Journal of Human Evolution 61 (2011) 583–596

Contents lists available at SciVerse ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

Dietary correlates of temporomandibular joint morphology in New World primates

Claire E. Terhune

Department of Community and Family Medicine, Duke University Medical Center, Box 104780, Durham, NC 27710, USA

ARTICLE INFO

Article history:
Received 19 March 2011
Accepted 10 August 2011

Keywords:
Geometric morphometrics
Primate feeding behavior
Masticatory morphology
Mandible
TMJ

ABSTRACT

Previous analyses of the masticatory apparatus have demonstrated that the shape of the temporomandibular joint (TMJ) is functionally and adaptively linked to variation in feeding behavior and diet in primates. Building on previous research, this study presents an analysis of the link between diet and TMJ morphology in the context of functional and dietary differences among New World primates. To evaluate this proposed relationship, I used three-dimensional morphometric methods to quantify TMJ shape across a sample of 13 platyrrhine species. A broad interspecific analysis of this sample found strong relationships among TMJ size, TMJ shape, and diet, suggesting that both size and diet are significant factors influencing TMJ morphology in New World primates. However, it is likely that at least some of these differences are related to a division of dietary categories along clade lines.

A series of hypotheses related to load resistance capabilities and range of motion in the TMJ were then tested among small groups of closely related taxa with documented dietary differences. These pairwise analyses indicate that some aspects of TMJ morphology can be used to differentiate among closely related species with different diets. However, not all of my predictions were upheld. The anteroposterior dimensions of the TMJ were most strongly consistent with hypothesized differences in ingestive/masticatory behaviors and jaw gape, whereas the predictions generated for variation in entoglenoid and articular tubercle height were not upheld. These results imply that while some features can be reliably associated with increased load resistance and facilitation of wider jaw gapes in the masticatory apparatus, other features are less strongly correlated with masticatory function.

Introduction

Temporomandibular joint (TMJ) form has been documented to vary both within humans (Sullivan, 1917; Weidenreich, 1943; Hinton and Carlson, 1979; Harvati, 2001; 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). The more recent of these analyses have directly linked aspects of this variation to functional differences among taxa in the masticatory apparatus (e.g., Bouvier, 1986a,b; Wall, 1995, 1999; Vinyard, 1999; Vinyard et al., 2003). Building upon experimental analyses of masticatory function by Hylander and colleagues (e.g., Hylander, 1975, 1979; Hylander and Bays, 1978, 1979; Hylander and Crompton, 1980), Smith et al. (1983) and Bouvier (1986a,b) first analyzed the biomechanical scaling of the TMJ both across anthropoids (Smith et al., 1983) and separately within cercopithecoids (Bouvier, 1986a) and platyrrhines (Bouvier, 1986b). More recent work by Wall and Vinyard (Wall, 1995, 1999; Vinyard, 1999; Vinyard et al., 2003) has more explicitly tested functional hypotheses related to TMJ shape in both anthropoids and strepsirrhines. All of these studies suggest that the form of the TMJ covaries with differences in feeding behavior among primates, principally in the dimensions of the joint (and particularly the mandibular condyle) in relation to load resistance, use of the anterior or posterior dentition, and relative gape.

Following on this research, it is the goal of this study to examine variation in TMJ morphology in the context of functional and dietary differences among New World primates. Platyrrhines are an excellent group to test this proposed association between feeding behavior and TMJ morphology for a number of reasons. Taxa within this clade vary considerably in their feeding behavior and body size, ranging from an annual fruit intake of as little as 8% in *Cebuella* to as much as 86% in *Ateles* (Norconk et al., 2009), and with body sizes varying between 0.11 and 11.4 kg in *Cebuella pygmaea* and *Alouatta pigra*, respectively (Smith and Jungers, 1997). Importantly, masticatory variation in this group has been extensively evaluated (e.g., Kinzey, 1974; Hylander, 1975; Kay, 1975; Rosenberger and Kinzey, 1976; van Roosmalen et al., 1988; Ayres, 1989; Rosenberger and

E-mail address: claire.terhune@duke.edu.

0047-2484/$ – see front matter © 2011 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jhevol.2011.08.003

Strier, 1989; Kinzey, 1992; Kinzey and Norconk, 1993; Anapol and Lee, 1994; Spencer, 1995; Wright, 2005; Constantino, 2007; Taylor and Vinyard, 2009; Norconk et al., 2009), and the material properties of food items ingested by a number of species in this clade have been comparatively well documented (Kinzey and Norconk, 1990; Wright, 2005; Norconk et al., 2009; Wright and Wright, 2010; Chalk et al., 2010). This study analyzed TMJ variation in this clade in two ways. First, TMJ morphology across the entire sample was quantified using geometric morphometric methods, and the extent to which this variation covaries with feeding behavior and body size was examined. Second, three separate sets of phylogenetically restricted pairwise comparisons were performed. These comparisons were designed to test a series of morphological predictions for TMJ shape based on existing experimental and behavioral data. These morphological predictions and their biomechanical basis are outlined in the following section and the ecological data for each of the comparative groups is reviewed.

Morphological predictions

Theoretical and experimental analyses of masticatory function have demonstrated that the magnitude of the joint reaction force varies depending upon the position of the bite point, the magnitude and position of the muscle resultant force, position of the TMJ in relation to the tooth row, as well as the overall geometry of the masticatory apparatus (e.g., Hylander, 1975, 1979, 2006; Greaves, 1978; Smith, 1978; Hylander and Bays, 1979; Brehnan et al., 1981; Spencer, 1995, 1999). For example, more anterior bite points produce relatively higher joint reaction forces (JRF), and the ratio of the JRF between the working and balancing sides becomes smaller as the bite force moves more posteriorly. Histological, experimental, and comparative studies have also shown that the loading within the joint is unlikely to be uniform (e.g., Moffett et al., 1964; Hylander, 1979, 2006; Richards, 1987, 1988).

Bony morphology may also help to facilitate or limit movements at the joint. These movements primarily occur in the anteroposterior and mediolateral planes and include rotation and translation of the condyle, or a combination of these two movements. During simple opening and closing movements of the mandible (as would occur with social display behaviors or incision, as well as at the beginning or end of a gape cycle during mastication), motion of the right and left condyles should be roughly equal, and is typically comprised of a combination of translation and rotation in primates (i.e., sagittal sliding). Cineradiographic analyses conducted by Wall (1995, 1999) indicate that sagittal sliding of the condyle is strongly correlated with linear gape between the incisors. By contrast, mastication occurs along the postcanine dentition and is characterized by mediolateral deviation of the mandible. This type of movement typically involves only slight rotation and lateral movement of the working side condyle with the balancing side condyle shifting downward (or forward) and medially along the (variably prominent) articular eminence (Byrd et al., 1978; Miyawaki et al., 2000; Komiyama et al., 2003; Hylander, 2006). Analyses of masticatory movements during the comminution of foods with different food material properties suggest that with more resistant foods, the amount of lateral deviation increases (Byrd et al., 1978; Anderson et al., 2002; Komiyama et al., 2003; Wall et al., 2006; but see Reed and Ross, 2010).

Although there are many factors that are likely to affect both force and range of motion at the TMJ, this study focuses on three (non-mutually exclusive) influences: food material properties, location of the bite point, and gape requirements. First, the material property of a food item influences the amount of muscle force required to process the food, which, in turn, influences the magnitude of the joint reaction force at the TMJ (e.g., Lucas, 2004; Williams et al., 2005). Second, the location of the bite point will influence the amount of muscle and bite force vs. joint reaction force, as well as the distribution of the joint reaction force across the balancing and working side condyles (e.g., Hylander, 1979; Hylander and Bays, 1979; Brehnan et al., 1981). Finally, behavioral and dietary demands associated with gape requirements (e.g., social display behaviors such as canine displays and/or food object size) are particularly likely to influence range of motion at the TMJ (e.g., Lucas, 1981, 1982; Wall, 1995, 1999; Vinyard et al., 2003; Hylander and Vinyard, 2006; Hylander et al., 2008). Based on this previous research regarding TMJ biomechanics, I generate a series of predictions regarding how TMJ forms are expected to vary in association with these factors in three separate clades of platyrrhines:

1) The surface area of the mandibular condyle should be relatively larger in taxa that masticate more resistant food objects and/or use their anterior dentition extensively for food processing. Increased joint reaction forces at the TMJ (as a consequence of increased muscle resultant forces and/or use of the anterior dentition) should necessitate relatively larger joint surface areas in order to improve the load resistance capabilities of the TMJ by increasing the area over which force is applied (Hylander, 1979; Smith et al., 1983; Bouvier, 1986a,b; Taylor, 2005).
2) The anteroposterior length of the TMJ will vary in association with the frequency of ingestive behavior. Taxa that use their anterior teeth extensively for ingestive behaviors (particularly large object feeders that must also generate large jaw gapes) should have a relatively anteroposteriorly elongated cranial articular surface (e.g., the glenoid should be anteroposteriorly longer in relation to condylar length so that more sagittal sliding can occur at the joint) (Wall, 1995, 1999; Vinyard et al., 2003).
3) The mediolateral width of the TMJ will vary as a consequence of the frequency of masticatory behaviors. Studies of joint remodeling and dysfunction have suggested that the lateral aspect of the TMJ experiences higher stresses than other portions of the joint (Moffett et al., 1964; Richards and Brown, 1981; Hinton, 1981; Richards, 1988). These increased stresses may be a result of twisting of the mandibular corpus and compression of the lateral aspect of the condyle during the power stroke and/or lateral shifting of the working side condyle during lateral deviation of the mandible (Hylander, 1979; Hylander and Bays, 1979; Bouvier, 1986a,b; Taylor, 2005, 2006). Consequently, it is predicted here that taxa masticating hard- and/or tough-food objects will exhibit mediolaterally expanded joint surfaces to withstand the increased stresses generated by increased twisting and lateral deviation of the mandible during mastication. This will be particularly true of taxa where the frequency (rather than just the magnitude) of the power stroke is increased (i.e., tough object feeders) and/or where intensive unilateral mastication of food items is emphasized (as with taxa that masticate hard- and/or tough-food objects on the postcanine dentition). 4) The entoglenoid process will be relatively larger in resistant-object feeders and taxa that use their postcanine dentition extensively for unilateral mastication when compared with taxa that do not rely heavily on unilateral mastication on the posterior teeth. Work by Wall (1995, 1999) demonstrated that the mandibular condyle contacts the entoglenoid process during masticatory movement, and that size and shape of the entoglenoid process and mandibular condyle were correlated. Functionally, Wall (1999) interpreted this congruence to indicate that the entoglenoid process acts to guide the mandibular

condyle during sagittal sliding, and possibly to prevent excessive mediolateral movements. Thus, a relatively large entoglenoid process may serve to guide medial movements of the balancing side condyle during mastication and to increase joint surface area and reduce joint stresses. 5) The articular tubercle should be relatively larger in resistant-object feeders compared with soft-object feeders. As the primary attachment site of the temporomandibular ligament (TML), the size of the articular tubercle is likely a reflection of the size of the TML (Wall, 1995). This ligament has been suggested to function to maintain contact between the mandibular and cranial components of the TMJ, therefore resisting tensile forces at the joint (Greaves, 1978; Hylander, 1979; Spencer, 1995; Wall, 1995). 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 during lateral deviation. It is therefore predicted that relatively larger articular tubercles should be found in taxa that exhibit increased lateral deviation (e.g., resistant-object feeders and taxa that use their postcanine dentition extensively for unilateral mastication) (Byrd et al., 1978; Anderson et al., 2002; Komiyama et al., 2003; Wall et al., 2006, but see Reed and Ross, 2010).

Dietary ecology, morphology, and predicted TMJ shape variation in the comparative groups

Analyses of TMJ shape were performed by examining three sets of closely related taxa with different feeding behaviors and diets: atelines, cebines, and pitheciines. This approach allows for multiple pairwise comparisons of TMJ morphology among closely related taxa in a single clade, thereby minimizing the effects of phylogeny on shape differences. The following section outlines the dietary ecology of the members of each of the comparative groups, reviews previous morphological findings for these species, and lays out the expected variation in TMJ morphology in each clade. These predictions rely heavily on previous descriptions of the dietary ecology of these species, and particularly on available data regarding food material properties (e.g., Williams et al., 2005; Wright, 2005; Norconk et al., 2009).

Atelines Five ateline species were studied in the pairwise analysis: *Ateles geoffroyi*, *Lagothrix lagothrica*, and three species of *Alouatta* (*Alouatta seniculus*, *Alouatta belzebul*, and *Alouatta palliata*). Among these taxa, *A. geoffroyi* and *L. lagothrica* are the most frugivorous, consuming between 74% and 87% fruit parts in their diets (Chapman, 1987, 1989; Peres, 1994; Di Fiore, 2004; Russo et al., 2005). These species differ, however, in their relative consumption of seeds and insect prey. Some data suggest that *L. lagothrica* is a seasonal seed predator and relies more heavily on insect parts than does *A. geoffroyi* (van Roosmalen and Klein, 1988; Peres, 1994; Di Fiore, 2004; Russo et al., 2005). In contrast, *Alouatta* is the most folivorous of all New World primates, although there is considerable variation in this group. *A. 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). Food items opened or breached and/or masticated by *Alouatta* are substantially more resistant than those utilized by *Ateles*, both in average and maximum toughness (Wright, 2004; Norconk et al., 2009). No comparable data are available for *Lagothrix*. Another consideration in this clade is the highly derived nature of the vocal apparatus in *Alouatta*. Members of this genus are characterized by their distinctive vocal behaviors (e.g., Carpenter, 1934; Hershkovitz, 1949; Altmann, 1959), which could be associated with relatively larger gapes. However, no behavioral data quantifying gape during vocalizations in these species are currently available.

Morphological differences in the masticatory apparatus of the atelines have also been extensively evaluated. The more folivorous *Alouatta* exhibits relatively higher occlusal relief and relatively greater molar area compared with the more frugivorous *Ateles* and *Lagothrix* (Hylander, 1975; Kay, 1975; Rosenberger and Kinzey, 1976; Rosenberger and Strier, 1989; Anapol and Lee, 1994). Similarly, *Alouatta* has been argued to exhibit a more robust masticatory apparatus (e.g., high TMJ, robust mandible, larger temporal fossa) compared with *Ateles* (Rosenberger and Strier, 1989; Spencer, 1995).

Given the ecological and morphological data, when compared with the relatively more gracile *Ateles*, *Alouatta* should have relatively larger condylar joint surface areas because of their heavy reliance on tough food objects. Increased use of the postcanine dentition in *Alouatta* predicts a relatively mediolaterally wider joint as well. However, *Alouatta* is also predicted to have relatively anteroposteriorly longer joints to facilitate generating relatively wider jaw gapes during their distinctive vocal behaviors. Additionally, *Alouatta* is predicted to have the relatively highest entoglenoid process and articular tubercle to guide movements of the condyle during masticatory and/or vocal behaviors. In contrast, *Lagothrix* and *Ateles* should have relatively smaller joint surface areas and processes, and also have relatively shorter joints in the anteroposterior dimension.

Cebines Three species of *Cebus* (subfamily Cebinae) were included in this study: *Cebus capucinus* and *Cebus albifrons* (non-apelloids), and *Cebus apella*. Although primarily frugivorous, all three 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). In addition, all three species use their anterior teeth during ingestive behaviors, including processing seeds (Terborgh, 1986; Janson and Boinski, 1992). However, *C. apella* exploits relatively greater amounts of resistant foods compared with the non-apelloid capuchins (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 and/or dental preparation, often in the form of the use of the canines as a wedge to further propagate cracks (Izawa and Mizuno, 1977; Izawa, 1979; Terborgh, 1983; Janson and Boinski, 1992).

Numerous morphological analyses of cebine masticatory morphology are consistent with the finding that *C. apella* exploits tougher and stiffer food objects than non-apelloids, and that these relatively large food items necessitate wide jaw gapes (Kinzey, 1974; Rosenberger and Kinzey, 1976; Teaford, 1985; Bouvier, 1986b; Cole, 1992; Daegling, 1992; Spencer, 1995; Wright, 2005; Norconk et al., 2009; Taylor and Vinyard, 2009). Interestingly, Spencer (1995) and Wright (2005) 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 configuration among species of *Cebus* and hypothesized instead that the ability of *C. apella* to utilize more resistant food objects was related to differences in soft tissue anatomy. In contrast, Wright (2005) found that the masticatory apparatus of *C. apella* was more advantageous for generating and dissipating higher masticatory forces (particularly along the anterior dentition) than other *Cebus* species, although these forces may be relatively infrequent.

Given these data, *C. apella* is expected to exhibit relatively larger condylar surface areas as a consequence of their assumed relatively larger joint reaction forces (Table 1). In addition, increased use of the anterior dentition and ingestion and biting of relatively large food objects along the postcanine dentition suggest *C. apella* should have a relatively anteroposteriorly longer glenoid and

Table 1
Predicted variation in aspects of TMJ shape in each comparative group examined in the dietary analyses.

	Atelines	Cebines	Pitheciines
Articular tubercle height	*Alouatta* > *Lagothrix*/*Ateles*	*C. apella* > *C. albifrons*/*C. capucinus*	*Pithecia* > *Cacajao*/*Chiropotes*
Entoglenoid height	*Alouatta* > *Lagothrix*/*Ateles*	*C. apella* > *C. albifrons*/*C. capucinus*	*Pithecia* > *Cacajao*/*Chiropotes*
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*
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*
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*
Condyle area	*Alouatta* > *Lagothrix*/*Ateles*	*C. apella* > *C. albifrons*/*C. capucinus*	*Cacajao*/*Chiropotes* > *Pithecia*
Glenoid length/condyle length ratio	*Alouatta* > *Lagothrix*/*Ateles*	*C. apella* > *C. albifrons*/*C. capucinus*	*Cacajao*/*Chiropotes* > *Pithecia*

mandibular condyle, which should facilitate achieving the larger gapes necessary for food processing. This increased gape is also expected to be accompanied by a relatively large entoglenoid process that acts to guide the movement of the condyle and function to increase the joint surface area of the TMJ, as well as an enlarged articular tubercle.

Pitheciines *Cacajao melanocephalus*, *Chiropotes satanas*, and *Pithecia pithecia* are included from the subfamily Pitheciinae. All three species feed primarily on seeds, particularly when fruits are less available (Buchannon et al., 1981; van Roosmalen et al., 1981, 1988; Ayres, 1989; Kinzey, 1992; Boubli, 1999). Collectively, 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 taxa, *Pithecia* has been suggested to be the least specialized for seed predation, primarily because of its more generalized masticatory morphology, lower molar relief, and less well-developed canines (Kinzey, 1992; Kinzey and Norconk, 1993). Spencer (1995) tested the hypothesis that *Pithecia* was more generalized than either *Chiropotes* or *Cacajao*, and found that the mechanical advantage of the masticatory muscles in *Pithecia* was substantially lower than in *Chiropotes* and *Cacajao*. Additionally, Norconk et al. (2009) found that among pitheciines, the masticatory apparatus of *Pithecia* has the lowest mechanical advantage for biting on the anterior teeth. This may be associated with the greater proportion of leaves in the diet of *Pithecia* compared with *Chiropotes* and *Cacajao*. However, *C. satanas* and *P. pithecia* ingest and masticate foods of comparable average and maximum toughness, and in fact, *Pithecia* has been documented to breach food items that are considerably tougher than those processed by *Chiropotes* (Wright, 2004; Norconk et al., 2009).

These data suggest that *Cacajao* and *Chiropotes* should both have relatively larger condylar surface areas as a consequence of their increased reliance on seed predation (and therefore presumably larger joint reaction forces) (Table 1). 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 and entoglenoid process as a result of their increased use of the postcanine dentition.

Materials and methods

To examine TMJ shape variation in the sample and to test the predictions, three-dimensional (3D) coordinate data describing the shape of the glenoid fossa and mandibular condyle were collected on females and males from 13 platyrrhine species (Table 2). Data were collected using a Microscribe G2X digitizer (Immersion Corp.). The measured accuracy for the Microscribe G2X is ±0.23 mm, and an analysis of intraobserver error for this dataset found an average error of approximately 0.03 mm for the skull and 0.04 mm for the mandible (Terhune, 2010). Three-dimensional renderings of the articular surfaces of the glenoid and mandibular condyle were created by collecting a dense cloud of 3D landmarks describing each of these surfaces 3D surface areas were then calculated using these point clouds.

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 were 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 was then visualized using wireframe diagrams. All configurations were scaled to the same unit centroid size, and the size of each configuration was retained as a separate variable (centroid size). In this study, shape variation was examined both for the entire sample and separately for each of the three comparative groups. This was done for both the glenoid and condylar configurations. 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 listed in Table 3 and illustrated in Fig. 1.

Analyses examining TMJ shape across the entire platyrrhine sample

Analyses of shape variation in the entire sample of 13 species included examining the extent to which shape variation is

Table 2
Comparative taxa used in this study.

Species	Female	Male
Alouatta belzebul	12	12
Alouatta palliata	12	12
Alouatta seniculus	12	12
Aotus trivirgatus	11	10
Ateles geoffroyi	12	12
Cacajao melanocephalus	11	11
Cebus albifrons	12	11
Cebus apella	11	12
Cebus capucinus	13	11
Chiropotes satanas	12	12
Lagothrix lagothrica	11	12
Pithecia pithecia	11	12
Saimiri sciurius	10	10

Table 3
Temporomandibular joint landmark definitions.

Landmark number	Landmark description
Glenoid landmarks	
1	Most inferior point on entoglenoid process
2	Most inferior point on articular tubercle
3	Most inferior point on postglenoid process
4	Deepest point in the mandibular fossa in the sagittal plane of the postglenoid process point
5	Most anterior point on the articular surface of the glenoid fossa
6	Most lateral point on the articular surface of the glenoid at the end of the long axis of the articular eminence
7	Most lateral point on the surface of the articular eminence
8	Most medial point on the surface of the articular eminence
9	Most medial point on the articular surface of the glenoid at the end of the long axis of the articular eminence
10	Midpoint of the crest of the articular eminence
11	Most anterior point on the articular surface of the glenoid along a line perpendicular to the long axis of the articular eminence
12	Point on the posterior edge of the articular eminence along a line perpendicular to the long axis of the articular eminence
Condyle landmarks	
13	Most lateral point on the articular surface of the mandibular condyle
14	Most medial point on the articular surface of the mandibular condyle
15	Midpoint of line connecting the medial and lateral poles of the mandibular condyle
16	Most posterior point on the articular surface of the mandibular condyle at the midpoint of the mediolateral curve
17	Most anterior point on the mandibular condyle at the midpoint of the mediolateral curve

correlated with diet and/or TMJ size. These analyses were performed for females and males separately. To assess the relationship between TMJ shape and size, Procrustes distance matrices describing shape 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 Microsoft Excel add-on PopTools. To assess the relationship between shape variation and diet (as a very rough proxy for food material properties (FMPs)), I compiled published data reporting the percentage of particular food items included in the diets of 11 of the 13 species (Table 4) and created a Euclidean distance matrix using PopTools. Two dietary matrices were created. The first matrix calculated Euclidean distances among taxa when the percentages of less resistant (e.g., fruit, flower, insects) and more resistant (e.g., seeds, leaves, bark, roots) food items were summed. Notably, this matrix did not distinguish between tough and hard food items such as leaves and seeds. As a result, I also computed a dietary matrix based on the summed percentages of these more qualitative dietary categories (e.g., fruits/insects, seeds, and leaves). Admittedly, these categories of food items are very rough proxies for food material properties, but many more data describing FMPs in platyrrhines (and across primates) are necessary before a similar matrix incorporating average and/or maximum fracture toughness or elasticity can be made.

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).

Pairwise comparisons

For each of the clades for which pairwise comparisons were performed, 3D geometric morphometric analyses first assisted in describing the variation in each clade and its correlation to size. Further analyses of shape variation in the sample were performed using linear measurements extracted from the coordinate data using the programs MacMorph (Spencer and Spencer, 1993) and Rhino 3D (Robert McNeel & Associates). Variables measured included anteroposterior glenoid and condyle length as well as mediolateral glenoid and condyle width, 3D glenoid and condylar surface area, preglenoid plane length (as a measure of functional glenoid length), entoglenoid process height, and articular tubercle height (Table 5). These variables were size adjusted by dividing each variable by either mandibular length (as a measure of the load-arm during incision) or the distance from the TMJ to M_1 (as a measure of the load-arm during mastication) (after Hylander, 1985; Vinyard, 2008). For the atelines, variables were standardized using the distance from the TMJ to M_1, whereas for the cebines and pitheciines these biomechanical shape ratios were created using mandibular length. Behavioral data upon which these determinations were made are outlined below.

Differences in these univariate measurements were analyzed using a one-tailed Student's *t*-test. Where these tests failed to find significant differences between the taxa, a two-tailed test was subsequently performed to assess whether there were differences in the direction opposite than that predicted. Taxa that were not specifically predicted to vary (e.g., *Ateles* vs. *Lagothrix*, *C. capucinus* vs. *C. albifrons*, and *Chiropotes* vs. *Cacajao*) were not compared. The critical $\alpha = 0.05$ was further adjusted for multiple comparisons using the sequential Bonferroni method (Rice, 1989). These analyses were performed separately for atelines, cebines, and pitheciines. Student's *t*-tests for significant differences between the sexes suggested that males and females do not significantly differ in most aspects of TMJ shape, and since I have no a priori expectation of functional differences between the sexes, their data were pooled. The *t*-tests were calculated using the program IBM SPSS (Version 19).

Results

Platyrrhine TMJ variation

In the geometric morphometric analysis of the entire sample (Fig. 2), PC 1 separates the three *Alouatta* species from the rest of the sample. This PC explains 43% of the sample variance and is significantly correlated with size in females ($r^2 = 0.497$, $p = 0.007$) and males ($r^2 = 0.680$, $p = 0.007$). Shape variation along this axis is primarily associated with postglenoid process projection, and to a lesser degree, the relative anteroposterior and mediolateral dimensions of the joint. PC2 (which explains approximately 25% of the sample variance) is not significantly correlated with size and separates the remaining atelines (*Lagothrix* and *Ateles*) and pitheciines from the cebines (including *Aotus* and *Saimiri*), although this separation is marginal. Shape variation along this PC is associated with entoglenoid process projection and to a lesser extent, mediolateral width of the glenoid fossa.

TMJ shape and diet are significantly correlated in both sexes, but only when seeds and leaves were summed separately and incorporated into the dietary matrix (Table 6). There is also a significant correlation between the shape and size matrices in both females and males. Partial Mantel tests were also performed to determine the relative influence of size and diet, and suggest that size is more strongly correlated with TMJ shape when diet is held constant (Table 6). However, diet was still significantly ($r = 0.3458$, $p = 0.011$)

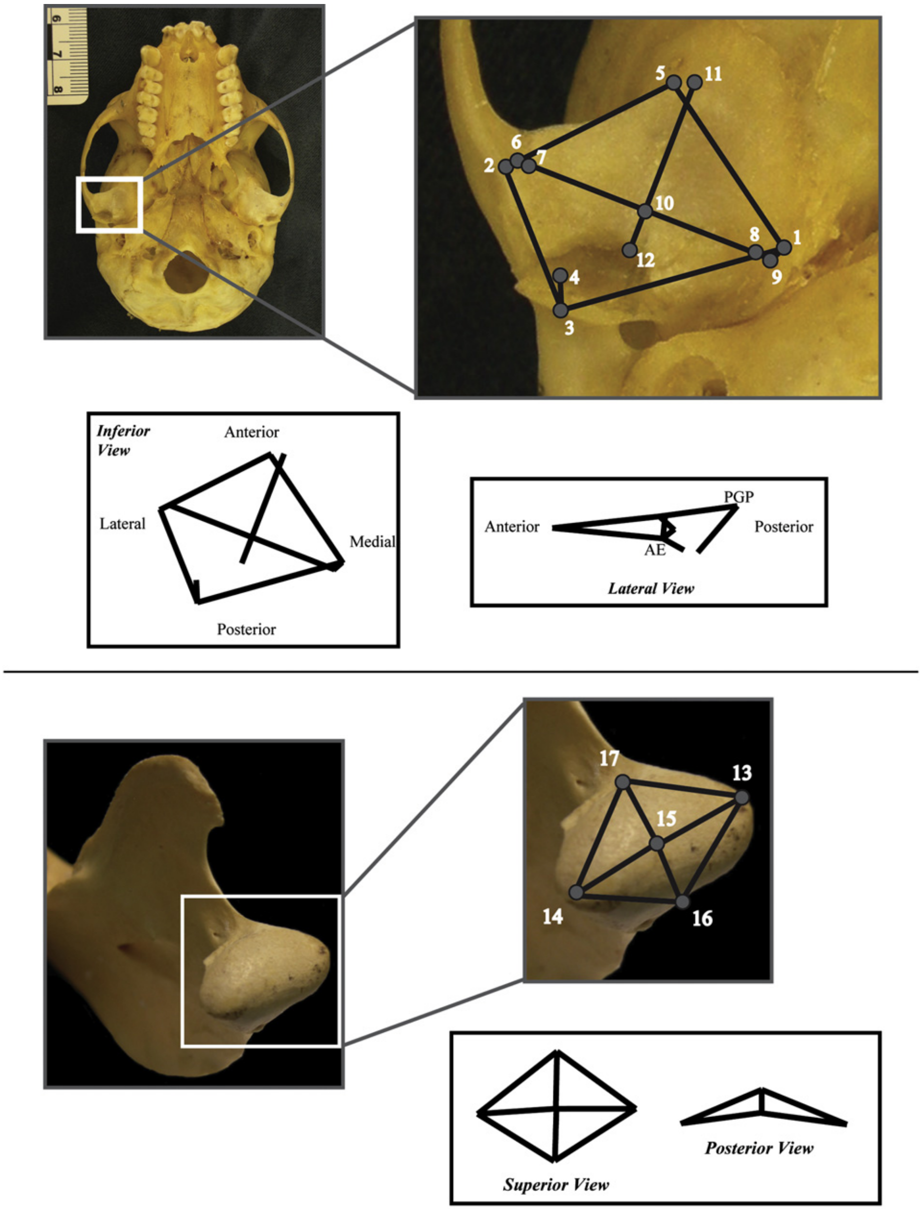

Figure 1. Inferior views of a *Cebus apella* glenoid (top) and mandibular condyle (bottom) showing landmarks and wireframe diagrams used in this study. Numbers correspond to landmarks listed in Table 3. Features indicated on the lateral view wireframe are the articular eminence (AE) and postglenoid process (PGP).

Table 4
Data used to calculate the dietary distance matrices.

	% Fruit	% Seeds	% Insects	% Leaves	% Bark, pith, wood, stems	% Flowers	% Other	References
Cebus apella	82.5	12.5			3.75		1.25[b]	Terborgh, 1983
Cebus albifrons	76	21			0.25		2.5[b]	Terborgh, 1983
Saimiri sciureus	55.1		44.9					Lima and Ferrari, 2003
Alouatta belzebul	35			61		4		DeSouza et al., 2002
Alouatta palliata	42.1			48.2		9.6		Milton, 1980
Alouatta seniculus	25.5		1.5	57	0.4	12.6		Julliot and Sabatier, 1993
Lagothrix lagotricha	74	7		16.2		3.1		Peres, 1994
Ateles geoffroyi	82.2			17.2		1		Russo et al., 2005
Chiropotes satanas	21.6	74.8	0.5	0.2		0.4		Kinzey and Norconk, 1993
Cacajao calvus[a]	18	67	5				6[c]	Ayres, 1986, 1989
Pithecia pithecia	27.8	60.6	2.3	7.1		2.2		Kinzey and Norconk, 1993

Totals do not necessarily add up to 100% because some food items were not identified by the original authors. ‘Soft’ food items = fruit, animal matter, flowers, and other; ‘hard’ food items = seeds; ‘tough’ food items = leaves, bark, pith, wood, and stems.

[a] Since data for *C. melanocephalus* were not available, data for *C. calvus* were substituted.

[b] Nectar, petiole, and meristem.

[c] Nectar.

Table 5
Measurements included in the univariate analysis.

Name	Definition	Abbreviation
Articular tubercle height	Inferior projection of the articular tubercle (Ldmk 2), as measured from the Frankfurt Horizontal plane	ArtTubHt
Entoglenoid height	Inferior projection of the entoglenoid process (Ldmk 1), as measured from the Frankfurt Horizontal plane	EntGlHt
Glenoid length	Linear distance between the most anterior point on the articular surface of the glenoid fossa to the most inferior point on the postglenoid process (Ldmks 3 and 5)	GlenLg
Glenoid width	Linear distance between the most lateral and most medial points of the glenoid fossa (Ldmks 6 and 9)	GlenWid
Glenoid area	Sum of the surface area of the polygons connecting a cloud of points covering the articular surface of the glenoid fossa (calculated in the program Rhino 3D)	3DGlenArea
Preglenoid plane length	Linear distance between the apex of the articular eminence and the most anterior point on the articular surface of the glenoid fossa (Ldmks 5 and 10)	PreglenLg
Condyle length	Distance between the most anterior and most posterior points on the mandibular condyle (Ldmks 16 and 17)	CondLg
Condyle width	Distance between the most medial and most lateral points on the mandibular condyle (Ldmks 13 and 14)	CondWid
Condyle area	Sum of the surface area of the polygons connecting a cloud of points covering the articular surface of the mandibular condyle (calculated in the program Rhino 3D)	3DCondArea
Glenoid length–condyle length ratio	Glenoid length divided by condyle length	GlenLg/CondLg
Mandible length	Distance from the center of the mandibular condyle to infradentale	MandLg
Distance from TMJ to M1	Distance from the center of the mandibular condyle to the lateral alveolar margin of mandibular M1	TMJ-M1

correlated with female glenoid shape even after holding centroid size constant.

Pairwise comparisons

Atelines PC1 1 accounts for 29% of the sample variation and is significantly correlated with centroid size ($r^2 = 0.57$, $p < 0.001$) (Fig. 3). This PC separates all three species of *Alouatta* from *Lagothrix* and *Ateles*. Variation in shape along this axis is associated with the relative size of the postglenoid process (PGP), which is considerably larger in *Alouatta*, but also with relative AP length of the glenoid. However, a separate geometric morphometrics analysis for the condylar configurations (not shown) did not separate these taxa.

Several trends are apparent from the pairwise comparisons of relative differences in TMJ shape (Table 7). Atelines generally exhibit the predicted differences in relative entoglenoid height, articular tubercle height, and some aspects of glenoid shape. Compared with *Ateles*, *Alouatta* has significantly more projecting entoglenoid processes and articular tubercles, a relatively anteroposteriorly longer glenoid, and a larger ratio of glenoid to condyle length. Only *A. palliata* was found to have relatively larger glenoid or condylar surface areas than *Ateles.* Similarly, *Alouatta* has a relatively more projecting entoglenoid process and larger ratio of glenoid to condylar length than does *Lagothrix*. But unlike the comparisons between *Alouatta* and *Ateles*, *Alouatta* has relatively smaller condylar length, condylar area, and (less consistently) glenoid width and preglenoid plane length than *Lagothrix*.

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 very slightly along PC 2 (15.2% of variation) (Fig. 4). No significant correlations were found between the top ten PC axes (which account for ∼90% of the sample variance) and centroid size. The wireframe diagrams indicate that *C. apella* differs from the other species in anteroposterior length and mediolateral width of the glenoid, and in the relative size of the postglenoid process. *C. apella* also separated from *C. albifrons* and *C. capucinus* in condylar morphology (Fig. 5), with *C. apella* exhibiting a relatively anteroposteriorly shorter condyle that is less mediolaterally convex.

Table 6
Results of the full and partial Mantel tests between the Procrustes distance (shape), centroid size, and dietary matrices.

	Female shape		Male shape	
	r	*p*-value	*r*	*p*-value
Centroid size	**0.692**	**<0.001**	**0.719**	**<0.001**
Diet (soft vs. resistant)	0.155	0.115	0.060	0.310
Diet (soft vs. hard vs. tough)	**0.488**	**<0.001**	**0.316**	**0.024**
Centroid size (controlling for diet)	**0.6303**	**<0.001**	**0.6812**	**<0.001**
Diet (controlling for size)	**0.3458**	**0.011**	0.029	0.425

Significant correlations are shown in bold.

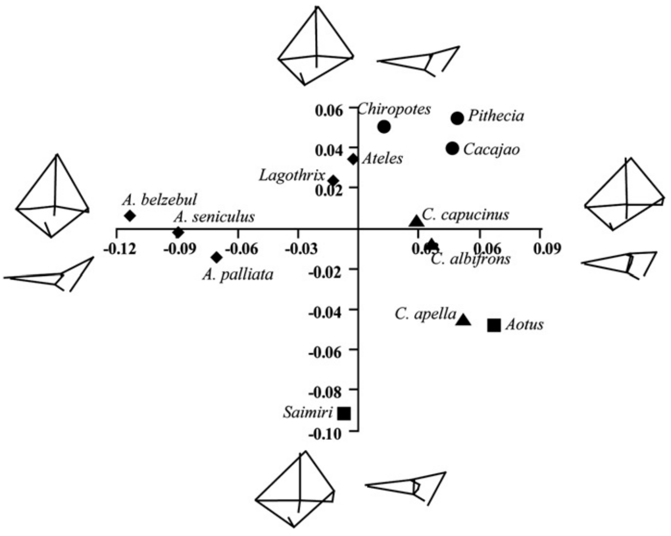

Figure 2. Bivariate plot of PC 1 (*x*-axis) and PC 2 (*y*-axis) from the PC analysis of the glenoid landmarks with wireframe diagrams illustrating shape variation in the sample. Platyrrhine females only included.

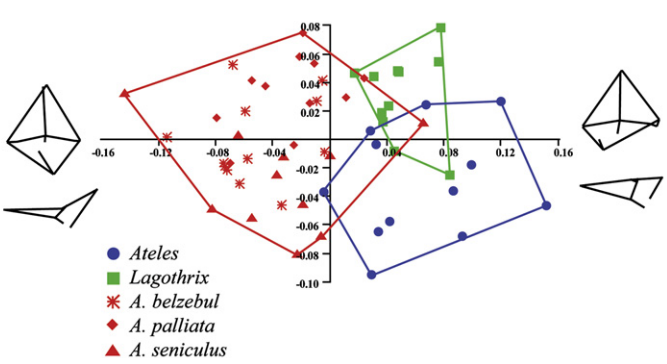

Figure 3. Bivariate plot of PC 1 (*x*-axis) and PC 2 (*y*-axis) from the PC analysis of the glenoid configurations in the Atelinae females. Wireframe diagrams illustrate the shape variation from the resistant to soft-object feeders in the sample.

Table 7
Means, standard deviations (SD), and *p*-values for the Student's *t*-tests among the atelines. Variables were scaled by the distance from the TMJ to the first molar (TMJ-M1).

Variable	Prediction	*A. belzebul*		*A. palliata*		*A. seniculus*		*Ateles*		*Lagothrix*	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
ArtTub/TMJ-M1	*Alouatta*>	0.141	0.017	0.155	0.012	0.159	0.019	0.119	0.015	0.156	0.012
EntGlHt/TMJ-M1	*Alouatta*>	0.176	0.021	0.177	0.013	0.180	0.014	0.140	0.017	0.151	0.018
GlenLg/TMJ-M1	*Alouatta*>	0.339	0.021	0.349	0.014	0.342	0.018	0.325	0.025	0.337	0.025
GlenWid/TMJ-M1	*Alouatta*>	0.266	0.018	0.300	0.018	0.278	0.021	0.291	0.019	0.294	0.016
PreGlLg/TMJ-M1	*Alouatta*>	0.195	0.017	0.202	0.013	0.187	0.016	0.196	0.020	0.205	0.020
GlenArea/TMJ-M1	*Alouatta*>	0.308	0.014	0.325	0.010	0.305	0.012	0.316	0.015	0.315	0.017
CondWid/TMJ-M1	*Alouatta*>	0.216	0.020	0.216	0.047	0.219	0.017	0.222	0.016	0.230	0.018
CondLg/TMJ-M1	*Alouatta*>	0.086	0.008	0.092	0.021	0.088	0.008	0.092	0.008	0.102	0.008
CondArea/TMJ-M1	*Alouatta*>	0.187	0.013	0.199	0.013	0.188	0.010	0.189	0.012	0.200	0.013
GlenLg/CondLg	*Alouatta* >	3.989	0.382	4.047	1.340	3.917	0.462	3.560	0.412	3.331	0.342

Variable	Prediction	*p*-values[a]					
		A. belzebul vs. *Ateles*	*A. palliata* vs. *Ateles*	*A. seniculus* vs. *Ateles*	*A. belzebul* vs. *Lagothrix*	*A. palliata* vs. *Lagothrix*	*A. seniculus* vs. *Lagothrix*
ArtTub/TMJ-M1	*Alouatta*>	**<0.00001/-**	**<0.00001/-**	**<0.00001/-**	**NS/0.002**	NS/NS	NS/NS
EntGlHt/TMJ-M1	*Alouatta*>	**<0.00001/-**	**<0.00001/-**	**<0.00001/-**	**0.00004/-**	**<0.00001/-**	**<0.00001/-**
GlenLg/TMJ-M1	*Alouatta*>	NS/NS	**<0.00001/-**	**0.0035/-**	NS/NS	NS/NS	NS/NS
GlenWid/TMJ-M1	*Alouatta*>	**NS/0.00003**	NS/NS	NS/NS	**NS/<0.00001**	NS/NS	NS/NS
PreGlLg/TMJ-M1	*Alouatta*>	NS/NS	NS/NS	NS/NS	NS/NS	NS/NS	**NS/0.001**
GlenArea/TMJ-M1	*Alouatta*>	NS/NS	**0.0076/-**	NS/NS	NS/NS	NS/NS	NS/NS
CondWid/TMJ-M1	*Alouatta*>	NS/NS	NS/NS	NS/NS	NS/NS	NS/NS	NS/NS
CondLg/TMJ-M1	*Alouatta*>	NS/NS	NS/NS	NS/NS	**NS/<0.00001**	NS/NS	**NS/<0.00001**
CondArea/TMJ-M1	*Alouatta*>	NS/NS	**0.0052/-**	NS/NS	**NS/0.005**	NS/NS	**NS/0.0005**
GlenLg/CondLg	*Alouatta*>	**0.0003/-**	NS/NS	**0.0035/-**	**<0.00001/-**	NS/NS	**<0.00001/-**

[a] *p*-values indicate the significance level for the one-tailed test, followed by a two-tailed, which was performed only if the one-tailed test failed to find a significant difference. A significant *p*-value for the two-tailed test indicates a statistically significant difference in the direction opposite to that originally predicted. Bolded values indicate a significant *p*-value, whereas NS indicates no significant difference in shape between the taxa examined.

In contrast to the geometric morphometric analyses, most pairwise comparisons between *C. apella* on the one hand, and *C. capucinus* and *C. albifrons* on the other, were not statistically significant, and several that were significant were not in the expected direction (Table 8). Thus, contrary to predictions, *C. apella* has a relatively smaller articular tubercle and entoglenoid process compared with *C. albifrons* and/or *C. capucinus*. However, *C. apella* tends to have relatively wider joints, and larger glenoid joint surface area compared with *C. albifrons* and/or *C. capucinus.*

Pitheciines For both glenoid and condylar morphologies, PC analysis of the 3D landmarks failed to significantly distinguish among *C. melanocephalus*, *C. satanas*, and *P. pithecia* (Figs. 6 and 7). However, centroid size was found to be significantly correlated with PC 1 ($r = 0.278$, $p = 0.003$). In contrast, significant differences in TMJ shape among these three species were identified in the univariate analyses (Table 8). As predicted, *C. satanas* and/or *C. melanocephalus* have relatively larger glenoid and condylar surface areas and dimensions compared with *P. pithecia*. Counter to expectations, *Pithecia* was not found to have a relatively wider joint compared with *Cacajao* and *Chiropotes*, or (at least in comparison to

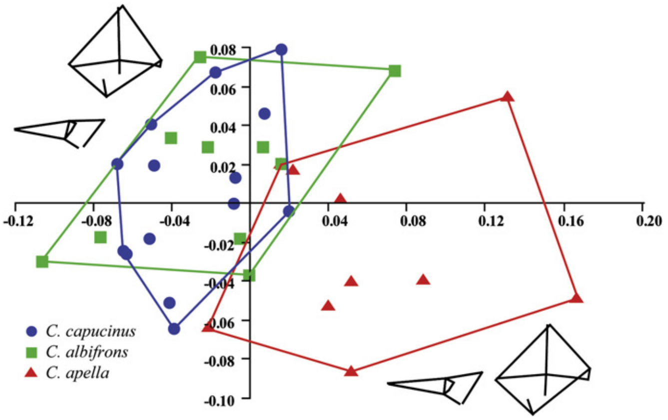

Figure 4. Bivariate plot of PC 1 (*x*-axis) and PC 2 (*y*-axis) from the PC analysis of the glenoid configurations in the Cebinae females. Wireframe diagrams illustrate the shape variation from the resistant to soft-object feeders in the sample.

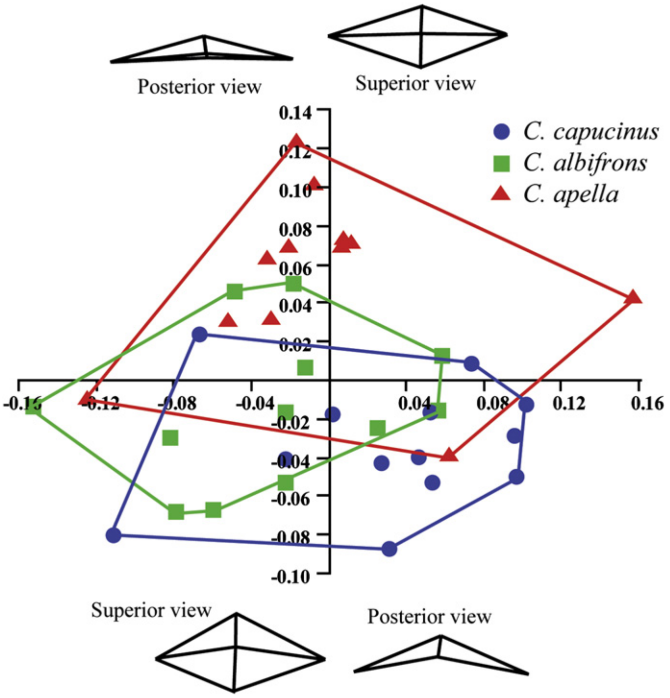

Figure 5. Bivariate plot of PC 1 (*x*-axis) and PC 2 (*y*-axis) from the PC analysis of the condylar configurations in the Cebinae females. Wireframe diagrams illustrate the shape variation from the resistant to soft-object feeders in the sample.

Table 8

Means, standard deviations (SD), and *p*-values for the Student's *t*-tests among the cebines (top) and pitheciines (bottom). Variables were scaled by mandible length.

Variable	Prediction	*C. apella*		*C. capucinus*		*C. albifrons*		*p*-value[a]	
		Mean	SD	Mean	SD	Mean	SD	*C. apella* vs. *C. capucinus*	*C. apella* vs. *C. albifrons*
ArtTub/MandLg	*C. apella*>	0.064	0.017	0.081	0.009	0.087	0.009	**NS/0.00009**	**NS/<0.00001**
EntGlHt/MandLg	*C. apella*>	0.069	0.011	0.081	0.009	0.080	0.010	**NS/0.0002**	**NS/0.002**
GlenLg/MandLg	*C. apella*>	0.219	0.019	0.207	0.011	0.213	0.016	NS/NS	NS/NS
GlenWid/MandLg	*C. apella*>	0.217	0.019	0.199	0.012	0.207	0.011	**0.0002/-**	NS/NS
PreGlLg/MandLg	*C. apella*>	0.123	0.015	0.122	0.011	0.124	0.017	NS/NS	NS/NS
GlenArea/MandLg	*C. apella*>	0.221	0.013	0.209	0.009	0.212	0.013	**0.0002/-**	NS/NS
CondWid/MandLg	*C. apella*>	0.166	0.013	0.155	0.016	0.153	0.012	NS/NS	**0.0004/-**
CondLg/MandLg	*C. apella*>	0.062	0.006	0.061	0.006	0.062	0.005	NS/NS	NS/NS
CondArea/MandLg	*C. apella*>	0.137	0.011	0.131	0.013	0.132	0.008	NS/NS	NS/NS
GlenLg/CondLg	*C. apella*>	3.563	0.407	3.418	0.346	3.474	0.358	NS/NS	NS/NS

Variable	Prediction	Pithecia		Chiropotes		Cacajao		*p*-value[a]	
		Mean	SD	Mean	SD	Mean	SD	*Pithecia* vs. *Chiropotes*	*Pithecia* vs. *Cacajao*
ArtTub/MandLg	*Pithecia*>	0.073	0.010	0.082	0.015	0.060	0.013	NS/NS	**0.0004**
EntGlHt/MandLg	*Pithecia*>	0.084	0.013	0.093	0.014	0.077	0.010	NS/NS	NS/NS
GlenLg/MandLg	*Pithecia*<	0.216	0.021	0.244	0.017	0.230	0.015	**<0.00001/-**	**0.0067/-**
GlenWid/MandLg	*Pithecia*>	0.200	0.015	0.225	0.014	0.225	0.014	**NS/<0.00001**	**NS/<0.00001**
PreGlLg/MandLg	*Pithecia*<	0.130	0.019	0.143	0.014	0.137	0.013	**0.0049/-**	NS/NS
GlenArea/MandLg	*Pithecia*<	0.212	0.013	0.234	0.011	0.231	0.007	**<0.00001/-**	**<0.00001/-**
CondWid/MandLg	*Pithecia*>	0.152	0.029	0.169	0.025	0.172	0.012	**NS/0.045**	**NS/0.006**
CondLg/MandLg	*Pithecia*<	0.061	0.013	0.076	0.014	0.072	0.009	**0.0004/-**	**0.0014/-**
CondArea/MandLg	*Pithecia*<	0.123	0.010	0.152	0.013	0.150	0.006	**<0.00001/-**	**<0.00001/-**
GlenLg/CondLg	*Pithecia*<	3.641	0.635	3.367	0.903	3.240	0.364	NS/NS	NS/NS

[a] *p*-values indicate the significance level for the one-tailed test, followed by a two-tailed, which was performed only if the one-tailed test failed to find a significant difference. A significant *p*-value for the two-tailed test indicates a statistically significant difference in the direction opposite to that originally predicted. Bolded values indicate a significant *p*-value, whereas NS indicates no significant difference in shape between the taxa examined.

Chiropotes) a more projecting articular tubercle. Glenoid and condylar length also tended to be longer in *Chiropotes* and *Cacajao* than in *Pithecia*.

Discussion

TMJ size and shape variation across platyrrhines

Analysis of TMJ variation across the platyrrhine sample highlights the wide range of variation in glenoid shape present in this clade. Importantly, this analysis found a relationship between size and shape of the TMJ and diet, particularly when seeds and leaves are considered separately. Assuming that dietary categories bear some relationship to food material properties, the results of this study further suggest that differentiating between seeds and leaves may be important for understanding functional differences in TMJ shape. 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; 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, insect 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 with 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.

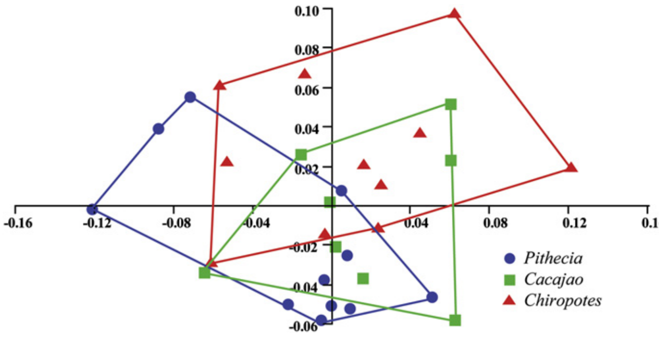

Figure 6. Bivariate plot of PC 1 (*x*-axis) and PC 2 (*y*-axis) from the PC analysis of the glenoid configurations in the Pitheciinae females.

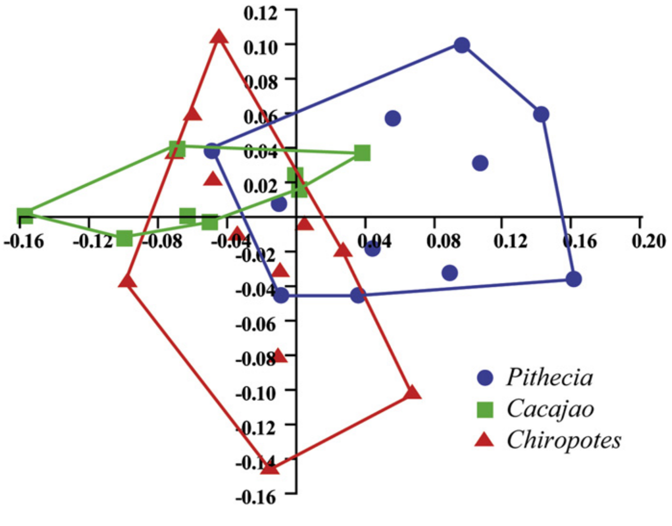

Figure 7. Bivariate plot of PC 1 (*x*-axis) and PC 2 (*y*-axis) from the PC analysis of the condylar configurations in the Pitheciinae females.

mature leaves), since these different categories may have different food material properties and/or require different masticatory abilities. As more data on food material properties become available, future work will be able to further refine the analyses performed in this study.

One reason for the increased resolution in the dietary signal of the TMJ when the percentage of seeds and leaves in the diets of these taxa are analyzed separately may be that these dietary categories separate along clade lines. For example, pitheciines are seed predators whereas the atelines and cebines have relatively larger percentages of leaves and fruit pulp, respectively, in their diets (e.g., Izawa, 1979; Gaulin and Gaulin, 1982; Terborgh, 1986; Chapman, 1987; Ayres, 1989; Kinzey, 1992; Janson and Boinski, 1992; Peres, 1994; Boubli, 1999). Thus, by separating these dietary categories, the correlation between morphology and diet increases. This therefore suggests that TMJ morphology varies both as a function of diet and as a function of phylogenetic differentiation of these groups. The goal of the restricted pairwise comparisons was to minimize this possible phylogenetic confound. Although not directly comparable analyses, the pairwise comparisons did not show as marked of a correlation between diet and TMJ shape as was demonstrated by the analysis across the entire platyrrhine sample. Thus, at lower taxonomic levels shape does not appear to be as strongly correlated with diet. In some instances, this may represent an overlap in the types of foods utilized by closely related taxa (e.g., *C. apella* and *C. albifrons*), or it could indicate an insignificant knowledge of the dietary breadth of taxa in particular clades (e.g., pitheciines). As a result, even though these pairwise comparisons give us the ability to specifically test biomechanical hypotheses of function, future analyses seeking to assess the morphological correlates of diet or feeding behavior may also benefit from broader interspecific analyses of shape with strong phylogenetic controls.

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, as well as taxa that utilize their anterior dentition extensively, were expected to have relatively larger condylar joint surface areas to improve the load resistance capabilities of the TMJ. However, this prediction was only supported in the pitheciine sample, and to a much lesser extent, the atelines. Thus, these data do not support an overwhelming pattern of differences in TMJ shape within cebines or atelines related to force production. This result is curious in light of food material property data for these species (Norconk et al., 2009). Average and maximum toughness values for food items opened or masticated by these taxa suggest that *C. apella* and *A. seniculus* generate considerably higher bite forces than do *C. olivaceus* and *Ateles paniscus*, respectively. That these differences in bite force magnitude are apparently not linked to differences in load resistance at the joint may imply that other morphological features of the mandible and/or TMJ (e.g., the articular eminence) act to mediate the magnitude of the joint reaction force in relation to the bite force, or that the TMJ is over designed and therefore does not reflect differences in joint loading.

Taxa were also predicted to differ significantly in the relative anteroposterior and mediolateral dimensions of the joint surfaces, depending on whether they rely more extensively on their anterior vs. posterior teeth for processing foods. Taxa that repetitively masticate tougher food items (e.g., leaves) on their posterior teeth were expected to have relatively mediolaterally wider joints than taxa that use their anterior teeth more extensively to process food items (Smith et al., 1983; Bouvier, 1986a,b). Mixed support was found for this prediction. The anteroposterior dimensions of the joint differed predictably and most consistently among the atelines and pitheciines. No differences in anteroposterior dimensions of the joint were found in the cebines. In the atelines, anteroposterior dimensions of the joint differed primarily between *Alouatta* and *Ateles*. Interestingly, in comparison with *Lagothrix*, *Alouatta* was either not significant or had smaller anteroposterior dimensions of the joint. However, despite these differences, *Alouatta* consistently had a larger glenoid to condylar length ratio than *Ateles* and *Lagothrix*. These data may therefore suggest subtle differences in the translatory potential of the TMJ among these species, such that *Alouatta* may have the ability to generate wider jaw gapes than either *Ateles* or *Lagothrix*. *Alouatta* tends to rely heavily on the postcanine dentition for the repetitive mastication of leaves, which is not necessarily a feeding behavior that necessitates generating relatively wide jaw gapes (although this may depend on the quantity of leaves consumed in a single bite). Therefore, the improved sagittal sliding and attendant capacity to generate relatively large jaw gapes could instead be related to the unique vocal behaviors of *Alouatta*. Although it is currently unknown whether *Alouatta* generates relatively wide jaw gapes during their vocal behaviors, if these vocal behaviors do require generating relatively large gapes this behavior could further be facilitated by differences in soft tissue anatomy, such as jaw adductor muscle position and fiber length.

Some significant differences in anteroposterior TMJ length were also found in the pitheciines. In the females, both glenoid and condylar length were larger in *Chiropotes* than in *Pithecia*. These differences could be indicative of masticatory specializations related to the extensive use of the anterior dentition to process hard or tough seeds in *Chiropotes* and *Cacajao* (e.g., Kinzey, 1992). However, the ratio between glenoid and condylar length did not vary significantly between these species, suggesting that these differences in the anteroposterior dimensions of the joint in the pitheciines do not necessarily translate into differences in gape capacity among these species (although other factors such as muscle architecture, muscle position, or mandibular morphology may also influence gape).

C. apella has also been documented to process food items using its anterior dentition (e.g., the canines, premolars, and even first molar (Wright and Wright, 2010; Reed and Ross, 2010)). I therefore predicted that this species would have relatively anteroposteriorly longer TMJs than *C. capucinus* or *C. albifrons*. However, no significant differences were found for variables reflecting TMJ length among these taxa. These data suggest that the species of *Cebus* examined here maintain roughly similar capacities for sagittal sliding at the TMJ. In fact, coupled with the relatively increased height of the TMJ above the occlusal plane in *C. apella* (Constantino, 2007), this finding may suggest that *C. apella* has relatively similar (or possibly smaller) maximum jaw gapes than *C. capucinus* or *C. albifrons*, since mandibular ramus height tends to be negatively correlated with gape (Herring and Herring, 1974; Smith, 1984; Singleton, 2005). Thus, minimally, these data suggest that TMJ morphology in this species is not adapted in such a way as to facilitate relatively larger gapes in *C. apella*. Together with recent analyses of masticatory muscle architecture in the cebines, these data further support previous suggestions that *C. apella* can generate relatively larger muscle and bite forces, while maintaining gapes similar to non-apelloid species (Spencer, 1995; Wright, 2005; Constantino, 2007; Taylor and Vinyard, 2009).

No significant differences in mediolateral width were found in the atelines, which ran counter to the expectation that *Alouatta* would have a relatively wider TMJ than *Ateles* or *Lagothrix*. Similarly, few differences in relative TMJ width were found in the *Cebus* sample, although *C. apella* does tend to have a wider glenoid and/or condyle than either *C. albifrons* or *C. capucinus*, a finding that is consistent with previous analyses by Bouvier (1986b). This may suggest increased joint reaction forces on the lateral aspect of the joint in *C. apella*, as would be consistent with increased unilateral mastication on the posterior dentition in this taxon. In the pitheciines, it was predicted that *Pithecia* would exhibit the relatively mediolaterally widest TMJ as a result of their heavier use of the postcanine dentition to masticate leaves. This was not the case, however, since all measures of TMJ width (and in fact, all measures of joint size except the ratio between glenoid and condyle length) were significantly larger in *Chiropotes* and *Cacajao* than in *Pithecia*. This finding suggests that joint reaction forces may be oriented more mediolaterally (as is expected to be the case with axial torsion of the mandible) in *Chiropotes* and *Cacajao* in comparison to *Pithecia*. Furthermore, the significantly larger joint dimensions in *Chiropotes* and *Cacajao* may be indicative of globally higher joint reaction forces in these taxa.

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. It was predicted that the relative size of both of these features would increase with increased joint reaction forces (i.e., to increase joint surface area of the joint), and/or with increased range of motion (i.e., to guide movement of the condyle and counteract tensile forces at the joint). Thus, in resistant-object feeders and taxa that extensively use their postcanine dentition, the entoglenoid process and articular tubercle should be relatively larger than in taxa that masticate relatively softer food objects and/or do not extensively use their postcanine dentition.

Again, results were mixed. The more resistant-object feeders among the atelines (e.g., *Alouatta*) and the pitheciines (e.g., *Chiropotes*) do have relatively larger articular tubercles and/or entoglenoid processes. However, contrary to predictions, *C. apella* has a smaller articular tubercle and entoglenoid process compared with the non-apelloids. Although no explicit comparisons were made between *Cacajao* and *Chiropotes*, it is particularly notable that the entoglenoid process is the only variable for which *Cacajao* and *Chiropotes* depart from one another. For all other variables, these two genera differ in the same direction from *Pithecia*, whereas for this variable, *Cacajao* has a smaller entoglenoid than *Pithecia* and the values for *Chiropotes* are larger (although neither species differs significantly from *Pithecia*). Differences in feeding ecology between *Cacajao* and *Chiropotes* are poorly documented, however, and it is therefore unclear whether these morphological differences may be associated with differences in masticatory (or ingestive) behavior.

Some of the observed variation in entoglenoid (and possibly articular tubercle) height may be related to the need for some of these taxa to generate relatively high jaw forces at relatively wide jaw gapes. In *Alouatta*, it is presumed that higher forces are generally generated along the postcanine dentition while jaw gapes are relatively low, whereas *C. apella* and all of the pitheciines have been observed to process relatively large and resistant objects using the anterior dentition (e.g., Izawa and Mizuno, 1977; Terborgh, 1983; van Roosmalen et al., 1988; Ayres, 1989; Janson and Boinski, 1992; Kinzey, 1992), which often necessitates large ingestive gapes (e.g., Norconk et al., 2009; Taylor and Vinyard, 2009). The relatively less projecting entoglenoid processes observed in these taxa may be advantageous for allowing increased mediolateral movements of the mandible during ingestive behaviors that involve the use of the anterior dentition. Experimental analyses of mandibular movements and glenoid morphology are necessary to further explore this proposed function of the entoglenoid process.

The TMJ and the masticatory apparatus as a whole

The TMJ is one portion of the much larger masticatory apparatus. Examining the functional morphology of the TMJ is informative, but only to the extent that functional variation in the masticatory apparatus is reflected in this joint. Here I examined morphology of the TMJ as it is assumed to be related to differences in force production and range of motion in the masticatory apparatus as a whole, and these data suggest that form of the TMJ does vary as a consequence of feeding behavior. Some features of the TMJ can be linked to hypothesized differences in joint reaction forces as well as movement at the joint, and these features should be taken into consideration in future evaluations of the masticatory apparatus in living and extinct primates. For example, this study provides further (albeit indirect) evidence that the anteroposterior dimensions of the joint are linked to gape capacity (Wall, 1999; Vinyard et al., 2003). If this is the case, then (along with other mandibular dimensions) we may be able to further refine our estimates of relative gape in fossil hominins such as *Australopithecus* or *Paranthropus*, which in turn has implications for diet and feeding behavior in these taxa (e.g., Demes and Creel, 1988; Teaford and Ungar, 2000; Ungar, 2004; Rak and Hylander, 2008; Strait et al., 2009).

The inferences that can be made using only TMJ morphology are limited, however. Large joint surface areas may imply relatively improved load resisting ability, but cannot be used to infer whether joint forces are of infrequent but high magnitude, or high frequency and low magnitude. This is of particular importance in considerations of critical function and fallback foods (e.g., Rosenberger and Kinzey, 1976; Rosenberger, 1992; Lambert et al., 2004; Marshall and Wrangham, 2007), where especially resistant food items may only be utilized in times of resource scarcity. The seasonal use of more resistant food items has been documented for species in all three of the clades examined here, and therefore these data indicate that the morphologies of these taxa may be specialized for the utilization of food items during food shortages, but what impact the utilization of these food items has in comparison with more commonly exploited foods is unclear. Further data comparing and contrasting the material properties of foods used during resource rich vs. resource poor times of the year are necessary to better understand how this differential resource use may impact the morphology and function of the masticatory apparatus.

Just as inferences from the TMJ regarding forces in the masticatory apparatus are limited, so are inferences regarding gape capacity. The data presented here suggest that some taxa have increased the extent to which sagittal sliding can occur at the joint, and these morphological differences are likely the be linked to differences in these taxa's ability to generate wide jaw gapes (e.g., Wall, 1999; Vinyard et al., 2003). However, a number of other features influence gape capacity. Height of the TMJ above the occlusal plane, jaw length, soft tissues structures in and around the joint, and the position and internal architecture of the masticatory muscles may all limit or facilitate wide jaw gapes (e.g., Herring and Herring, 1974; Smith, 1984; Wall, 1995, 1999; Hylander and Vinyard, 2006; Taylor and Vinyard, 2009; Taylor et al., 2009; Terhune et al., 2011), and it is therefore imperative that other features of the masticatory apparatus be considered when drawing definitive conclusions regarding gape capacity in primates.

Conclusions

The data presented here suggest mixed correlations between feeding behavior and the morphology of the TMJ in platyrrhine primates. The correlations observed among the shape, size, and dietary matrices suggest relationships among all of these datasets, and demonstrate that both size and diet are significant factors influencing TMJ morphology in New World primates. Analyses of 3D TMJ shape variation in each of the three comparative groups further indicated that some aspects of TMJ morphology can be used to differentiate among closely related species with different diets. Subsequent univariate analyses of TMJ shape demonstrated statistically significant differences in multiple aspects of TMJ shape in each of these comparative groups. Results for some of these analyses were consistent with the predictions outlined at the outset of this study, while others were not. The anteroposterior dimensions of the TMJ were most strongly consistent with these initial predictions, whereas the predictions generated for variation in entoglenoid and articular tubercle height were not upheld. These results imply that while some features can be reliably associated with increased load resistance and facilitation of wider jaw gapes in the masticatory apparatus, other features are less strongly correlated with masticatory function. Further analyses, particularly regarding the articular tubercle and entoglenoid process are necessary to fully understand the functions of these specific features.

One major way in which we will be able to further evaluate TMJ function is through a better understanding of the functional implications of anterior vs. posterior tooth use. 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 vs. 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, 1979; Hylander and Bays, 1979; Brehnan et al., 1981), but it is unclear how forces generated during repetitive processing of food items on the posterior teeth compare to these high magnitude but less frequent forces. As concluded by Daegling and McGraw (2007), more data on the use of the anterior vs. 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.

In sum, these data indicate that TMJ shape is influenced by the function of the masticatory apparatus, including variation in the use of foods with presumably different material properties, use of the dentition, and jaw 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 New World primates. Further analyses will explore these relationships in cercopithecoids and hominoids and will seek to draw further links between TMJ morphology and masticatory function.

Acknowledgments

Thanks go to all of the individuals and institutions that made collections available for this research: American Museum of Natural History, the Department of Primatology at the State Collection of Anthropology and Paleoantomy, the National Museum of Natural History, the Field Museum, and the Royal Museum for Central Africa. Valuable feedback was received from Bill Kimbel, Gary Schwartz, Mark Spencer, Andrea Taylor, Christine Wall, Chris Vinyard, David Begun and two anonymous reviewers. Any faults remaining are my own. This research was supported by funding from the National Science Foundation (BCS 0752661), the Leakey Foundation, and the Graduate and Professional Student Association of Arizona State University.

References

Altmann, S.A., 1959. Field observations on a howling monkey society. J. Mammal. 40, 317–330.

Anapol, F., Lee, S., 1994. Morphological adaptation to diet in platyrrhine primates. Am. J. Phys. Anthropol. 94, 239–261.

Anderson, K., Throckmorton, G.S., Buschang, P.H., Hayasaki, H., 2002. The effects of bolus hardness on masticatory kinematics. J. Oral Rehabil. 29, 689–696.

Ashton, E.H., Zuckerman, S., 1954. The anatomy of the articular fossa (fossa mandibularis) in man and apes. Am. J. Phys. Anthropol. 12, 29–61.

Ayres, J.M., 1986. The White Uakaris and the Amazonian Flooded Forest. Ph.D. Dissertation, Cambridge University.

Ayres, J.M., 1989. Comparative feeding ecology of the uakari and bearded saki, *Cacajao* and *Chiropotes*. J. Hum. Evol. 18, 697–716.

Bonnet, E., Van de Peer, Y., 2002. zt: a software tool for simple and partial Mantel tests. J. Stat. Soft. 7, 1–12.

Boubli, J.P., 1999. Feeding ecology of black-headed uacaris (*Cacajao melanocephalus melanocephalus*) in Pico da Neblina National Park, Brazil. Int. J. Primatol. 20, 719–749.

Bouvier, M., 1986a. A biomechanical analysis of mandibular scaling in Old World monkeys. Am. J. Phys. Anthropol. 69, 473–482.

Bouvier, M., 1986b. Biomechanical scaling of mandibular dimensions in New World monkeys. Int. J. Primatol. 7, 551–567.

Brehnan, K., Boyd, R.L., Laskin, J.L., Gibbs, C.H., Mahan, P.E., 1981. Direct measurement of loads at the temporomandibular joint in *Macaca arctoides*. J. Dent. Res. 60, 1820–1824.

Buchannon, D.B., Mittermeier, R.A., van Roosmalen, M.G.M., 1981. The saki monkeys, genus *Pithecia*. In: Coimbra-Filho, A.F., Mittermeier, R.A. (Eds.), Ecology and Behavior of Neotropical Primates. Academia Brasiliera de Ciencias, Rio de Janeiro, pp. 391–417.

Byrd, K.E., Milberg, D.J., Luschei, E.S., 1978. Human and macaque mastication: a quantitative study. J. Dent. Res. 57, 834–843.

Carpenter, C.R., 1934. A field study of the behavior and social relations of howling monkeys. Comp. Psychol. Monog. 10, 1–168.

Chalk, J., Wright, B.W., Lucas, P.W., Richmond, B.G., Fragaszy, D., Visalberghi, E., Izar, P., Ottoni, E.B., 2010. Food mechanical property variation during ontogeny in *Cebus libidinosus*. Am. J. Phys. Anthropol. 141 (S50).

Chapman, C., 1987. Flexibility in the diets of three species of Costa Rican primates. Folia Primatol. 49, 90–105.

Chapman, C.A., 1989. Primate seed dispersal: the fate of dispersed seeds. Biotropica 21, 148–154.

Chapman, C.A., Fedigan, L.M., 1990. Dietary differences between neighboring *Cebus capucinus* groups: local traditions, food availability or responses to food profitability? Folia Primatol. 54,177–54,186.

Cole, T.M., 1992. Postnatal heterochrony of the masticatory apparatus in *Cebus apella* and *Cebus albifrons*. J. Hum. Evol. 23, 253–282.

Constantino, P.J., 2007. Primate Masticatory Adaptations to Fracture-Resistant Foods. Ph.D. Dissertation, George Washington University.

Daegling, D.J., 1992. Mandibular morphology and diet in the genus *Cebus*. Int. J. Primatol. 13, 545–570.

Daegling, D.J., McGraw, W.S., 2007. Functional morphology of the mangabey mandibular corpus: relationship to dental specializations and feeding behavior. Am. J. Phys. Anthropol. 134, 50–62.

DeSouza, L.L., Ferrari, S.F., DaCosta, M.L., Kern, D.C., 2002. Geophagy as a correlate of folivory in red-handed howler monkeys (*Alouatta belzebul*) from Eastern Brazilian Amazonia. J. Chem. Ecol. 28, 1613–1621.

Demes, B., Creel, N., 1988. Bite force, diet, and cranial morphology of fossil hominids. J. Hum. Evol. 17, 657–670.

Di Fiore, A., 2004. Diet and feeding ecology of woolly monkeys in a western Amazonian rain forest. Int. J. Primatol. 25, 767–801.

Elgart-Berry, A., 2004. Fracture toughness of mountain gorilla (*Gorilla gorilla beringei*) food plants. Am. J. Primatol. 62, 275–285.

Freese, C., Oppenheimer, J.R., 1981. The capuchin monkeys, genus *Cebus*. In: Coimbra-Filho, A.F., Mittermeier, R.A. (Eds.), Ecology and Behavior of Neotropical Primates. Academia Brasiliera de Ciencias, Rio de Janeiro, pp. 331–390.

Gaulin, S.J.C., Gaulin, C.K., 1982. Behavioral ecology of *Alouatta seniculus* in Andean cloud forest. Int. J. Primatol. 3, 1–32.

Greaves, W., 1978. The jaw lever system in ungulates: a new model. J. Zool. Lond. 184, 271–285.

Harvati, K., 2001. The Neanderthal problem: 3-D geometric morphometric models of cranial shape variation within and among species. Ph.D. Dissertation, City University of New York.

Herring, S.W., Herring, S.E., 1974. The superficial masseter and gape in mammals. Am. Nat. 108, 561–576.

Hershkovitz, P., 1949. Mammals of northern Colombia. Preliminary report No. 4: monkeys (Primates), with taxonomic revisions of some forms. Proc. Am. Nat. Mus. 98, 323–427.

Hinton, R.J., 1981. Changes in articular eminence morphology with dental function. Am. J. Phys. Anthropol. 54, 439–455.

Hinton, R.J., Carlson, D.S., 1979. Temporal changes in human temporomandibular joint size and shape. Am. J. Phys. Anthropol. 50, 325–334.

Hylander, W.L., 1975. The human mandible: lever or link? Am. J. Phys. Anthropol. 43, 227–242.

Hylander, W.L., 1979. An experimental analysis of temporomandibular joint reaction force in macaques. Am. J. Phys. Anthropol. 51, 433–456.

Hylander, W.L., 1985. Mandibular function and biomechanical stress and scaling. Am. Zool. 25, 315–330.

Hylander, W.L., 2006. Functional anatomy and biomechanics of the masticatory apparatus. In: Laskin, J.L., Greene, C.S., Hylander, W.L. (Eds.), Temporomandibular Disorders: an Evidenced Approach to Diagnosis and Treatment. Quintessence Pub Co, New York, pp. 1–34.

Hylander, W.L., Bays, R., 1978. Bone strain in the subcondylar region of the mandible in *Macaca fascicularis* and *Macaca mulatta*. Am. J. Phys. Anthropol. 48, 408.

Hylander, W.L., Bays, R., 1979. An in vivo strain-gauge analysis of the squamosal-dentary joint reaction force during mastication and incisal biting in *Macaca mulatta* and *Macaca fascicularis*. Arch. Oral Biol. 24, 689–697.

Hylander, W.L., Crompton, A.W., 1980. Loading patterns and jaw movements during the masticatory power stroke in macaques. Am. J. Phys. Anthropol. 52, 239.

Hylander, W.L., Vinyard, C.J., 2006. The evolutionary significance of canine reduction in hominins: functional links between jaw mechanics and canine size. Am. J. Phys. Anthropol. 129, 107.

Hylander, W.L., McMillan, A.S., Lam, E.W.N., Watanabe, M., Langenbach, G.E.J., Stavness, I., Peck, C.C., Palla, S., 2008. From movements to models: a tribute to Professor Alan G. Hannam. J. Orofac. Pain 22, 307–316.

Izawa, K., 1979. Foods and feeding behavior of wild black-capped capuchin (*Cebus apella*). Primates 20, 57–76.

Izawa, K., Mizuno, A., 1977. Palm-fruit cracking behavior of wild black-capped capuchin (*Cebus apella*). Primates 18, 773–792.

Janson, C.H., Boinski, S., 1992. Morphological and behavioral adaptations for foraging in generalist primates: the case of the cebines. Am. J. Phys. Anthropol. 88, 483–498.

Julliot, C., 1996. Fruit choice by red howler monkeys (*Alouatta seniculus*) in a tropical rain forest. Am. J. Primatol. 40, 261–282.

Julliot, C., Sabatier, D., 1993. Diet of the red howler monkey (*Alouatta seniculus*) in French Guiana. Int. J. Primatol. 14, 527–550.

Kay, R.F., 1975. The functional adaptation of primate molar teeth. Am. J. Phys. Anthropol. 43, 195–216.

Kinzey, W.G., 1974. Ceboid models for the evolution of hominoid dentition. J. Hum. Evol. 3, 193–203.

Kinzey, W., 1992. Dietary and dental adaptations in the Pitheciinae. Am. J. Phys. Anthropol. 88, 499–514.

Kinzey, W.G., Norconk, M.A., 1990. Hardness as a basis of fruit choice in two sympatric primates. Am. J. Phys. Anthropol. 81, 5–15.

Kinzey, W.G., Norconk, M.A., 1993. Physical and chemical properties of fruit and seeds eaten by *Pithecia* and *Chiropotes* in Surinam and Venezuela. Int. J. Primatol. 14, 207–227.

Komiyama, O., Asano, T., Suzuki, H., Kawara, M., Wada, M., Kobayashi, K., Ohtake, S., 2003. Mandibular condyle movement during mastication of foods. J. Oral Rehabil. 30, 592–600.

Lambert, J.E., Chapman, C.A., Wrangham, R.W., Conklin-Brittain, N.L., 2004. Hardness of cercopithecine foods: implications for the critical function of enamel thickness in exploiting fallback foods. Am. J. Phys. Anthropol. 145, 363–368.

Lima, E.M., Ferrari, S.F., 2003. Diet of a free-ranging group of squirrel monkeys (*Saimiri sciureus*) in Eastern Brazilian Amazonia. Folia Primatol. 74, 150–158.

Lockwood, C.A., Lynch, J.M., Kimbel, W.H., 2002. Quantifying temporal bone morphology of great apes and humans: an approach using geometric morphometrics. J. Anat. 201, 447–464.

Lucas, P.W., 1981. An analysis of canine size and jaw shape in some Old and New World non-human primates. J. Zool. 195, 437–448.

Lucas, P.W., 1982. An analysis of the canine tooth size of Old World higher primates in relation to mandibular length and body weight. Arch. Oral Biol. 27, 493–496.

Lucas, P.W., 2004. Dental Functional Morphology: How Teeth Work. Cambridge University Press, New York.

Mantel, N., 1976. The detection of disease clustering and a generalized regression approach. Cancer Res. 27, 209–220.

Marshall, A.J., Wrangham, R.W., 2007. Evolutionary consequences of fallback foods. Int. J. Primatol. 28, 1219–1235.

Milton, K., 1980. The Foraging Strategy of Howler Monkeys: A Study in Primate Economics. Columbia University Press, New York.

Miyawaki, S., Ohkochi, N., Kawakami, T., Sugimura, M., 2000. Effect of food size on the movement of the mandibular first molars and condyles during deliberate unilateral mastication in humans. J. Dent. Res. 79, 1525–1531.

Moffett Jr., B.C., Johnson, L.C., McCabe, J.B., Askew, H.C., 1964. Articular remodeling in the adult human temporomandibular joint. Am. J. Anat. 115, 119–141.

Norconk, M.A., Wright, B.W., Conklin-Brittain, N.L., Vinyard, C.J., 2009. Mechanical and nutritional properties of food as factors in platyrrhine dietary adaptations. In: Garber, P.A., Estrada, A., Bicca-Marques, C., Heymann, E., Strier, K. (Eds.), South American Primates: Testing New Theories in the Study of Primate Behavior, Ecology, and Conservation. Springer Science, New York, pp. 279–319.

O'Higgins, P., Jones, N., 1998. Facial growth in *Cercocebus torquatus*: an application of three dimensional geometric morphometric techniques to the study of morphological variation. J. Anat. 193, 251–272.

Peres, C.A., 1994. Diet and feeding ecology of gray woolly monkeys (*Lagothrix lagotricha cana*) in central Amazonia: comparisons with other atelines. Int. J. Primatol. 15, 333–372.

Rak, Y., Hylander, W.L., 2008. What else is the tall mandibular ramus of the robust australopiths good for? In: Vinyard, C.J., Ravosa, M.J., Wall, C.E. (Eds.), Primate Craniofacial Function and Biology. Springer, New York, pp. 431–442.

Reed, D.A., Ross, C.F., 2010. Modulation of jaw kinematics to food material properties in *Cebus*. Am. J. Phys. Anthropol. 141, 196.

Rice, W.R., 1989. Analyzing tables of statistical tests. Evolution 43, 223–225.

Richards, L.C., 1987. Temporomandibular joint morphology in two Australian aboriginal populations. J. Dent. Res. 66, 1602–1607.

Richards, L.C., 1988. Degenerative changes in the temporomandibular joint in two Australian aboriginal populations. J. Dent. Res. 67, 1529–1533.

Richards, L.C., Brown, T., 1981. Dental attrition and degenerative arthritis of the temporomandibular joint. J. Oral Rehabil. 8, 293–307.

Rosenberger, A.L., 1992. Evolution of feeding niches in New World monkeys. Am. J. Phys. Anthropol. 88, 525–562.

Rosenberger, A.L., Kinzey, W.G., 1976. Functional patterns of molar occlusion in platyrrhine primates. Am. J. Phys. Anthropol. 45, 281–298.

Rosenberger, A.L., Strier, K.B., 1989. Adaptive radiation of the ateline primates. J. Hum. Evol. 18, 717–750.

Russo, S.E., Campbell, C.J., Lawrence Dew, J., Stevenson, P.R., Suarez, S.A., 2005. A multi-forest comparison of dietary preferences and seed dispersal by *Ateles* spp. Int. J. Primatol. 26, 1017–1037.

Singleton, M., 2005. Functional shape variation in the cercopithecine masticatory complex. Patterns. In: Slice, D.E. (Ed.), Modern Morphometrics in Physical Anthropology. Kluwer Academic/Plenum Publishers, New York, pp. 319–348.

Slice, D.E., Bookstein, F.L., Marcus, L.F., Rohlf, F.J., 1998. A Glossary for Geometric Morphometrics. http://life.bio.sunysb.edu/morph/glossary/gloss1.html (accessed 17.02.2005.).

Smith, R.J., 1978. Mandibular biomechanics and temporomandibular joint function in primates. Am. J. Phys. Anthropol. 49, 341–349.

Smith, R.J., 1984. Comparative functional morphology of maximum mandibular opening (gape) in primates. In: Chivers, D.J., Wood, B.A., Bilsborough, A. (Eds.), Food Acquisition and Processing in Primates. Plenum Press, New York, pp. 231–255.

Smith, R.J., Jungers, W.L., 1997. Body mass in comparative primatology. J. Hum. Evol. 32, 523–559.

Smith, R.J., Petersen, C.E., Gipe, D.P., 1983. Size and shape of the mandibular condyle in primates. J. Morphol. 177, 59–68.

Smouse, P.E., Long, J.C., Sokal, R.T., 1986. Multiple regression and correlation extensions of the Mantel test of matrix correspondence. Syst. Zool. 35, 627–632.

Spencer, M.A., 1995. Masticatory System Configuration and Diet in Anthropoid Primates. Ph.D. Dissertation, State University of New York at Stony Brook.

Spencer, M.A., 1999. Constraints on masticatory system evolution in anthropoid primates. Am. J. Phys. Anthropol. 108, 483–506.

Spencer, M.A., Spencer, G.S., 1993. MacMorph Data Acquisition Package. Stony Brook, NY.

Strait, D.S., Weber, G.W., Neubauer, S., Chalk, J., Richmond, B.G., Lucas, P.W., Spencer, M.A., Schrein, C., Dechow, P.C., Ross, C.F., Grosse, I.R., Wright, B.W., Constantino, P., Wood, B.A., Lawn, B., Hylander, W.L., Wang, Q., Byron, C., Slice, D.E., Smith, A.L., 2009. The feeding biomechanics and dietary ecology of *Australopithecus africanus*. Proc. Nat. Acad. Sci. 106, 2124–2129.

Sullivan, L.R., 1917. Variations in the glenoid fossae. Am. Anthropol. 19, 19–23.

Sun, Z., Liu, Z.J., Herring, S.W., 2002. Movement of temporomandibular joint tissues during mastication and passive manipulation in miniature pigs. Arch. Oral Biol. 47, 293–305.

Taylor, A.B., 2005. A comparative analysis of temporomandibular joint morphology in the African apes. J. Hum. Evol. 48, 555–574.

Taylor, A.B., 2006. Feeding behavior, diet, and the functional consequences of jaw form in orangutans, with implications for the evolution of *Pongo*. J. Hum. Evol. 50, 377–393.

Taylor, A.B., Vinyard, C.J., 2009. Jaw-muscle fiber architecture in tufted capuchins favors generating relatively large muscle forces without compromising jaw gape. J. Hum. Evol. 57, 710–720.

Taylor, A.B., Eng, C.M., Anapol, F.C., Vinyard, C.J., 2009. The functional correlates of jaw-muscle fiber architecture in tree-gouging and non-gouging callitrichid monkeys. Am. J. Phys. Anthropol. 139, 353–367.

Teaford, M.F., 1985. Molar microwear and diet in the genus *Cebus*. Am. J. Phys. Anthropol. 66, 363–370.

Teaford, M.F., Ungar, P.S., 2000. Diet and the evolution of the earliest human ancestors. Proc. Nat. Acad. Sci. 97, 13506–13511.

Terborgh, J., 1983. Five New World Primates. Princeton University Press, Princeton, New Jersey.

Terborgh, J., 1986. Community aspects of frugivory in tropical forests. In: Estrada, A., Fleming, T.H. (Eds.), Frugivores and Seed Disperal. D.W. Junk Publ., Dordrecht, pp. 371–384.

Terhune, C.E., 2010. The Temporomandibular Joint in Anthropoid Primates; Functional, Allometric, and Phylogenetic Influences. Ph.D. Dissertation. Arizona State University.

Terhune, C.E., Kimbel, W.H., Lockwood, C.A., 2007. Variation and diversity in *Homo erectus*: a 3D geometric morphometric analysis of the temporal bone. J. Hum. Evol. 53, 41–60.

Terhune, C.E., Iriarte–Diaz, J., Taylor, A.B., Ross, C.F., 2011. The instantaneous center of rotation of the mandible in non-humanprimates. J. Int. Comp. Biol. 51, 320–332.

Ungar, P., 2004. Dental topography and diets of *Australopithecus afarensis* and early *Homo*. J. Hum. Evol. 46, 605–622.

van Roosmalen, M.G.M., Klein, L.L., 1988. The spider monkeys, genus *Ateles*. In: Mittermeier, R.A., Rylands, A.B., Coimbra-Filho, A., Fonseca, G.A.B. (Eds.), Ecology and Behavior of Neotropical Primates, vol. 2. World Wildlife Fund, Washington D.C., pp. 455–538.

van Roosmalen, M.G.M., Mittermeier, R.A., Milton, K., 1981. The bearded sakis, genus *Chiropotes*. In: Coimbra–Filho, A.F., Mittermeier, R.A. (Eds.), Ecology and Behavior of Neotropical Primates. Academia Brasiliera de Ciencias, Rio de Janeiro, pp. 419–441.

van Roosmalen, M.G.M., Mittermeier, R.A., Fleagle, J.G., 1988. Diet of the northern bearded saki (*Chiropotes satanas chiropotes*): a neotropical seed predator. Am. J. Primatol. 14, 11–35.

Vinyard, C., 1999. Temporomandibular Joint Morphology and Function in Strepsirrhine and Eocene Primates. Ph.D. Dissertation, Northwestern University.

Vinyard, C.J., 2008. Putting shape to work: making functional interpretations of masticatory apparatus shapes in primates. In: Vinyard, C.J., Ravosa, M.J., Wall, C.E. (Eds.), Primate Craniofacial Function and Biology. Springer Science, New York, pp. 357–386.

Vinyard, C.J., Wall, C.E., Williams, S.H., Hylander, W.L., 2003. Comparative functional analysis of skull morphology of tree-gouging primates. Am. J. Phys. Anthropol. 120, 153–170.

Wall, C.E., 1995. Form and Function of the Temporomandibular Joint in Anthropoid Primates, Ph.D. Dissertation, State University of New York at Stony Brook.

Wall, C.E., 1999. A model of temporomandibular joint function in anthropoid primates based on condylar movements during mastication. Am. J. Phys. Anthropol. 109, 67–88.

Wall, C.E., Vinyard, C.J., Johnson, K.R., Williams, S.H., Hylander, W.L., 2006. Phase II jaw movements and masseter muscle activity during chewing in *Papio anubis*. Am. J. Phys. Anthropol. 129, 215–224.

Weidenreich, F., 1943. The skull of *Sinanthropus pekinensis*: a comparative odontography of the hominids. Palaeontol. Sin. D 10, 1–484.

Williams, S.H., Wright, B.W., Truong, V.D., Daubert, C.R., Vinyard, C.J., 2005. Mechanical properties of foods used in experimental studies of primate masticatory function. Am. J. Primatol. 67, 329–346.

Wright, B.W., 2004. Ecological Distinctions in Diet, Food Toughness, and Masticatory Anatomy in a Community of Six Neotropical Primates in Guyana, South America. Ph.D. Dissertation. Urbana-Champaign, University of Illinois.

Wright, B.W., 2005. Craniodental biomechanics and dietary toughness in the genus *Cebus*. J. Hum. Evol. 48, 473–492.

Wright, B.W., Wright, K.A., 2010. You are how you eat: hard food feeding behavior in primates. Am. J. Phys. Anthropol. 141, 248.

Yamashita, N., 2003. Food procurement and tooth use in two sympatric lemur species. Am. J. Phys. Anthropol. 121, 125–133.

Yamashita, N., Vinyard, C.J., Tan, C.L., 2009. Food mechanical properties in three sympatric species of *Hapalemur* in Ranomafana National Park, Madagascar. Am. J. Phys. Anthropol. 139, 368–381.

Zelditch, M.L., Swiderski, D.L., Sheets, H.D., Fink, W.L., 2004. Geometric Morphometrics for Biologists: A Primer. Elsevier Academic Press, London.