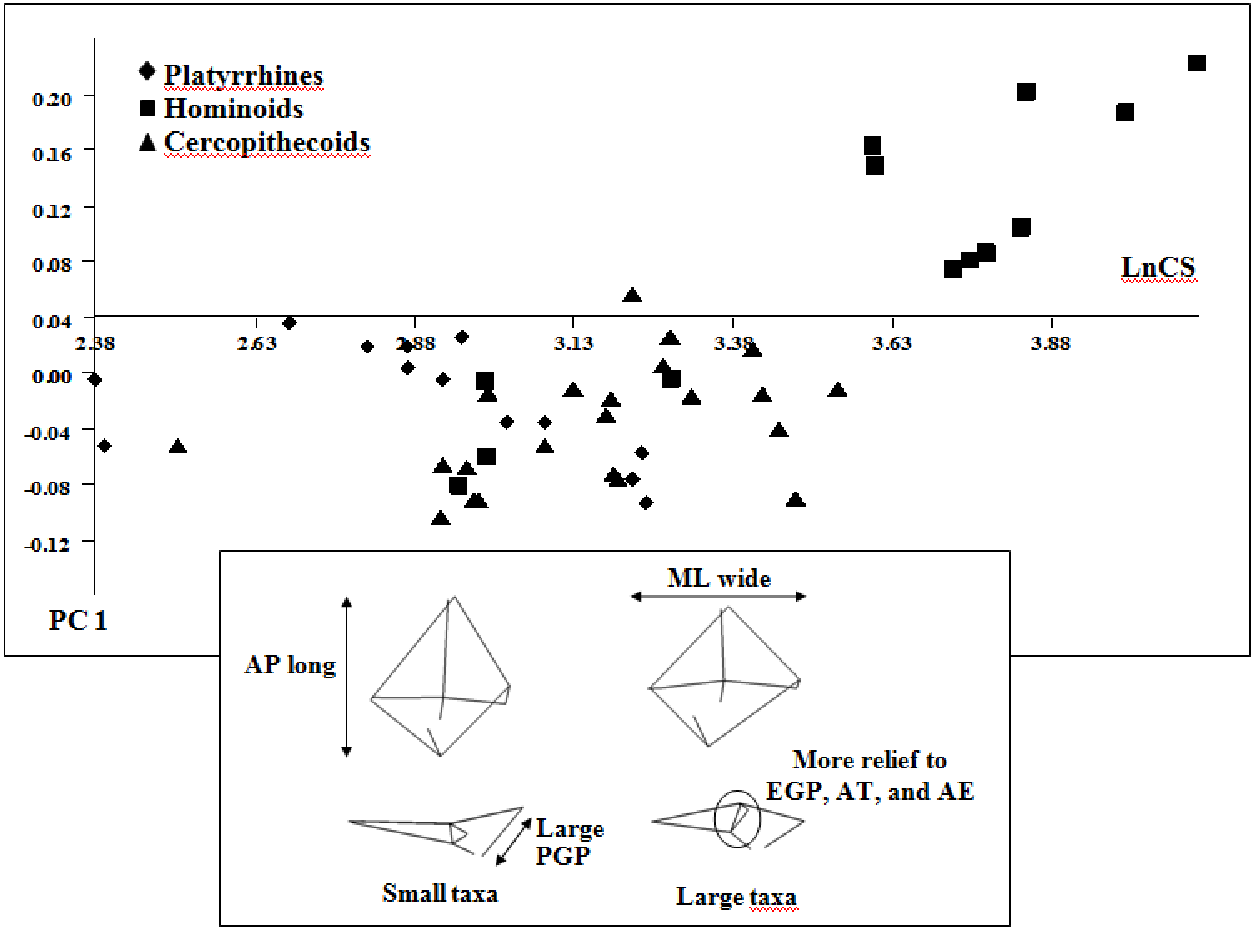


Fig. 5-2. PC results for the entire sample (females only). Axes shown are centroid size (x-axis) and PC 1 (y-axis), which are significantly correlated (r-squared = 0.422, p-value< 0.001). Wireframe diagrams show shape variation between the small and large taxa within the analysis.

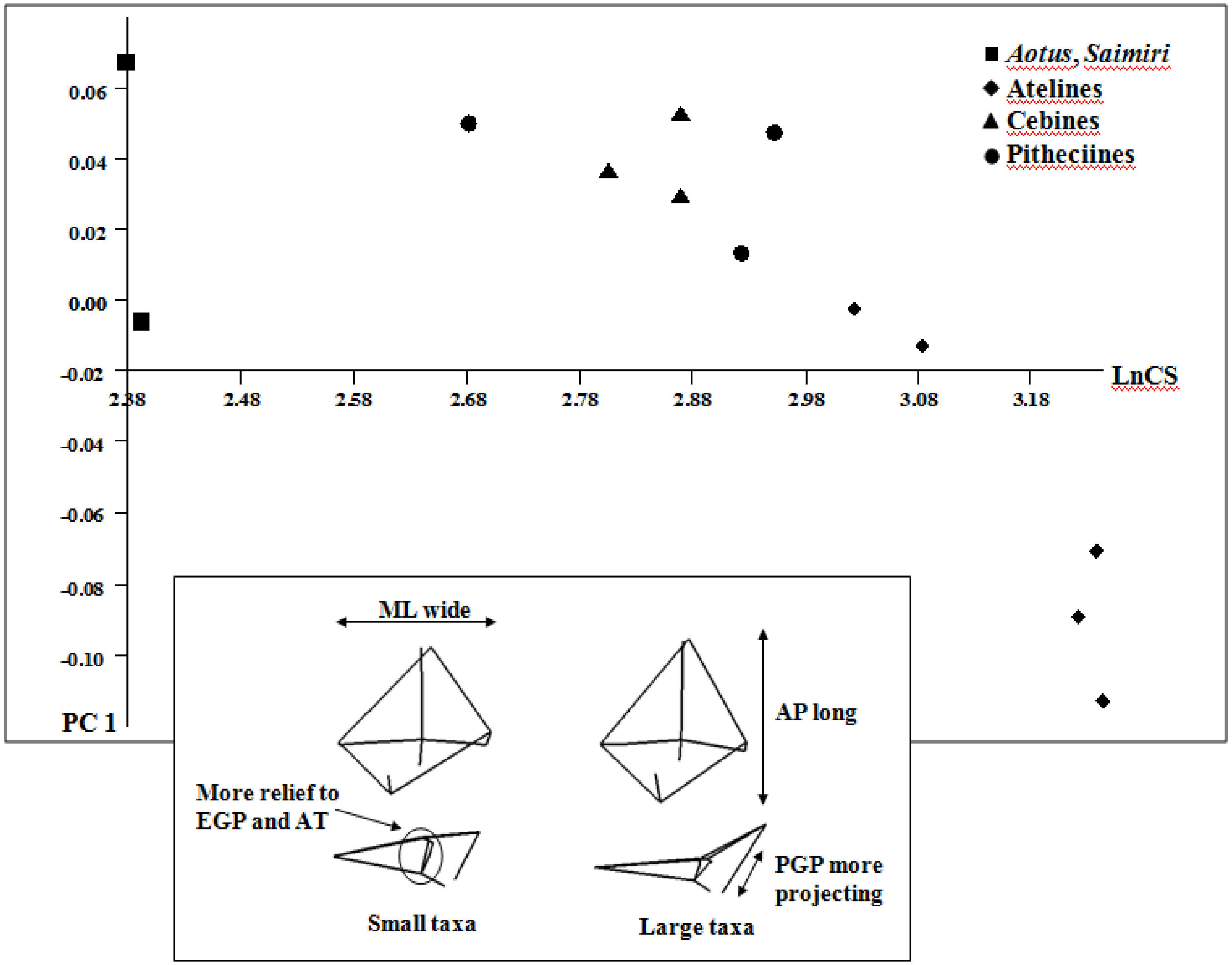


Fig. 5-3. PC results for the platyrrhine sample (females only). Axes shown are centroid size (x-axis) and PC 1 (y-axis), which are significantly correlated (r-squared = 0.497, p-value= 0.007). Wireframe diagrams show shape variation between the small and large taxa within the analysis.

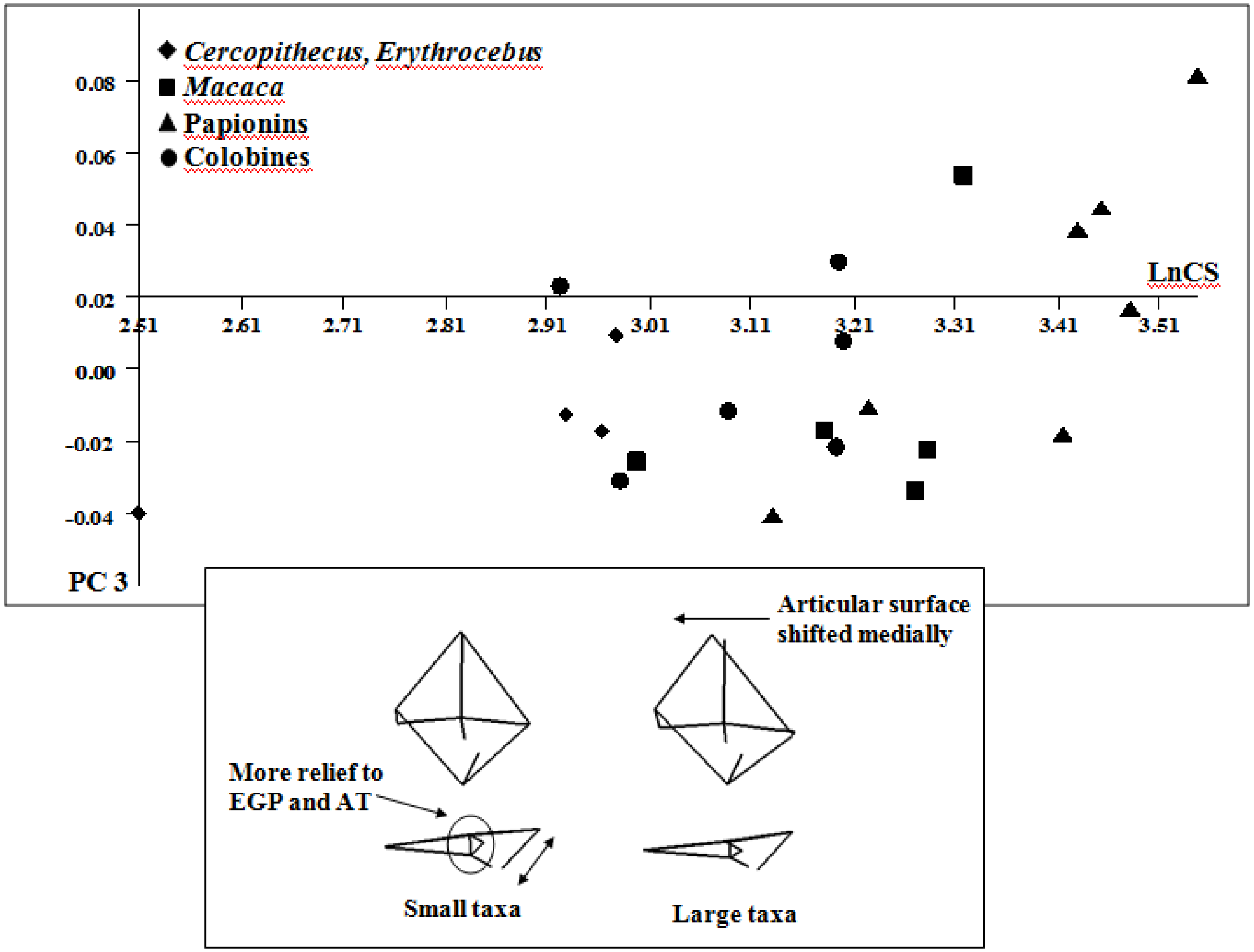


Fig. 5-4. PC results for the cercopithecoid sample (females only). Axes shown are centroid size (x-axis) and PC 3 (y-axis), which are significantly correlated (r-squared = 0.314, p-value= 0.007). Wireframe diagrams show shape variation between the small and large taxa within the analysis.

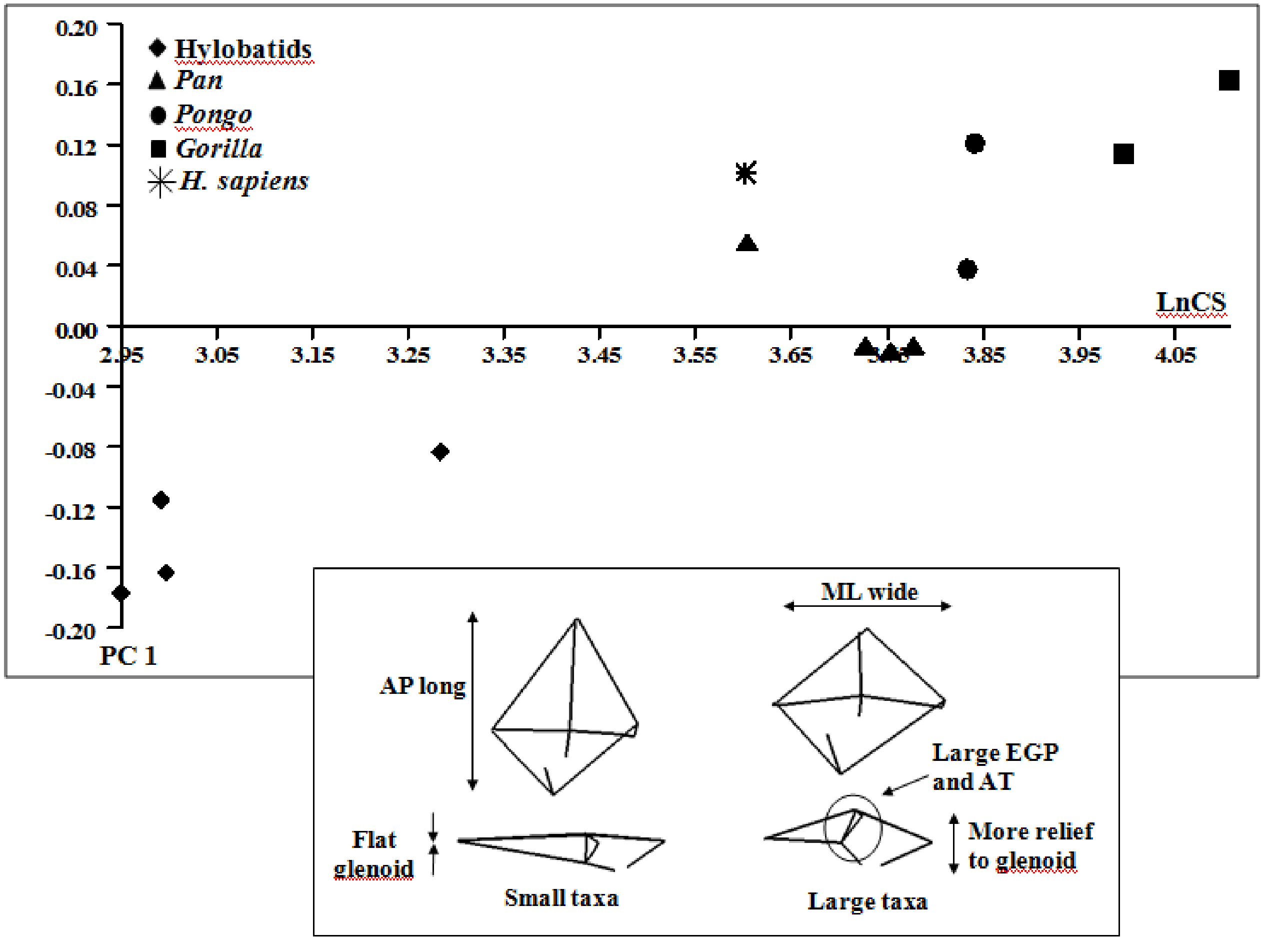


Fig. 5-5. PC results for the hominoid sample (females only). Axes shown are centroid size (x-axis) and PC 1 (y-axis), which are significantly correlated (r-squared = 0.804, p-value < 0.001). Wireframe diagrams show shape variation between the small and large taxa within the analysis.

Size related shape variation was not particularly marked in cercopithecoids (Fig. 5-4), even after *M. talapoin* was removed from the analysis because of its considerably smaller body size. In larger bodied taxa, the preglenoid plane appeared slightly longer, the entoglenoid process and articular tubercle slightly more projecting in larger species, and the articular eminence was somewhat more inferiorly inclined (i.e., more raised) in larger bodied taxa. However, in general, shape stayed relatively the same as size increased in this group.

Finally, hominoids displayed the strongest relationship between size and glenoid shape, with clear and marked differences in glenoid shape between smaller (e.g., *Hylobates*) and larger bodied (e.g., *Gorilla* and *Pongo*) taxa (Fig. 5-5). Smaller taxa tend to have a very flat glenoid region, with little topographic relief, that is very anteroposteriorly long and mediolaterally narrow. In contrast, larger bodied taxa have a very raised articular eminence, larger postglenoid and entoglenoid processes and articular tubercle, with an anteroposteriorly short and very mediolaterally wide glenoid shape.

Regressions of condylar shape on centroid size. Fewer significant correlations between centroid size and condylar shape were found (Table 5-16), and the r-squared values were generally lower for condylar shape than for glenoid shape. These results suggest that variation in condylar shape among taxa is less strongly related to size than is glenoid shape variation, or that condylar shape is too plastic. No significant correlations were found between PC 1 and centroid size; instead, significant correlations were found between centroid size and PCs 3 and 4 when the uncorrected PC scores were used. When contrasts were used in place of the original PC scores, significant correlations were found between centroid size and PCs 2 and 4, but only for the cercopithecoid sample.

Shape variation in relation to size in the mandibular condyle was also evaluated, but because of the general lack of strong correlations between size and shape, visualization of the

TABLE 5-16. Results for the regression of PC scores against centroid size for the mandibular condyle. Critical alpha was set at 0.05/4= 0.0125. Highlighted cells indicate significant relationships.

		Condyle Points				Condyle Points- Contrasts			
		Females		Males		Females		Males	
		R-sq	p-value	R-sq	p-value	R-sq	p-value	R-sq	p-value
PC 1	All taxa	0.002	0.790	0.027	0.266	0.018	0.363	0.002	0.739
	Platyrrhine	0.157	0.180	0.219	0.106	0.000	0.985	0.017	0.687
	Cercopithecoid	0.109	0.133	0.026	0.472	0.037	0.404	0.010	0.669
	Hominoid	0.154	0.185	0.122	0.242	0.182	0.166	0.144	0.224
PC 2	All taxa	0.012	0.452	0.002	0.781	0.046	0.147	0.024	0.297
	Platyrrhine	0.040	0.513	0.370	0.027	0.001	0.916	0.094	0.333
	Cercopithecoid	0.031	0.430	0.075	0.218	0.263	0.018	0.386	0.003
	Hominoid	0.026	0.599	0.149	0.192	0.013	0.729	0.013	0.723
PC 3	All taxa	0.133	0.011	0.084	0.046	0.081	0.053	0.042	0.166
	Platyrrhine	0.073	0.371	0.011	0.737	0.009	0.775	0.028	0.603
	Cercopithecoid	0.286	0.010	0.002	0.859	0.274	0.015	0.021	0.528
	Hominoid	0.394	0.022	0.422	0.016	0.186	0.161	0.162	0.195
PC 4	All taxa	0.072	0.066	0.001	0.857	0.002	0.789	0.036	0.200
	Platyrrhine	0.058	0.429	0.003	0.859	0.001	0.934	0.036	0.557
	Cercopithecoid	0.006	0.732	0.312	0.007	0.004	0.781	0.377	0.003
	Hominoid	0.081	0.345	0.098	0.298	0.043	0.516	0.017	0.689
PC 5	All taxa	0.037	0.193	0.039	0.180	0.005	0.636	0.006	0.611
	Platyrrhine	0.027	0.591	0.125	0.236	0.101	0.314	0.151	0.212
	Cercopithecoid	0.001	0.885	0.024	0.493	0.006	0.748	0.089	0.188
	Hominoid	0.000	0.993	0.053	0.449	0.024	0.627	0.141	0.229

shape changes related to size was not particularly meaningful, and is not discussed here. This may be a result of the fact that only five landmarks were used to quantify the shape of the mandibular condyle.

DISCUSSION

The goal of this chapter was to evaluate the extent to which aspects of the bony morphology of the TMJ scale in relation to body and cranial size. Given previous analyses of scaling in the masticatory apparatus and TMJ, it was predicted that features of the TMJ should scale primarily with positive allometry. Furthermore, several specific biomechanical scaling hypotheses were generated to further test the predictions of TMJ function outlined in Chapter 4. The first of these hypotheses posited that, if dietary resistance increases with body size, it was predicted that the size of the TMJ and its processes should scale with positive allometry against either body or cranial size. The second hypothesis predicted that features of the TMJ associated with gape would show negative allometry, since relative food-object size should decrease with increasing body size.

To test these hypotheses, a number of univariate regression and geometric morphometric analyses were performed. Results of the univariate regression analyses indicate that features of the TMJ scale, for the most part, with positive allometry against size, as was predicted based on previous research. These results were somewhat dependent upon whether the TMJ variables were scaled against body mass or the cranial geometric mean, since cranial size scaled with strong negative allometry when regressed against body mass. Since the cranial geometric mean represents aspects of calvarial size, this scaling relationship likely reflects the strong negatively allometric relationship that has been previously documented between body and brain size (e.g., Gould, 1975b; Hoffman, 1982; Martin and Harvey, 1985; Pagel and Harvey, 1988).

Of the specific features within the TMJ, the height of processes in the joint (the entoglenoid process, postglenoid process, and articular tubercle) all tended to scale with positive allometry in platyrrhines and cercopithecoids, but to a lesser extent in hominoids. Overall, these data support the hypothesis that the size of the TMJ and its various processes scale with positive allometry. Since dietary resistance and daily ingested feeding volume have been suggested to scale with positive allometry against body size (Hylander, 1985; Sailer et al., 1985; Ross et al., 2009), this finding provides further support for Prediction 1 from Chapter 4, that resistant-object feeders have relatively larger joint surface areas and processes than closely related taxa that masticate more compliant food objects.

Similarly, glenoid length and preglenoid plane length scaled with slight positive allometry in platyrrhines and cercopithecoids, but with isometry or slight negative allometry in hominoids. The negative allometry/ isometry observed for preglenoid plane length in hominoids may indicate decreased relative gape in larger bodied hominoids, since preglenoid plane length has been shown by Vinyard et al. (2003) to be positively correlated with relative gape, and particularly translation potential of the mandibular condyle during jaw opening. However, given the mixed nature of these results, these data suggest that there is unlikely to be a significant relationship between food-object size and body size, such that relative gape does not necessarily decrease with size as was suggested by Singleton (2005).

Regression of the principal component axes representing shape on centroid size in the geometric morphometric analyses suggest that glenoid shape tends to have a strong relationship with size in hominoids and platyrrhines, but less so in cercopithecoids. This finding is reflected in the evaluation of the wireframe diagrams that suggest shape does not vary as much in cercopithecoids as in platyrrhines and particularly hominoids. One possible explanation for this lack of size-related shape variation may be phylogenetic constraint within this group. Although recent analyses (Steiper et al., 2004) suggest a molecular divergence date of 29.2 to 34.5 million years ago (Ma) between cercopithecoids and hominoids, fossil data indicate a much more recent adaptive radiation of the cercopithecoids beginning in the Miocene, and peaking in the Pliocene and Pleistocene (Delson, 1994; Benefit, 1999; Benefit and McCrossin, 2002; Jablonski, 2002; Elton, 2007). Species of extant cercopithecoids represent this relatively recent radiation, and the diversity of adaptations within this group has made this clade highly successful. However, the rapidity and recency of this radiation has resulted in conserved skeletal and dental morphology and a general lack of morphological differentiation among lineages that may otherwise be expected if lineages had diverged more distantly (Schultz, 1970; Disotell, 1996; Jablonski, 2002). Moreover, several instances of morphological convergence among cercopithecoid primates have recently been indicated by molecular analyses (e.g., Disotell, 1994, 1996). The conserved nature of the morphology of this group has therefore made the interpretation of cercopithecoid evolution a complicated endeavor. This analysis supports these previous observations, and suggests that the bony morphology of the TMJ is relatively stable among taxa, despite the relatively high degree of size variation within this group. This could potentially indicate that the masticatory apparatus functions in very similar ways across body sizes. This result is not necessarily unexpected given the dietary heterogeneity of this group, and particularly of the species within this clade, which have often been noted to have very diverse diets (e.g., Wheatley, 1976, 1980; Dunbar, 1977; Moreno-Black and Maples, 1977; Hamilton et al., 1978; Crockett and Wilson, 1980; Maruhashi, 1980; Drucker, 1982; Deag, 1983; Lucas and Corlett, 1991; Whiten et al., 1991; Byrne et al., 1993; Iwamoto, 1993; Jablonski, 1993; Hill, 1997; Menard and Vallet, 1997; Fleagle, 1999; Pochron, 2000; Chapman et al., 2002; Hill and Dunbar, 2002; Lambert 2002; Menard, 2002; Swedell, 2002; Lambert et al., 2004; Tsuji et al., 2006).

Notably, however, the results of the geometric morphometric and univariate analyses yielded strikingly different signals for the cercopithecoid sample. In the univariate analyses, cercopithecoids showed the most consistent scaling patterns, where many of the variables examined scaled with strong positive allometry, particularly when measured against the cranial geometric mean. However, as discussed above, the geometric morphometric analyses failed to find a very high correlation between size and shape. It is unclear why these analyses differ. It is possible that the combination of variables that are included in the overall shape of the TMJ in this group is not able to discern among the scaling patterns of the individual features, as the univariate analyses do, and that perhaps the different patterns of scaling for these features cancel one another out in the geometric morphometric analyses. Further analyses will be necessary to determine whether this is indeed the case, and perhaps increased sample sizes at lower taxonomic levels (e.g., cercopithecines vs. colobines) will allow for examination of scaling patterns within the cercopithecoid sample.

In contrast, hominoids show a more drastic amount of shape change between small and large bodied taxa, which is likely a result of the two size classes included in this group: the smaller bodied hylobatids and large bodied hominids. As evidenced by the regression analyses where humans were excluded, humans tended to represent outliers in comparison to the rest of the hominoid sample. This result highlights the unique shape of the TMJ in this species, and indicates that humans tend not to lie along the same scaling trajectory as the rest of the hominoids. Analyses of TMJ morphology in fossil hominin species could help shed light on exactly when the hominin lineage began to deviate from this hominoid scaling pattern, and whether this morphology is at all related to increases in brain size and shape (and concurrently basicranial and facial morphology and position) in hominins (e.g., Todd, 1930; Weidenreich, 1943; Kimbel et al., 1984; Ross and Ravosa, 1993).

Interestingly, the pattern of shape changes with size in platyrrhines and hominoids differs substantially, with opposite size-related shape changes from small to large bodied taxa. In particular, the overall dimensions of the glenoid vary such that in platyrrhines, the glenoid is mediolaterally wide and anteroposteriorly short in small-bodied taxa, and gradually becomes both anteroposteriorly long and mediolaterally narrow in larger species. In hominoids this is reversed. These data could be interpreted to indicate a case of convergence between large bodied atelines (i.e., *Alouatta*) and the small-bodied hylobatids. Both of these groups are noted for their unique vocal behaviors, and although no analyses have quantified gape during vocalization in these taxa, it could be hypothesized that these vocal behaviors should necessitate relatively larger gapes. Gape data recently collected by Hylander et al. (2008) indicate that gibbons and siamangs do indeed have relatively large gapes, although the few data points currently available for *Alouatta* may suggest relatively smaller gapes in this genus (Hylander, personal communication). However, mandibular and canine morphology differs radically between *Alouatta* and hylobatids, with the TMJ raised well above the occlusal plane in howlers, while the TMJ is positioned very close to the occlusal plane in gibbons and siamangs. As a result, even given the same amount of condylar translation in these two groups, hylobatids would attain greater relative gapes than *Alouatta*, simply by virtue of their mandibular configuration (Herring and Herring, 1974; Singleton, 2005). This substantial difference in mandibular morphology is likely a consequence of the radical reorganization of the cranial base in *Alouatta*, as associated with the enlargement of the vocal apparatus (Hershkovitz, 1949; Hill, 1962; Fleagle, 1999). A number of features of the cranial base and masticatory apparatus have been previously linked to the highly autapomorphic vocal apparatus in this genus, including a small cranial capacity, decreased cranial flexion, increased bigonial breadth, a deep mandibular corpus with an enlarged and rounded gonial angle, and a TMJ raised above the occlusal plane (Watanabe, 1982; Anapol and Lee, 1994; Fleagle, 1999). Among these, several characters can also be interpreted as providing increased mechanical advantage for the mastication of tough food objects such as leaves, which *Alouatta* relies on heavily. In particular, the raised TMJ of *Alouatta* can be interpreted as acting to maximize the dispersion of bite forces along the postcanine dentition (Greaves, 1980; Spencer, 1995). Thus, the unique configuration of the masticatory apparatus and TMJ in *Alouatta* is likely due to a combination of factors, which further analyses of variation within this genus may be able to tease apart.

Comparisons to previous research

These findings are broadly consistent with the scaling relationships documented previously by Smith et al. (1983), Bouvier (1986a,b), and Vinyard (1999), although with some important differences. Smith et al. (1983) found that the dimensions of the mandibular condyle scaled with slight positive allometry, whereas most of the data here indicate that the condylar dimensions scale with strong positive allometry when regressed against cranial size, but only scaled with positive allometry in hominoids and female cercopithecoids when regressed against body mass. Smith et al. did not split their sample into smaller taxonomic groups, and therefore the positive allometry in the hominoid and cercopithecoid samples likely swamped the isometric relationships identified in platyrrhines here.

Similarly, Bouvier (1986a,b) analyzed scaling of the condylar dimensions in platyrrhines and cercopithecoids separately and found that these dimensions scaled with isometry in both groups; the data here are consistent with Bouvier’s results for platyrrhines, but not for cercopithecoids, which tended to scale more with positive allometry in the current study. Although the number of cercopithecoid species analyzed was identical and 14 of the 22 species included were the same, the difference in these results is likely to have occurred for several methodological reasons. First, Bouvier (1986b) used ordinary least squares rather than reduced major axis regression. Next, Bouvier regressed condylar width, length, and area against body mass and found that these variables all scaled with isometry. This result was also found in this study; however, additional variables analyzed (articular tubercle, entoglenoid, and postglenoid height) were all found to scale with positive allometry against body mass. Finally, regression of variables against the cranial geometric mean in this study resulted in substantially more positively allometric relationships than did regression against body mass. Bouvier (1986a,b) recognized that body mass may not have been the most appropriate measure of size, but did not assess scaling relationships against overall cranial size, (instead she regressed her variables against mandibular length as a measure of biomechanical function).

Vinyard (1999)'s data are not directly comparable to this analysis because only strepsirrhines were included in his analyses. However, the patterns identified by Vinyard are largely consistent with the analysis conducted here, with most dimensions of the condyle and glenoid scaling with positive allometry, with the notable exception of condylar and glenoid length, which was also the case here (although to a lesser extent for condylar length than for glenoid length).

CONCLUSIONS

The data presented in this chapter indicate that many aspects of TMJ shape scale with positive allometry, particularly when regressed against cranial size. These findings are consistent with previous findings that suggest most aspects of the masticatory apparatus are positively allometric. Furthermore, these results support the conclusions arrived at in the preceding chapter; that is, aspects of the TMJ shape tend to vary in association with functional differences among anthropoid taxa.

Phylogenetically, these analyses suggest that the taxonomic groups examined do not vary in the same ways. The inconsistency in the pattern of scaling relationships among platyrrhines, cercopithecoids, and hominoids may indicate underlying adaptive strategies present in each of these groups that can influence phylogenetic patterns. In particular, this can be demonstrated well for the atelines, with the large bodied *Alouatta* displaying a unique behavioral trait that is likely to have a significant influence over TMJ function and shape (Fleagle, 1999; Halenar, 2008).

CHAPTER 6: TEMPOROMANDIBULAR JOINT VARIATION IN PHYLOGENETIC PERSPECTIVE

INTRODUCTION

There is a long history of use of the cranial base, and particularly features on the temporal bone, in taxonomic and phylogenetic analyses of extant and fossil primate species (e.g., Weidenreich, 1943; Tobias, 1967; Olson, 1981; Kimbel, 1986; Strait et al., 1997; Martinez and Arsuaga, 1997; Kimbel et al., 2004). Many authors have suggested that particular portions of the cranium may be more phylogenetically informative because they are less prone to variation caused by environmental variables (Olson, 1981; Strait et al., 1997; Lieberman et al., 2000; Harvati, 2001; Wood and Lieberman, 2001; Harvati and Weaver, 2006a,b). The basicranium in particular has been a focus of attention, because this region forms very early during fetal growth and primarily ossifies endochondrally (Scheuer and Black, 2000; White, 2000). This region also mirrors the shape of the developing brain, the morphology of which is relatively constrained (Houghton, 1996). Practically speaking, the cranial base is one of the most frequently preserved portions of the cranium in the hominin fossil record, and the complex morphology of this region lends itself well to analyses of both discrete and continuous characters (Weidenreich, 1943; Dean and Wood, 1981, 1982; Olson, 1981, 1985; Kimbel et al., 1984, 2004; Rightmire, 1984, 1990; Wood, 1984; Andrews, 1984; Kimbel, 1986; Lockwood et al., 2002; Villmoare, 2005; Terhune et al., 2007).

Recent analyses of the temporal bone and cranial base have centered on the use of the temporal region for distinguishing among species and subspecies of extant great apes and for quantifying expected levels of variation within fossil and extant taxa (Harvati, 2001, 2003; Lockwood et al., 2002, 2004, 2005; Terhune et al., 2007). Lockwood et al. (2002, 2004) demonstrated that three-dimensional (3D) coordinate data describing temporal bone morphology (including aspects of mandibular fossa shape) could be used to differentiate among species and subspecies of extant apes and modern humans, and a phenogram created using these data was nearly identical to published molecular phylogenies of these species. Similarly, several recent analyses have assessed the extent to which temporal bone morphology reflects genetic variation among modern human populations, with results suggesting that the temporal bone covaries significantly with molecular variation, particularly in contrast to other regions of the skull (Harvati and Weaver, 2006a,b; Smith et al., 2007; HF Smith, 2009; von Cramon-Taubadel, 2009). Finally, temporal bone morphology has also been used to test hypothesized taxonomic divisions among late Pleistocene hominins (Harvati, 2001, 2003) and *Homo erectus* (Terhune et al., 2007), and to evaluate morphological variation in extant and fossil papionins (Gilbert, 2008).

These analyses all rely on the use of the temporal bone (including aspects of the mandibular fossa) for the reconstruction of phylogenetic history, and therefore assume that morphological variation is a reliable indicator of genetic relatedness. The goal of this chapter, therefore, is to evaluate variation in the TMJ in a phylogenetic context, and particularly to assess the extent to which TMJ morphology covaries with molecular phylogenies of anthropoid taxa.

Phenetic vs. cladistic approaches to phylogenetic reconstruction

Considerable debate has taken place in the evolutionary biology community regarding the most appropriate methodology for classifying biological organisms and for inferring phylogenetic relatedness. The two prevailing schools of thought in this debate are phenetics and cladistics (e.g., Hennig, 1966; Bock, 1973; Sokal, 1986; Mayr, 1994; Sneath, 1995). Phenetics as an approach relies on the overall similarity of organisms for classification. Similar organisms are inferred to be more closely related to one another than more dissimilar organisms. This approach therefore assumes that morphological similarity is proportional to genetic relatedness (Bock, 1973). However, there is no assumption in phenetics that a particular character state is more or less evolutionarily derived than another, and therefore phenetics does not require knowledge of the evolutionary history of the feature(s) in question. Proponents of cladistics (aka phylogenetic systematics) reject the use of measures of similarity, and instead rely on the presence or absence of derived (e.g., apomorphic) features (Hennig, 1966). In other words, related taxa must share one or more derived features, and hierarchical classifications are then based on hierarchies of derived characters. This methodology therefore requires knowledge of the evolutionary history of the feature in question.

The analyses presented here are inherently phenetic in nature. This approach was taken for several reasons. The complex morphology of the TMJ is not particularly amenable to analyses that require the identification of discrete character states (as would be necessary with cladistics). Instead, the continuous variation in this region lends itself well to analyses such as geometric morphometrics, which are inherently phenetic in nature (Rohlf, 1990; Bookstein, 1991; Sneath, 1995). In other words, geometric morphometric analyses search for patterns of similarity in morphology and further analyses using the resulting geometric morphometric data (e.g., UPGMA) clustering were designed specifically to analyze matrices that describe “dissimilarity” among the operational taxonomic units in question (Rohlf and Sokal, 1981). The use of geometric morphometric data is therefore well suited to analyses such as those performed here, which seek to evaluate the covariance between a complex morphological region such as the TMJ and other datasets.

RESEARCH QUESTIONS

As outlined in the introduction, TMJ shape may or may not be covary with phylogenetic variation. Previous research suggests that the morphology of the temporal bone as a whole strongly reflects phylogenetic variation. Similarly, TMJ morphology may also reflect phylogenetic variation across anthropoid primates. Alternatively, TMJ morphology may not strongly reflect genetic variation, and may instead be more strongly tied to other factors. Many factors influence the ways in which taxa in a particular clade become phylogenetically distinct. For example, dietary differences among conspecific taxa may drive speciation such that differences in diet (and perhaps also masticatory configuration) map onto genetic or morphological phylogenies with a high degree of consistency. Thus, results indicating high levels of congruence between the genetic and morphological data are not unexpected. In other words, adaptive explanations for the observed variation in TMJ morphology cannot be excluded where TMJ morphology strongly reflects genetic relationships. Alternatively, instances of low congruence between these datasets may serve to highlight morphologies in more distantly related taxa that are convergent upon one another. Such examples will then necessitate further analysis to evaluate potential reasons for this convergence.

The objective of this analysis was to assess the extent to which TMJ morphology reflects known genetic relationships among primate taxa. Although many studies place an emphasis on the reliability of molecular data, and elevate results obtained from genetic analyses over analyses of morphology, this is not the intent of this chapter. Genetic analyses may indeed uncover the “true” phylogeny of a clade; however, genetic analyses are impractical, or more commonly, impossible for fossil species, and therefore morphological analyses must necessarily be relied upon. This chapter therefore sought to compare these two datasets in an attempt to evaluate their congruence.

The analyses presented here will therefore provide a discussion of the congruence of the morphological and molecular data for each clade examined, and will also evaluate the extent to which phylogenies created using TMJ morphology covary with other potential influences over TMJ shape, such as dietary or body size variation. These potential alternative influences over TMJ shape will likely vary among the clades being examined as part of this study. Notably, these factors are not mutually exclusive and can therefore work in conjunction with one another to produce a unique pattern of morphology. In particular, it is likely that diet and body size differences are not independent of one another, as body size is known to vary as a function of diet (Kay, 1975; Hylander, 1985; Sailer et al., 1985; Ravosa, 1996, 2000). Alternatively, a lack of correlation between the molecular data and any of these factors could suggest that stochastic processes were primarily responsible for the evolutionary relationships observed among extant taxa, or simply that the main influence(s) over the observed variation are not addressed by this study.

MATERIALS AND METHODS

Data used in this study included three-dimensional (3D) coordinate data describing glenoid fossa and mandibular condyle morphology (refer to Chapter 3 for landmark definitions). These data included twelve landmarks on the glenoid fossa and five landmarks on the mandibular condyle. These two regions were analyzed separately in all analyses to minimize potential error associated with attempting to place these two configurations in the same reference system. For all analyses, Generalized Procrustes Analysis (GPA) was used to superimpose landmark configurations, and subsequent analyses were performed on the rotated coordinate data.

Shape variation within the sample as a whole was examined first, so that the extent to which clades were distinguishable in morphospace could be assessed. Differences among taxa were summarized and described using principal components analysis (PCA), and shape variation along the principal component (PC) axes was visualized using wireframe diagrams representing glenoid and condylar morphology (refer to Fig. 3-2). Procrustes distances among species in morphospace were then calculated and a matrix of distances created. All geometric morphometric analyses, including the calculation of Procrustes distances, were performed in the program *Morphologika* (O'Higgins and Jones, 1998). Using the top fifteen PC axes (which together represented approximately 95% of the sample variation) a Discriminant Function Analysis (DFA) with jackknife cross-validation was then conducted to examine the extent to which specific clades were able to be differentiated on the basis of TMJ morphology. Prior probabilities for classification were set equal to group sizes. DFAs were conducted using SPSS (version 11.0.1).

Two types of analyses were performed using the Procrustes distance matrices. First, UPGMA cluster diagrams were created to illustrate phenetic similarities among species at various taxonomic levels using the program Neighbor, which is part of the PHYLIP package (version 3.68, Felsenstein, 2008). These trees were then compared visually to a consensus molecular phylogeny compiled from Purvis (1995), with supplemental data from Disotell (1996), Morales and Melnick (1998), Canavez et al. (1999), Page et al. (1999), Tosi et al. (2000, 2005), Page and Goodman (2001), Cortes-Ortiz et al. (2003), Newman et al. (2004), Takacs et al. (2005), Xing et al. (2005), Opazo et al. (2006), Whittaker et al. (2007), and Ting et al. (2008) (refer to Fig. 5-1). Because similarities among trees containing more than approximately nine taxa were difficult to ascertain visually, the program TreeDist (also from PHYLIP) was used to compare complex tree topologies. This program compares two input trees and calculates the Symmetric Difference of Robinson and Foulds (1981) between the two trees of interest. This statistic is simply a count of the number of partitions among the two trees that are present on one tree but not the other. For example, given two trees, {A, C | B, D, E} and {A, D | B, C, E}, which each contain the same species but which are partitioned differently, the symmetric difference between the two trees is two (Felsenstein, 2006). The maximum number of differences among two trees was calculated using the formula $2n$-3, where n equals the number of species examined (Pattengale et al., 2007; Bryant and Steel, 2009).

To assess the influence of size variation, all Procrustes distance matrices were compared to size matrices that calculated the absolute difference in centroid size among groups using a Mantel test (Mantel, 1976; Smouse et al., 1986) in the free Excel add-on PopTools. The influence of dietary variation was examined by assessing the extent to which taxa with diets composed of similar food material properties or mechanical demands (as outlined in Chapter 3) clustered together. In addition, published dietary data reporting the percentage of particular food items included in the diets of approximately 38 of the 48 species were compiled and a Euclidean distance matrix was created using PopTools. This was done by summing the percentage the food items that were relatively less resistant (e.g., fruit, flower, animal prey) versus more resistant food items (e.g., leaves, bark, roots) for each taxon for which these data were available (Table 6-1). Mantel tests were then used to examine the correlation between TMJ shape and dietary variation. Where shape was significantly correlated with both size and diet, partial Mantel tests were used to examine the correlation between shape and size while controlling for diet, and the correlation between shape and diet while controlling for size. Partial Mantel tests were performed in the free program zt.exe (Bonnet and Van de Peer, 2002).

For the principal component and Procrustes distance analyses, the data points included were species means, separated by sex. For the DFA, individual specimens were analyzed. All analyses were also performed at multiple taxonomic levels; data were first analyzed for the entire sample, then at the level of superfamily (ceboids [e.g., platyrrhines], cercopithecoids, and hominoids), and finally at the subfamily level, although the cercopithecoids were separated into a papionin and macaque sample (classification follows Fleagle, 1999).

Predictions

Prior to analysis, predictions regarding which potential factors may covary with morphological variation were formulated for each group based on existing descriptions of morphological, dietary, and behavioral variation among the taxa included in this study. These factors may covary with morphology regardless of whether the morphological and genetic data are congruent with one another. All body mass data reported below were compiled from Fleagle (1999) and Smith and Jungers (1997).

TABLE 6-1. Dietary data compiled from previously published analyses, indicating the percentage of soft vs. resistant food items consumed by each species. Data for some species do not add up to 100% because some authors chose to only report selected values, and because of rounding errors.

Species	%Soft	%Resistant	References
Alouatta belzebul	39	61	DeSouza et al., 2002
Alouatta palliata	51.7	48.2	Milton, 1980
Alouatta seniculus	38.1	57	Julliot and Sabatier, 1993
Ateles geoffroyi	83.2	17.2	Russo et al., 2005
Lagothrix lagotricha	84.1	16.2	Peres, 1994
Cebus apella	96.25	3.75	Terborgh, 1983
Cebus albifrons	99.5	0.25	Terborgh, 1983
Saimiri sciureus	102	0	Terborgh, 1983
Chiropotes satanas	97.3	0.2	Kinzey and Norconk, 1993
Pithecia pithecia	92.9	7.1	Kinzey and Norconk, 1993
Cacajao calvus	96	0	Ayres, 1986, 1989
Erythrocebus patas	93.82	0.82	Nakagawa, 2003
Cercopithecus mitis	72	24.5	Cords, 1986; Fairgrieve, 1995
Cercopithecus nictitans	77.6	22.4	Tutin et al., 1997
Papio ursinus	52	47	Kamilar, 2006
Theropithecus gelada	7.45	95.73	Dunbar, 1977
Cercocebus torquatus	78.75	20	Mitani, 1989
Lophocebus albigena	78.5	18.7	Lambert et al., 2004
Mandrillus sphinx	84.9	15	Tutin et al., 1997
Macaca fascicularis	82.9	17.2	Yeager, 1996
Macaca sylvanus	45.5	45	Menard and Vallet, 1996
Macaca fuscata	63.9	36.3	Hill, 1997
Semnopithecus entellus	45	48	Hladik, 1977
Nasalis larvatus	53	47	Bennett and Sebastian, 1988
Presbytis obscurus	35	56	Curtin, 1980
Procolobus badius	25	48	Marsh, 1981
Colobus polykomos	37.2	56.1	Dasilva, 1994
Procolobus verus	25	69	Oates, 1988
Hylobates agilis	62	39	Gittins, 1979
Hylobates klossii	97	2	Whitten, 1984
Hylobates lar	70	29	Raemakers, 1984
Symphalangus syndactylus	57	43	Raemakers, 1984
Pan troglodytes troglodytes	85.1	14.8	Tutin et al., 1997
Pan troglodytes verus	77	10	McGrew et al., 1988
Pongo abelii	80	19	Fox et al., 2004
Pongo pygmaeus	65	26	Galdikas, 1988
Gorilla beringei	1.38	96.96	Watts, 1984
Gorilla gorilla	71.1	29.1	Tutin et al., 1997

Entire sample. For the entire sample, the scaling data presented in Chapter 5 suggest that there is a large allometric component to the observed shape variation, and therefore morphological variation is predicted to covary with body size, which itself may be associated with dietary differences (Kay, 1975; Hylander, 1985; Sailer et al., 1985; Ravosa, 1996, 2000).

Platyrrhines. Allometry may significantly influence variation in the platyrrhine sample, as indicated in Chapter 5. In addition, there is considerable dietary variation in this group (e.g., Rosenberger, 1992; Anapol and Lee, 1994), and this variation may not necessarily map onto molecular relationships. However, a rapid dietary radiation of the platyrrhines has been suggested to have been a primary factor in the early evolution of this clade (Rosenberger, 1980, 1992), and therefore it could be expected that the morphological data covary with diet in this group

Atelines. Because of the unique vocal specializations and marked dietary differences of *Alouatta* in comparison to other atelines (e.g., Hershkovitz, 1949; Hill, 1962; Hladik and Hladik, 1969; Gaulin and Gaulin 1982; Chapman, 1987, 1989; Julliot, 1996; Di Fiore, 2004; Russo et al., 2005), it is expected that species in this genus should consistently cluster together to the exclusion of the other taxa in this group, *At. geoffroyi* and *L. lagothrica*. A high degree of congruence between the, morphological, dietary, and behavioral data is therefore expected in this clade.

Cebines. Morphological variation in the cebines could covary with either diet or size. If similarities in diet are driving phenetic similarities among taxa, then *Cebus apella* and *C. albifrons* should cluster together as a result of their relatively more similar diets (Izawa, 1979; Izawa and Mizuno, 1977; Terborgh, 1983, 1986; Janson and Boinski, 1992). However, if size is a significant source of variation in this group, *C. apella* and *C. capucinus* should cluster together because of their similar body sizes (3,085 g and 3,110 g, respectively, versus 2,735 g for *C. albifrons*).

Pitheciines. Pitheciine taxa are differentiated primarily on the basis of diet, and therefore it is predicted that dietary variation in this group will covary with TMJ morphology. Furthermore, *Ch. satanas* and *C. melanocephalus* are more similar in diet and body size than either is to *P. pithecia* (Ayres, 1989; Kinzey, 1992; Kinzey and Norconk, 1993; Boubli, 1999), and therefore body size may also covary with TMJ shape.

Cercopithecoids. Data presented in Chapter 5, which suggest that TMJ shape tends not to vary significantly as a function of size in cercopithecoids, indicate that, of the three super-family analyses, allometric variation may be less important in this clade (at least in the geometric morphometric analyses). However, members of this clade vary considerably in diet, and broad dietary divisions should reflect phylogenetic variation (e.g., the split between cercopithecines and colobines; Fleagle, 1999). Therefore it is possible that dietary variation in this clade covaries with morphology.

Macaques. Morphological variation in the sample of macaques may be associated with diet or body size variation. If dietary differences are an important source of variation, then macaque species that tend to have more similar diets may be expected to be more similar morphologically. If this is the case, it might also be predicted that the congruence between the morphological and genetic data be low, since those taxa with more similar diets tend to be very distantly related. For example, *M. fuscata* and *M. fascicularis* are closely related (Purvis, 1995). However, *M. fuscata* and *M. sylvanus* both exploit relatively harder food objects than *M. fascicularis* (Menard and Vallet, 1996; Yeager, 1996; Hill, 1997), and therefore if dietary differences are driving the morphological differences in TMJ shape in this genus, these two taxa should be more similar in shape than either is to *M. fascicularis*. However, *M. fuscata* and *M. sylvanus* have quite disparate body sizes (*M. fuscata* = 9,515 g and *M. sylvanus*= 13,500 g [Fleagle, 1999]), and therefore if allometry covaries with morphology, then these two taxa may be relatively morphologically distinct.

Papionins. Molecular analyses have recently played an important role in resolving the phylogenetic relationships among taxa in this group, which was previously obscured by drastic size and dietary differences among papionin species (Disotell 1994, 1996). As a result, it is unlikely that the morphological phylogeny will be congruent with the genetic data. Instead, if size differences among taxa are driving phenetic similarities, *Lophocebus albigena* and *Cercocebus torquatus* (7,135 g and 8,615 g, respectively) should cluster together to the exclusion of the other papionin taxa (15,350 to 22,250 g). If dietary differences are a significant source of variation in this group, then *Mandrillus sphinx*, *C. torquatus*, and *L. albigena* should cluster together as a result of their reliance on relatively hard food objects (Hoshino, 1985; Norris, 1988; Mitani, 1989; Olupot et al., 1997; Olupot 1998; Poulsen et al., 2001; Lambert et al., 2004), to the exclusion of all other taxa. Gape may also be a consideration in this group; if this is the case, taxa with relatively large gapes (potentially gauged by mandible length) such as *Papio* and *Mandrillus* should be more similar morphologically than those taxa with relatively shorter mandibles (e.g., *Theropithecus* and the mangabeys).

Colobines. If the morphological data approximate the molecular relationships among the colobine taxa, then there should be a division between the Asian and African colobines. If body size is driving morphological variation within the sample, *Colobus polykomos*, *Semnopithecus entellus*, and *Presbytis obscurus* are all likely to cluster together because of their similar body sizes (9,100, 11,445, and 7,080 grams, respectively), while *Nasalis larvatus* (15,110 g) and *Procolobus verus* (4,450 g) should be distinct. Since fewer dietary data are available to compare the mechanical properties of food items consumed by colobines, it is difficult to formulate predictions based on dietary variation. However, at least in the African sample, *P. badius* and *C. polykomos* are more similar because of their heavy reliance on seeds and leaves, while *P. verus* relies more heavily on mature leaves, rather than seeds, and therefore *P. badius* and *C. polykomos* would be expected to cluster together to the exclusion of *P. verus* (e.g., Oates, 1994; Wachter et al., 1997; Davies et al., 1999; Daegling and McGraw, 2001; Korstjens et al., 2007; McGraw and Zuberbuhler, 2007).

Hominoids. There is a great deal of size variation in the hominoids (5,620 to 130,000 g), and much of the observed variation in TMJ shape can be linked to allometry (as indicated in Chapter 5). It is therefore expected that the morphology of the TMJ in this group will covary strongly with size, and size as a function of dietary differences among taxa. The division between the hylobatids and the hominids should be relatively easily reflected in morphology given the size differences between these two groups.

Hylobatids. Dietary and size differences are likely a significant source of variation between *Hylobates* and *Symphalangus.* However, variation within *Hylobates* could be a function of diet, with the more distantly genetically related *H. lar* and *H. klossii* expected to cluster together based on the relatively lower percentage of leaves in their diet in comparison to *H. agilis* (Chivers, 1974; MacKinnon and MacKinnon, 1978; Gittins, 1979; Raemakers 1984; Whitten, 1984; Palombit, 1997). Body size estimates for these three taxa are virtually indistinguishable, however, suggesting that body size in *Hylobates* is unlikely to strongly covary with TMJ morphology.

Hominids. Temporal bone variation in the hominid taxa examined here was previously evaluated by Lockwood et al. (2002, 2004) and was found to reliably reflect molecular relationships. Therefore, if the TMJ represents a significant component of this phylogenetic signal, then there should be a high degree of congruence between TMJ morphology and the molecular data as well. Taxa within this clade differ significantly in diet, but it has been suggested that this ecological differentiation drove the phylogenetic differentiation of these taxa (e.g., Fleagle, 1999; Pilbeam, 2002; Taylor, 2002), particularly in the case of *Pan* and *Gorilla* and for the species within each of the three genera examined. As a result, dietary differences among species should map onto the molecular phylogeny well. However, *Pongo* and *Gorilla* both consume relatively more resistant food objects than *Pan* (Watts, 1984; Galdikas, 1988; Williamson et al., 1990; Tutin and Fernandez, 1993; Nishihara, 1995; Wich et al., 2006), and both have relatively larger body sizes than *Pan*; therefore body size and dietary differences may covary with morphological variation, regardless of the congruence between the morphological and genetic data. .

RESULTS

Principal component analysis

All taxa. In the PC analysis performed for the glenoid landmarks and including all taxa (Fig. 6-1), the first PC axis summarizes approximately 42% of the sample variance and separates hominids from cercopithecoids, platyrrhines, and the hylobatids. This PC axis is correlated with size in both females ($r^2=0.422$, $p<0.001$) and males ($r^2=0.352$, $p<0.001$), although given these relatively low coefficients of variation, most of this variation is likely to be unrelated to size. Shape variation along this PC is primarily associated with the relative mediolateral (ML) and anteroposterior (AP) dimensions of the glenoid, as well as the overall topographic relief of the glenoid region. Hominids, which load positively along PC 1, have very ML wide and AP short joints, with a great deal of topographic relief provided by an enlarged entoglenoid process and

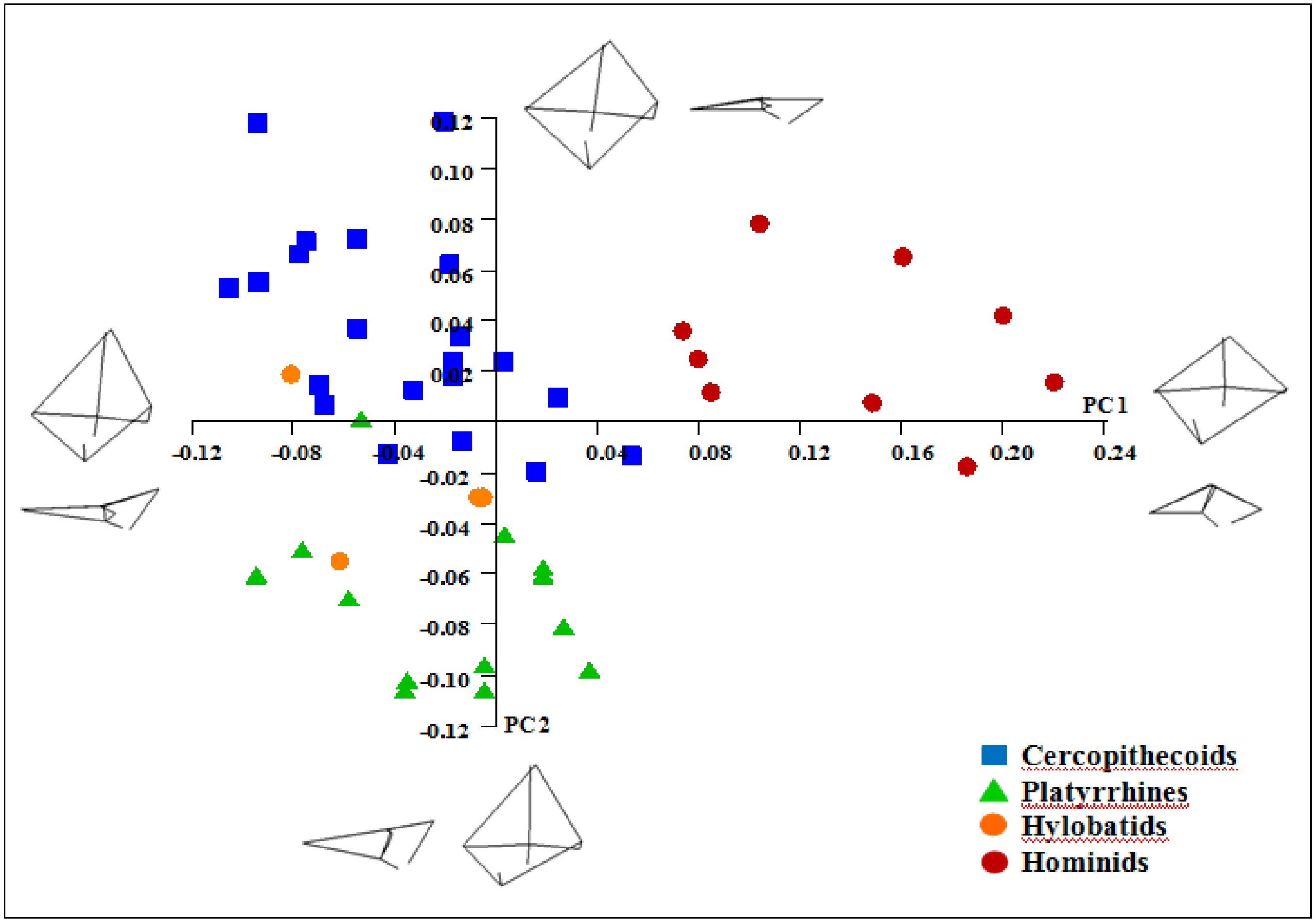


Fig. 6-1. Bivariate plot of PC 1 (x-axis) and PC 2 (y-axis) from the PC analysis of the glenoid landmarks with wireframe diagrams illustrating shape variation in the sample. All taxa included (females only).

articular tubercle, as well as a raised articular eminence. Conversely, all other taxa have relatively AP longer joints that have considerably less topographic relief.

The second PC axis represents approximately 22% of the variation in the sample, and separates cercopithecoids and platyrrhines (and to some extent platyrrhines vs. catarrhines as a whole). Shape variation along this PC axis mostly concerns the topography of the joint and the size of the postglenoid process. Taxa loading negatively (i.e., platyrrhines), have relatively large articular tubercles, entoglenoid processes, and postglenoid processes. To some extent, the apparent enlargement of the articular tubercle and entoglenoid process is associated with the ML concave nature of the glenoid fossa in this clade. Cercopithecoids, which load positively along this axis, have very flat glenoids with little topography in comparison.

Principal component axis three (Fig. 6-2) explained 7% of the sample variance, and separates out the hylobatids, although *S. syndactylus* does not group with *Hylobates* on this axis. *Hylobates* loads at the positive end of this PC, while *S. syndactylus* is solidly in the middle of the cercopithecoid and platyrrhine scatter. Shape variation along this axis is associated with ML and AP variation in the joint, but primarily has to do with the size of the postglenoid process. In particular, *Hylobates* is distinguished by its AP long glenoid and small postglenoid process.

Platyrrhines. In the platyrrhine analysis (Fig. 6-3), PC 1 (which explains 43% of the sample variance) separates the three *Alouatta* species from the rest of the taxa. This PC is significantly correlated with size in females (r^2= 0.497, p=0.007) and males (r^2= 0.680, p=0.007), and shape variation along this axis is primarily associated with size of the postglenoid process, and to a lesser degree, the relative AP and ML dimensions of the joint. Axis two separates the remaining atelines (*Lagothrix* and *Ateles*) and pitheciines from the cebines (including *Aotus* and *Saimiri*). This axis is not correlated with size, and shape variation along this PC is associated with the angle of the entoglenoid process and to a lesser extent, ML width of the glenoid fossa.

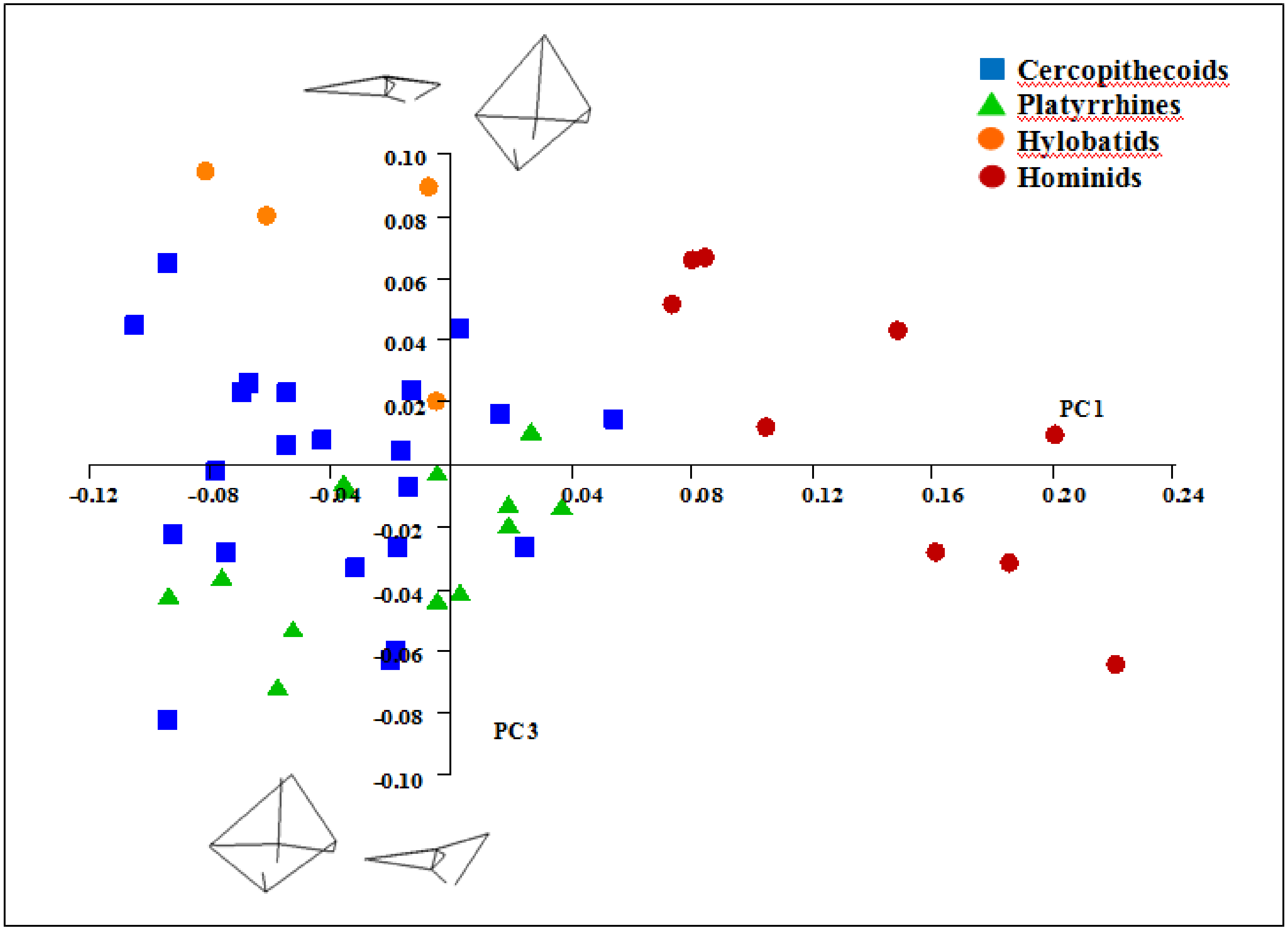


Fig. 6-2. Bivariate plot of PC 1 (x-axis) and PC 3 (y-axis) from the PC analysis of the glenoid landmarks with wireframe diagrams illustrating shape variation in the sample. All taxa included (females only).

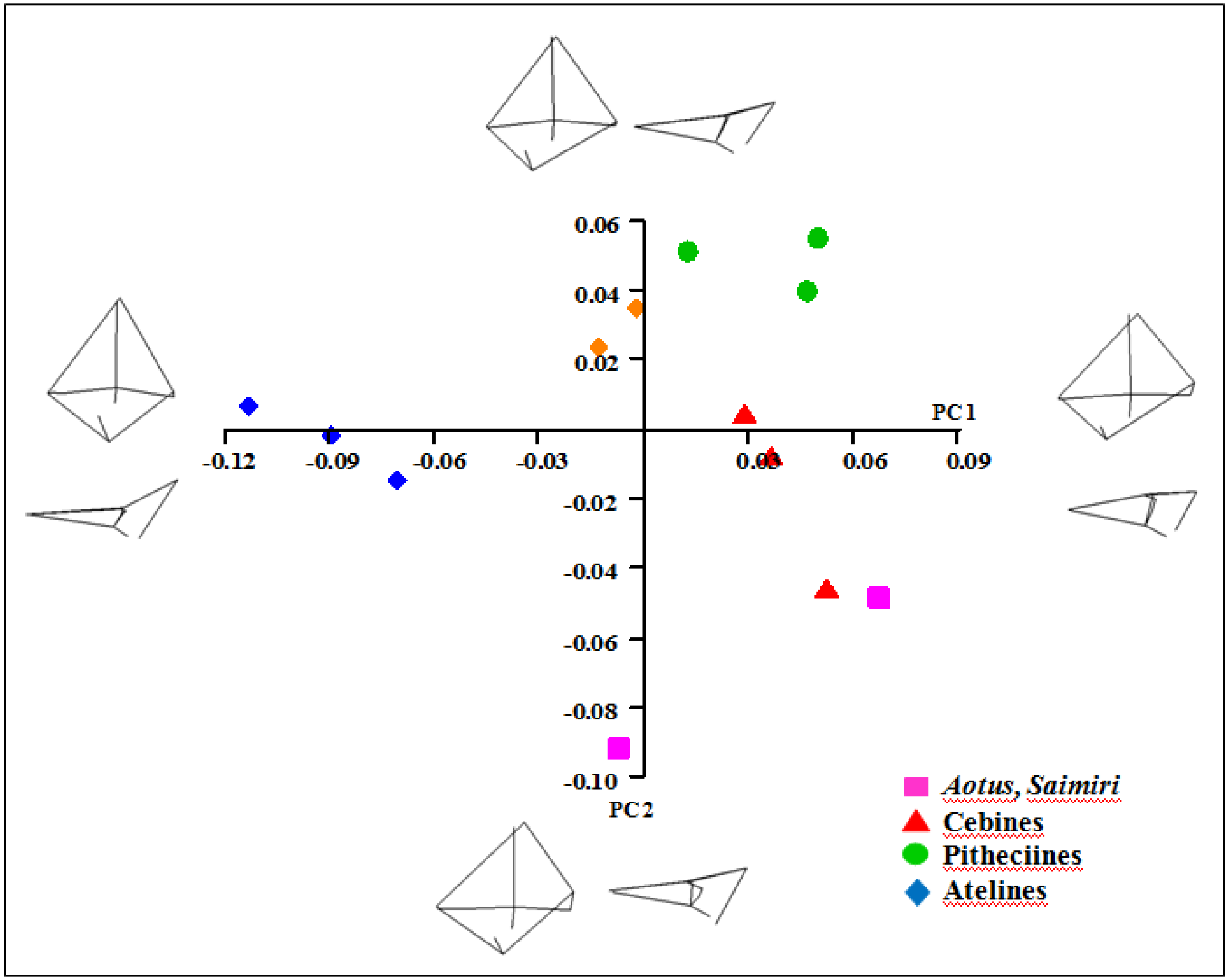


Fig. 6-3. Bivariate plot of PC 1 (x-axis) and PC 2 (y-axis) from the PC analysis of the glenoid landmarks with wireframe diagrams illustrating shape variation in the sample. Platyrrhine females only included.

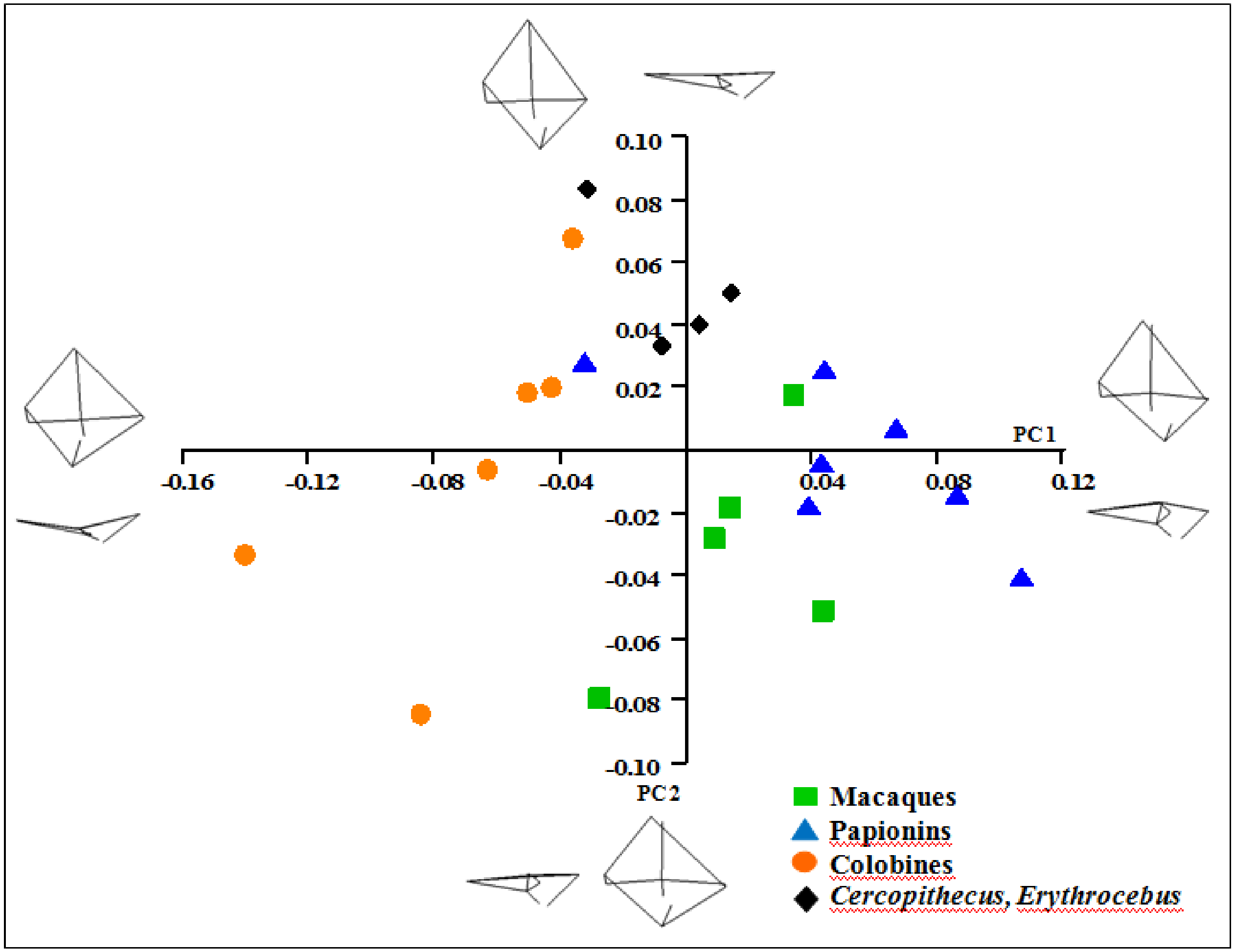


Fig. 6-4. Bivariate plot of PC 1 (x-axis) and PC 2 (y-axis) from the PC analysis of the glenoid landmarks with wireframe diagrams illustrating shape variation in the sample. Cercopithecoid females only included.

Cercopithecoids. In the cercopithecoids (Fig. 6-4), PC 1 (40% of the sample variance) separates the colobines and cercopithecines. Variation in glenoid shape along this axis is associated with size and ML placement of the postglenoid process, ML dimensions of the glenoid, height of the articular eminence, and potentially also angling of the glenoid in the sagittal plane. Principal component two doesn't separate taxa in any meaningful way, but does represent variation in AP length of the glenoid, inclination of the articular eminence, and a small amount of variation in postglenoid process size. Similarly, PC 3 (13% of the sample variance) does not meaningfully separate any specific taxonomic groups within the cercopithecoid sample, but it is significantly correlated with size in females (r^2=0.314, p=0.007) and males (r^2=0.548, $p<0.001$). Shape variation along this axis is primarily related to angulation of the glenoid in the sagittal plane, and also the size of the various processes within the joint.

Hominoids. In the hominoid taxa (Fig. 6-5), PC 1 (72% of sample variance) is strongly correlated with size in both sexes (females: r^2 = 0.804, $p<0.001$; males: r^2=0.803, $p<0.001$), and separates the small-bodied hylobatids and the large-bodied hominids. Shape variation along this axis is related to the relative ML and AP dimensions of the joint, and with increased topographic relief of the joint in hominids. The second PC axis (9.6% of variance) separates *H. klossii* from the other hylobatids, and also *Pan*, *Pongo*, and *H. sapiens* from *Gorilla*. This axis is not significantly correlated with size, and shape variation along this axis is mostly related to the relative height of the various processes in the joint.

Condylar data. Shape variation in condylar morphology was also examined using PCA (Fig. 6-6). However, unlike the glenoid configurations, there was no clear separation among taxa in condylar morphology. Shape variation along PC 1 was associated with the AP length of the condyle and the convexity of the articular surface. Variation in shape along PC 2 was driven by

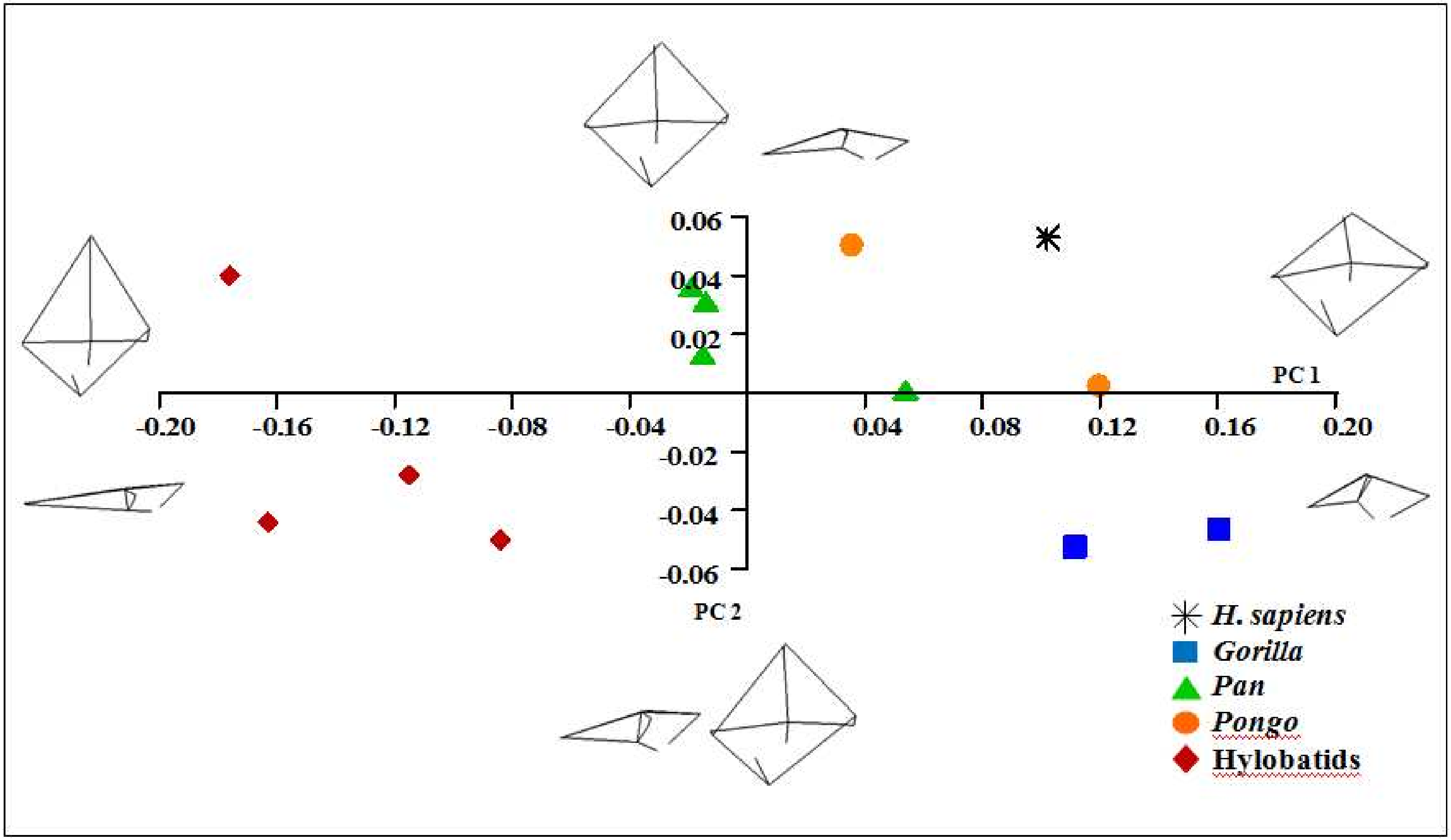


Fig. 6-5. Bivariate plot of PC 1 (x-axis) and PC 2 (y-axis) from the PC analysis of the glenoid landmarks with wireframe diagrams illustrating shape variation in the sample. Hominoid females only included.

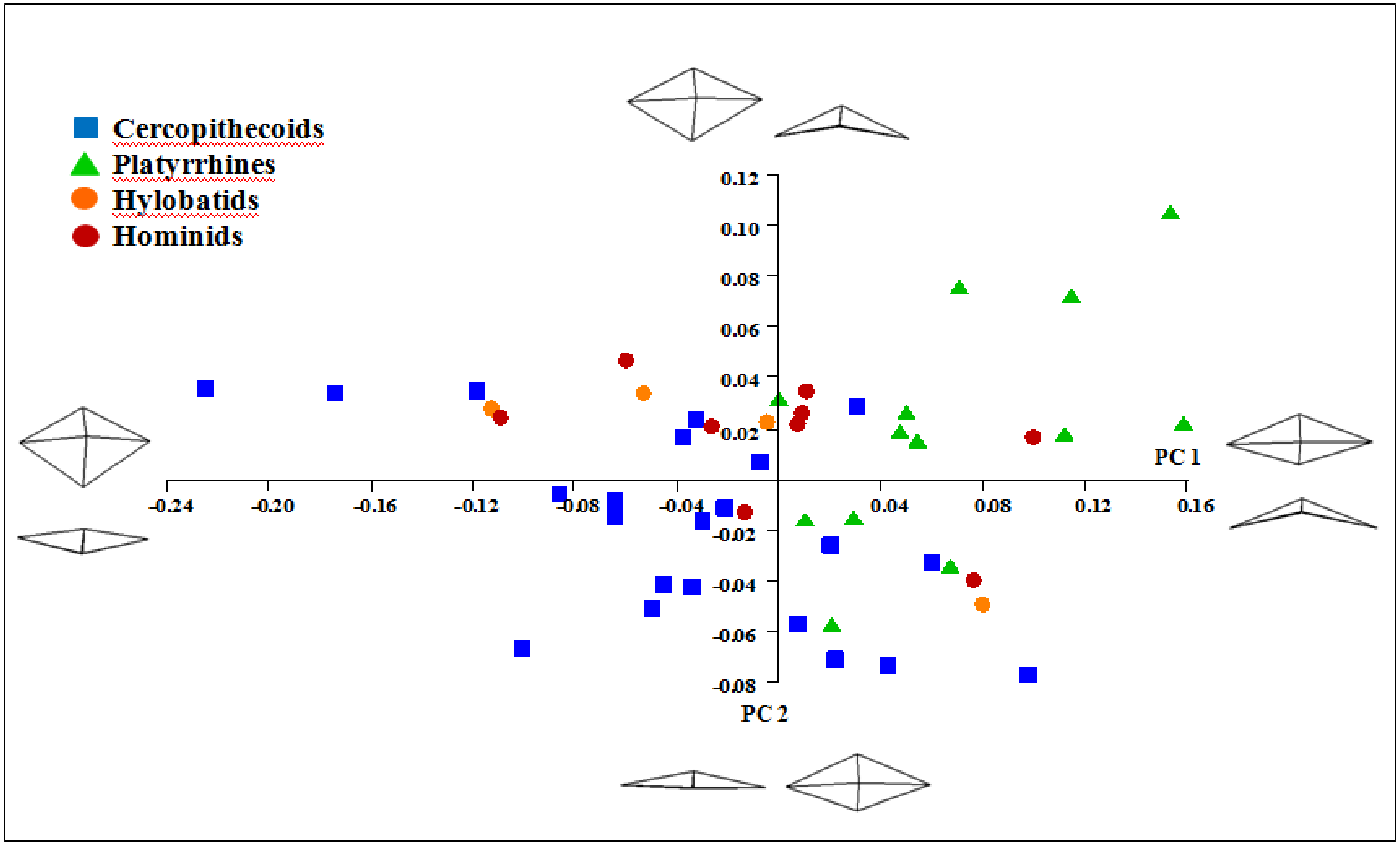


Fig. 6-6. Bivariate plot of PC 1 (x-axis) and PC 2 (y-axis) from the PC analysis of the condyle landmarks with wireframe diagrams illustrating shape variation in the sample. All taxa included (females only).

these same variables, although to a lesser degree. There was very little correlation between centroid size and any of the PC axes, suggesting that size does not drive variation within condylar morphology. As a result of this analysis, no Procrustes distance analyses were performed on the condylar landmarks, since these data suggest little to no phylogenetic patterning in condylar morphology across the entire sample.

Discriminant function analysis

The results of the discriminant function analysis with cross-validation indicate that specimens can frequently be correctly allocated to super- and sub-family groupings at relatively high frequencies on the basis of glenoid morphology (Tables 6-2 and 6-3). When specimens were categorized by superfamily (e.g., platyrrhine vs. cercopithecoid, vs. hominoid) correct classification rates were approximately 87.5%, with a range between 81.2 and 90.9% correct. In this analysis, platyrrhines were most frequently correctly identified to clade, while hominoids were the least frequently correctly allocated. These classification rates dropped slightly when specimens were identified to subfamily, with an average correct classification rate of 78.3%, with a range of 66.7 to 94.8%. Hylobatids and cebines were correctly identified the least number of times, and were either misidentified as cercopithecines (in the case of the hylobatids) or as atelines, pitheciines or cercopithecines (in the case of the cebines). Hominids had a very high frequency of correct classification (94.8% correct).

Procrustes distance analyses

All taxa. UPGMA cluster analyses that included all species (Fig. 6-7 and 6-8) in the sample indicate that many taxa that are distantly genetically related cluster together on the basis of morphological similarities in the glenoid. Visual inspection of the cluster diagrams for females (Fig. 6-7) indicate that the platyrrhines primarily cluster together, but some taxa (notably *C.*

TABLE 6-2. Classification results of the discriminant function analysis using jackknife cross-validation at the superfamily level. A priori probabilities of a specimen randomly being placed in the correct group were based on group sample size. Each horizontal row summarizes the number of correct classifications for each group, as well as misclassifications.

	% Correct	Platyrrhine	Cercopithecoid	Hominoid
Platyrrhine	90.9	251	19	6
Cercopithecoid	89.4	21	356	21
Hominoid	81.2	20	31	220

TABLE 6-3. Classification results of the discriminant function analysis using jackknife cross-validation at the subfamily level. A priori probabilities of a specimen randomly being placed in the correct group were based on group sample size. Each horizontal row summarizes the number of correct classifications for each group, as well as misclassifications.

	% Correct	Ateline	Cebine	Pitheciine	Aotine	Cercopithecine	Colobine	Hylobatid	Hominid
Ateline	69.7	76	4	20	2	6	0	1	0
Cebine	66.7	8	54	8	0	7	0	4	0
Pitheciine	69.2	7	8	45	0	1	0	4	0
Aotine	85.7	0	2	1	18	0	0	0	0
Cercopithecine	83.3	5	7	1	0	220	23	5	3
Colobine	68.7	2	0	0	0	39	92	1	0
Hylobatid	66.7	4	0	6	0	14	0	52	2
Hominid	94.8	0	0	0	0	3	2	5	183

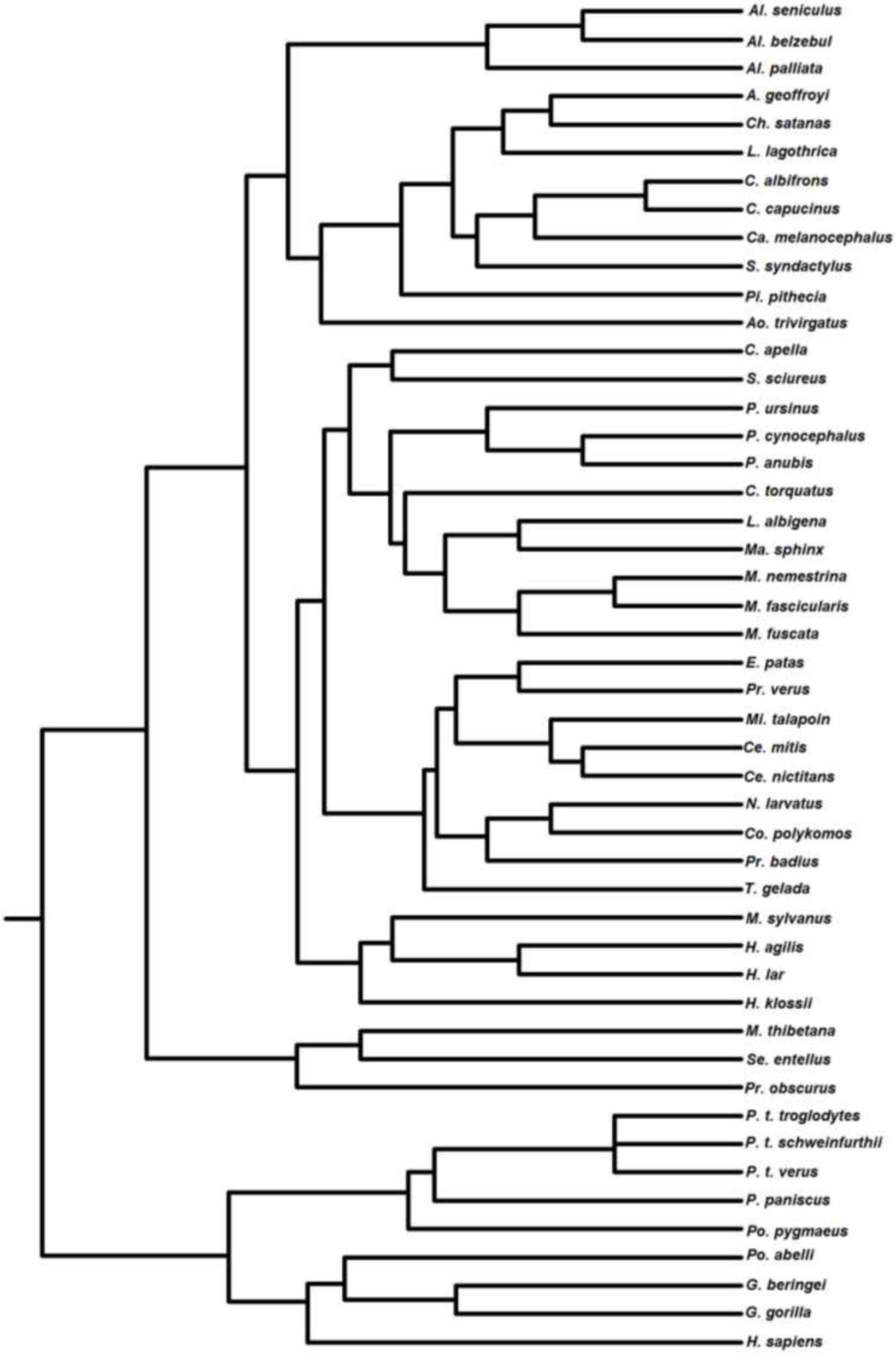


Fig. 6-7. UPGMA cluster diagram showing phenetic similarities among all taxa (females only).

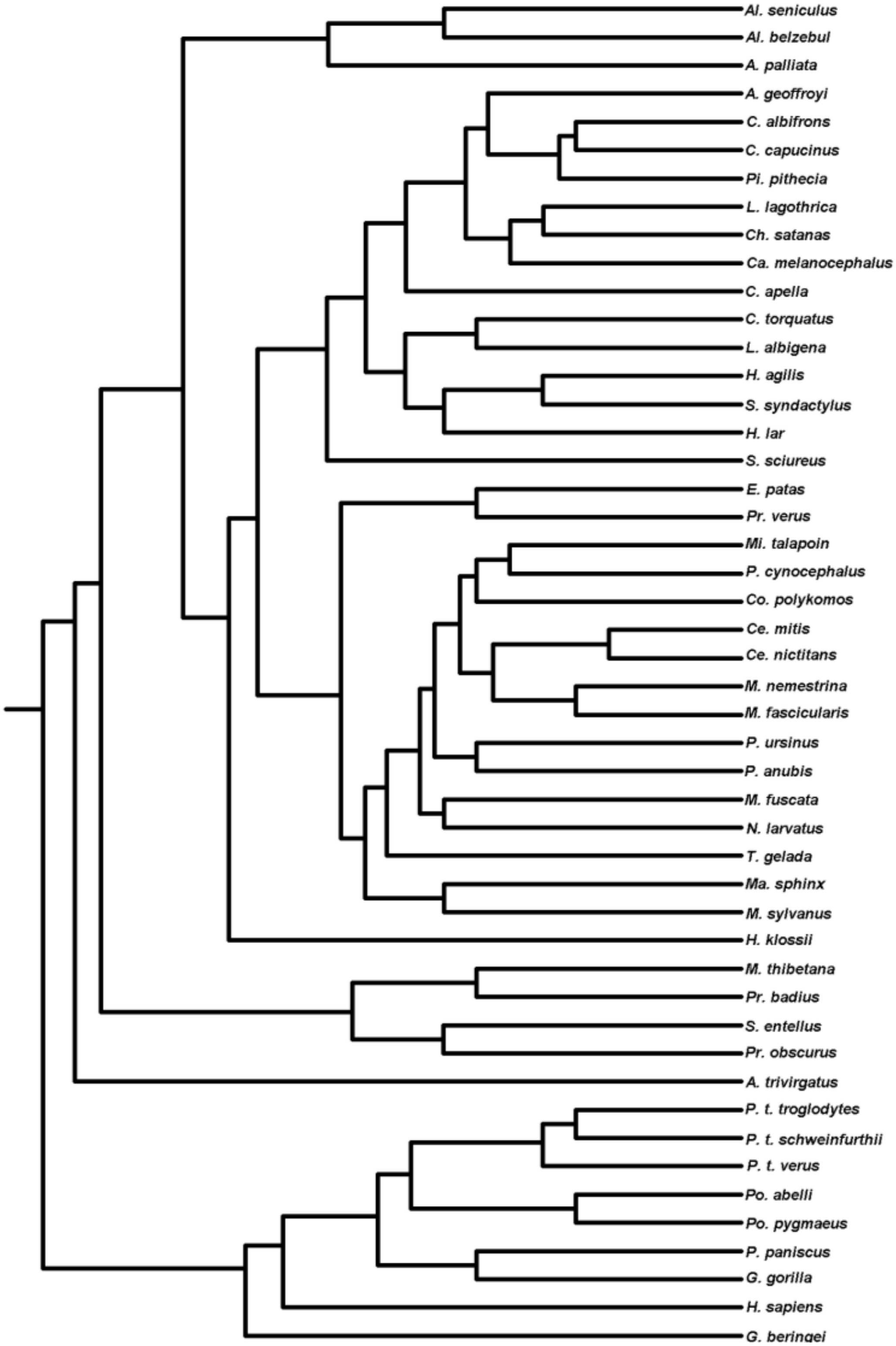


Fig. 6-8. UPGMA cluster diagram showing phenetic similarities among all taxa (males only).

apella and *S. sciureus*) group with the cercopithecines. Interestingly, the hylobatids have a tendency to cluster with the cercopithecoids (in the female analysis) and with platyrrhines (in the male analysis). In both sexes, *S. syndactylus* groups with the platyrrhines. This could be due to the overall low topography of the hylobatid glenoid, which is more similar to cercopithecoids and platyrrhines than to hominids. *Macaca thibetana* clusters with several colobine species (potentially suggesting some influence of diet since this species of *Macaca* is highly folivorous). The hominid taxa consistently cluster together to the exclusion of all other taxa.

Comparison of the morphological and molecular trees for both sexes similarly indicates a substantial number of differences between the datasets. In the female sample, there were 66 symmetric differences between the morphological and molecular trees, while in the male sample there were 74 differences (out of a possible 93 differences). These data indicate substantial incongruence of the morphological and molecular data when all taxa are analyzed together.

The Mantel tests indicate a strong correlation between the shape and size matrices (Table 6-4) for the female analysis ($r = 0.576$, $p < 0.001$) and slightly less so for males ($r = 0.459$, $p < 0.001$), suggesting a significant size component to the observed variation in glenoid morphology for both sexes. In addition, the shape and diet matrices were also significantly correlated in both sexes (females: $r = 0.235$, $p = 0.004$; males: $r = 0.263$, $p = 0.001$), although these correlations were relatively low. Results of the partial mantel test further indicate that size is the major factor influencing shape variation across the entire sample (Table 6-5), while diet is marginally significant when size is held constant.

Platyrrhines. In all analyses (by sex, and for the family-level analyses, e.g., atelines only; Fig. 6-9), the three species of *Alouatta* cluster together, and their pattern of clustering, with *Al. seniculus* and *Al. belzebul* more similar to one another than to *Al. palliata*, is consistent with the molecular data regarding the phylogenetic relationships among these taxa. All other taxa cluster to the

TABLE 6-4. Results of the mantel tests between the Procrustes distance (shape) matrices and the centroid size matrices (top) and the dietary matrices (bottom). Mantel tests were only performed for clades with more than three species. Significant correlations are shown in bold.

		Female		**Male**	
vs. size	**n**	**r**	**p-value**	**r**	**p-value**
All Taxa	48	**0.576**	**<0.001**	**0.459**	**<0.001**
Platyrrhines	13	**0.718**	**<0.001**	**0.760**	**<0.001**
Cercopithecoids	22	0.047	0.327	-0.058	0.667
Hominoids	13	**0.764**	**<0.001**	**0.706**	**<0.001**
Atelines	5	**0.924**	**0.014**	**0.628**	**0.005**
Cebines	3	n/a			
Pitheciines	3	n/a			
Macaques	5	-0.333	0.755	0.123	0.267
Papionins	7	0.351	0.105	**0.615**	**0.012**
Colobines	6	-0.004	0.489	0.116	0.279
Hylobatids	4	n/a			
Hominids	9	**0.543**	**0.003**	**0.519**	**0.008**
vs. diet					
All Taxa	38	**0.235**	**0.004**	**0.263**	**0.001**
Platyrrhines	11	**0.599**	**<0.001**	**0.736**	**<0.001**
Cercopithecoids	17	0.159	0.100	0.202	0.074
Hominoids	10	0.278	0.067	0.287	0.093
Atelines	5	**>0.999**	**0.008**	**0.665**	**0.017**
Cebines	2	n/a			
Pitheciines	3	n/a			
Macaques	3	n/a			
Papionins	5	0.300	0.217	-0.058	0.492
Colobines	6	-0.119	0.378	0.021	0.433
Hylobatids	4	n/a			
Hominids	7	**0.332**	**0.025**	**0.667**	**0.022**

TABLE 6-5. Results of the partial mantel tests between the Procrustes distance (shape) matrices and size (controlling for diet) and the dietary matrices (controlling for size). Significant correlations are shown in bold.

		Female		**Male**	
vs. size (no diet)	**n**	**r**	**p-value**	**r**	**p-value**
All Taxa	48	**0.612**	**<0.001**	**0.520**	**<0.001**
Platyrrhines	13	**0.501**	**0.013**	0.319	0.075
Atelines	22	0.669	0.075	0.069	0.458
Hominids	13	0.444	0.100	**0.761**	**0.004**
vs. diet (no size)					
All Taxa	38	**0.146**	**0.031**	**0.201**	**0.008**
Platyrrhines	11	**0.279**	**0.045**	**0.384**	**0.035**
Atelines	17	0.528	0.133	0.287	0.217
Hominids	10	-0.143	0.281	**0.674**	**0.040**

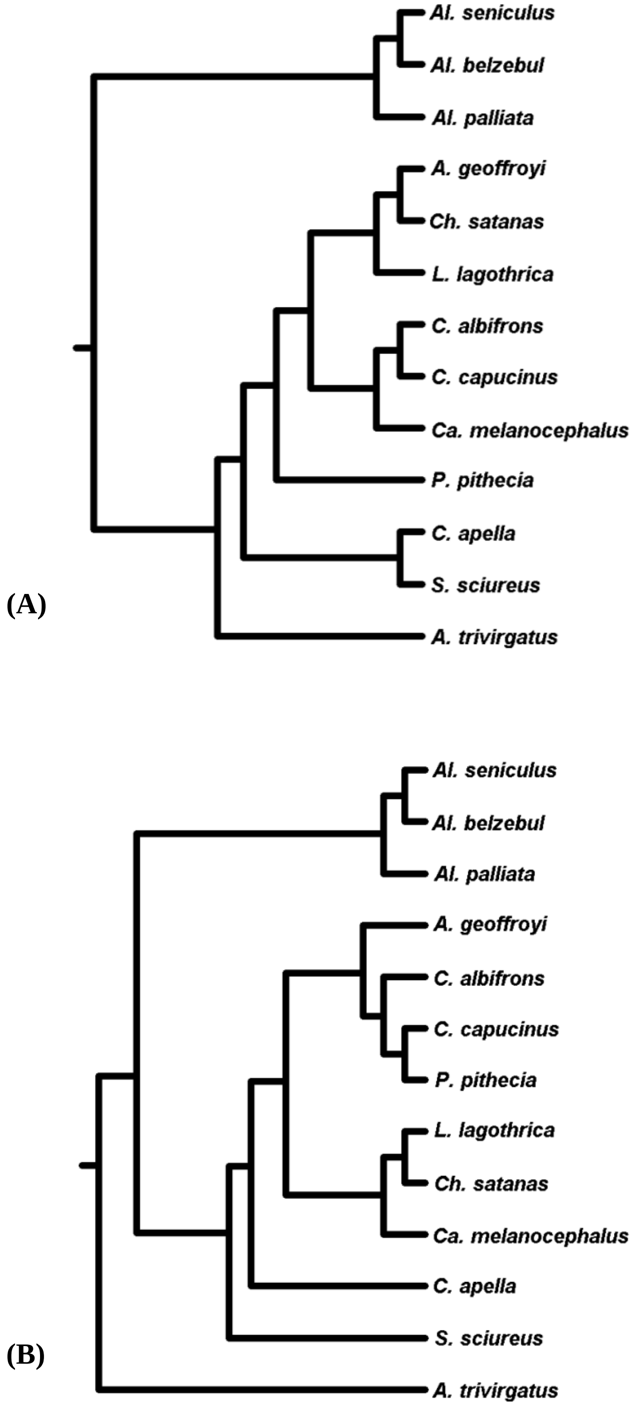


Fig. 6-9. UPGMA cluster diagram showing phenetic similarities among platyrrhine females (A) and males (B).

exclusion of *Alouatta*, including the other atelines, *Ateles* and *Lagothrix*. Patterns of clustering among these taxa are relatively inconsistent between the female and male samples and are not consistent with molecular variation. Calculation of the symmetric differences between the morphological and molecular trees further support this interpretation, with 14 and 16 symmetric differences for the female and male analyses, respectively (out of 23 possible differences). Although there is no obvious clustering of species with similar diets, the mantel test between the shape and dietary matrices indicates a strong correlation between diet and shape in both sexes (females: $r = 0.599$, $p < 0.001$; males: $r = 0.736$, $p < 0.001$). There is also a significant correlation between the shape and size matrices for both females ($r = 0.718$, $p < 0.001$) and males ($r = 0.760$, $p < 0.001$). Partial mantel tests were also performed to determine the relative influence of size and diet, and suggest that size is the primary factor (Table 6-5), while diet is not as significant of an influence on glenoid shape.

Similar patterns were observed at lower taxonomic levels. In the atelines (Fig. 6-10A), the three *Alouatta* species clustered together to the exclusion of *Ateles* and *Lagothrix*; this clustering is consistent with molecular data regarding the relationships among these taxa, suggesting a congruence between the genetic and morphological data in this clade. Furthermore, size and diet were also significantly correlated with shape (Tables 6-4 and 6-5), although the partial mantel did not have enough power with this small sample to differentiate between these two influences. A phylogenetic signal was also observed in the cebine sample (Fig. 6-10B), with *C. capucinus* and *C. albifrons* clustering together to the exclusion of *C. apella*; this pattern is identical to the molecular relationships among these taxa. Finally, the morphological and molecular data were also consistent with one another for the pitheciines (Fig. 6-10C), with *Ch. satanas* and *C. melanocephalus* clustering together to the exclusion of *Pithecia*.

Cercopithecoids. The cercopithecoid taxa generally did not cluster on the basis of phylogenetic relatedness (Fig. 6-11), although some taxa did consistently cluster together in multiple analyses, including *M. nemestrina* with *M. fascicularis*, *C. mitis* with *C. nictitans*, *E. patas* with *P. verus*, and *M. thibetana* with several colobine species (*S. entellus*, *P. badius*, and *P. obscurus*). This final example may suggest a convergence in TMJ morphology associated with increased utilization of tough food objects, as is the case for *M. thibetana* and the colobines. The number of symmetric differences between the molecular and morphological trees was also relatively high, further suggesting the lack of congruence between the genetic and morphological data in this clade, with 30 differences found for females and 34 for males (out of 41 possible differences). No significant correlation between the size and shape matrices or the shape and dietary matrices for the cercopithecoid sample were found for either sex.

This general lack of phylogenetic patterning was also found at lower taxonomic levels. In the colobines (Fig. 6-12A and 6-12B), there was no separation of the Asian and African taxa. Similarly, there was no observable influence of diet on the clustering of taxa, although taxa with similar body sizes (*S. entellus*, *P. obscurus*, and *P. badius*) did tend to cluster together. However, there was no significant correlation between the shape, size, or dietary matrices (Table 6-4). Although there was little congruence between morphology and genetics in the papionin sample, taxa in this clade did seem to cluster on the basis of diet and size in females and males, respectively (Fig. 6-12C and 6-12D). In the female analysis, taxa with relatively similar diets (e.g., the three *Papio* species, and *Mandrillus*, *Cercocebus*, and *Lophocebus*) clustered together, with *T. gelada* distinct from the rest of the sample. However, no significant correlation between the shape and dietary matrices was found. Conversely, in papionin males, taxa of similar body sizes tended to cluster together. In addition, there was a correlation between the size and shape matrices (r=0.615, p=0.012) in male papionins, further suggesting that these taxa clustered on the basis of size. Similarly, there appears to be a combined body size/ dietary signal in the macaque

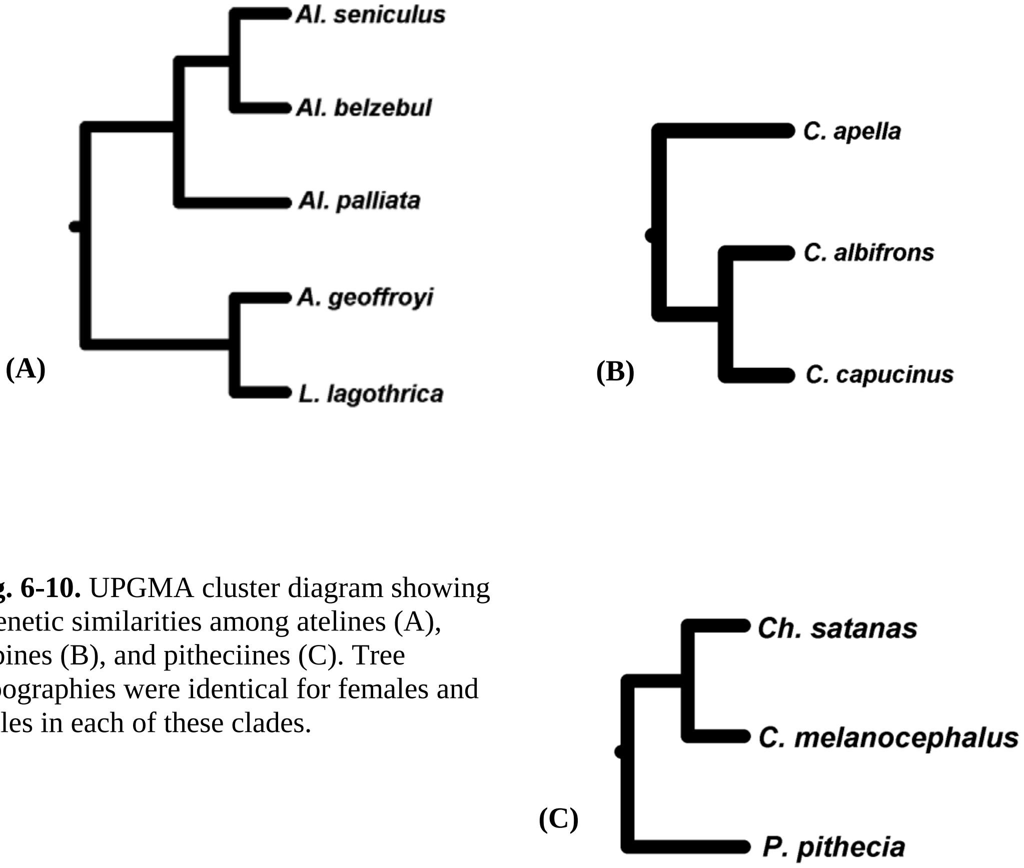


Fig. 6-10. UPGMA cluster diagram showing phenetic similarities among atelines (A), cebines (B), and pitheciines (C). Tree topographies were identical for females and males in each of these clades.

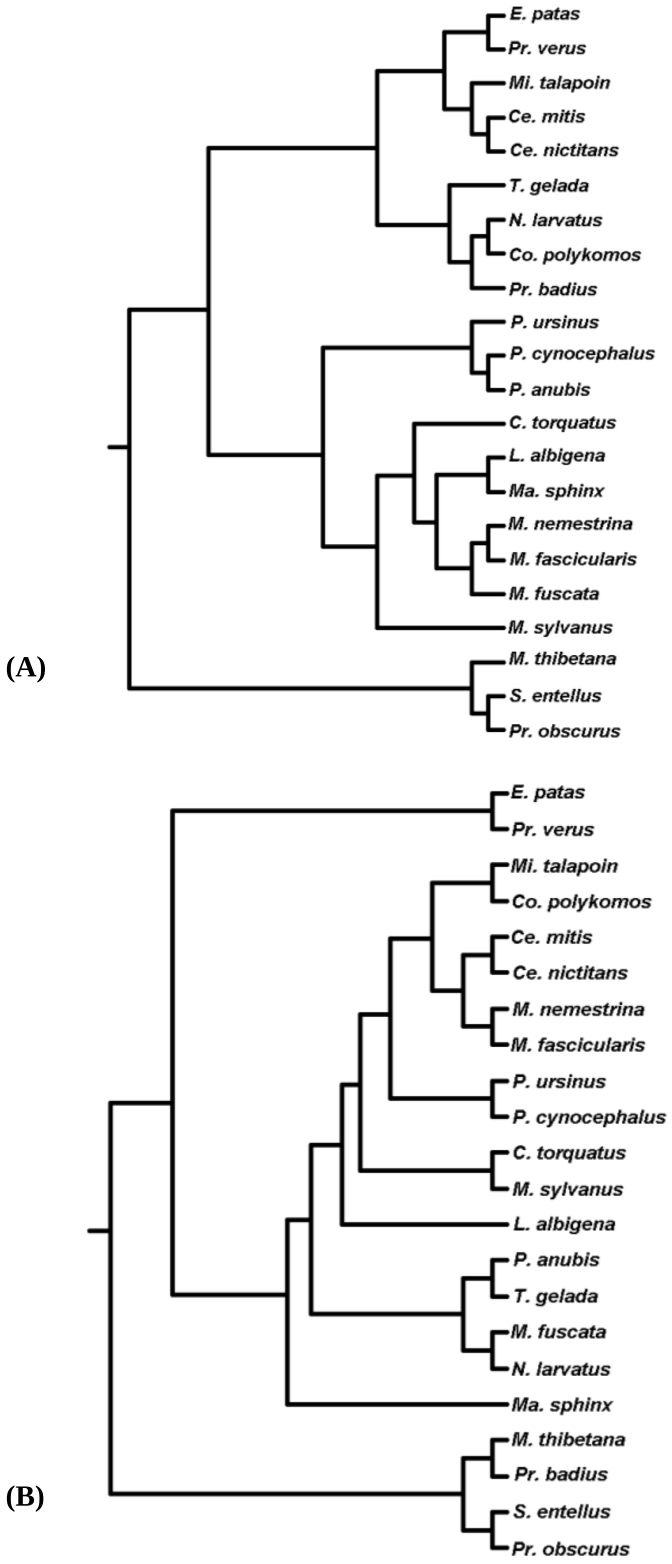


Fig. 6-11. UPGMA cluster diagram showing phenetic similarities among female (A) and male (B) cercopithecoids.

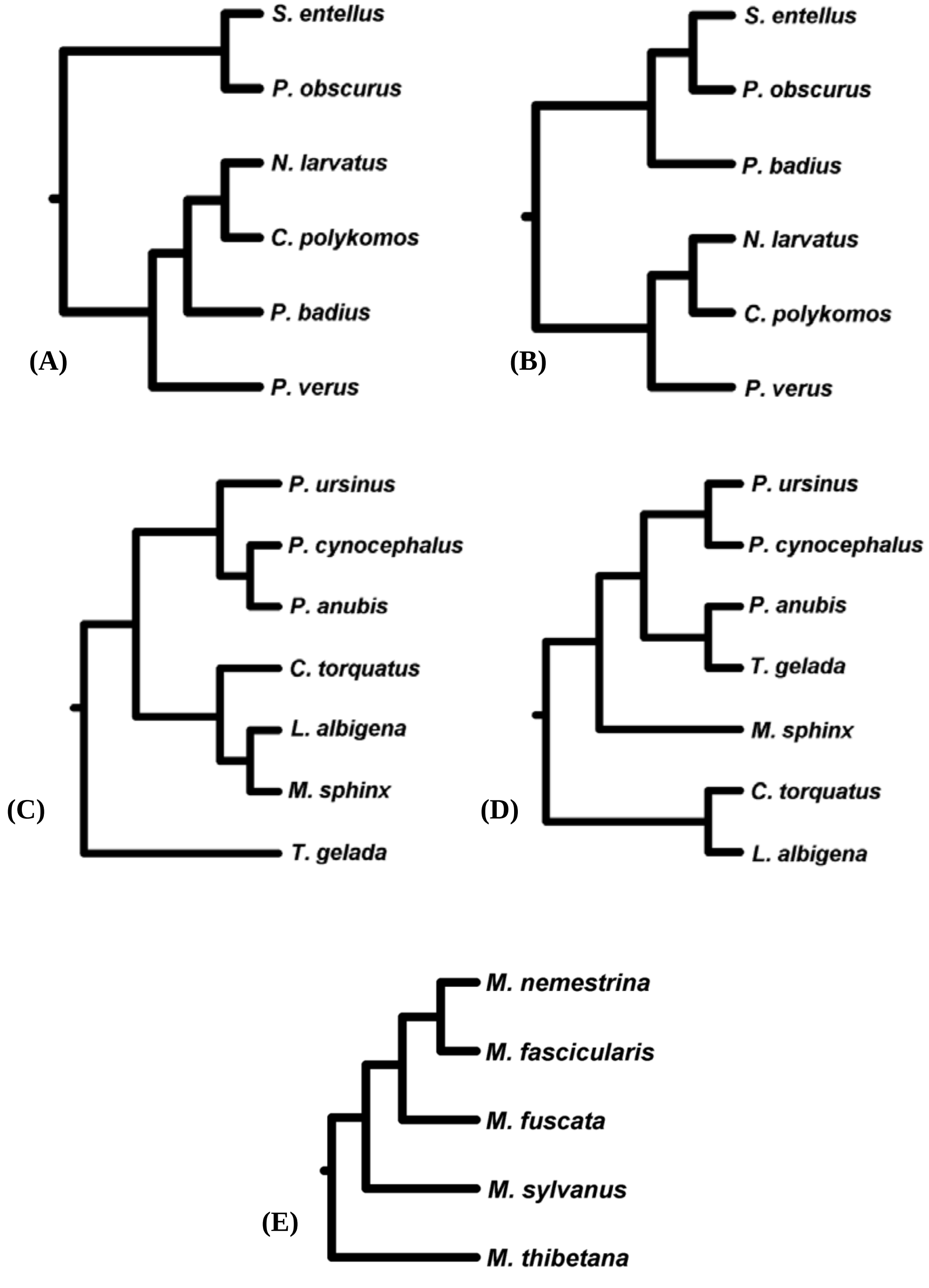


Fig. 6-12. UPGMA cluster diagram showing phenetic similarities among female colobines (A), male colobines (B), female papionins (C), male papionins (D), and macaques (E). Tree topographies were identical for females and male macaques.

sample that is not consistent with the molecular data (Fig. 6-12E). The smallest two taxa, *M. nemestrina* and *M. fascicularis*, which also tend to eat the least resistant food objects, clustered together in both males and females to the exclusion of all other taxa. However, no significant correlation between the diet, size, or shape matrices was found for either males or females.

Hominoids. The UPGMA cluster analysis for the hominoid sample clearly separates the hylobatids and the hominids (Fig. 6-13). There is a strong correlation between the size and shape matrices in this clade for both females (r =0.764 p<0.001) and males (r =0.706, p<0.001). This result is unsurprising given the substantial difference in body size among these two clades, which helps to distinguish them morphologically. Overall, there was a relatively strong congruence between the morphological and genetic data in this sample, potentially as a result of the division between the hylobatids and the hominids; 12 symmetric differences between the morphological and molecular trees were found for both sexes (out of 23 possible differences). This number is lower than the number of differences found in the cercopithecoid and platyrrhines analyses, although comparison of these numbers may not be statistically meaningful since there is no way to assign significance to these values (Felsenstein, 2006).

In the hylobatids (Fig. 6-14A and 6-14B), neither the male nor female trees were consistent with the molecular data, since *S. syndactylus* was not found to be the most basal as is suggested by genetic analysis (e.g., Whittaker et al., 2007). Additionally, in the females, the most closely related taxa (*H. agilis* and *H. lar*) did cluster together; this was not the case in the male analysis, however. Although size was not able to be examined statistically in this group due to small samples, the observed shape variation does not seem to be correlated with size given the placement of the relatively large bodied *S. syndactylus*. There may be a dietary signal present in the males, however, with *H. agilis* and *S. syndactylus* clustering together, potentially on the basis of their increased consumption of more resistant food objects (Chivers, 1974; Gittins, 1979).

Clustering of taxa was relatively variable in the hominid analysis (Fig. 6-14C and 6-14D), and although the clustering of some taxa was consistent with molecular data (e.g., the subspecies of *P. troglodytes*, and to some extent *Pongo* and *Gorilla*), congruence between the molecular and morphological datasets was relatively low. Notably, several more distantly related taxa clustered together. For example, in the female analysis *P. pygmaeus* was most similar to the species and subspecies of *Pan*, whereas for both sexes, humans were more similar to *Gorilla* than to *Pan*. These results may suggest similarities in masticatory function in these species, such that their TMJ morphology is convergent.

A strong correlation was found between the size and shape matrices for both sexes (females: r =0.543 p=0.003; males: r =0.519, p=0.008), suggesting that the taxa in this clade tende to cluster together on the basis of size. In addition, a significant correlation between the shape and dietary matrices (Table 6-4) was found for both sexes (females: r =0.332 p=0.025; males: r =0.667, p=0.022); results of the partial mantel tests, however, indicated a significant influence of both diet and size over glenoid variation in the male hominids, but not in the females (Table 6-5).

DISCUSSION

The goal of this chapter was to assess the extent to which the bony morphology of the TMJ maps onto genetic relationships among anthropoid primate taxa. The results of these analyses indicate that, although there are differences in TMJ shape that reflect broad phylogenetic differences, phylogenies created using TMJ morphology are not generally congruent with molecular phylogenies. Furthermore the level of congruence between the morphological and genetic datasets was variable across taxonomic groups and levels. The datasets were least

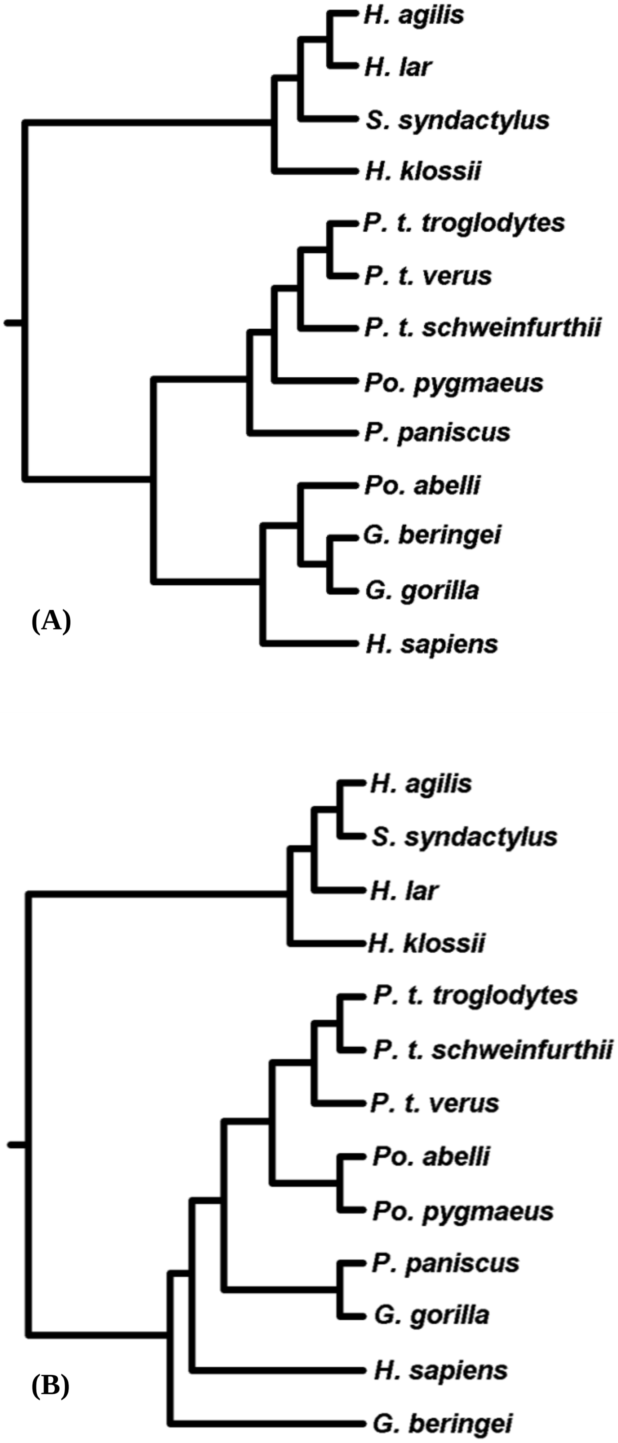


Fig. 6-13. UPGMA cluster diagram showing phenetic similarities among female (A) and male (B) hominoids.

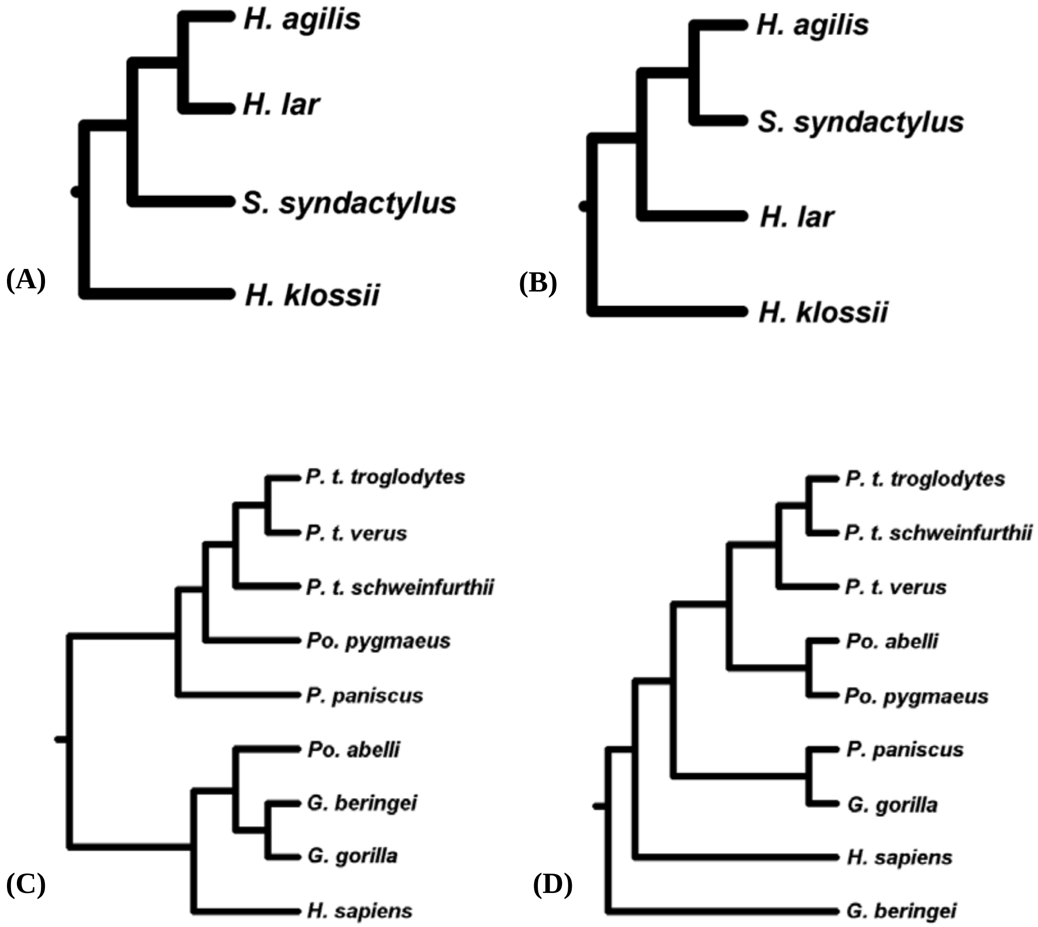


Fig. 6-14. UPGMA cluster diagram showing phenetic similarities among female hylobatids (A), male hylobatids (B), female hominids (C), and male hominids (D).

congruent when all of the taxa were examined. However, broad differences in TMJ shape among platyrrhines, cercopithecoids, and hominoids did allow these groups to be distinguished from one another at high frequencies. At the subfamily level, platyrrhine taxa tended to show the most congruence between morphology and genetics, whereas the least amount of congruence was found in the cercopithecoid subfamilies examined. Many of the clades examined also showed strong correlations with the size and dietary matrices, therefore suggesting that the morphology of the TMJ is strongly tied to differences in feeding behavior, as indicated by the analyses presented in Chapter 4. These findings are discussed in more detail below.

Morphological variation in the TMJ

As indicated by the principal components analysis, the anthropoid glenoid varies considerably in anteroposterior and mediolateral dimensions, and the relative topographic relief of the joint as related to the inclination of the articular eminence, and the size of the various processes in the joint is highly variable. The hominid taxa in particular can be distinguished relatively easily from the rest of the species examined, based on their mediolaterally wide joints with raised articular eminences and large processes. In contrast, platyrrhines and cercopithecoids tend to have very flat joints, although these two clades also differ from one another in the relative amount of relief in the glenoid region. The discriminant function analysis further indicates the disparity in glenoid shape among taxa at the superfamily and subfamily levels. It also suggests that taxa can be relatively reliably distinguished on the basis of glenoid morphology. In addition, this analysis further highlights the unique glenoid morphology observed in hominids.

These results for the glenoid provide an interesting contrast to the results obtained from the morphology of the mandibular condyle. Principal components analysis of condylar morphology suggests that this region is not useful for distinguishing among anthropoid taxa. Instead, this region tends to show less variation that is attributable to phylogeny. These results could be explained in two ways. First, the methods used here to capture condylar shape may not have been adequate to capture those aspects of shape that vary as a function of phylogenetic relationships. This is entirely plausible, since only five landmarks were used to describe condyle shape. Alternatively, there may simply be too much variation in condyle shape as a consequence of plastic changes in condylar morphology related to diet, or there is simply too little (or no) systematic variation in this morphology. This explanation is favored here since visual observation during data collection indicated a high degree of variation in condylar morphology within species, indicating that condylar morphology is not meaningful in the context in which it was employed here. Analyses of remodeling in the TMJ have previously indicated that the frequency of condylar remodeling increases with age and is also associated with anterior tooth wear (Richards, 1990). These data suggest that the mandibular condyle undergoes extensive remodeling throughout the life of an individual and that the extent of remodeling likely varies among individuals as a function of masticatory demands. However, this result may be tempered by additional findings of the same author suggesting that the cranial component of the TMJ begins to show degenerative changes at earlier ages than does the condyle (Richards and Brown, 1981; Richards, 1988).

Correlations with TMJ morphology

The Procrustes distance analyses provided a different view of glenoid variation in the study sample. At the level of superfamily, there is relatively little phylogenetic patterning of TMJ shape. This could partially be a result of the branching diagrams used here which could be misleading since they may force two taxa to cluster together to the exclusion of another species that may differ only in very subtle aspects of its morphology, therefore over-exaggerating the differences among taxa.

A large influence of size variation was identified in this analysis. This is particularly true for the platyrrhines and hominoids, but not for the cercopithecoids; these findings are consistent with the results presented in Chapter 5, which indicate that cercopithecoids tend to have very little size-related shape variation in glenoid morphology. Diet was also found to be a reasonably significant influence on glenoid shape variation, especially in platyrrhines and hominids. These results are also consistent with the data present in Chapter 4, which indicated a strong relationship between TMJ shape and masticatory function.

However, one caveat regarding the dietary analyses that should be addressed is the imperfection of the data used to create the dietary matrices. The ideal dataset for this analysis would include the food material properties for each food item ingested by the species included in this analysis. This type of analysis (see Wright, 2005) would then allow for the direct comparison of the masticatory demands of particular food items (or classes of food items) among taxa. However, these data are currently available for very few primate species (Kinzey and Norconk, 1990; 1993; Elgart-Berry, 2004; Williams et al., 2005; Wright, 2005; Chalk et al., 2008; Wright et al., 2008; Yamashita et al., 2009). Instead, the data used here represented the percentage of feeding records and/or the percentage of time spent feeding on foods of a particular group (e.g., leaves, animal prey, fruit, etc.). One major problem with these data is that these categories of food types are not standardized across analyses, and therefore may not be comparable to one another. In addition, some researchers differentiate among the parts of a specific food item (e.g., seeds vs. fruit pulp) or the relative maturation of food items (e.g., young vs. mature leaves), since these different categories may have different food material properties and/or require different masticatory abilities. If all researchers presented these types of data, it is possible that the dietary matrix used here would be more accurate; unfortunately, several categories that would have been particularly important to distinguish from one another (fruit pulp vs. seeds, for instance) could not be included and instead were summed into a single fruit category. Future work will hopefully be able to incorporate the continuously growing dataset regarding food material properties to refine these analyses.

Platyrrhines. The three species of *Alouatta* included in this analysis have a unique glenoid shape in comparison to *Ateles* and *Lagothrix*. Given the highly specialized nature of the vocal apparatus and basicranium in *Alouatta*, it is hypothesized that this unique glenoid morphology is correlated with their vocal behaviors. However, this genus is also distinct from *Ateles* and *Lagothrix* in both size and diet, potentially suggesting a combination of factors that contribute to this unique glenoid morphology. Whatever the reason for this unique morphology, variation in all of these factors (diet, size, and vocal behaviors) maps onto the molecular phylogeny of these species with a high degree of congruency. Furthermore, the only other groups within this study that showed phenetic clustering identical to the genetic data were the cebines and pitheciines. These results therefore suggest that variation in glenoid morphology in platyrrhines reflects phylogenetic relationships in this group. This could be a result of adaptive radiations within platyrrhines that were associated with dietary diversification which drove speciation events within this clade, as has been discussed extensively by Rosenberger (1980, 1992). These findings are largely consistent with the predictions laid out for each of these subfamilies (and platyrrhines as a whole) above.

Cercopithecoids. Very little congruence between the morphological and genetic data was found in the glenoid region in the cercopithecoid sample. Instead, the cercopithecoid clades analyzed tend to show a more consistent relationship between morphological variation and the diet/size data, particularly in papionins and macaques. Most interestingly, these correlations varied between sexes; in the papionin sample the female configurations tended to cluster on the basis of diet, while the males clustered on the basis of size. Since many of these taxa are highly sexually dimorphic (Fleagle, 1999) these results may indicate a potentially important role of shape dimorphism in glenoid morphology within species. This pattern of variation (e.g., that males tend to cluster on the basis of body size rather than diet) could also be indicative of increased sexual selection for larger body sizes, which results in more disparate glenoid morphologies between the sexes. The high levels of sexual dimorphism in these species could be also associated with differences in resource utilization (e.g., females access foods with different material properties than do males). Further data regarding the diets of these species, and particularly comparing and contrasting resources used by males and females, would be useful in this regard.

These results were partly expected given the predictions outlined for these clades above. Both size and diet were expected to covary significantly with morphology in the cercopithecoids, and low correlations between the morphological and genetic data were expected given previous difficulties with classification of these taxa (e.g., mangabeys).

Hominoids. The hominoids also showed a mixture of potential influences on glenoid shape that were somewhat consistent with the predictions for this group outlined at the beginning of this chapter. In the hylobatids, the most basal taxon of the sample, *S. syndactylus*, which is also generally considered to be dietarily distinct and is double the body mass of *Hylobates* (Fleagle, 1999), did not have a distinct glenoid shape in comparison to the three *Hylobates* species examined. However, the similarity in glenoid shape between *H. agilis* and *S. syndactylus* males (although not females) suggests that perhaps similarity in diet (both of these taxa have been documented to eat relatively more resistant food objects that *H. lar* and *H. klossii*) is associated with morphological variation in this group.

Given previous research by Lockwood et al. (2002, 2004), the most surprising result of this analysis was the general lack of phylogenetic patterning of glenoid morphology in the hominid species examined. Although some taxa that were more closely related to one another tended to cluster together (the subspecies of *Pan troglodyt*es, for instance), other species that were expected to be more similar in morphology given their close molecular relationships (e.g., *P. paniscus* and *P. troglodytes; P. abelii* and *P. pygmaeus*; and *G. gorilla* and *G. beringei*) did not reliably cluster together. For example, in the female analysis *P. pygmaeus* was found to be most similar to *Pan*, suggesting similar masticatory function in these taxa. As noted in Chapter 4, both *P. pygmaeus* and *Pan* tend to rely more heavily on the anterior dentition for food processing behaviors (or in the case of *P. pygmaeus*, bark stripping) than does *Gorilla*. Therefore, some of the morphological similarity between *P. pygmaeus* and *Pan* may be associated with this increased use of the anterior dentition. Similarly, the *H. sapiens* sample most consistently clustered with *Gorilla*, likely on the basis of the strongly reduced preglenoid plane and more inclined articular eminence, which suggests similarities in relative gape capacity in these two taxa.

Thus, at least for the glenoid region, the congruence between the morphological and genetic data is relatively low, although this may in part be associated with the strong influence of allometry in this clade (as discussed in Chapter 5). Given the previous findings that the hominid temporal bone as a whole tends to reflect phylogenetic history (Lockwood et al., 2002, 2004; Harvati and Weaver, 2006a,b; Smith et al., 2007), these results suggest an additional hypothesis, that different regions of the temporal bone (e.g., the glenoid region vs. the tympanic and petrous portions) are more or less useful for discerning phylogenetic relationships among taxa. Preliminary analyses support this hypothesis, and indicate that the tympanic and petrous portions of the temporal bone are driving the previously documented phylogenetic signal in this region of the cranium (Terhune, unpublished data).

Phylogenetic utility of the TMJ

In all, these results suggest that the relationship between morphology and genetics as exhibited by TMJ shape is not consistent across anthropoid primates. This is likely a result of the many and varied selective pressures that have shaped the evolutionary history of this primate group. Results presented in the prior chapter on scaling indicate that TMJ shape scales largely with positive allometry and isometry, and therefore the clustering of similarly sized taxa in several of the analyses presented above is unsurprising. Critically, it is important to realize that none of these factors (genetics, diet, body size) are likely to be independent of one another. Dietary differentiation among primate taxa has frequently been cited as a possible explanation for speciation events (e.g., the radiation of platyrrhines [Rosenberger, 1980, 1992]; cercopithecines and colobines [Jablonski, 2002]; and the great apes [Fleagle, 1999; Pilbeam, 2002]), and for subsequent differences in ontogenetic scaling among taxa which allow for the attainment of different adult body sizes and exploitation of different resources (e.g., Shea, 1984, 1985). As illustrated by the platyrrhine data, dietary or size differences among taxa need not be incongruent with known genetic relationships among species. In fact, it seems highly likely that dietary divergence, and subsequent changes in body size, may have been the primary factors which drove the widespread adaptive radiation observed in the platyrrhines (Rosenberger, 1992).

The initial impetus for the research presented in this chapter came from the inability of molecular analyses to adequately address relationships among extinct species. Examinations of these relationships must therefore necessarily rely upon analyses of morphology, which is assumed to have a genetic component. The basicranium in particular, because of its unique development and relation to the brain, has been frequently identified as a region of morphology that more accurately reflects molecular relationships (Lockwood et al., 2004; Smith et al., 2007; HF Smith, 2009; von Cramon-Taubadel, 2009), at least within humans and great apes. However, as identified here, the TMJ appears to be less reliable than the basicranium or temporal bone in this regard. This is not to say that previous analyses incorporating aspects of TMJ shape should be disregarded, but rather that phylogenetic analyses solely of TMJ shape are likely to be considerably less reliable than analyses of the basicranium or temporal bone as a whole. This interpretation is demonstrated well here in the case of the great apes. Previous analyses of the entire temporal support the conclusion that this region reliably reflects molecular relationships (i.e., Lockwood et al., 2004), but when only the glenoid region is examined, the congruence between these two datasets decreases considerably. Additional analyses will be necessary to evaluate whether this pattern holds true for groups other than the great apes and humans, but given the range of results found here, it seems likely that the congruence of the molecular data and the morphology of the TMJ and the entire basicranium varies considerably among taxonomic groups, probably as a result of the variation in selective pressures driving morphological variation among these groups.

CONCLUSIONS

The goal of this analysis was to assess the extent to which TMJ morphology reflects genetic relationships among anthropoid primates. The data presented here suggest that, althgouh TMJ morphology does not strongly reflect phylogenetic variation among species, TMJ shape does vary in association with diet, body size, and other ecological specializations among taxa. This does not mean that TMJ morphology is not useful in a phylogenetic context; in several clades TMJ morphology was strongly congruent with genetic variation. However, a lack of congruence between the morphological and genetic data in other clades indicates that phylogenetic inferences based on aspects of glenoid or condylar morphology are limited without the analysis of additional temporal bone morphology. These data highlight the myriad ways in which multiple factors may influence TMJ shape, which may or may not be congruent with known genetic relationships among taxa. These factors, which are clearly not mutually exclusive, have worked in concert with one another to result in the wide range of glenoid and condylar morphologies observed in extant anthropoid primates.

CHAPTER 7: DISCUSSION

I began this dissertation with a discussion of known variation in TMJ morphology across primates. This review highlighted the current lack of a broad framework comparing and contrasting TMJ morphology in anthropoid primates. However, knowledge of variation in TMJ form is crucial for further understanding the form and function of the masticatory apparatus. Three main avenues of research regarding TMJ morphology were identified. These included assessing functional variation in TMJ shape, evaluating TMJ form in the context of changes in body or cranial size, and use of the TMJ to infer phylogenetic history.

The first of these research areas is perhaps the most critical given the integral role the TMJ plays in the masticatory apparatus. Previous research has shown that this joint is indeed load bearing (Hylander, 1979a; Smith, 1978; Brehnan and Boyd, 1979; Brehnan et al., 1981; Boyd et al., 1982, 1990), and the masticatory apparatus in general is best classified as a class three lever system (Hylander, 1975, 1979a, 1991, 2006; Hylander and Crompton, 1980; Hylander and Johnson, 1985; Hylander et al., 1992; Hylander et al., 2005). In such a system, the joint reaction force and bite force must cancel out the muscle resultant force to maintain static equilibrium. However, there is likely to be considerable variation in the magnitude of the joint reaction force vs. the bite force depending upon multiple variables, such as muscle firing patterns, position of the bite point, height of the TMJ above the occlusal plane, and the overall configuration of the masticatory apparatus. The goal of a major portion of this dissertation was therefore to evaluate shape variation in the TMJ, and to link this variation to differences in feeding behavior among anthropoid primates. Three main research predictions were generated in this regard. These predictions had to do with three primary ways in which the TMJ is likely to vary as a function of masticatory demands: food material properties, bite point location, and gape requirements.

In regard to variation in food material properties, it was predicted that taxa who tend to consume more resistant food objects (whether this utilization is continuous or only as a fallback food) should exhibit adaptations in their TMJs associated with increased joint reaction force and range of motion, such as increased joint surface area and larger joint processes (entoglenoid process and articular tubercle).

Similarly, the second prediction posited that the TMJs of taxa that intensively use their anterior teeth should show adaptations to resist larger centrally or medially located joint reaction forces. Taxa that repetitively load their posterior teeth should show adaptations within their TMJs related to increased joint reaction forces on the lateral surface of the TMJ. These adaptations would be represented by changes in the relative mediolateral and anteroposterior dimensions of the joint and the size of the entoglenoid process and articular tubercle.

Finally, I predicted that taxa with relatively large gapes (whether for behavioral or dietary reasons) should have adaptations in their TMJ related to increased range of motion (e.g., sagittal sliding), such as an anteroposteriorly longer TMJ, large preglenoid plane, and anteroposteriorly flat mandibular condyle.

Results of the detailed analyses of the comparative groups examined (in Chapter 4) suggest that these predictions are supported, although with some exceptions. In almost all of the comparative groups, those taxa with more resistant diets (especially those that use their posterior teeth more extensively) tended have significantly larger joint surface areas, relatively mediolaterally (ML) wider and anteroposteriorly (AP) shorter TMJs, and larger entoglenoid processes. In contrast, taxa that utilize resistant food objects, but process them on their anterior teeth (e.g., *Cebus apella* and *Pongo pygmaeus*) were found to have relatively small entoglenoid processes. This may suggest that the entoglenoid process is associated with increasing the range of motion of the condyle at larger gapes. A smaller entoglenoid process at wide gapes would allow for increased range of motion of the condyle, and consequently the anterior dentition, which would be necessary when using the canines in food processing as is the case for these two species (Izawa and Mizuno, 1977; Izawa, 1979; Terborgh, 1983; Rodman, 1988; Janson and Boinski, 1992). These data therefore strongly suggest that TMJ shape varies as a function of food material property and relative use of the anterior or posterior dentition. However, further data regarding the magnitude of joint forces on the anterior teeth in comparison to taxa that repetitively load their posterior teeth is necessary to evaluate which of these patterns of masticatory loading are most significantly linked to TMJ shape variation.

A very strong correlation between measures of gape (e.g., canine crown height and height of the TMJ above the occlusal plane) and aspects of the AP length of the glenoid (glenoid length and preglenoid plane length) was also found in this analysis. These data indicate that the amount of translation occurring at the TMJ during jaw opening and closing is important for maximizing linear gape, and those taxa with relatively wider gapes have more extensive anterior excursion of the mandibular condyle during wide jaw opening. These finding are consistent with recent analyses by Hylander and colleagues (Hylander and Vinyard, 2006; Hylander et al., 2008), who found a significant correlation between relative gape and canine crown height, and support the hypothesis that increased gape is partly manifested by alterations in joint surface area (Hylander, personal communication). Similarly, these data support the findings of Vinyard et al., (2003) who found that tree-gouging primates tended to have relatively AP longer glenoids than closely related taxa that do not practice tree-gouging.

Any consideration of functional variation must also account for variation in size across the sample in question. Previous research on scaling in the masticatory apparatus has yielded mixed results. Multiple analyses have indicated that some features of the masticatory apparatus scale with positive allometry (Smith et al., 1983; Hylander, 1985; Ravosa, 1996; 2000; Vinyard, 1999; Anapol et al., 2008). Several authors have interpreted this scaling pattern to indicate a size-related increase in dietary toughness across primates. Other researchers have suggested that some of these features scale instead with isometry (Cachel, 1984; Bouvier, 1986a,b; Anton, 1999, 2000; Perry and Wall, 2008). It was predicted here that most features of the TMJ should scale with positive allometry, particularly if the hypothesis of a size-related increase in dietary toughness is correct. Scaling of food items relative to body size also suggests that, as taxa grow larger, food items should be relatively smaller, and therefore negative allometry in aspects of gape was predicted.

Results of the scaling analyses (presented in Chapter 5) indicated that many features of the TMJ do indeed tend to scale with positive allometry, but when these patterns are evaluated in platyrrhines, cercopithecoids, and hominoids separately, several distinct trends emerge. In both platyrrhines and cercopithecoids, the size of the processes in the joint (e.g., entoglenoid, postglenoid, and articular tubercle) scales with positive allometry, but these same relationships in hominoids are generally isometric. Similarly, glenoid length and preglenoid plane length tend to show a slightly negatively allometric scaling relationship in hominoids whereas in platyrrhines and cercopithecoids these variables scale with either isometry or positive allometry. These data may point to relative differences in gape in hominoids, since previous analyses by Vinyard et al. (2003) have demonstrated a correlation between relative gape and the anteroposterior length of the TMJ that is further supported by the strong correlation found here between aspects of glenoid shape and canine length and height of the TMJ above the occlusal plane.

The geometric morphometric analyses of scaling in the TMJ provide an interesting contrast to the univariate analyses conducted. The geometric morphometric scaling data indicated that TMJ shape is strongly correlated with variation in body size in platyrrhines and hominoids, but not in cercopithecoids, and that the pattern of TMJ shape change as related to size is reversed in platyrrhines and hominoids. These disparate patterns of shape change may again be associated with relative differences in gape, such that the larger bodied platyrrhines (e.g., *Alouatta*) and the smaller bodied hominoids (e.g., hylobatids) have similarly increased gape requirements that necessitate relatively anterioposteriorly long glenoids that would facilitate increased translation of the mandibular condyle during jaw opening and closing. However, mandibular and canine morphology differs considerably between these groups. *Alouatta* has a TMJ raised well above the occlusal plane and relatively smaller canines, while the hylobatids have TMJs that are considerably closer to the occlusal plane but very large canines. In *Alouatta*, increased AP translation of the condyle on the glenoid articular surface may somewhat compensate for the reduced linear gape associated with such high TMJs, regardless of the canine size in this taxon. In contrast, hylobatids may have wider gapes as a consequence of their enlarged canines.

Recent work with the temporal bone suggests that this region is particularly useful for uncovering the phylogenetic history of primate clades (Lockwood et al., 2002, 2004; Harvati and Weaver, 2006a,b; Smith et al., 2007; HF Smith, 2009; von Crammon-Taubadel, 2009). This has been demonstrated for great apes and humans, but it remains unclear whether this technique is broadly applicable across primates. Furthermore, whether different portions of the temporal bone are more or less useful for phylogenetic reconstruction is unknown. Yet researchers rely heavily on features of the temporal bone (including aspects of TMJ shape) to evaluate taxonomic and phylogenetic hypotheses, particularly in the fossil hominins. The third and final research question that was addressed in this dissertation investigated the extent to which TMJ morphology is congruent with genetic data.

Analyses of the congruence between the genetic and morphological data for the TMJ in Chapter 6 indicated that these datasets are not generally congruent, although again, this relationship varied across taxonomic groups and levels. The highest degree of congruence was observed in platyrrhines; in all three of the platyrrhine family groups phylogenies created using the genetic data and TMJ morphology were highly congruent. In contrast, the least congruence between these datasets was found for cercopithecoids. The analyses of the hominid sample presented a particularly interesting result. Previous analyses by Lockwood et al. (2002, 2004), have indicated that temporal bone shape in this group can be used reliably to reflect phylogenetic relationships. This finding was not replicated when only landmarks on the glenoid fossa were used, suggesting that the bulk of the phylogenetic signal of the temporal bone lies in the petrous and tympanic portions. In general, the results of the phylogeny chapter indicate that the relationship between the molecular and morphological data is not consistent across anthropoid primates, and caution is therefore warranted in future analyses of TMJ and basicranial variation of fossil and extant primates.

Further analysis of the covariance between TMJ morphology and distance matrices describing size and dietary variation in the sample found strong correlations among these datasets in several clades. Shape variation in the platyrrhines and hominoids in particular was strongly correlated with body diet and size. Coupled with the relative congruence between the morphological and genetic datasets for the platyrrhines, these findings suggest that perhaps dietary differences, accompanied by changes in relative body size, were the main selective pressure driving the adaptive radiation of this clade that has previously been suggested by Rosenberger (1992). In contrast, data for the cercopithecoids do not suggest any particularly strong correlations among morphology, body size, or diet; although the observed patterns of variation in each of these datasets may suggest that the relative influence of these factors varies across taxa in this group.

In sum, the analyses presented here indicate that the morphology of the TMJ covaries strongly with both masticatory function and body size, and to some extent TMJ morphology reflects phylogenetic history. To what extent are the findings of the dietary, scaling, and phylogenetic analyses related to one another? As discussed throughout this dissertation, none of the three factors analyzed are likely to function in isolation, nor are they likely to be the only influences over TMJ shape variation. Dietary differentiation among closely related populations or species can easily drive changes in body size and ultimately lead to phylogenetic differentiation. For example, the data examined here seem to suggest that dietary divergence in platyrrhines is strongly correlated with both size and phylogenetic divergence, perhaps indicating that initial diversification of this clade was related to differences in feeding behavior (Rosenberger, 1980, 1992). Similarly, changes in body size as a result of other selective pressures (e.g., predation, climate, etc.) could necessitate a shift in nutritional requirements and therefore dietary intake. The goal of this study was to examine whether TMJ morphology accurately reflects differences in feeding behavior, body size, or phylogeny. The results presented here suggest that the extent to which these factors were acting on TMJ morphology varies across anthropoid primates, and, perhaps most critically, these data indicate that no single factor is responsible for the variation in TMJ morphology observed across primates. Functional differences in the masticatory apparatus appear to be particularly important in hominids and atelines, but both of these groups also tended to show a strong allometric signal, suggesting that, at least in these groups, diet and body size are interrelated. Results of the biomechanical scaling analysis also suggest this may be the case across the entire sample, as the overall size and most features of the TMJ scale with positive allometry against cranial size. This finding is consistent with previous analyses suggesting that dietary resistance also scales with positive allometry with body size (Kay, 1975; Hylander, 1985; Sailer et al., 1985; Ravosa, 1996, 2000).

OTHER POTENTIAL INFLUENCES OVER TMJ MORPHOLOGY

Other factors that may influence TMJ shape that were not evaluated as part of this study include adaptive plasticity and soft tissue structures of the TMJ. Adaptive plasticity is defined as the ability of an organism to respond to altered environmental conditions during ontogeny (Gotthard and Nylin, 1995; Ravosa et al., 2007). In Chapter 5, plastic variation in condylar morphology was discussed as a potential explanation for the lack of patterning in condylar morphology. In particular, Richard’s (1990) data suggest that the mandibular condyle undergoes increased remodeling with age and as a function of masticatory demands. Studies by Bouvier and Hylander (1982, 1984) and more recently by Ravosa and colleagues (2007, 2008) indicate that the mandibular condyle experiences varying levels of remodeling as a result of variation in masticatory function. In particular, these studies demonstrated that condylar dimensions and articular disc thickness were significantly larger in lab animals (Bouvier and Hylander = rats and macaques, Ravosa et al. = rabbits) that were habitually fed a more resistant diet, in comparison to other groups that were not required to masticate hard or tough food objects. These data suggest that the plastic response of the TMJ to changes in loading magnitude and/or frequency is important for continual adjustment of the form-function relationship during an organism's lifespan. What is unclear from these studies, however, is whether some taxa are more able to respond plastically to changes in masticatory function than others. In other words, how do the reaction norms differ among taxa, and to what extent were modifications of an ancestral reaction norm selected for or against in particular taxa (e.g., Gotthard and Nylin, 1995)? Furthermore, the mandibular condyle has frequently been studied as it has been considered to be more sensitive to variation in the local mechanical environment (e.g., Petrovic et al., 1975, 1981; Burke and McNamara, 1979; McNamara and Carlson, 1979; Carlson et al., 1980; Beecher and Corruccini, 1981; McNamara, 1981). It remains unclear whether the morphology of the glenoid fossa is more or less plastic than the mandibular condyle, and a future extension of the research presented here, in conjunction with the morphological data on rabbit TMJ morphology from Ravosa and colleagues, will hopefully help to elucidate this relationship.

This study evaluated only the bony components of the TMJ. However, soft tissue structures of the TMJ are critical for regulating loads and range of motion at the TMJ. The articular disc in particular is likely to play a major role in TMJ function, as it is interposed between the cranial and mandibular components of the joint. But while the morphology of the articular disc has been extensively analyzed in humans, few studies have evaluated the articular disc of non-human primates. The disc itself is an oval pad of dense avascular connective tissue (rather than hyaline cartilage) that is thinnest centrally and thickened peripherally. Osborn (1985) suggested that this thin intermediate zone develops during ontogeny as a result of increased compressive forces, and analyses of loading of the disc suggest that the highest loads are incurred in this region (DeVocht et al., 1996; Beek et al., 2000, 2001). As with other soft tissue structures associated with joints that are incongruent (e.g., the knee), the soft tissue structures are assumed to decrease the contact pressure of the components of the joint by increasing the contact area of the joint surfaces (Beek et al., 2000), thereby decreasing or preventing high-magnitude stresses that could consequently result in degeneration and perforation of the disc (Tanaka and van Eijden, 2003). More analyses need to be conducted to evaluate the extent to which the morphology of the articular disc varies in non-human primates, but it is likely that this structure exhibits a diversity of form that is linked to the bony morphology of the joint.

These two areas of research represent major considerations in studies of TMJ shape. Remodeling of the joint may significantly influence the morphology observed such that it is difficult to determine whether shape variation is a consequence of adaptation or plastic changes over an individual’s lifetime. Given these considerations it is therefore particularly important that studies of TMJ shape be conducted using wild-caught populations rather than zoo collections, where feeding behaviors are less likely to be consistent with wild behaviors. A consideration of soft tissue structures at the TMJ is equally important, as these structures may significantly influence the function of the bony components of the joint, and particularly may alter the range of motion or the distribution of forces in the joint such that these variables are not inferable from the bony morphology alone.

TMJ VARIATION IN FOSSIL HOMININS

One major goal of the research presented here was to provide a framework for analyses of fossil craniofacial variation. How might previously observed variation in TMJ morphology across hominins be explained in light of the data presented here? In order to address this question, the following section provides an overview of previous analyses regarding TMJ shape variation in fossil hominins. I will conclude by presenting several outstanding research questions that can be addressed using the methodology and data presented in this dissertation.

Fossil hominin morphology

In many respects, the morphology of the TMJ (particularly the glenoid fossa) in fossil hominins is intermediate between the great ape and modern human conditions. In the australopiths, this morphology is considerably more primitive and thus more similar to that of the great apes (although the robust australopiths are an important exception), whereas the morphology of the species of the genus *Homo* are more like the glenoid of modern humans. Many of these differences in morphology may potentially be explained by differences in masticatory function, as discussed below. Body size differences among these taxa are also important to consider given the scaling relationships identified in this study. However, current data regarding body size estimates for fossil hominins suggest there may not be appreciable differences in body mass among species, except between the australopiths/ early *Homo* and later species of *Homo* (e.g., Jungers, 1988; McHenry, 1992; Kappelman, 1996).

The australopiths. Few details are available regarding the morphology of the glenoid fossa of the earliest australopith, *Australopithecus anamensis.* Information that has been published suggests that this morphology is relatively primitive, with a very shallow glenoid fossa, an indistinct articular eminence, and a small entoglenoid process (Leakey et al., 1995; Ward et al., 1999). In comparison, the glenoid fossa of *A. afarensis* is slightly more derived, with increased relief, but this morphology is still extremely ape-like, as it retains many primitive characteristics (Kimbel, 1986; Kimbel et al., 2004), including a large, “open” fossa with an extensive preglenoid plane, a weakly developed articular eminence, and an inflated and laterally placed postglenoid process. In comparison to the apes, the glenoid fossa of *A. afarensis* is shortened anteroposteriorly, but is very broad mediolaterally. The *A. africanus* glenoid differs somewhat in this regard, with a slightly longer, narrower glenoid. There is a great deal of overlap, however, in the morphology of the glenoid between *A. afarensis* and *A. africanus,* with some representatives of the former species displaying a markedly flatter "open" glenoid than is present in *A. africanus*, in which the articular eminence is slightly more raised, resulting (on average) in a marginally deeper fossa in this species (Aiello and Dean, 1990; Kimbel et al., 2004). Additionally, one particular *A. africanus* specimen (MLD 37/38) is distinctly more derived in some characters than other specimens attributed to this taxon, displaying a more bar-like articular eminence, which is also twisted around its transverse axis (as is observed in *Homo*) (DuBrul, 1974; Kimbel et al., 2004). Laterally, DuBrul (1974) describes a strong articular tubercle in this species, a feature which does not seem to be as distinct in *A. afarensis*.

Given the comparative analyses conducted here, these data indicate that the glenoid region of the "gracile australopiths" is very similar to that of *Pan*, with an AP elongated glenoid articular surface which is likely suggestive of increased translation of the mandibular condyle and thus wider gapes. This could indicate that these species still relied heavily on the use of the anterior dentition for food processing. This observation is consistent with reviews of the dentition in *A. afarensis* and *A. africanus,* which suggest these species retained relatively larger incisors (although incisor size is slightly reduced in *A. africanus* in comparison to *A. afarensis*), as well as relatively large canines (see measurements in Kimbel and Delezene, 2009). However, increased size of the postcanine dentition and thickened enamel on the molars (e.g., Rak, 1983; Grine and Martin, 1988; Schwartz, 2000; Kimbel et al., 2004; White et al., 2006; Olejniczak et al., 2008; Kimbel and Delezene, 2009) may indicate that these species also utilized their postcanine dentition extensively for the mastication of more resistant food objects, at least in comparison to *Pan* and older species of hominins. This interpretation is supported by the somewhat mediolaterally wider TMJs found in *A. afarensis* and *A. africanus*, which indicate increased lateral shifting of the mandible during mastication.

How can the observed differences in TMJ morphology between *A. afarensis* and *A. africanus* be explained? As noted above, the TMJ of *A. africanus* is slightly anteroposteriorly longer, with a more raised articular eminence. Data presented in this dissertation suggest that both of these morphologies may be linked to increased height of the TMJ above the occlusal plane. If canine size is comparable in these two species (Kimbel and Delezene, 2009), but the TMJ is positioned higher above the occlusal plane in *A. africanus*, then more anteroposterior translation of the condyle would be necessary to achieve the same amount of linear gape, thus requiring a anteroposteriorly longer preglenoid plane. Increased height of the TMJ above the occlusal plane would also explain the increased inclination of the articular eminence in *A. africanus*, as indicated by the strong correlation between these variables observed in the extant species examined in this study. However, current data regarding ramus height in *A. afarensis* and *A. africanus* are scarce, and perhaps do not currently support the suggestion of a higher TMJ in *A. africanus* (W. Kimbel, personal communication). Further data regarding differences in glenoid (and more generally masticatory system) shape in these two taxa are necessary to identify how extensively these species differ in this morphology.

Geologically younger *Australopithecus* species primarily include the "robust australopiths." Phylogenetically, these species (which include *A. aethiopicus, A. robustus,* and *A. boisei*), have been considered to be both monophyletic and paraphyletic (Skelton et al., 1986; Wood, 1988; Skelton and McHenry, 1992; Lieberman et al., 1996; Strait et al., 1997; Kimbel et al., 2004). The argument for paraphyly of this group has centered around the suggestion that, as the masticatory apparatus is a functional complex, characters associated with such a complex should be more prone to homoplasy (Skelton et al., 1986; Skelton and McHenry, 1992; McHenry, 1994). If this is the case, then it would be reasonable to expect that multiple taxa with the same adaptive characters may arise independently (Skelton et al., 1986; Skelton and McHenry, 1992). More recently, however, there is a growing consensus that these specimens are most appropriately considered a monophyletic group, which some researchers attribute to a separate genus, *Paranthropus* (e.g., Jungers and Grine, 1986; Grine, 1988; Grine and Daegling, 1993; Strait, 1998, 2001; Wood and Constantino, 2007; Villmoare, 2008).

In *A. robustus*, although the shape of the glenoid is generally similar to *A. africanus*, the size of the fossa is considerably larger (Kimbel et al., 2004). The fossae of these two taxa differ primarily in the deeper glenoid of *A. robustus*, which is associated with a distinctly stronger articular eminence. Additionally, the glenoid can be characterized as somewhat more anteroposteriorly compressed than in *A. africanus*, although again, the glenoid is absolutely larger in *A. robustus* (Aiello and Dean, 1990; Kimbel et al., 2004). Like the bulk of *A. afarensis* specimens, however, the articular eminence is not ‘twisted’ and the preglenoid plane is roughly the same size (Aiello and Dean, 1990; Sherwood, 1995; Sherwood et al., 2002; Kimbel et al., 2004).

Australopithecus boisei, on the other hand, is distinctly more derived in morphology than is *A. robustus*, a characteristic that was first noted by DuBrul (1974, 1977). Specifically, the glenoid fossa is considerably deeper than in any earlier hominins. This is, again, a consequence of changes in several characters, including a steeply sloped articular eminence, as well as a vertically oriented tympanic which is merged with the small, medially placed postglenoid (Kimbel et al., 2004; Aiello and Dean, 1990; Sherwood, 1995; Sherwood et al., 2002). With this reorientation of the tympanic and concomitant reduction in postglenoid size, the tympanic replaces the postglenoid as the posterior wall of the fossa, as is observed in *Homo* (Kimbel et al., 2004). Additionally, the preglenoid plane is markedly reduced in overall size, both in AP and ML dimensions. The morphology of the entoglenoid is particularly of note, as the articular eminence is twisted so that the entoglenoid is directed posteriorly, overlapping the tympanic element and creating a unique morphology: the "medial glenoid plane" as termed by DuBrul (1977). This researcher devotes a significant amount of time to discussion of this character, as it is distinct from that observed in *A. africanus*. As noted by DuBrul (1977: 315, italics in original):

> "Medially, however, the eminence has no wall. As the articular eminence was lowered anteriorly to increase its steepness the entoglenoid process was rotated up and back to wall the fossa instead of the eminence. The lower border of the process… is well rounded and forms an extensive *medial* glenoid plane."

Thus, in essence the medial glenoid plane of DuBrul is a flattened platform between the medial edge of the articular fossa and the foramen ovale (Kimbel et al., 2004). DuBrul (1974, 1977) hypothesized that the small, posteriorly directed entoglenoid, which helps to form the "medial glenoid plane," would be necessary in taxa that require increased excursion of the mandibular condyle during mastication.

As noted, the morphology of the glenoid region in *A. boisei* is highly derived. Furthermore, this morphology shares many similarities with the morphology of the glenoid region in modern humans. Another quote from DuBrul (1974: 26) sums this similarity up nicely: "This entire arrangement is amazingly similar to that of modern man except for its enormous dimensions."

In contrast to the synapomorphic morphologies of *A. robustus* and *A. boisei*, the glenoid fossa of *A. aethiopicus* is distinctly *dissimilar* in morphology, with the majority of the glenoid composed of primitive, rather than derived features (Kimbel et al., 1988; Leakey and Walker, 1988; Kimbel et al., 2004). This distinction is notable, as the type specimen for this species has also been considered instead to be an early representative of *A. boisei* (Walker et al., 1986). If this is the case, this early specimen could represent a more generalized form, which eventually evolved into the highly apomorphic morphology traditionally linked to *A. boisei* (Kimbel et al., 2004). Nonetheless, this specimen, KNM-WT 17000, retains the primitive glenoid shape, characterized by a shallow fossa with a large preglenoid plane and a large, laterally placed postglenoid process that is separated from the tympanic. Moreover, twisting of the articular eminence and posterior inclination of the entoglenoid are conspicuously lacking in this taxon.

In general, the morphology of the glenoid region in the robust australopiths can be summed up as more “closed” in shape, with a raised articular eminence and anteroposteriorly compressed articular surface with a small preglenoid plane. Furthermore, the joint surface area is considerably larger in the robust australopiths when compared to either *A. afarensis* or *A. africanus*. These morphological changes are consistent with an increase in joint reaction forces at the TMJ as might be associated with increased reliance on the posterior dentition for masticatory behaviors. This interpretation is unsurprising given the massive postcanine dentition of the robust australopiths and the overall robusticity of their masticatory apparatus, which strongly suggests extensive use of the postcanine dentition for the mastication of resistant food objects (Tobias, 1967; Rak, 1983; Demes and Creel, 1988; Kay and Grine, 1988; Hylander, 1988; Wood, 1991; Wood and Strait, 2004; Constantino, 2007; Wood and Constantino, 2007).

Given the data presented here, the robust australopith glenoid configuration further suggests that this taxon had smaller linear gapes (as evidenced by AP compression of the joint), although AP length of the joint decreases considerably from *A. aethiopicus* to *A. robustus* and finally to *A. boisei*. This suggests that *A. aethiopicus* retained a relatively large gape in association with relatively larger anterior dentition (Walker et al., 1986; Kimbel et al., 1988). Inclination of the articular eminence also appears to increase from *A. aethiopicus* to *A. boisei*; this morphology is most likely correlated with the increased height of the TMJ above the occlusal plane in these taxa. These findings, along with the reduced anterior dentition of these species (Tobias, 1967; Hylander, 1975a; Wood, 1991; Wood and Constantino, 2007; Kimbel and Delezene, 2009) strongly indicate that these species did not rely on the anterior dentition for food processing.

The morphology of the entoglenoid process is unique in *A. boisei*. The analyses presented here found mixed results for the hypothesis that entoglenoid variation is associated with overall size of the joint and processing and/or mastication of resistant food-objects. Several taxa examined here (*Cebus apella* and *Pongo pygmaeus*) that process hard food objects were actually found to have relatively smaller entoglenoid processes than other closely related species. It was therefore suggested that the small entoglenoid processes in these taxa facilitated use of the anterior dentition during food processing. This interpretation may be generalized to indicate increased mediolateral movement of the mandible during food processing, which would be facilitated by a relatively small entoglenoid process. This finding is consistent with DuBrul's (1974, 1977) hypothesized function for the "medial glenoid plane" of *A. boisei*, and suggests that masticatory behaviors in this species involved considerable amount of mediolateral movement of the mandible (as recently discussed by Rak and Hylander, 2008).

The genus *Homo*. Descriptions of the glenoid region in the genus *Homo*, while still figuring prominently in the literature, seem somewhat less detailed, and are primarily embedded within more general descriptions of individual crania (e.g., Rightmire, 1993; Delson et al., 2001). Furthermore, understanding these descriptions is complicated by a lack of standardized terms for many of the characters being discussed (i.e., the articular tubercle, 'Glaserian fissure' and medial recess of Weidenreich [1943]), and somewhat nebulous descriptions of morphology for particular taxa or specimens which are phrased only in relation to other taxa. For instance, many authors state that the glenoid of *H. habilis* is shallower than in *H. erectus* (Picq, 1990; Martinez and Arsuaga, 1997), but what does such a statement imply—especially in light of the fact that there is a large amount of variation in this character in *H. erectus*? These problems make comprehensive descriptions of the glenoid for several of the species of *Homo* difficult. Compounding this is the fact that few empirical analyses of variation in temporal bone morphology have been conducted for these taxa (but see Martinez and Arsuaga, 1997).

With the appearance of early *Homo* (which here includes both *H. habilis* and *H. rudolfensis*), the glenoid region is much more modern human-like. The early *Homo* glenoid is frequently categorized as being narrow and deep, with an articular eminence that is more pronounced than in the gracile australopiths (i.e., *A. anamensis*, *A. afarensis, A. africanus*), but which is flatter on average than in *H. erectus* and later *Homo*, with the possible exception of Neandertals (Sherwood, 1995; Martinez and Arsuaga, 1997). Deepening of the fossa is, as in the robust australopiths and modern humans, primarily a consequence of the vertical reorientation of the tympanic plate, which is merged with a reduced postglenoid process (Kimbel, 1986; Kimbel and Rak, 1993), as well as a slightly more inclined articular eminence (Martinez and Arsuaga, 1997). Early *Homo* is also unique in that this taxon has a preglenoid plane which is reduced in size and is directed anteriorly, rather than inferiorly (Kimbel, 1986). Medially, the articular eminence is not twisted, and the entoglenoid process, which is reduced in size, is relatively small in comparison to the australopiths. Within this group, Wood (1993) recognizes two distinct species: *H.habilis* and *H. rudolfensis*, and cites a shallower glenoid fossa as one of the characters differentiating these two taxa, with *H. habilis* having a deeper glenoid fossa than *H. rudolfensis*, although few details regarding this distinction are provided and this difference is not quantified.

The condition of the glenoid in *Homo erectus* (sensu lato) has been better described in the literature, primarily as a result of disputes regarding taxonomic diversity within this species (i.e., are the African specimens more appropriately attributable to *H. ergaster*? [e.g., Wood, 1984; Andrews, 1984]), as well as the detailed analysis of temporal bone morphology discussed for the *Sinanthropus* materials from Zhoukoudian by Weidenreich (1943). The glenoid of the African specimens is on average more similar to the early *Homo* condition described above; the articular eminence is more gently sloping, with a deeper glenoid fossa than in early *Homo*, as well as a reduced postglenoid that is merged with the tympanic. The preglenoid plane appears to be approximately the same size as in early *Homo*, and the articular eminence is not twisted and terminates medially in a large, inferiorly projecting entoglenoid process.

In contrast, the condition observed in the Asian *H. erectus* specimens is more derived, with a glenoid that is, on average, considerably reduced in size in comparison to the African specimens, and is also markedly deeper. This deepening is a result of a highly angled articular eminence, as well as a marked anteroposterior compression of the fossa, which is coincident with a reduction in size of the preglenoid plane (a feature which in some specimens is virtually non-existent) (Weidenreich, 1943; Condemi, 1989; Pope, 1992; Etler, 1994; Martinez and Arsuaga, 1997; Terhune et al., 2007). Medially, the articular eminence is twisted, and the reduced entoglenoid is directed slightly posteriorly and inferiorly (Weidenreich, 1943; Howells, 1980; Rightmire, 1985, 1993; Martinez and Arsuaga 1997).

Like early *Homo* and *Homo erectus* (s.l.), the collection of specimens frequently referred to as “Archaic *Homo sapiens*” or generally *H. heidelbergensis* (Stringer et al., 1979; Rightmire, 1993, 1998; Clarke, 1990; Martinez and Arsuaga, 1997; Arsuaga et al., 1997; Manzi et al., 2003) also displays a large amount of variation in glenoid morphology. The glenoid fossa morphology of the Middle Pleistocene specimens from Africa is, on average, distinct from that of the European specimens (Martinez and Arsuaga, 1997), although further research is necessary to quantify any such differences. In comparison to the earlier African specimens that have been attributed to *H. erectus*, the glenoid fossa is deeper in the African Middle Pleistocene specimens (e.g., Omo 2, ES-11693, Kabwe), which have a steeper articular eminence; how this morphology compares to the Asian representatives of *H. erectus* is unclear, however, although Martinez and Arsuaga (1997) place the articular eminence in *H. erectus* (s.l.) at approximately the same degree of slope as found in the African Middle Pleistocene specimens. In contrast, the articular eminence of the European specimens (as represented primarily by the Sima de los Huesos remains) is much more gradually sloping, with a shallower glenoid fossa overall (Arsuaga et al., 1993; Martinez and Arsuaga, 1997).

As demonstrated by Martinez and Arsuaga (1997), the postglenoid process in African *H. heidelbergensis* is approximately the same size as that of African *H. erectus*, both of which fall within the size range of modern humans. In contrast, the postglenoid of Asian *H. erectus* is smaller than in both of these taxa; moreover, it is also considerably smaller than the postglenoid of the European *H. heidelbergensis* specimens, which is large and inflated (Arsuaga et al., 1993; Martinez and Arsuaga, 1997). The features of the medial portion of the glenoid fossa in both the African and European *H. heidelbergensis* specimens have rarely been described other than to say that the entoglenoid is large and inferiorly projecting (Rightmire, 1993). This finding is consistent with observations by the author that suggest that the twisting of the articular eminence is variable within both of these groups, although this feature needs to be quantified in further detail for any substantial conclusions to be drawn.

More authors have evaluated the morphology of the Neandertal glenoid region than of the *H. heidelbergensis* samples discussed above. However, analyses focusing on the temporal bone in Neandertals tend to dwell on the unique morphology of the mastoid region in this taxon (Weidenreich, 1943; Vallois, 1969; Vandermeersch, 1981; 1985; Stringer and Trinkaus, 1981; Trinkaus, 1983; Aiello and Dean, 1990), rather than the morphology of the mandibular fossa. Consequently, concrete comparative data are still relatively rare (but see Martinez and Arsuaga, 1997). Further complicating matters, though, is the debate regarding the morphology of the glenoid. While most authors agree that the glenoid fossa is very large (Smith, 1976; Vallois, 1969; Stringer and Trinkaus, 1981) and that the articular eminence is flattened (Vandermeersch, 1981; Trinkaus, 1983; Condemi, 1989; Aiello and Dean 1990; Bar Yosef and Vandermeersch, 1991; Martinez and Arsuaga 1997) there is debate regarding the size and development of the postglenoid process. Some authors have suggested that Neandertals have a mediolaterally well developed postglenoid that forms the posterior wall of the articular fossa (Vandermeersch, 1981; Condemi, 1989; Bar Yosef and Vandermeersch, 1991). Others, (Martinez and Arsuaga, 1997) suggest that the height of the postglenoid is the same as observed in modern humans, which is inconsistent with previous descriptions of a well developed postglenoid in this taxon (Vallois, 1969; Smith, 1976).

Few authors have made reference to the size or projection of the entoglenoid in Neandertals or to the twisting of the articular eminence, though observations made in association with this discussion would suggest that, while twisting of the articular eminence is variable (and also hard to assess given the high degree of degenerative remodeling that has taken place on some of the Neandertal glenoids), the entoglenoid is well developed and appears to project inferiorly, rather than infero-posteriorly.

These descriptions indicate that, although the glenoid morphology of the genus *Homo* is more derived than that of the gracile australopiths, the morphology of this region begins primitively in early *Homo* and becomes more derived in younger taxa. In early *Homo*, the glenoid is considerably more australopith like, with a larger preglenoid plane and relatively flat articular eminence. The morphology of African *H. erectus* is also primitive, and it is not until Asian *H. erectus* and *H. heidelbergensis* that the morphology of the glenoid becomes more similar to the modern human configuration. These data suggest that masticatory function may have been similar in the gracile australopiths and early *Homo*, particularly in regard to the degree of anteroposterior translation at the glenoid, and that geologically younger taxa may have had decreased translatory potential (and joint reaction forces?) at the TMJ. Neandertals may represent a departure from this pattern however; if the joint surface areas of Neandertals are indeed larger than in *H. heidelbergensis*, this may suggest increased loading of the TMJ during masticatory (or paramasticatory) behaviors.

Some of the observed variation in TMJ shape in the genus *Homo* may be correlated with height of the TMJ above the occlusal plane. Few data regarding variation in this feature are available, however, as a result of infrequent fossilization of the entire ascending ramus of the mandible. Several authors have discussed the very low glenoid of Neandertals (Rak et al., 2003; Nicholson and Harvati, 2006), which is consistent with the relatively flat articular eminence observed in this species. More data are necessary to determine whether variation in articular eminence inclination across hominins is a function of TMJ height above the occlusal plane.

One further consideration is variation in entoglenoid morphology. Although the entoglenoid is generally smaller in *Homo* than in the australopiths, the descriptions provided above seem to indicate that entoglenoid shape varies considerably among taxa. However, few of these descriptions directly compare entoglenoid shape among species, and therefore it is unclear which species possess relatively larger or smaller processes. This present lack of comparative data across hominins precludes any meaningful discussion of what this variation may signify in regard to masticatory function.

Trends in fossil hominin glenoid morphology. The goal of this review was to highlight the large amount of variation in glenoid fossa form throughout the hominin lineage. In general, the glenoids of the earliest hominins are very ape-like in character, with very little relief (i.e., a very flat articular eminence), enlarged surface areas, and an anteroposteriorly elongated joint. This morphology, along with other features of the masticatory apparatus and dentition, suggest that these species tended to rely more heavily on use of the anterior dentition for food processing. In contrast, more derived morphologies, as observed in the robust australopith species as well as later *Homo*, indicate a shift toward more intensive use of the posterior dentition and/or decreased reliance on the anterior dentition. This is evidenced primarily by changes in joint surface area and anteroposterior dimensions of the joint. In the case of the robust australopiths, joint surface area is considerably larger than earlier species, indicating increased joint reactions forces as would be associated with mastication of very resistant food objects. For species of later *Homo*, joint surface areas do not appear to change considerably among species (except possibly in Neandertals), but the glenoid becomes considerably more anteroposterioly compressed, perhaps indicating decreased relative gape in these species.

All of these findings are strongly consistent with previous analyses of masticatory variation across the hominin lineage that indicate an increase in masticatory size likely associated with the use of more resistant food objects (Walker, 1981; Teaford and Ungar, 2000; Wood and Strait, 2004; Laden and Wrangham, 2005; Constantino, 2007; Ungar, 2007; Kimbel and Delezene, 2009). This initial trend culminated in the extreme masticatory configuration observed in the robust australopiths, and was followed by a gradual gracilization of the masticatory apparatus in the genus *Homo*, which may have been associated with an increase in premasticatory food processing (e.g., cooking) (Ungar et al., 2006; Ungar, 2007 and chapters therein).

Future research questions

If there is one conclusion that can be drawn from the data above, it is that there is considerable variation in glenoid morphology across extinct hominins. However, the data presented above are all qualitative; more quantitative data are necessary to fully evaluate differences in TMJ morphology across fossil hominin species. Knowledge of this variation may be useful for elucidating differences in masticatory function among species, and/or could be indicative of body size differences among taxa. Analyses of TMJ scaling may be particularly useful in this regard. Given the suggestion that dietary resistance decreased through time in the genus *Homo* (likely as a function of increased premasticatory food processing; Ungar et al., 2006; Ungar, 2007), we might hypothesize a negatively allometric relationship between body/ cranial size and TMJ surface area in this genus. If dietary resistance increased through time in the australopiths (Walker, 1981; Teaford and Ungar, 2000; Wood and Strait, 2004; Laden and Wrangham, 2005; Ungar, 2007; Kimbel and Delezene, 2009) then we may expect a positively allometric relationship between glenoid area and body/cranial size in this clade, as was observed for the extant taxa examined here. Furthermore, changes in TMJ shape throughout hominin evolution may have been a consequence of the trade-off between relative gape and height of the TMJ above the occlusal plane (Hylander and Vinyard, 2006; Hylander et al., 2008). More comprehensive data regarding TMJ height is therefore necessary to evaluate this relationship.

Given the above review of glenoid morphology in hominins, there are several specific research questions that can be addressed by the research protocol presented here. The morphologies of the modern human and robust australopith glenoid fossae are remarkably similar. A number of authors have discussed this resemblance (DuBrul, 1974, 1977; Kimbel et al., 1984, 2004), and attention has also been drawn to similarity in the morphology of the basicranium in these two groups (Dean and Wood, 1981, 1982). Many current cladistic reconstructions regard *Homo* and the robust australopiths as sister taxa, although *A. africanus* is also frequently included as a sister taxon to the robusts. These reconstructions therefore suggest two possible reasons for the morphological similarities between *Homo* and the robust australopiths; these characters are either homoplastic or homologous. However, the discovery of *A. aethiopicus*, which is considered a basal robust australpith that is considerably morphologically more primitive than *A. boisei* and *A. robustus,* suggests that the apomorphies of the robust and human TMJ discussed above are homoplastic, rather than synapomorphic (Wood, 1988; Kimbel et al., 1988; Kimbel et al., 2004). In fact, Kimbel et al. (1984, 2004) identified a number of derived characteristics shared by *Homo*, *A. robustus*, and *A. boisei* (e.g., an anteriorly placed and horizontal foramen magnum, vertically oriented tympanic plates and coronally oriented petrous bones, and a strong rounded articular eminence) that they identified as being homoplastic as a result of increased flexion of the cranial base and upper facial orthognathism. Preliminary analyses conducted for this dissertation, however, evaluated the correlations among these features in anthropoid primates, and only found weak correlations between basicranial length and glenoid length (r=0.41, p=0.04) and between degree of prognathism and articular eminence inclination (r=0.486, p=0.043); neither correlation was significant after Bonferroni correction.

Many studies have focused primarily on the implications of similarities among robust australopith species for reconstructing phylogenetic relationships (Kimbel et al., 1984; Skelton and McHenry, 1992; Strait, 1998, 2001; Kimbel et al., 2004; Villmoare, 2008), and several possible functional implications of this morphology have been suggested (DuBrul, 1974, 1977). Additional quantification of the TMJ in the robust australopiths, particularly in comparison to members of the genus *Homo*, would prove useful in understanding specifically how similar these morphologies truly are, and in placing these morphologies into a broader context describing variation in the primate TMJ. Analyses of masticatory function which compare and contrast the robust australopith and modern human masticatory apparatus would further assist in determining whether the observed similarities in TMJ morphology are functionally analogous.

Temporomandibular joint variation may also be useful for evaluating the validity of the anterior dental loading hypothesis (ADLH) (Smith, 1983; Rak, 1986; Spencer and Demes, 1993) which has been proposed to explain variation in Neandertal cranial morphology. This hypothesis states that the unique morphology of the Neandertal facial skeleton (e.g., large anterior dentition, marked midfacial prognathism, a retromolar space, an anterior broad and squared off palate, backward sweeping zygomatic arches, etc. [Howells, 1974; Smith, 1983; Stringer et al., 1984; Rak, 1986; Trinkaus, 1987; Smith and Paquette, 1989; Franciscus, 1999, 2003]) is adapted for heavy and/or repeated stresses that result from increased use of the anterior dentition (Smith, 1983; Trinkaus, 1983, 1987; Rak, 1986; Demes, 1987; Spencer and Demes, 1993). Most recently this hypothesis has been evaluated by Spencer and Demes (1993) and O’Connor et al. (2005), but these authors came to contrasting conclusions. Spencer and Demes (1993) evaluated the ADLH in the context of Greaves (1978) biomechanical model of masticatory function and concluded that Neandertals exhibited specializations of the masticatory apparatus that increased the efficiency of inciscal use in comparison to the less specialized early *Homo sapiens* specimens they examined. In contrast, O'Connor et al (2005) also examined the biomechanical configuration of the Neandertal masticatory apparatus in comparison to anatomically modern *H. sapiens*, and concluded that masticatory biomechanics were not the primary selective force by which the Neandertal facial skeleton evolved.

If the anterior dental loading hypothesis is correct, there should be predictable differences in TMJ shape in Neandertals when compared with less specialized "archaic" *Homo sapiens*. Specifically, Neandertals should have relatively larger joint surface areas (which, as discussed above, previous work suggests may be the case), with an anteroposteriorly elongated joint, as would be expected with increased use of the anterior dentition.

CONCLUDING THOUGHTS

The goal of this dissertation was to test a series of predictions designed to investigate the extent to which feeding behavior, body size, and phylogeny influence variation in the shape of the anthropoid TMJ. The results of this study suggest that TMJ morphology covaries significantly with feeding behavior, body size, as well as phylogeny, and therefore these three factors are intertwined. However, the relative influence of each of these factors was found to vary among the taxonomic groups examined. Particularly strong correlations between body size, dietary variation, and TMJ shape were found in the atelines and hominids, potentially suggesting that size and dietary variation covary significantly in these groups.

Several gaps in our current understanding of primate masticatory function were also identified during this research. Our current knowledge regarding variation in food material properties among primate taxa is growing, but still lags behind our knowledge of variation in the morphology of the masticatory apparatus. Enhanced data regarding the frequency at which foods with particular material properties are processed and/or masticated is particularly important for elucidating the extent to which masticatory morphology tracks feeding behavior. Further data are also needed regarding the extent to which anterior versus posterior tooth use impacts the form of the masticatory apparatus. Experimental analyses of masticatory function would be particularly helpful for elucidating whether it is the frequency of bite forces or their peak magnitude which are most important for influencing masticatory shape. Until these data are available, it will be particularly difficult to identify whether critical resources, such as those used during times of food scarcity, are important determinants of masticatory function. In addition, the extent to which the morphology of the TMJ responds to changes in loading during development are critical for understanding the adaptive plasticity of this joint, and further studies of soft tissue variation in the joint are also warranted to fully understand the influence of the articular disc on TMJ function.

Although the TMJ is only a small portion of the skeleton, the morphology of this joint can provide valuable information with which to infer or reconstruct the biology of primate taxa. As reviewed here, there is considerable variation in TMJ shape in fossil hominins, but the implications of this variation are unclear. Several ways in which TMJ morphology can be used to examine fossil hominin variation were subsequently proposed. The findings presented here will hopefully provide a framework within which these future studies of fossil hominin TMJ variation can be evaluated.

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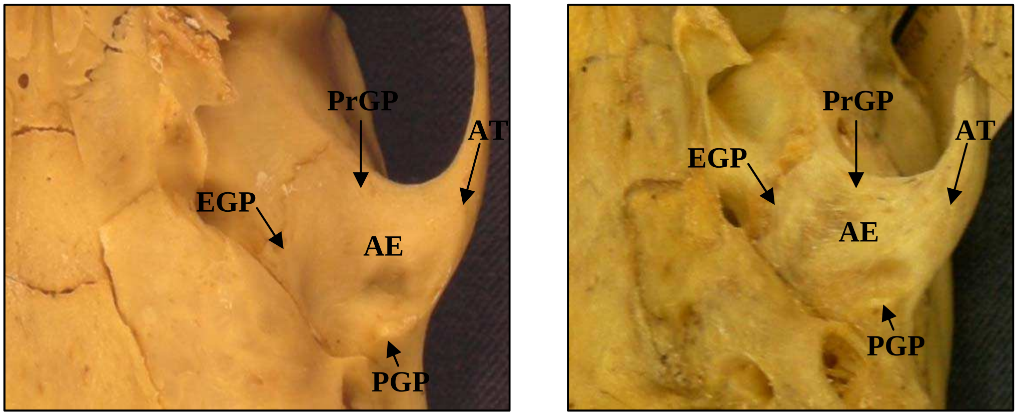
APPENDIX A

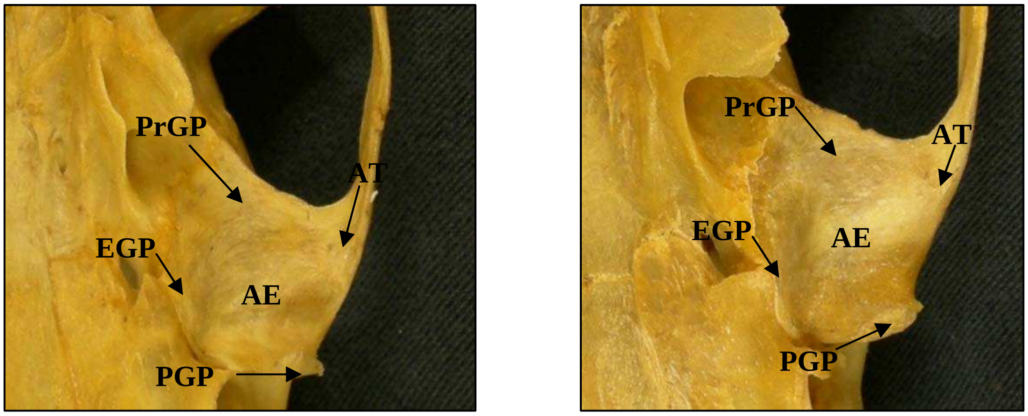
PHOTOS OF GLENOID MORPHOLOGY IN COMPARATIVE GROUPS

This appendix provides photographs of the glenoid morphology for many of the species included in the comparative groups. Where possible, photos of female (left side of page) and male (right side of page) anatomy are shown. All glenoids shown are from the left side of the cranium. Features indicated are the entoglenoid process (EGP), articular tubercle (AT), articular eminence (AE), preglenoid plane (PrGP), and postglenoid process (PGP).

***Ateles geoffroyi* (female/ male)**



***Alouatta seniculus* (female/ male)**



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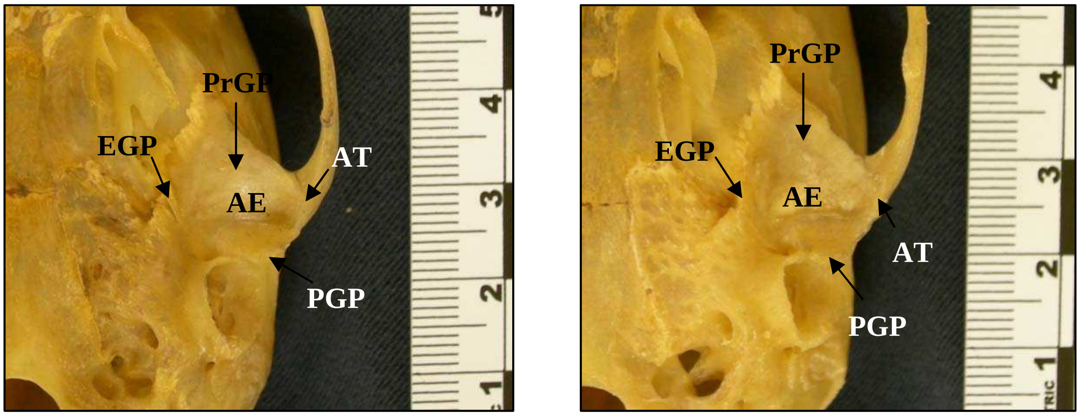
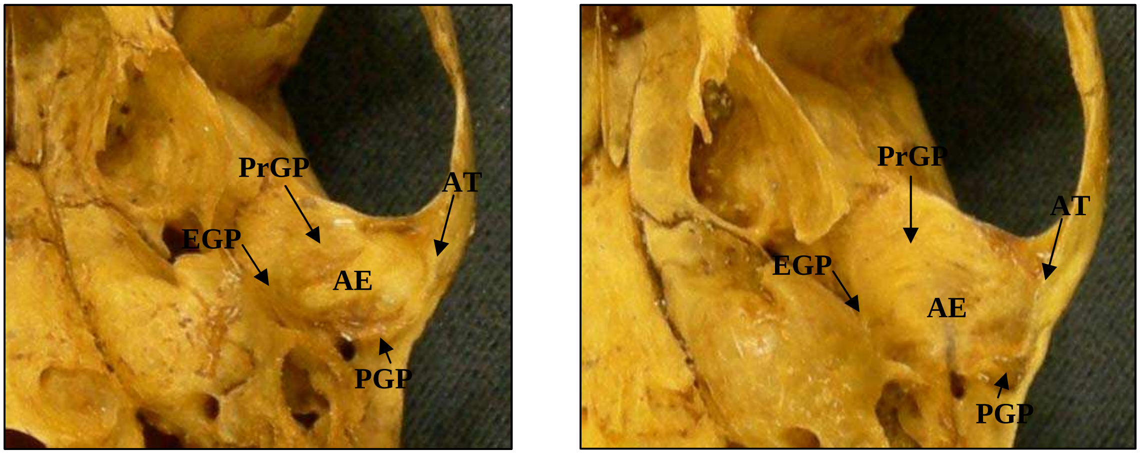
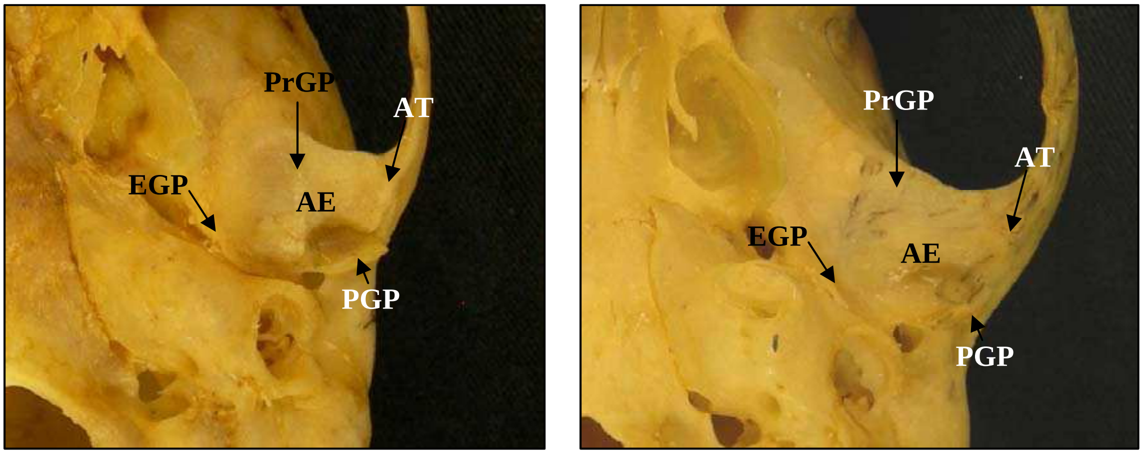


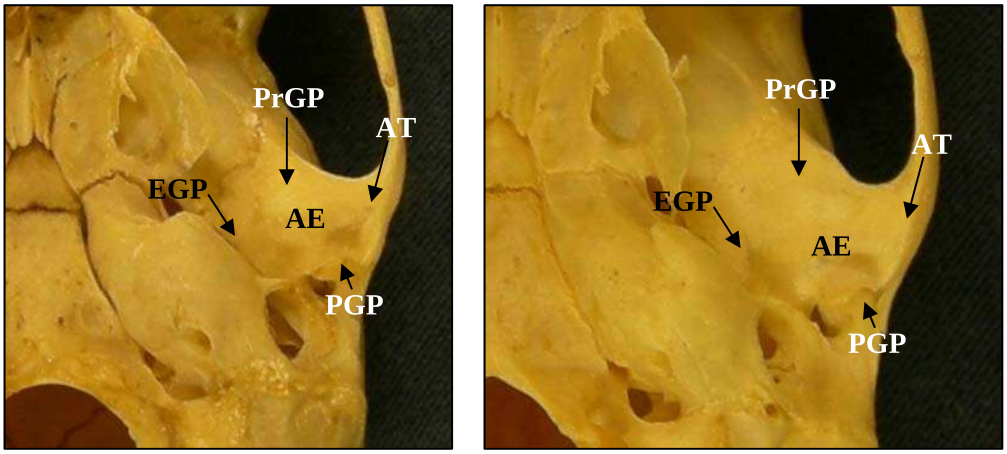
Cebus albifrons **(female/ male)**



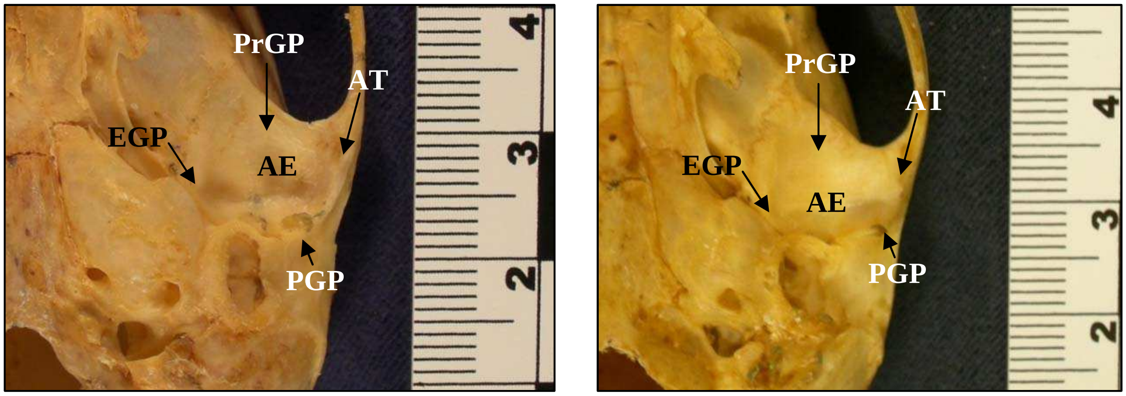
Cebus apella **(female/ male)**



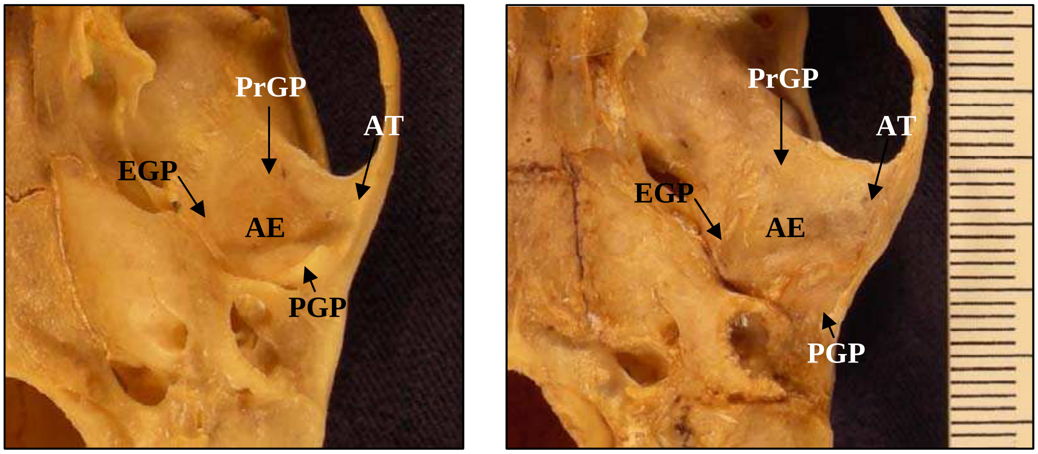
Cebus capucinus **(female/ male)**



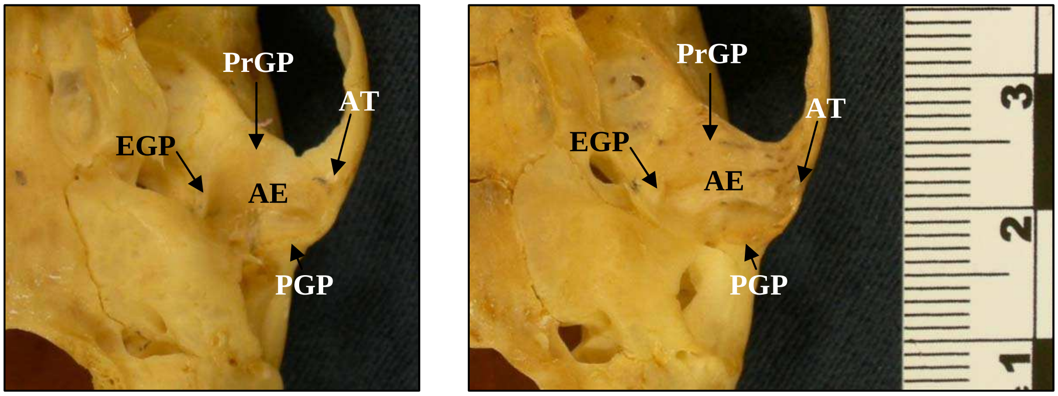
***Cacajao melanocephalus* (female/ male)**



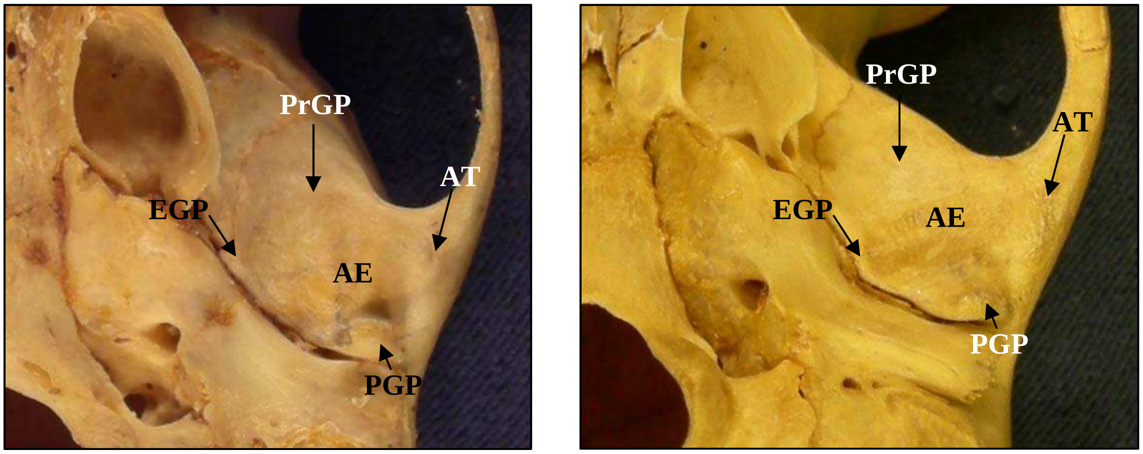
***Chiropotes satanas* (female/ male)**



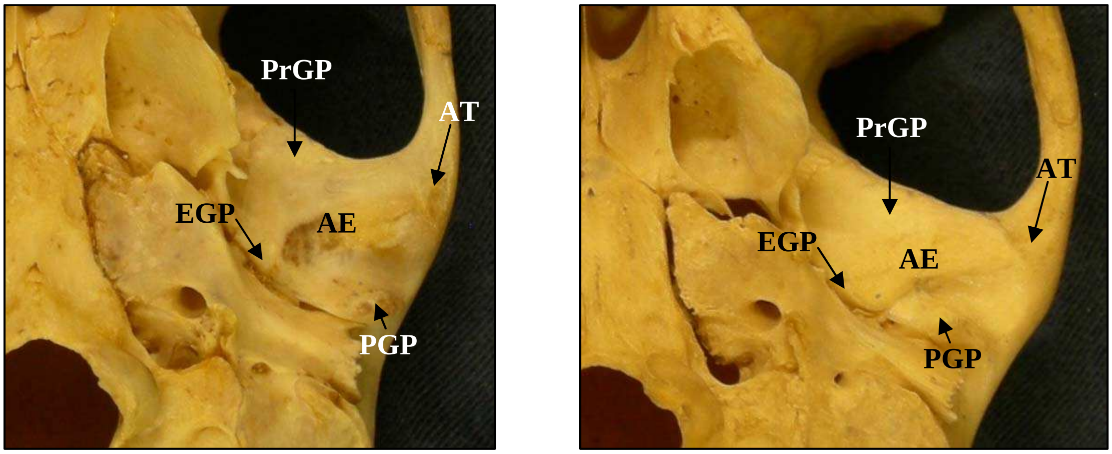
***Pithecia pithecia* (female/ male)**



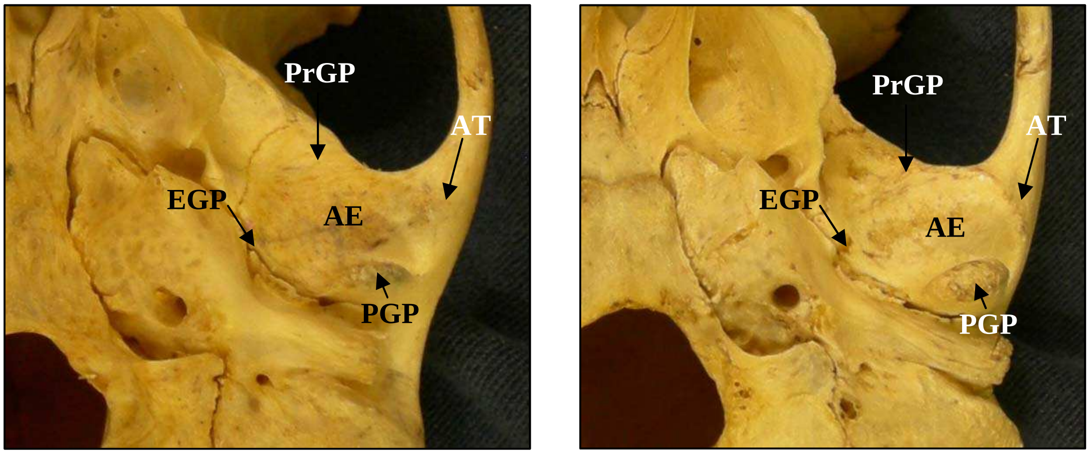
***Macaca fascicularis* (female/ male)**



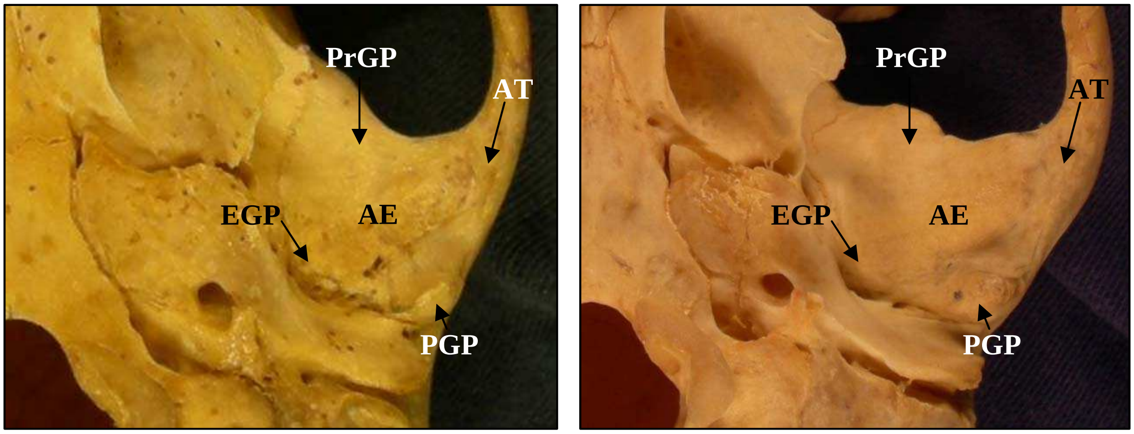
***Macaca fuscata* (female/ male)**



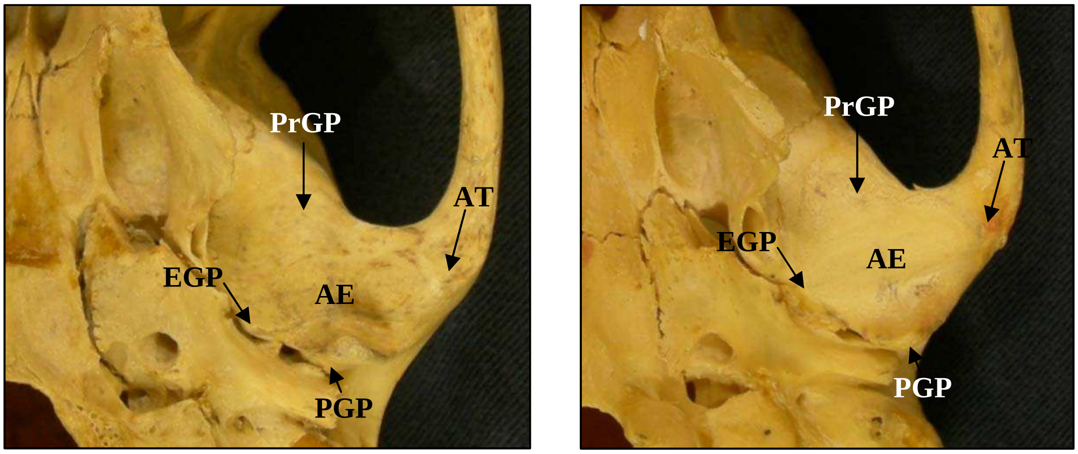
***Macaca nemestrina* (female/ male)**



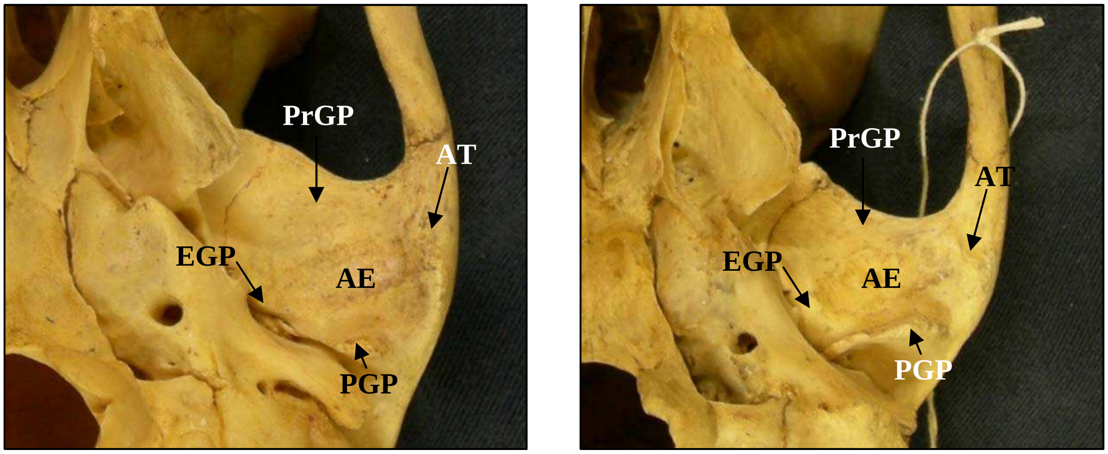
***Macaca sylvanus* (female/ male)**



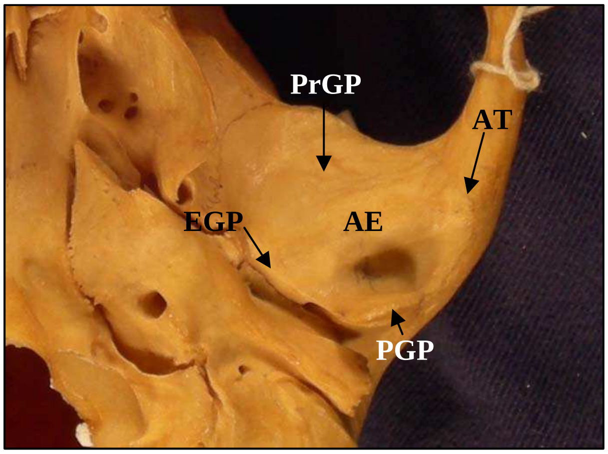
***Macaca thibetana* (female/ male)**



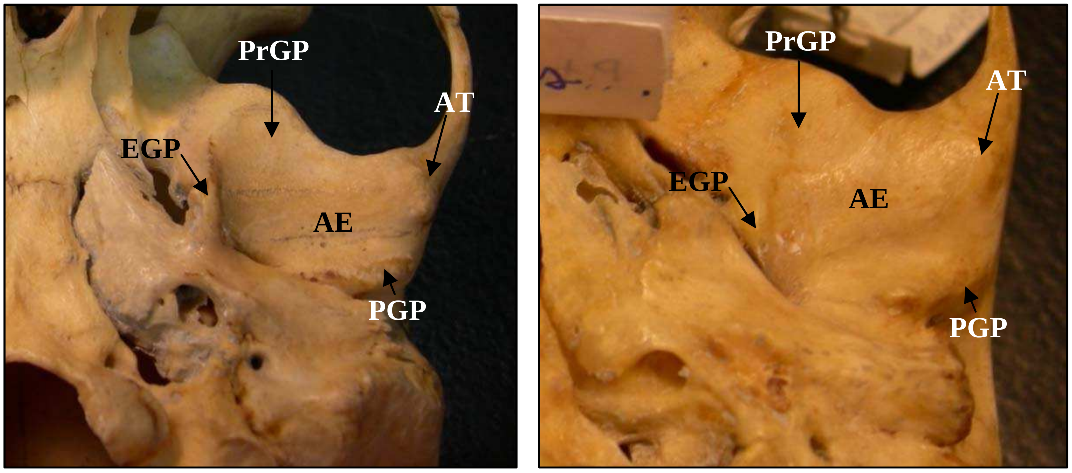
***Papio cynocephalus* (female/ male)**



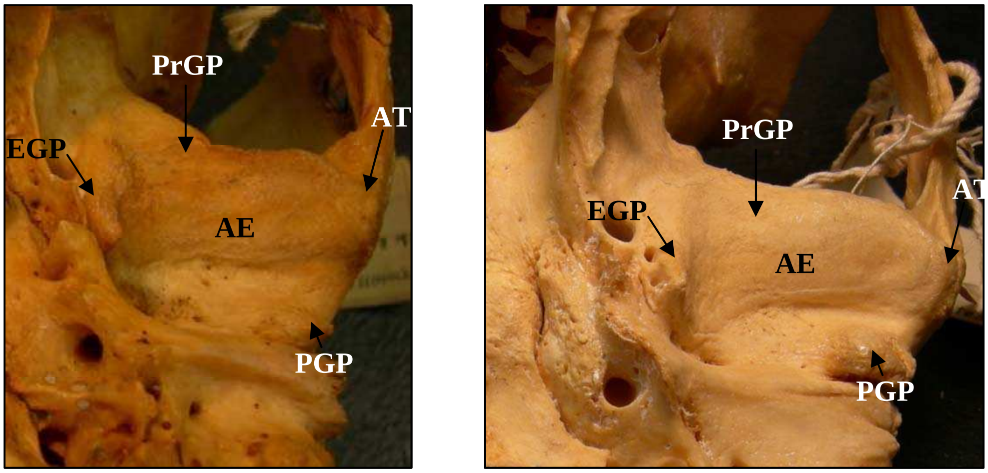
***Theropithecus gelada* (female)**



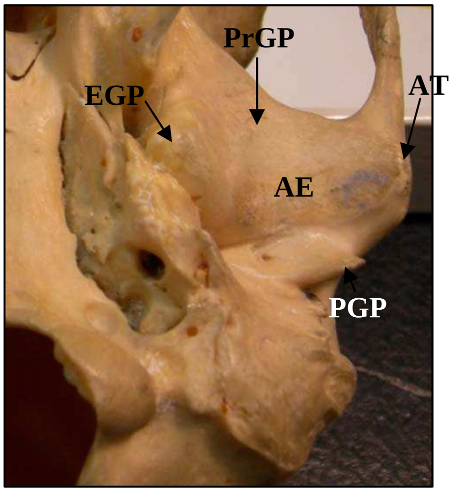
***Pan troglodytes* (male)/ *Pan paniscus* (female)**



***Gorilla gorilla* (female)/ *Gorilla beringei* (female)**



***Pongo pygmaeus* (female)**

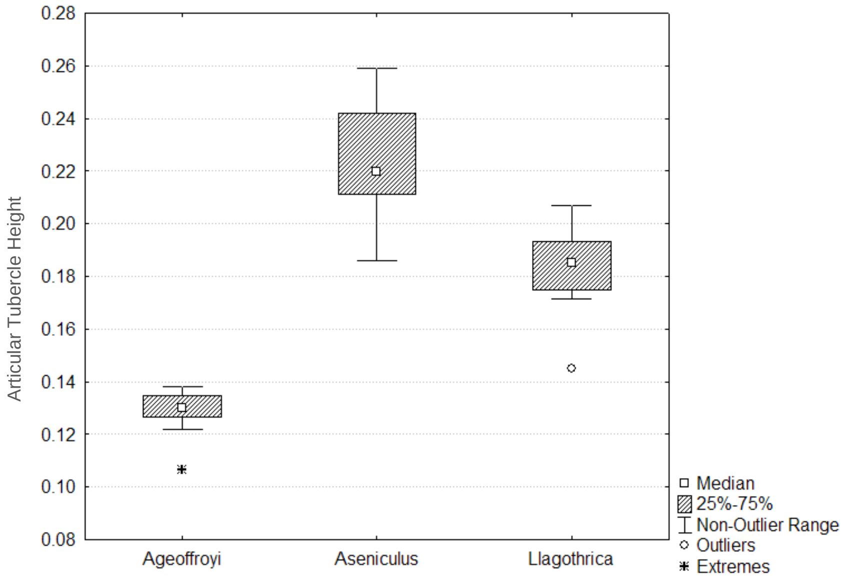


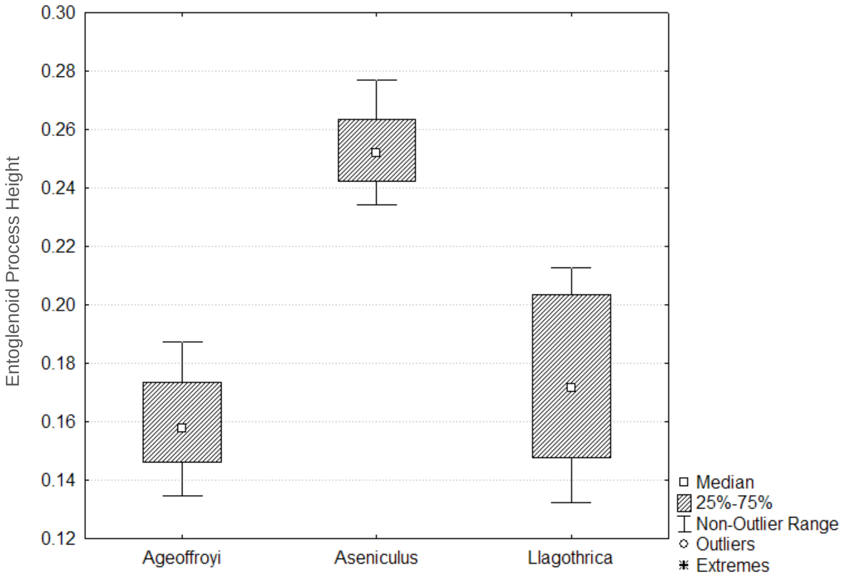
APPENDIX B

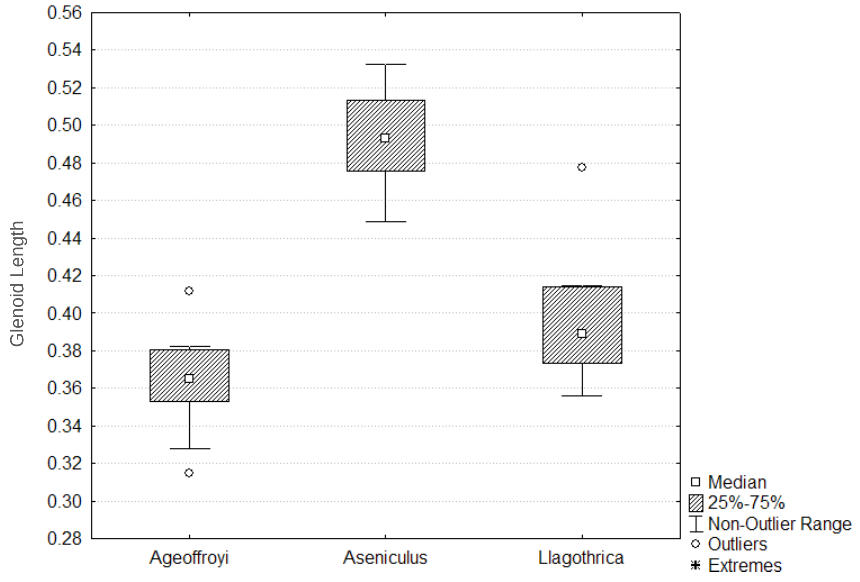
BOX PLOTS FOR COMPARATIVE GROUPS

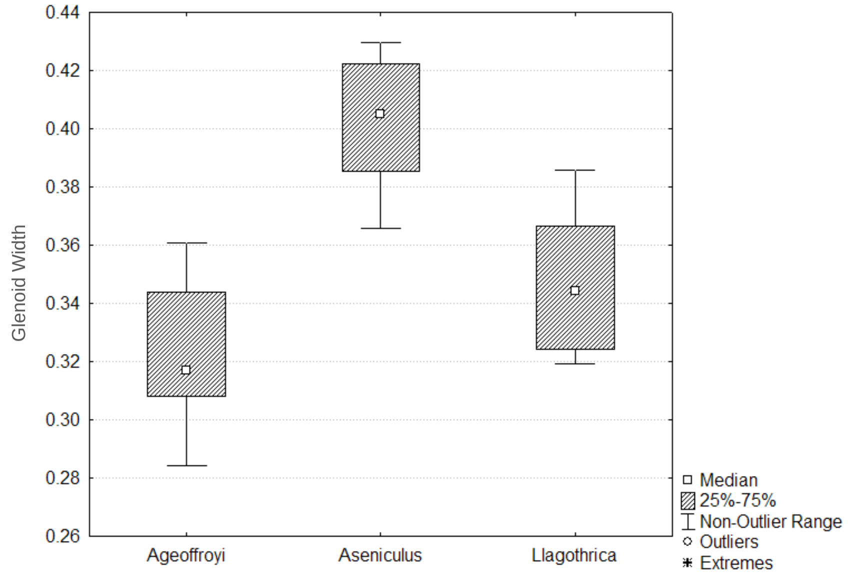
This appendix provides box plots for variables that differ significantly among species in each of the six comparative groups analyzed in Chapter 4. Figures are organized by comparative group, and illustrate the median, 50% confidence interval, outliers, and extreme values for each variable.

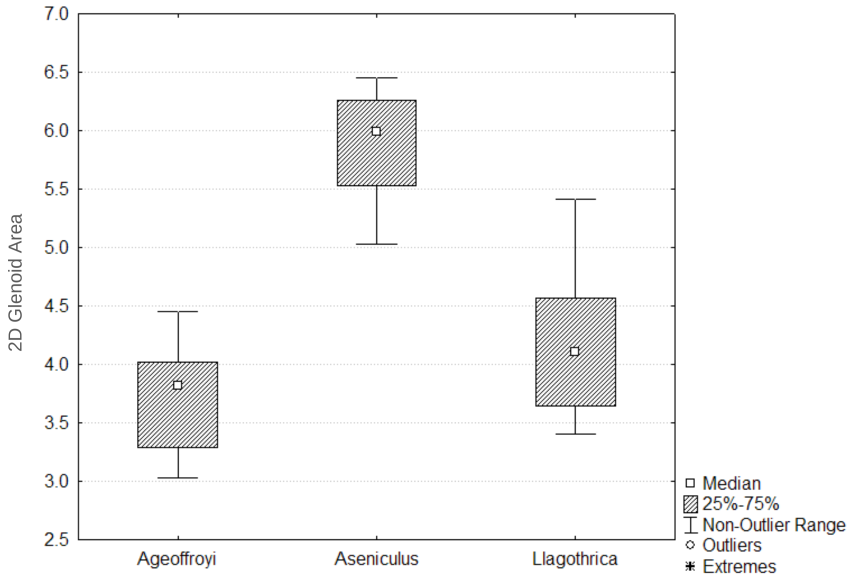
ATELINES

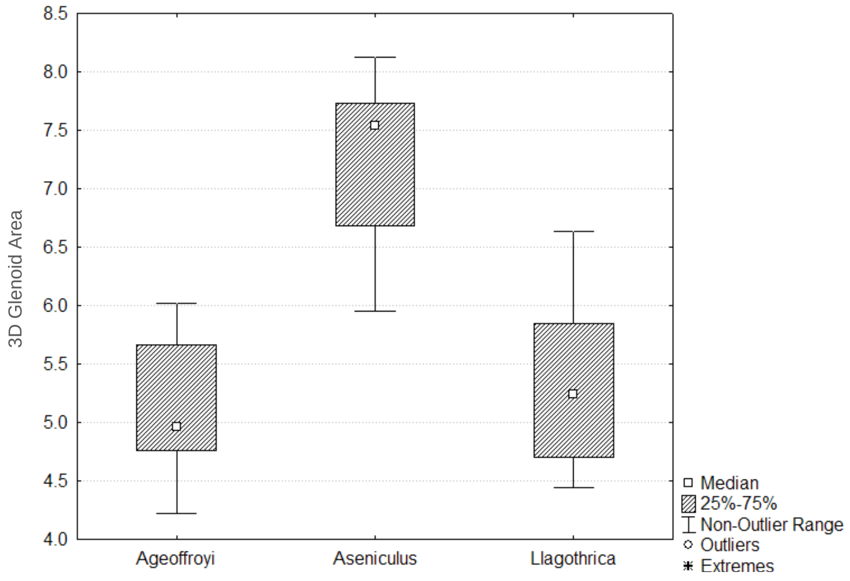


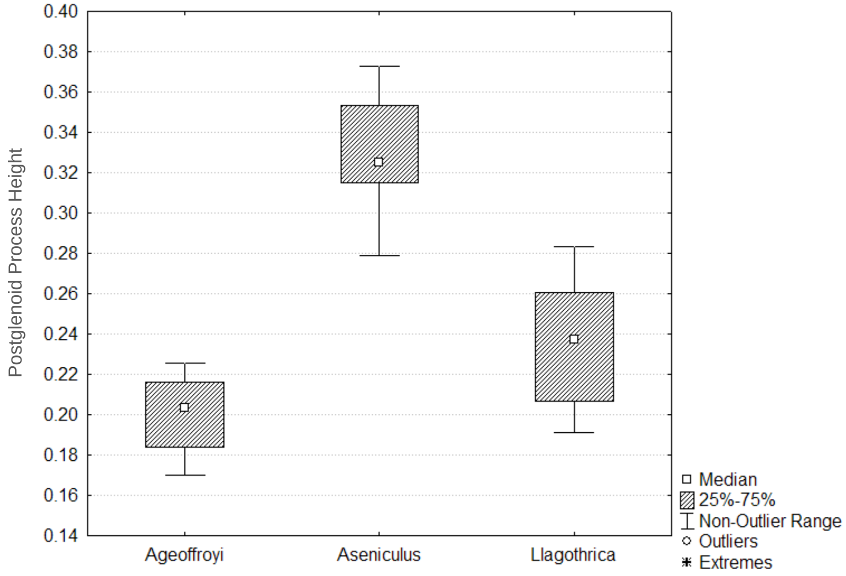


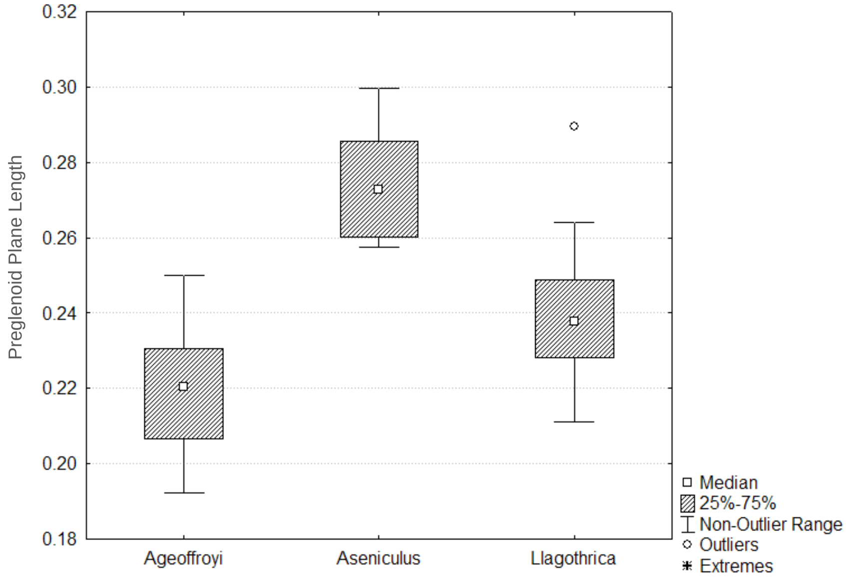

Glenoid Length
0.56
0.54
0.52
0.50
0.48
0.46
0.44
0.42
0.40
0.38
0.36
0.34
0.32
0.30
0.28
Ageoffroyi
Aseniculus
Llagothrica
□ Median
▨ 25%-75%
Non-Outlier Range
○ Outliers
* Extremes

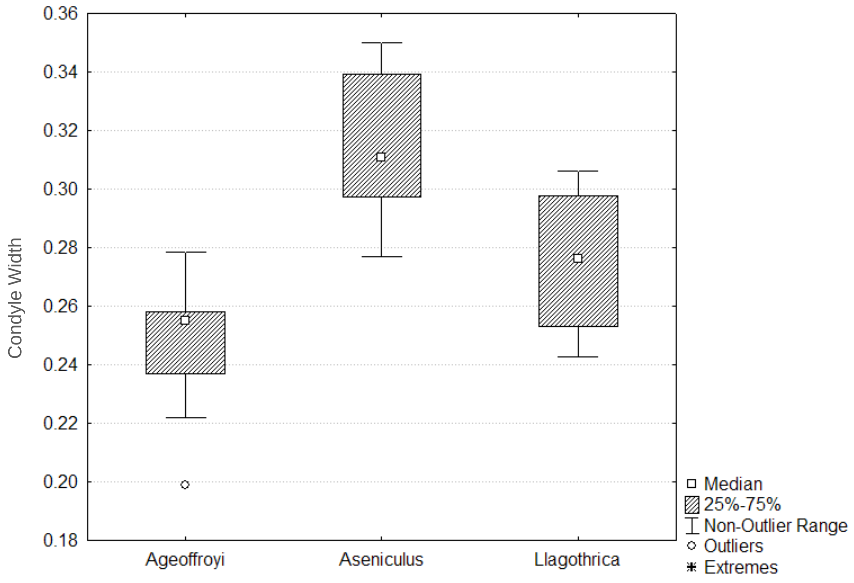

Glenoid Width
0.44
0.42
0.40
0.38
0.36
0.34
0.32
0.30
0.28
0.26
Ageoffroyi
Aseniculus
Llagothrica
□ Median
▨ 25%-75%
Non-Outlier Range
○ Outliers
* Extremes

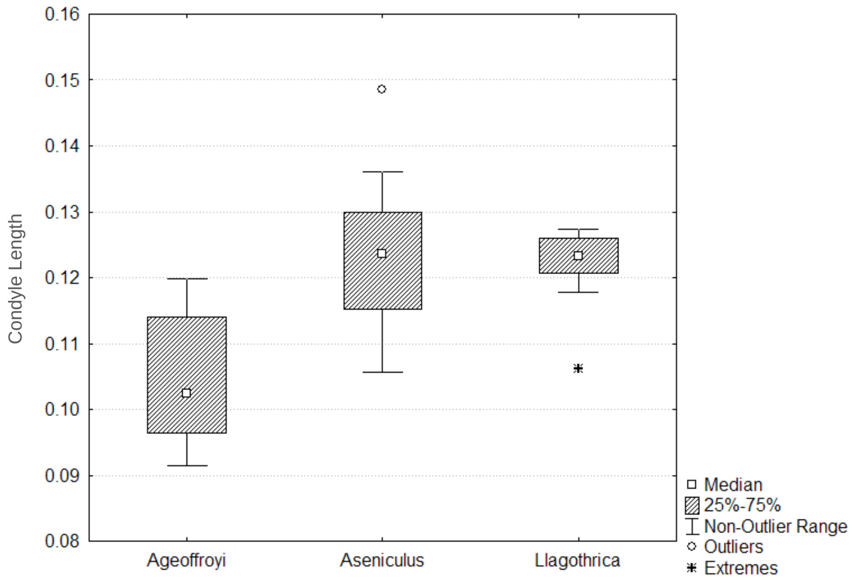

2D Glenoid Area
7.0
6.5
6.0
5.5
5.0
4.5
4.0
3.5
3.0
2.5
Ageoffroyi
Aseniculus
Llagothrica
□ Median
▨ 25%-75%
Ι Non-Outlier Range
○ Outliers
* Extremes

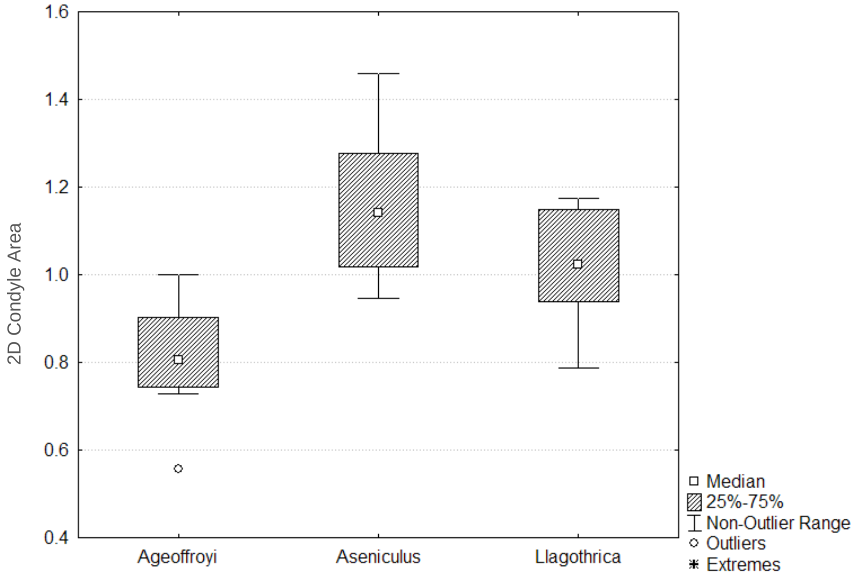

3D Glenoid Area
8.5
8.0
7.5
7.0
6.5
6.0
5.5
5.0
4.5
4.0
Ageoffroyi
Aseniculus
Llagothrica
□ Median
▨ 25%-75%
Ι Non-Outlier Range
○ Outliers
* Extremes

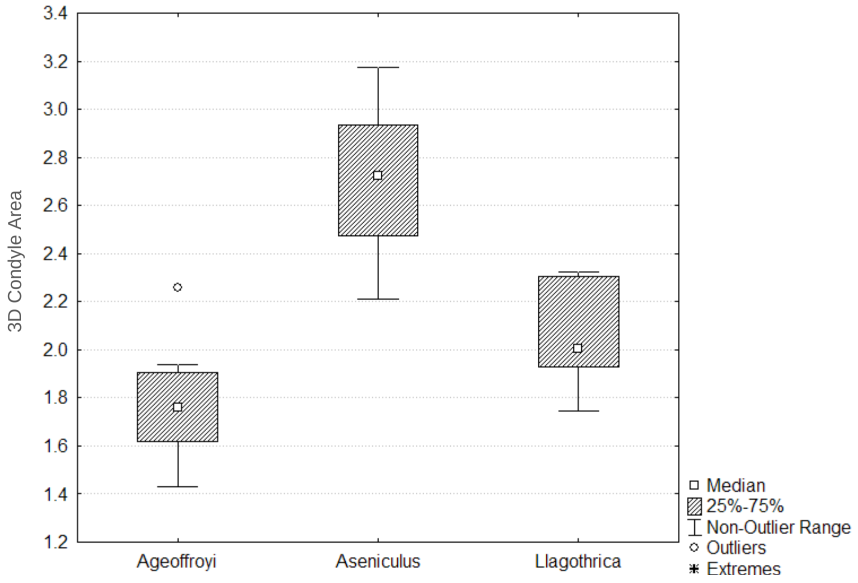

Postglenoid Process Height
0.40
0.38
0.36
0.34
0.32
0.30
0.28
0.26
0.24
0.22
0.20
0.18
0.16
0.14
Ageoffroyi
Aseniculus
Llagothrica
□ Median
▨ 25%-75%
⌶ Non-Outlier Range
○ Outliers
✳ Extremes

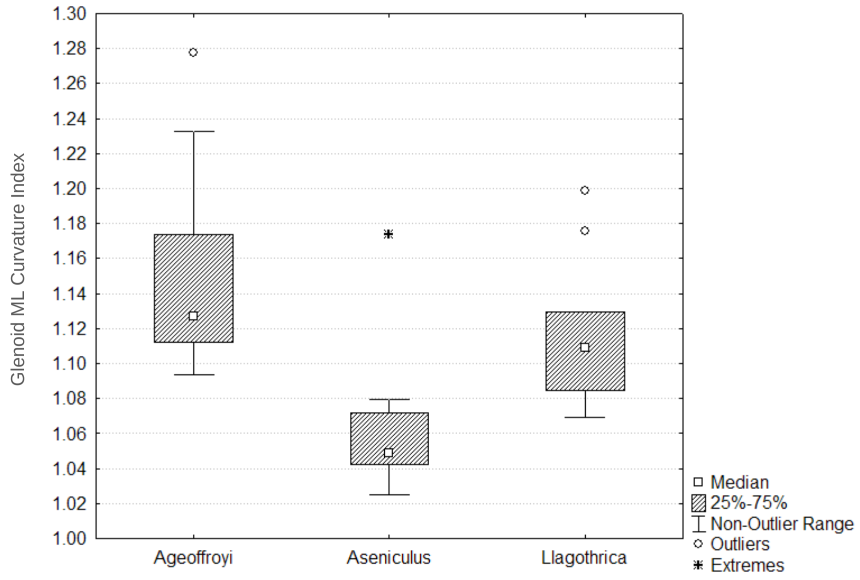

Preglenoid Plane Length
0.32
0.30
0.28
0.26
0.24
0.22
0.20
0.18
Ageoffroyi
Aseniculus
Llagothrica
□ Median
▨ 25%-75%
⌶ Non-Outlier Range
○ Outliers
✳ Extremes


Condyle Width
0.36
0.34
0.32
0.30
0.28
0.26
0.24
0.22
0.20
0.18
Ageoffroyi
Aseniculus
Llagothrica
□ Median
▨ 25%-75%
⌶ Non-Outlier Range
○ Outliers
✱ Extremes

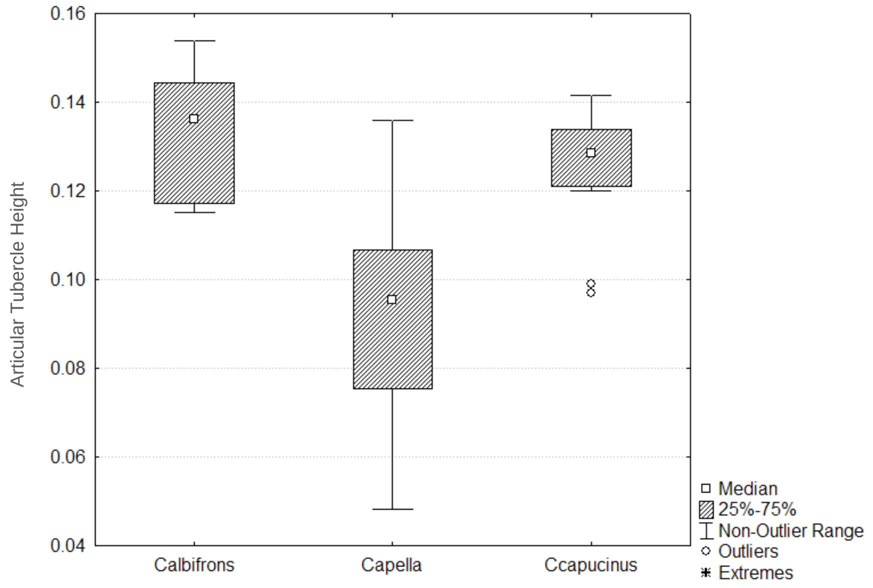

Condyle Length
0.16
0.15
0.14
0.13
0.12
0.11
0.10
0.09
0.08
Ageoffroyi
Aseniculus
Llagothrica
□ Median
▨ 25%-75%
⌶ Non-Outlier Range
○ Outliers
✱ Extremes

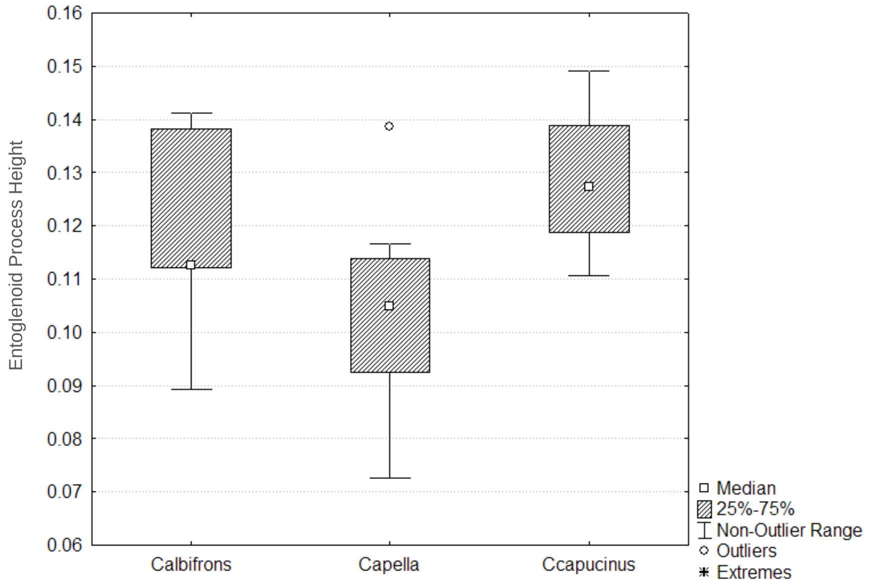

2D Condyle Area
1.6
1.4
1.2
1.0
0.8
0.6
0.4
Ageoffroyi
Aseniculus
Llagothrica
□ Median
▨ 25%-75%
⌶ Non-Outlier Range
○ Outliers
✱ Extremes

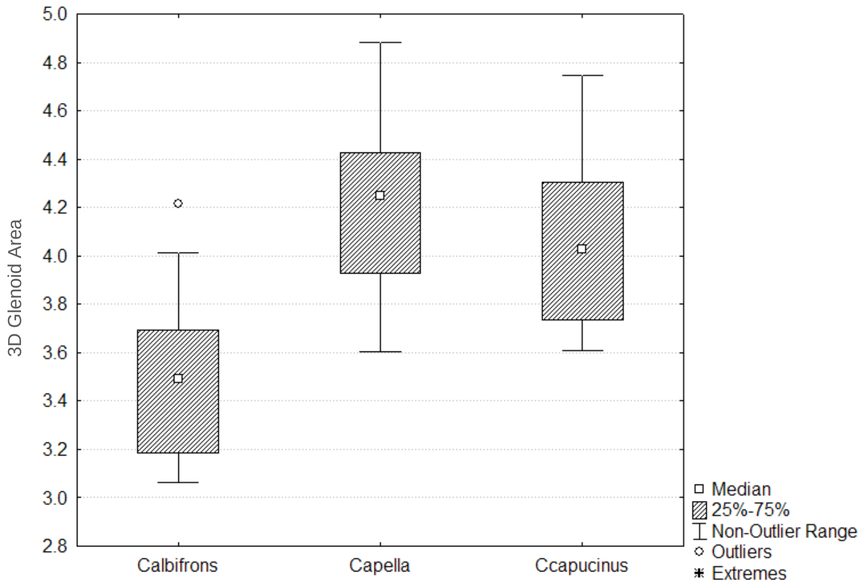

3D Condyle Area
3.4
3.2
3.0
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
Ageoffroyi
Aseniculus
Llagothrica
□ Median
▨ 25%-75%
⌶ Non-Outlier Range
○ Outliers
✱ Extremes

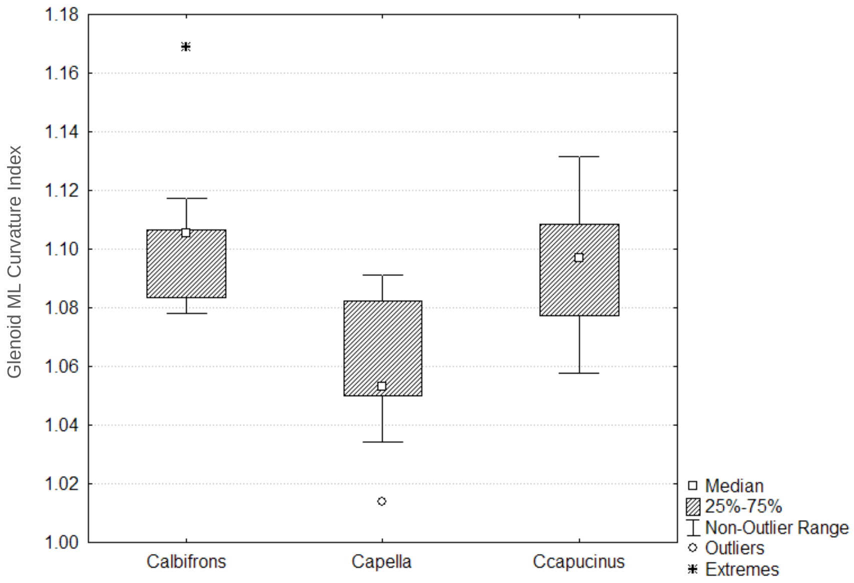

Glenoid ML Curvature Index
1.30
1.28
1.26
1.24
1.22
1.20
1.18
1.16
1.14
1.12
1.10
1.08
1.06
1.04
1.02
1.00
Ageoffroyi
Aseniculus
Llagothrica
Median
25%-75%
Non-Outlier Range
Outliers
Extremes

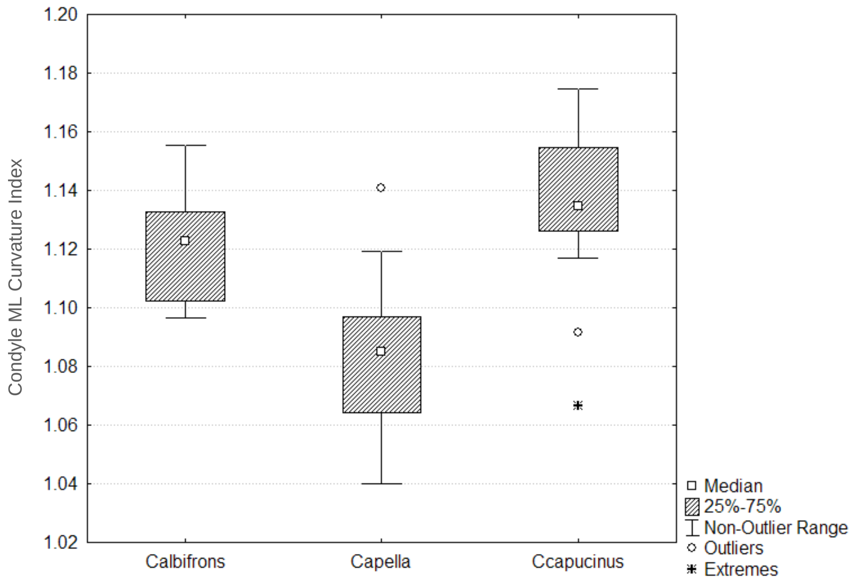
CEBINES


Articular Tubercle Height
0.16
0.14
0.12
0.10
0.08
0.06
0.04
Calbifrons
Capella
Ccapucinus
□ Median
▨ 25%-75%
Non-Outlier Range
○ Outliers
✱ Extremes

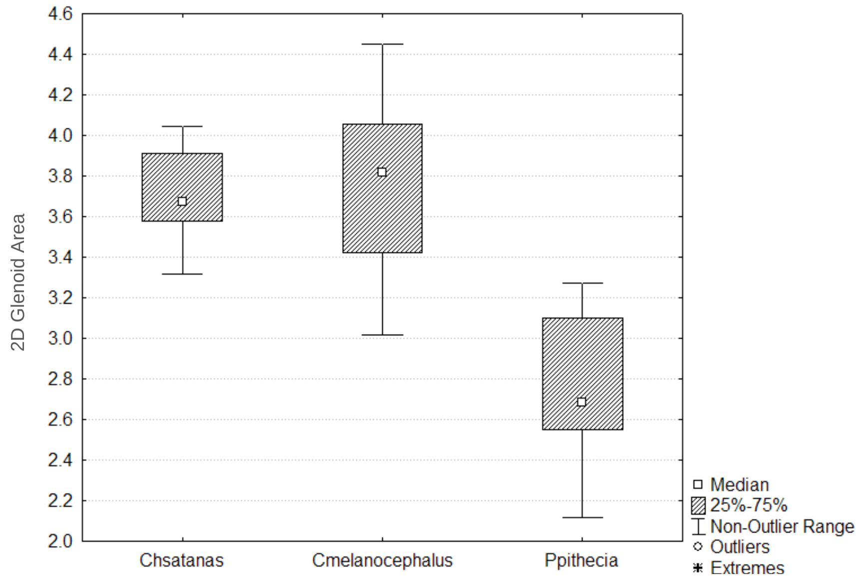

Entoglenoid Process Height
0.16
0.15
0.14
0.13
0.12
0.11
0.10
0.09
0.08
0.07
0.06
Calbifrons
Capella
Ccapucinus
□ Median
▨ 25%-75%
Non-Outlier Range
○ Outliers
✱ Extremes

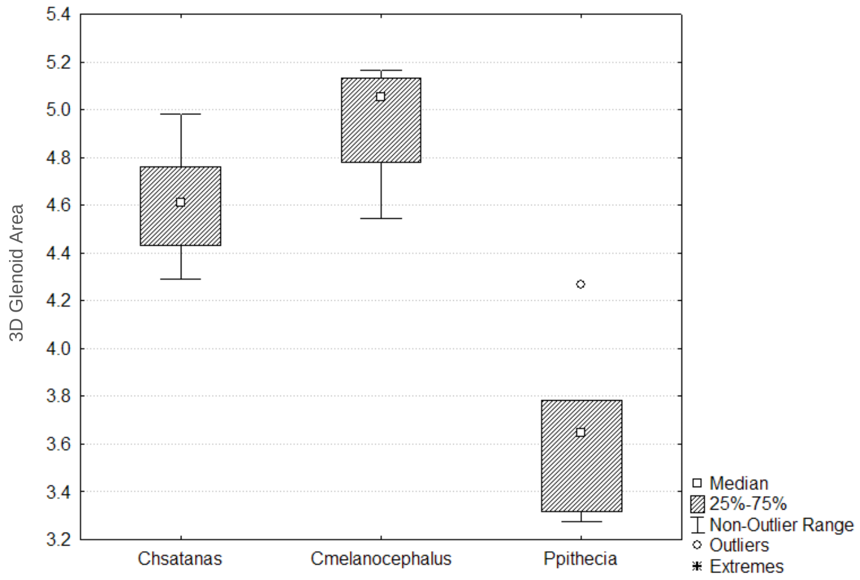

3D Glenoid Area
5.0
4.8
4.6
4.4
4.2
4.0
3.8
3.6
3.4
3.2
3.0
2.8
Calbifrons
Capella
Ccapucinus
□ Median
▨ 25%-75%
Ɪ Non-Outlier Range
○ Outliers
✱ Extremes

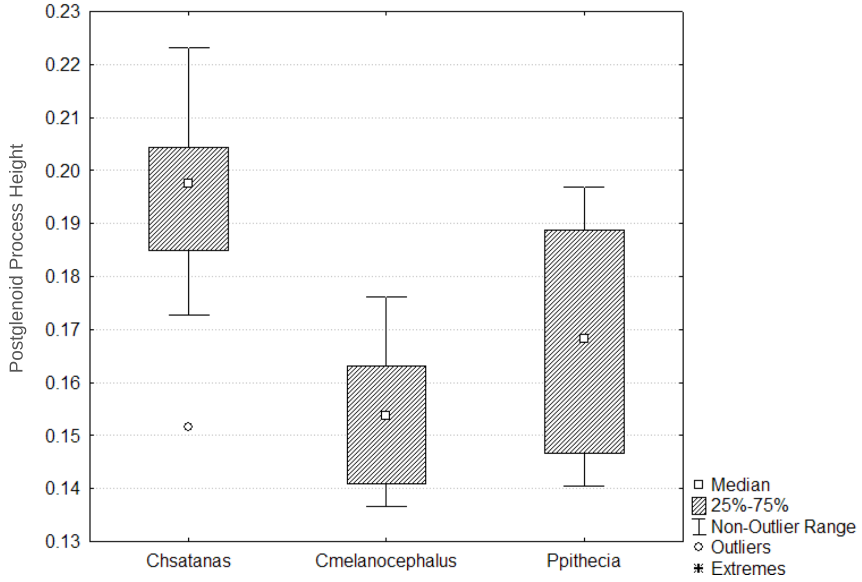

Glenoid ML Curvature Index
1.18
1.16
1.14
1.12
1.10
1.08
1.06
1.04
1.02
1.00
Calbifrons
Capella
Ccapucinus
□ Median
▨ 25%-75%
Ɪ Non-Outlier Range
○ Outliers
✱ Extremes

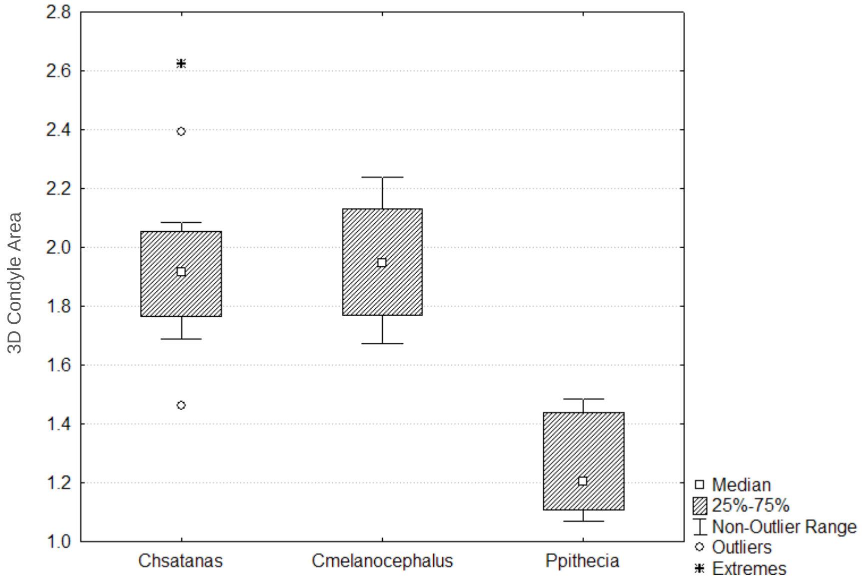

Condyle ML Curvature Index
1.20
1.18
1.16
1.14
1.12
1.10
1.08
1.06
1.04
1.02
Calbifrons
Capella
Ccapucinus
□ Median
▨ 25%-75%
Ɪ Non-Outlier Range
○ Outliers
✱ Extremes

PITHECIINES

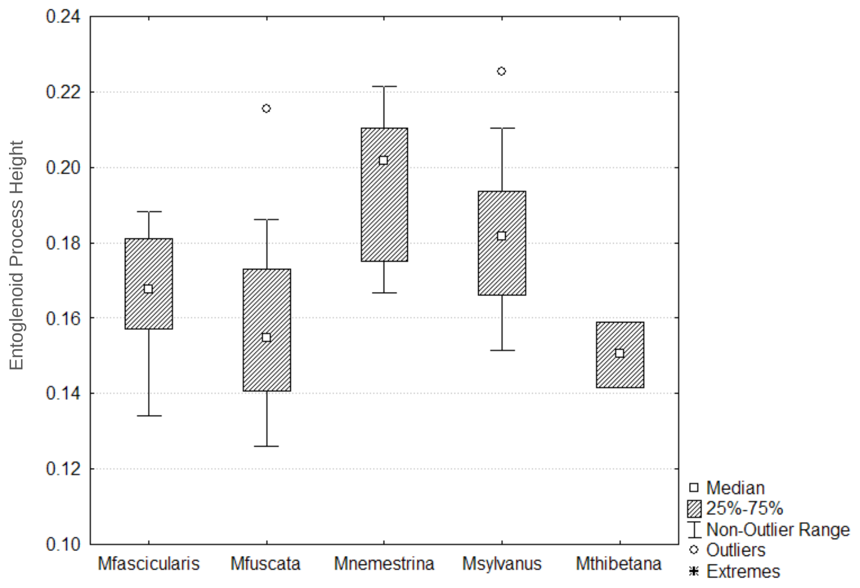


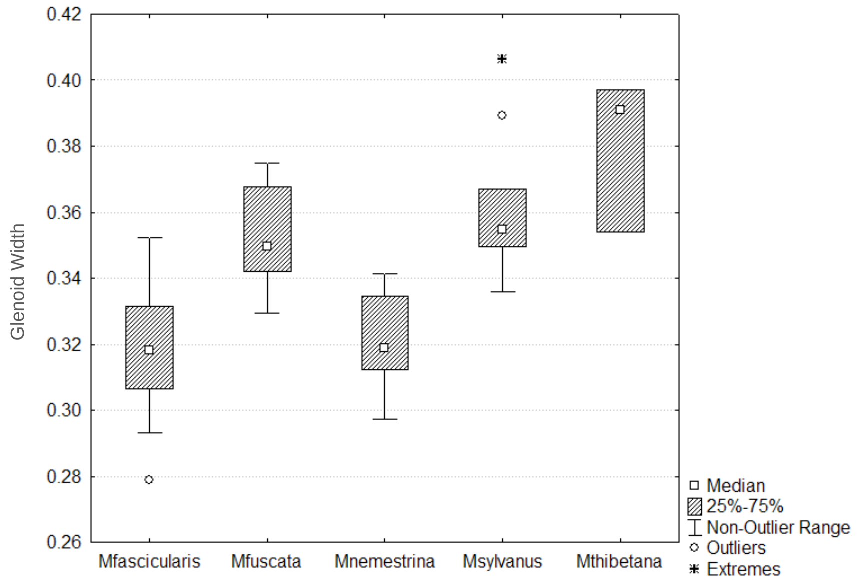


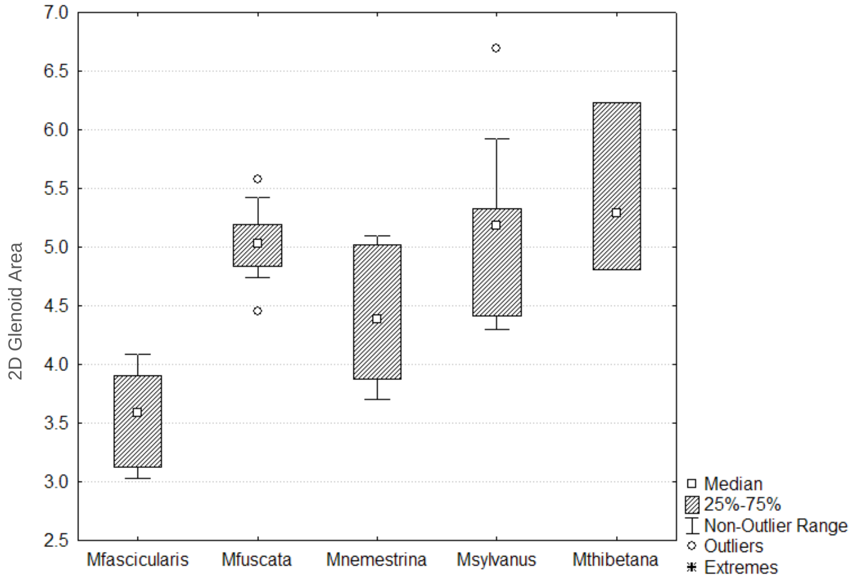

Postglenoid Process Height
0.23
0.22
0.21
0.20
0.19
0.18
0.17
0.16
0.15
0.14
0.13
Chsatanas
Cmelanocephalus
Ppithecia
Median
25%-75%
Non-Outlier Range
Outliers
Extremes

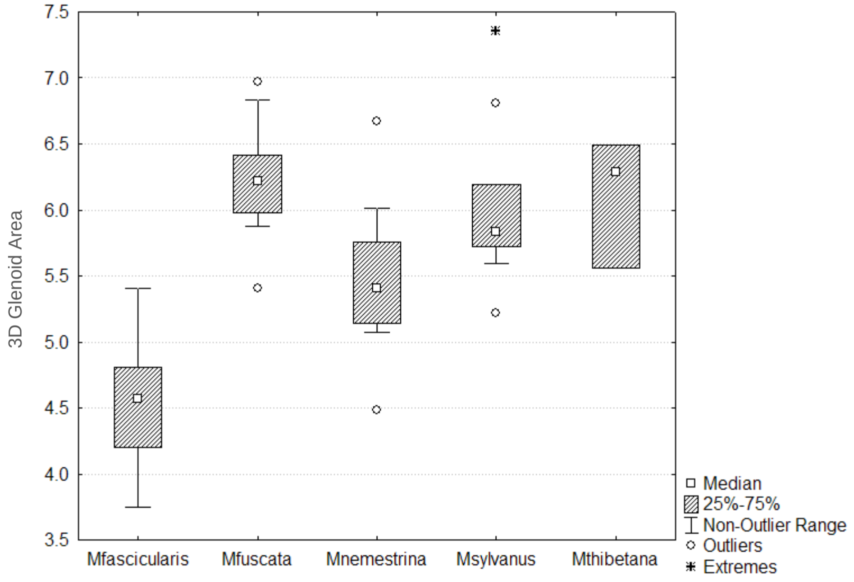

3D Condyle Area
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
Chsatanas
Cmelanocephalus
Ppithecia
Median
25%-75%
Non-Outlier Range
Outliers
Extremes

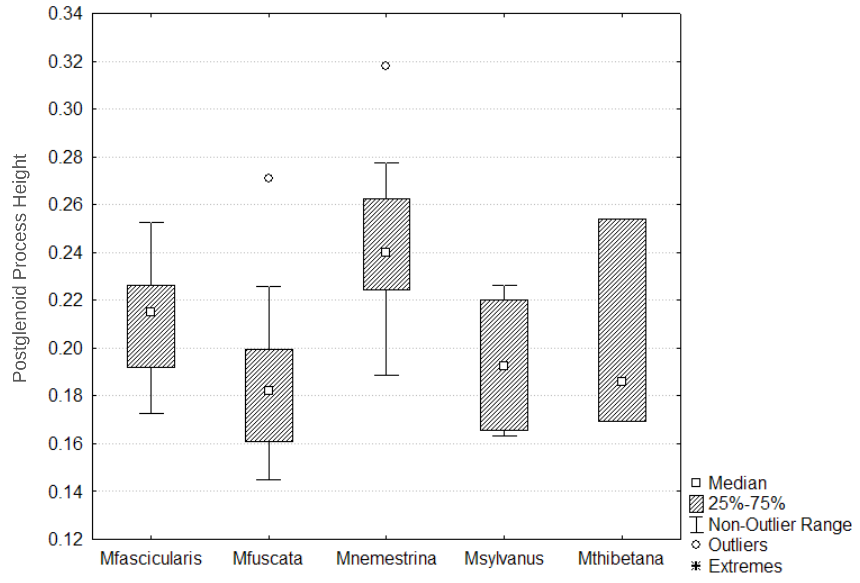
MACACA

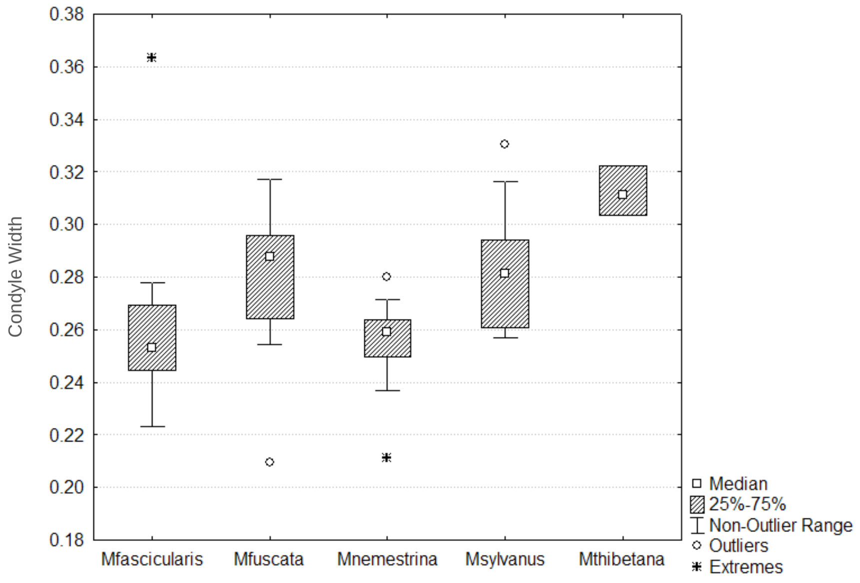

Entoglenoid Process Height
0.24
0.22
0.20
0.18
0.16
0.14
0.12
0.10
Mfascicularis
Mfuscata
Mnemestrina
Msylvanus
Mthibetana
Median
25%-75%
Non-Outlier Range
Outliers
Extremes

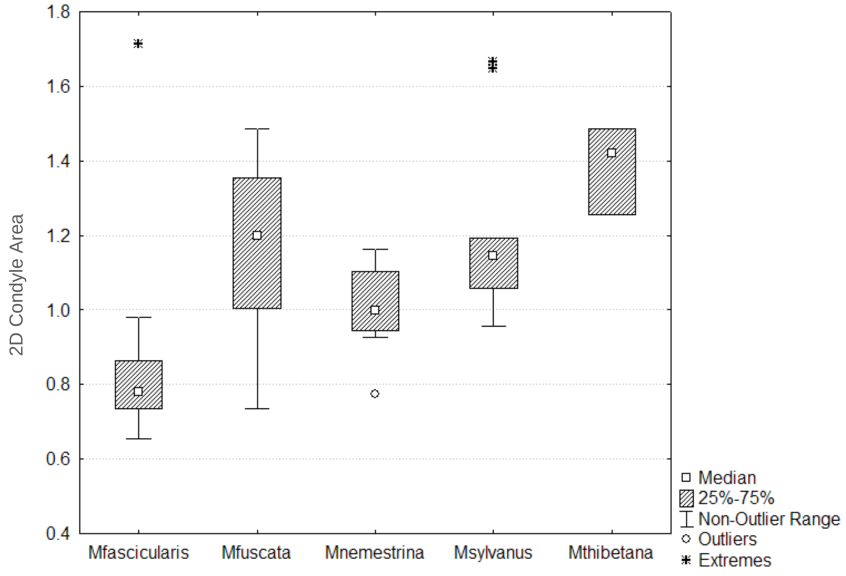

Glenoid Width
0.42
0.40
0.38
0.36
0.34
0.32
0.30
0.28
0.26
Mfascicularis
Mfuscata
Mnemestrina
Msylvanus
Mthibetana
Median
25%-75%
Non-Outlier Range
Outliers
Extremes

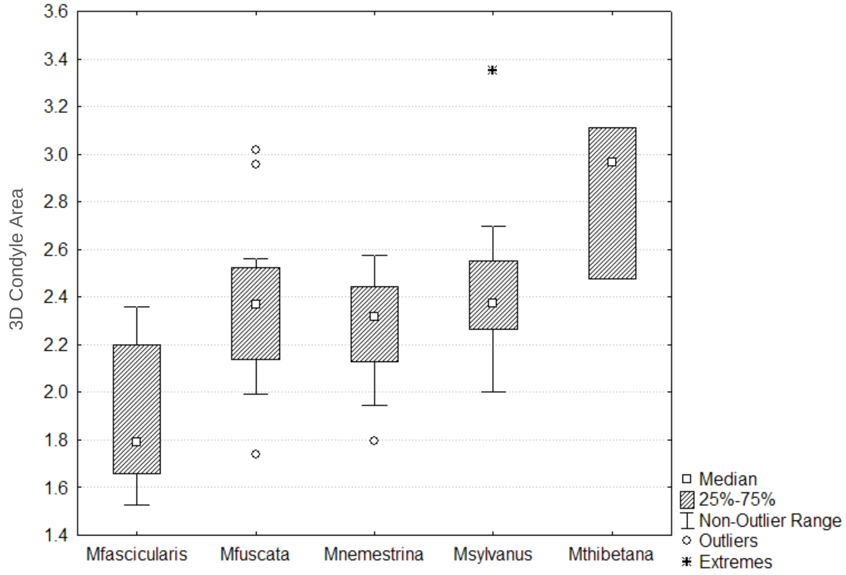

2D Glenoid Area
7.0
6.5
6.0
5.5
5.0
4.5
4.0
3.5
3.0
2.5
Mfascicularis
Mfuscata
Mnemestrina
Msylvanus
Mthibetana
□ Median
▨ 25%-75%
Non-Outlier Range
○ Outliers
✱ Extremes

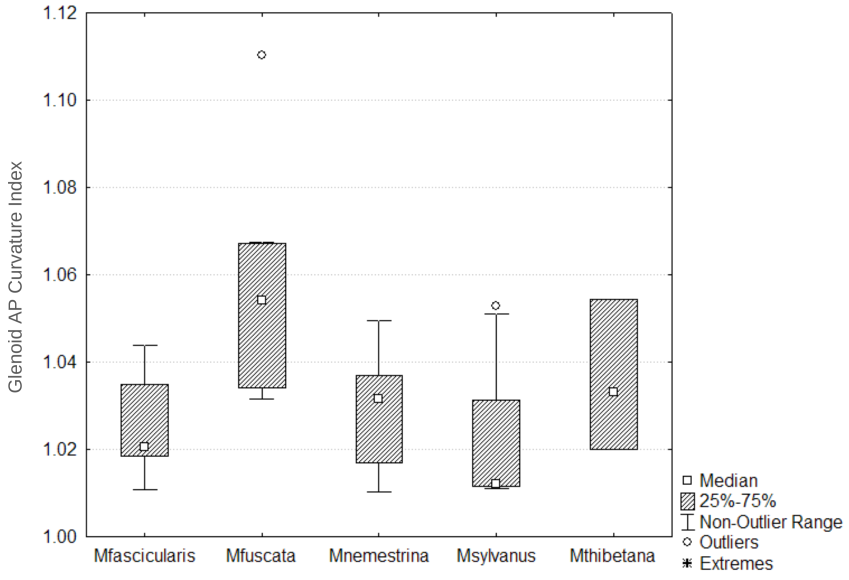

3D Glenoid Area
7.5
7.0
6.5
6.0
5.5
5.0
4.5
4.0
3.5
Mfascicularis
Mfuscata
Mnemestrina
Msylvanus
Mthibetana
□ Median
▨ 25%-75%
Non-Outlier Range
○ Outliers
✱ Extremes


Postglenoid Process Height
0.34
0.32
0.30
0.28
0.26
0.24
0.22
0.20
0.18
0.16
0.14
0.12
Mfascicularis
Mfuscata
Mnemestrina
Msylvanus
Mthibetana
Median
25%-75%
Non-Outlier Range
Outliers
Extremes

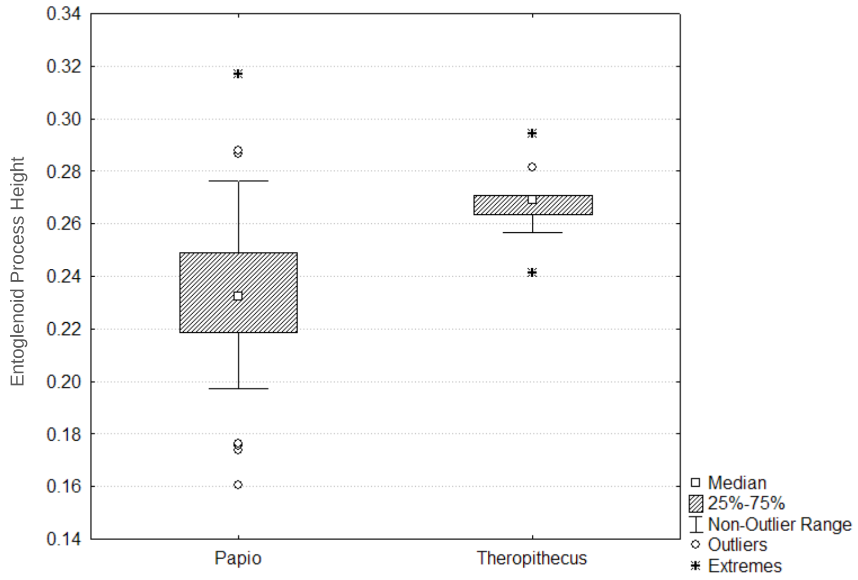

Condyle Width
0.38
0.36
0.34
0.32
0.30
0.28
0.26
0.24
0.22
0.20
0.18
Mfascicularis
Mfuscata
Mnemestrina
Msylvanus
Mthibetana
Median
25%-75%
Non-Outlier Range
Outliers
Extremes

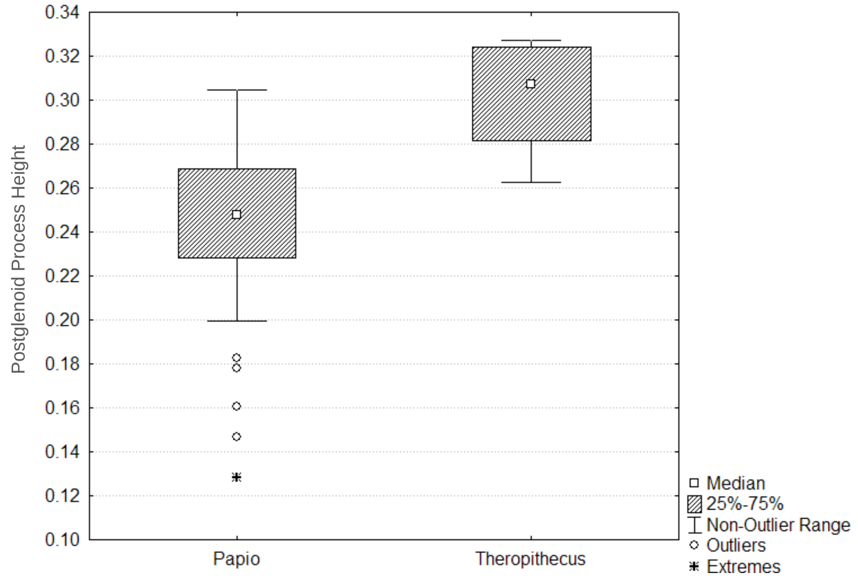

2D Condyle Area
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
Mfascicularis
Mfuscata
Mnemestrina
Msylvanus
Mthibetana
□ Median
▨ 25%-75%
⌶ Non-Outlier Range
○ Outliers
✱ Extremes

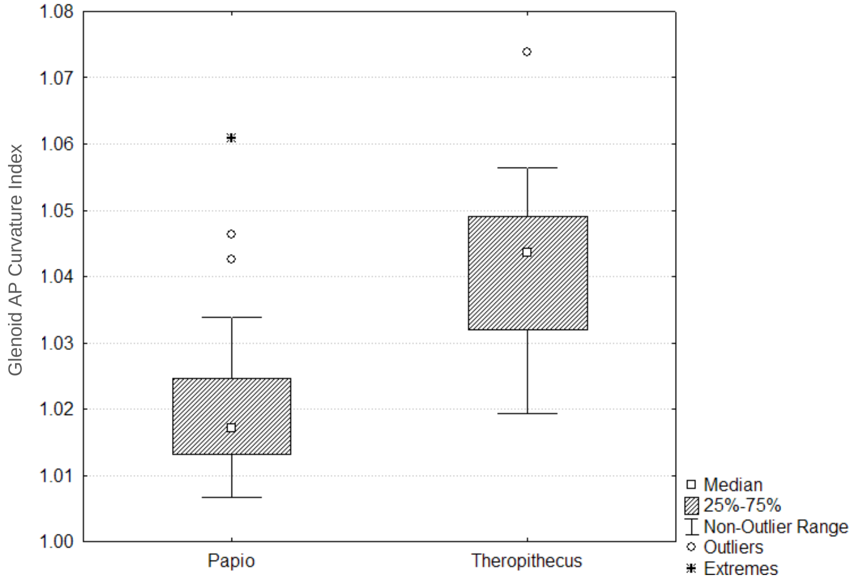

3D Condyle Area
3.6
3.4
3.2
3.0
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
Mfascicularis
Mfuscata
Mnemestrina
Msylvanus
Mthibetana
□ Median
▨ 25%-75%
⌶ Non-Outlier Range
○ Outliers
✱ Extremes


Glenoid AP Curvature Index
1.12
1.10
1.08
1.06
1.04
1.02
1.00
Mfascicularis
Mfuscata
Mnemestrina
Msylvanus
Mthibetana
□ Median
▨ 25%-75%
⌶ Non-Outlier Range
○ Outliers
✱ Extremes

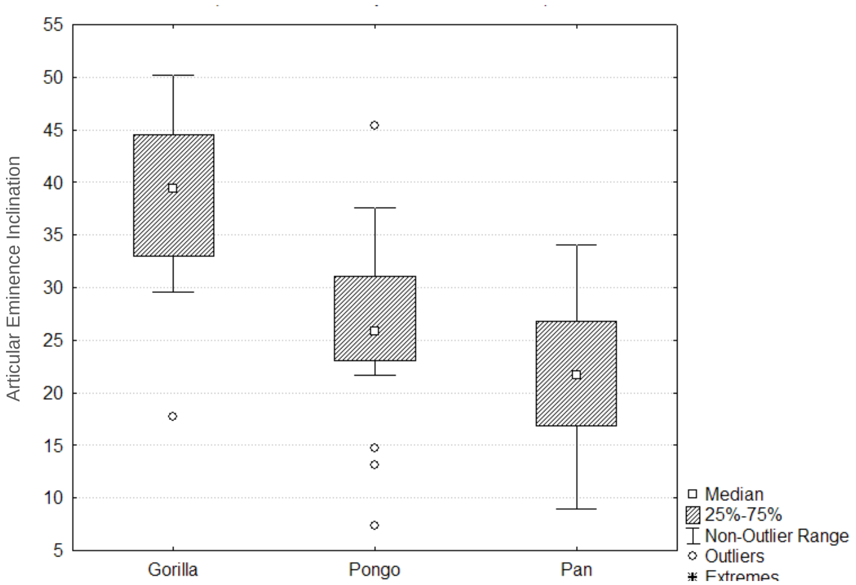
PAPIO VS. *THEROPITHECUS*

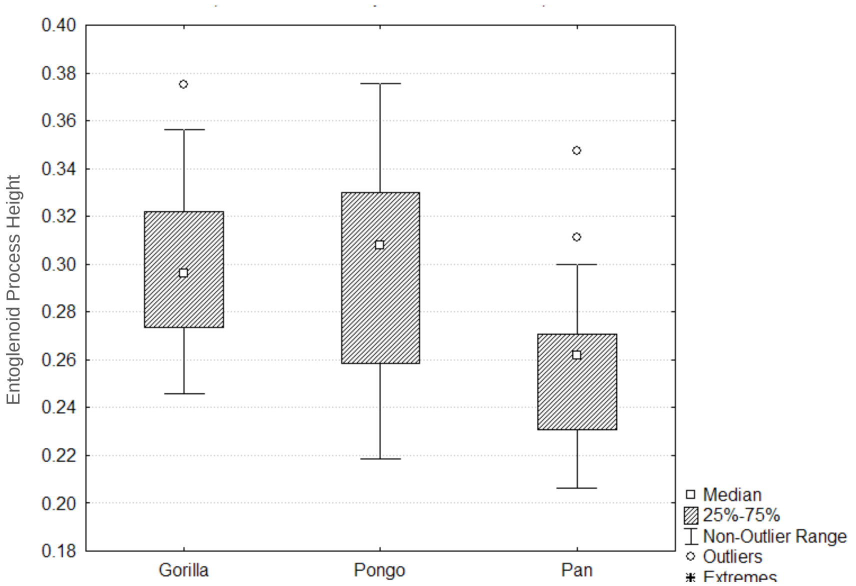


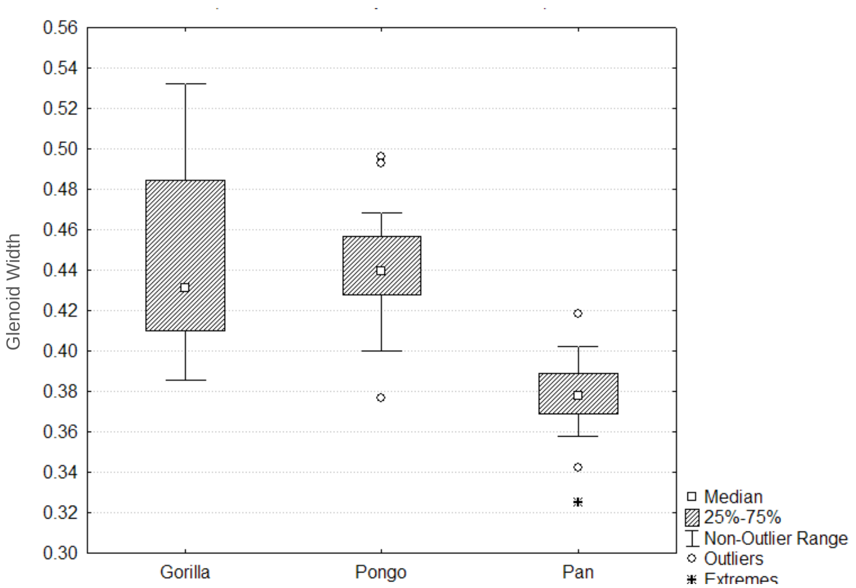


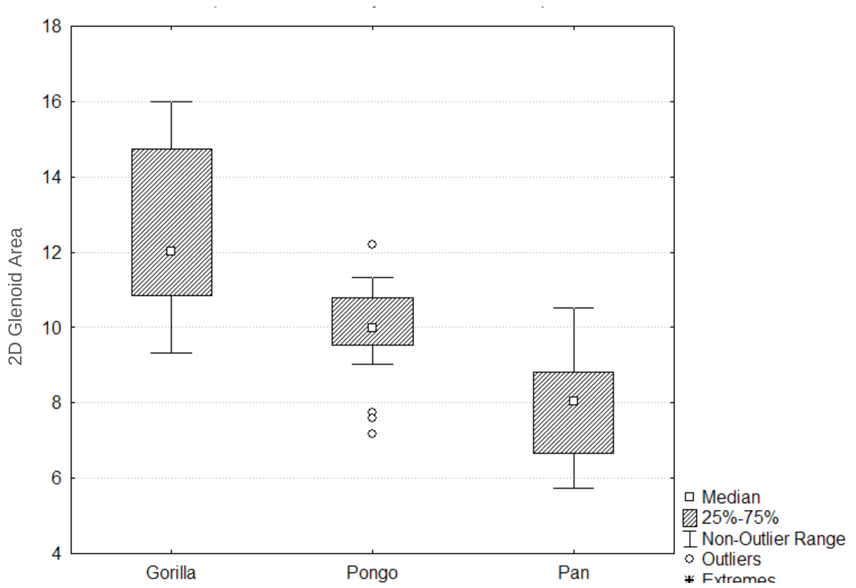

Glenoid AP Curvature Index
1.08
1.07
1.06
1.05
1.04
1.03
1.02
1.01
1.00
Papio
Theropithecus
Median
25%-75%
Non-Outlier Range
Outliers
Extremes

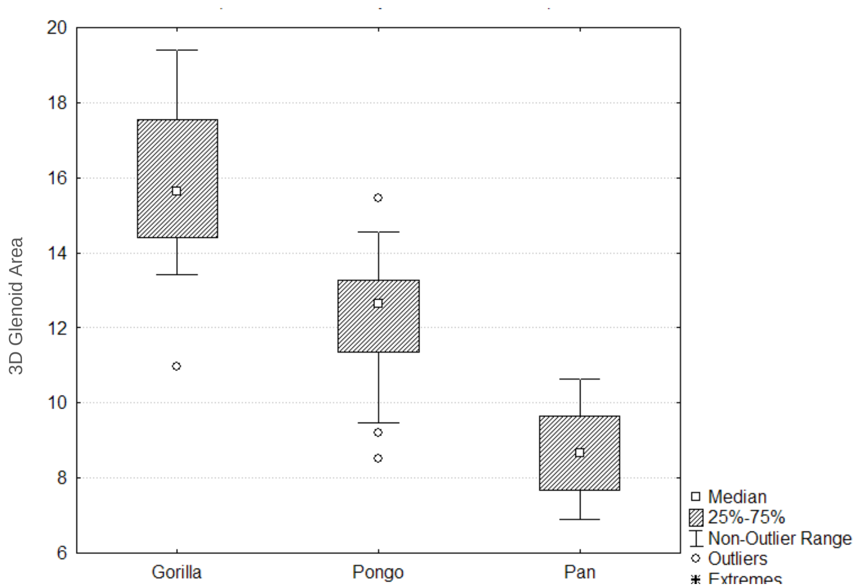
HOMINIDS

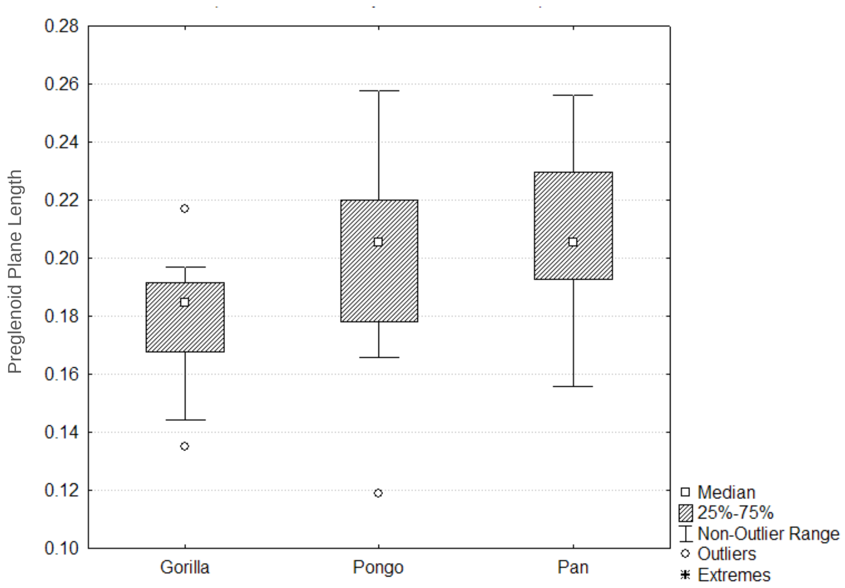

Articular Eminence Inclination
55
50
45
40
35
30
25
20
15
10
5
Gorilla
Pongo
Pan
□ Median
▨ 25%-75%
⌶ Non-Outlier Range
○ Outliers
✱ Extremes

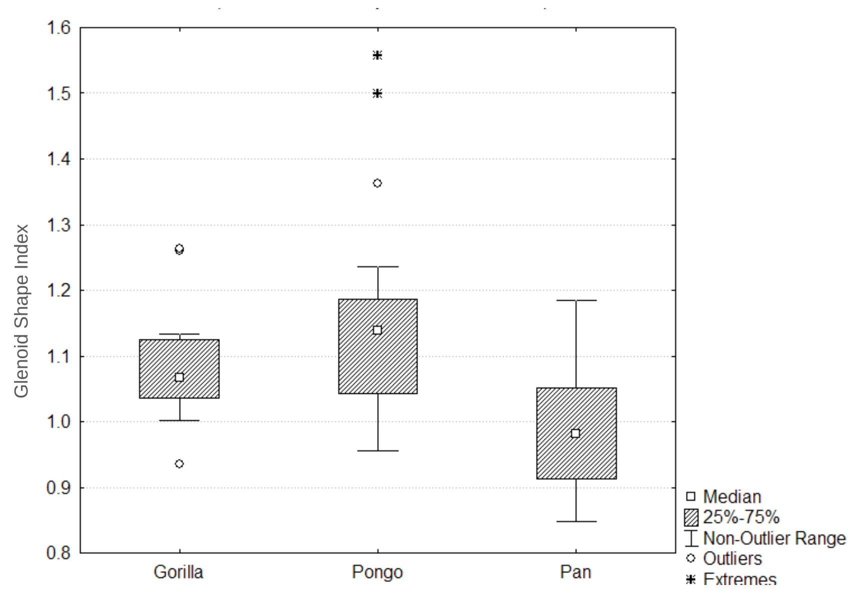

Entoglenoid Process Height
0.40
0.38
0.36
0.34
0.32
0.30
0.28
0.26
0.24
0.22
0.20
0.18
Gorilla
Pongo
Pan
□ Median
▨ 25%-75%
⌶ Non-Outlier Range
○ Outliers
✱ Extremes

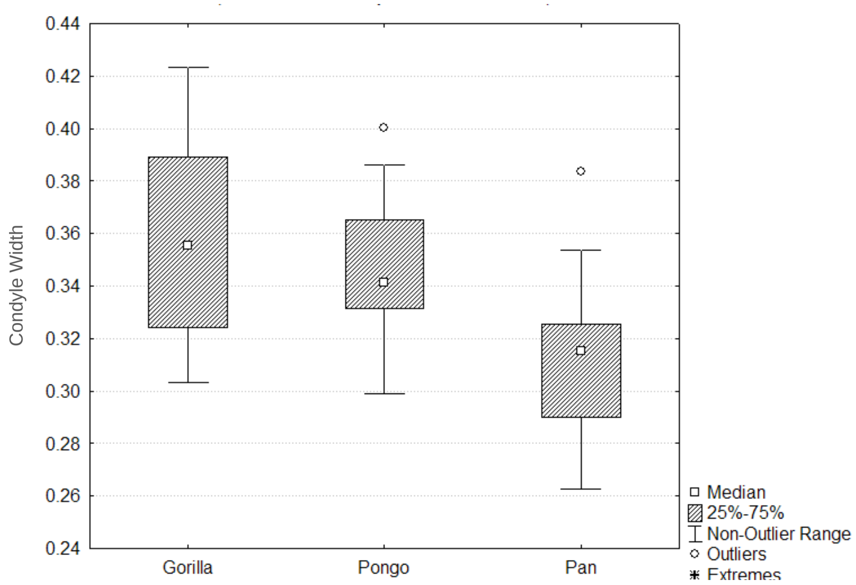

Glenoid Width
0.56
0.54
0.52
0.50
0.48
0.46
0.44
0.42
0.40
0.38
0.36
0.34
0.32
0.30
Gorilla
Pongo
Pan
Median
25%-75%
Non-Outlier Range
Outliers
Extremes

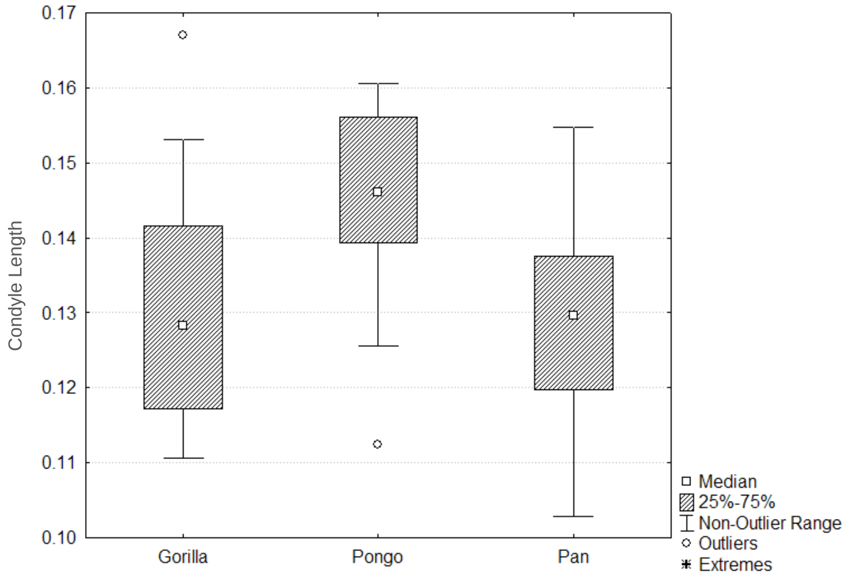

2D Glenoid Area
18
16
14
12
10
8
6
4
Gorilla
Pongo
Pan
Median
25%-75%
Non-Outlier Range
Outliers
Extremes

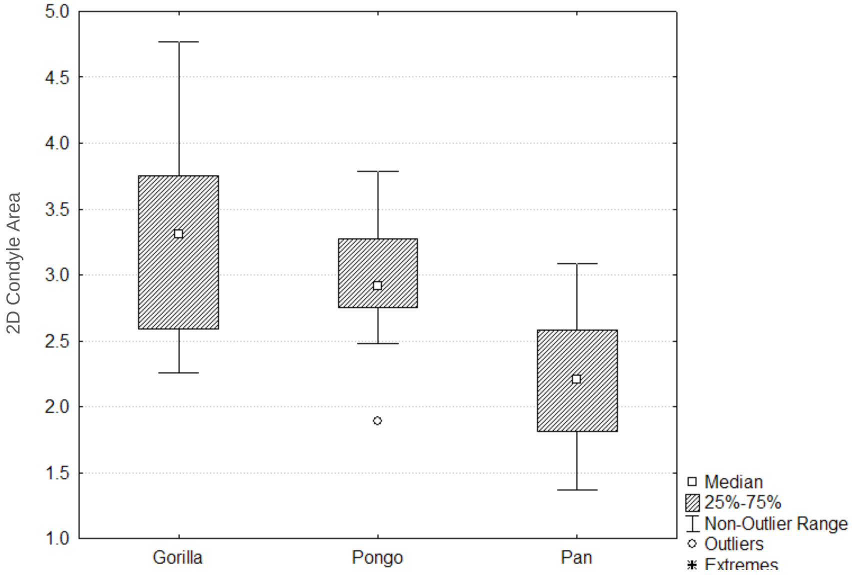

3D Glenoid Area
20
18
16
14
12
10
8
6
Gorilla
Pongo
Pan
□ Median
▨ 25%-75%
Non-Outlier Range
○ Outliers
* Extremes

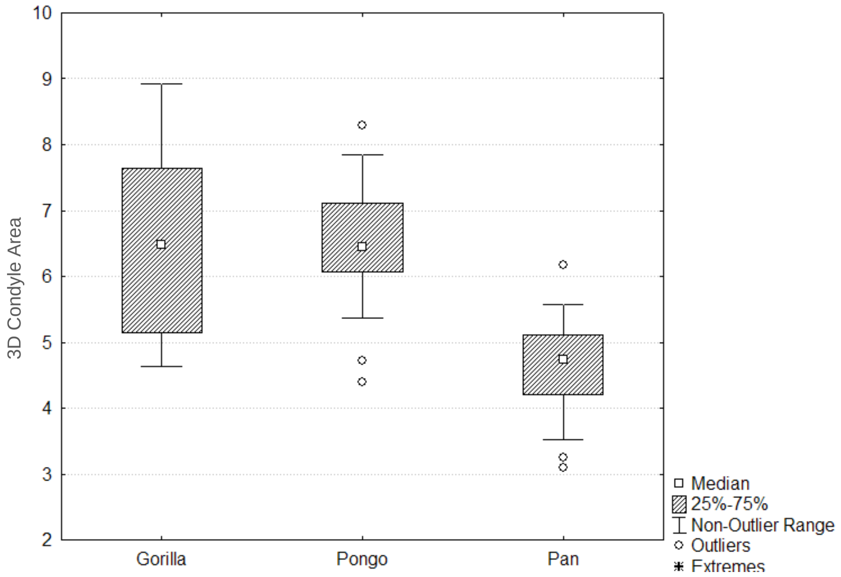

Preglenoid Plane Length
0.28
0.26
0.24
0.22
0.20
0.18
0.16
0.14
0.12
0.10
Gorilla
Pongo
Pan
□ Median
▨ 25%-75%
Non-Outlier Range
○ Outliers
* Extremes

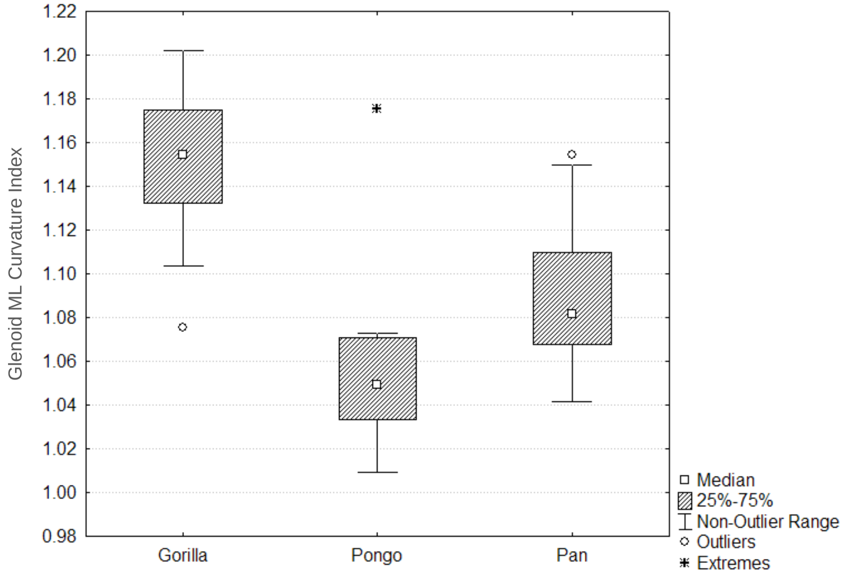

Glenoid Shape Index
1.6
1.5
1.4
1.3
1.2
1.1
1.0
0.9
0.8
Gorilla
Pongo
Pan
□ Median
▨ 25%-75%
Ⲓ Non-Outlier Range
○ Outliers
✱ Extremes

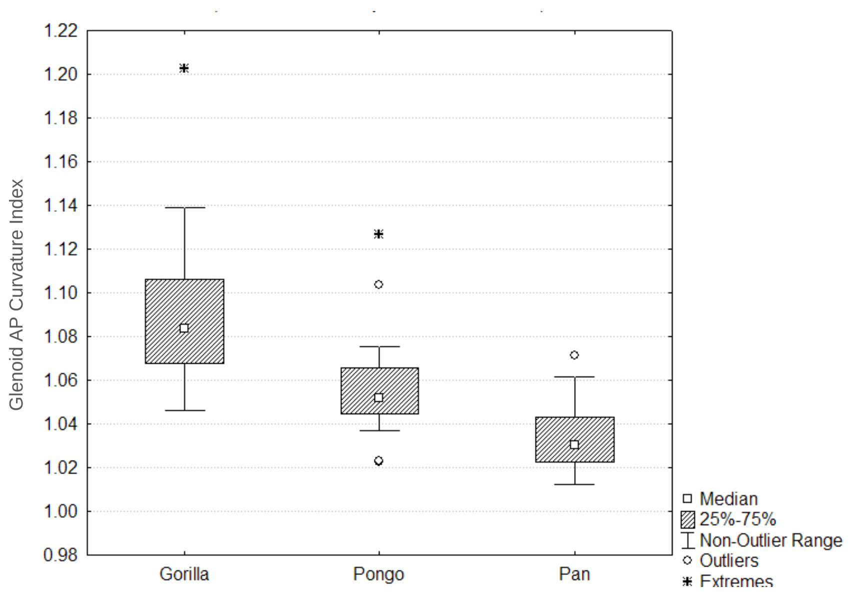

Condyle Width
0.44
0.42
0.40
0.38
0.36
0.34
0.32
0.30
0.28
0.26
0.24
Gorilla
Pongo
Pan
□ Median
▨ 25%-75%
Ⲓ Non-Outlier Range
○ Outliers
✱ Extremes


0.17
0.16
0.15
0.14
0.13
0.12
0.11
0.10
Condyle Length
Gorilla
Pongo
Pan
□ Median
▨ 25%-75%
Non-Outlier Range
○ Outliers
✱ Extremes


5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
2D Condyle Area
Gorilla
Pongo
Pan
□ Median
▨ 25%-75%
Non-Outlier Range
○ Outliers
✱ Extremes


10
9
8
7
6
5
4
3
2
3D Condyle Area
Gorilla
Pongo
Pan
Median
25%-75%
Non-Outlier Range
Outliers
Extremes


1.22
1.20
1.18
1.16
1.14
1.12
1.10
1.08
1.06
1.04
1.02
1.00
0.98
Glenoid ML Curvature Index
Gorilla
Pongo
Pan
Median
25%-75%
Non-Outlier Range
Outliers
Extremes


Glenoid AP Curvature Index
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1.20
1.18
1.16
1.14
1.12
1.10
1.08
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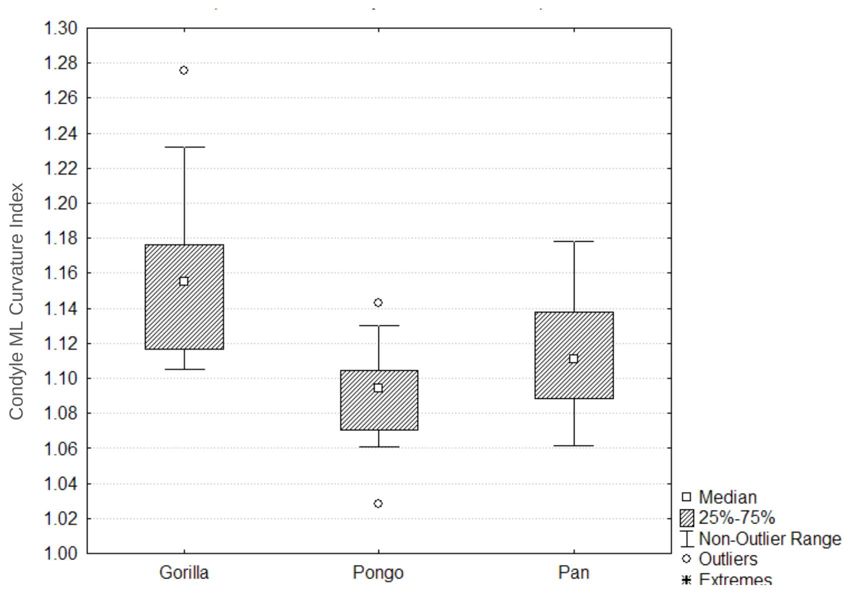
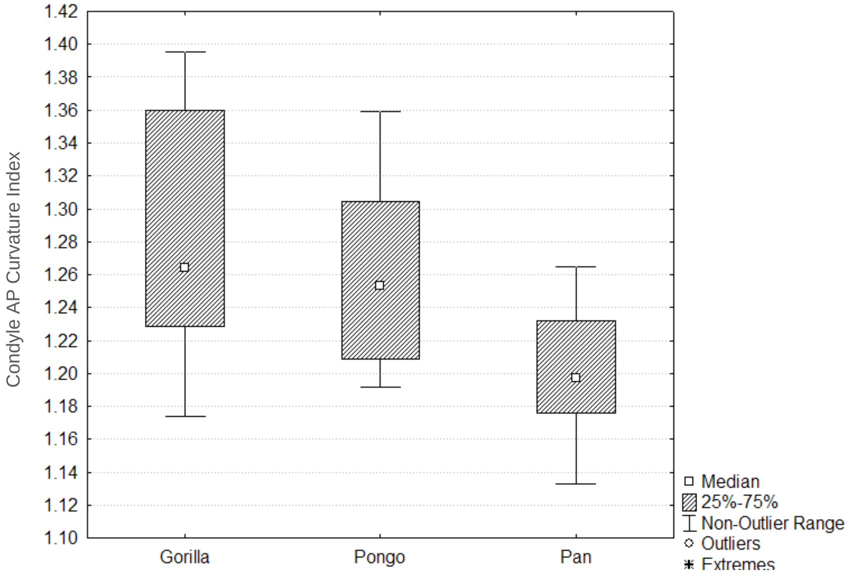
1.02
1.00
0.98
Gorilla
Pongo
Pan
Median
25%-75%
Non-Outlier Range
Outliers
Extremes


Condyle ML Curvature Index
1.30
1.28
1.26
1.24
1.22
1.20
1.18
1.16
1.14
1.12
1.10
1.08
1.06
1.04
1.02
1.00
Gorilla
Pongo
Pan
Median
25%-75%
Non-Outlier Range
Outliers
Extremes


Condyle AP Curvature Index
1.42
1.40
1.38
1.36
1.34
1.32
1.30
1.28
1.26
1.24
1.22
1.20
1.18
1.16
1.14
1.12
1.10
Gorilla
Pongo
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Median
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Non-Outlier Range
Outliers
Extremes