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Dietary Correlates of Temporomandibular Joint Morphology in the Great Apes

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ABSTRACT Behavioral observations of great apes have consistently identified differences in feeding behavior among species, and these differences have been linked to variation in masticatory form. As the point at which the mandible and cranium articulate, the temporomandibular joint (TMJ) is an important component of the masticatory apparatus. Forces are transmitted between the mandible and cranium via the TMJ, and this joint helps govern mandibular range of motion. This study examined the extent to which TMJ form covaries with feeding behavior in the great apes by testing a series of biomechanical hypotheses relating to specific components of joint shape using linear measurements extracted from three-dimensional coordinate data. Results of these analyses found that taxa differ significantly in TMJ shape, particularly in the mandibular fossa. Chimpanzees have relatively more anteroposteriorly elongated joint surfaces, whereas gorillas tend to have relatively anteroposteriorly compressed joints. Orangutans were most commonly intermediate in form between *Pan* and *Gorilla*, perhaps reflecting a trade-off between jaw gape and load resistance capabilities. Importantly, much of the observed variation among taxa reflects differences in morphologies that facilitate gape over force production. These data therefore continue to emphasize the unclear relationship between mandibular loading and bony morphology, but highlight the need for further data regarding food material properties, jaw gape, and ingestive/food processing behaviors. Am J Phys Anthropol 150:260–272, 2013. ©2012 Wiley Periodicals, Inc.

Observations of African ape feeding behavior suggest a gradient in dietary resistance[1] across taxa. Chimpanzees consume less resistant foods compared to mountain gorillas (Watts, 1984; Williamson et al., 1990), while bonobos and lowland gorillas fall between these two extremes (Badrian and Malenky, 1984; Tutin and Fernandez, 1993; Malenky and Wrangham, 1994). A similar gradient has been documented within and between orangutan species (Galdikas, 1988; Knott, 1998; Fox et al., 2004; Wich et al., 2006), and comparisons of African and Asian apes suggest orangutans consume food items, such as seeds, that are at least as—if not considerably more—resistant than foods consumed by gorillas (Elgart-Berry, 2004; Vogel et al., 2008). Food processing behaviors also vary across ape taxa, with orangutans and chimpanzees relying more consistently on their anterior teeth for processing than gorillas (Lucas et al., 1994; Ungar, 1994; Lambert, 1999). A number of researchers have attempted to link these feeding behaviors to great ape craniofacial variation with varying success (e.g., Krogman, 1931a,b; Schultz, 1969; Daegling, 1989, 2007; Taylor, 2002, 2005, 2006a,b, 2009; Constantino, 2007; McCollum, 2007; Taylor et al., 2008). Though this prior work suggests differences in masticatory form among the great apes in general (e.g., Taylor, 2002, 2003, 2006a,b), and the TMJ in particular (Taylor, 2005), this work did not incorporate all functionally important aspects of this joint, including the cranial component of the TMJ and condylar curvature. The study presented here addresses this gap by linking known differences in diet and feeding behavior to variation in both the cranial and mandibular components of the TMJ.

The great apes are an important clade in which to evaluate craniofacial and TMJ variation for several reasons. Temporal bone morphology, including the mandibular (i.e., glenoid) fossa, has been used to distinguish among extant great ape taxa, for quantifying expected levels of variation in fossil taxa, and for recovering phylogenetic relationships among great apes (Harvati, 2003; Lockwood et al., 2002, 2004; Terhune et al., 2007). Similarly, temporal bone form, again, including the mandibular fossa, has been shown to reflect genetic variation among modern humans (Smith et al., 2007; von Cramon-Taubadel, 2009). Thus, further evaluating great ape TMJ shape from a functional perspective, especially the relatively less studied cranial component of this joint, may help to elucidate the extent to which phylogenetic variation in this clade reflects functional differences in the masticatory system. Finally, examining the functional correlates of TMJ shape in the great apes will add to a growing body of data describing TMJ form across primates (e.g., Smith et al., 1983; Bouvier, 1986a,b; Wall, 1995, 1999; Vinyard, 1999; Vinyard et al., 2003; Taylor, 2005; Terhune, 2010, 2011a,b) and may assist in reconstructions of feeding behavior in fossil taxa.

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[1] I use the term "resistant" here to collectively refer to foods that are fracture resistant (tough) and/or stress-limited (stiff) (Lucas, 2004; Williams et al., 2005).

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GREAT APE FEEDING ECOLOGY

Although all great apes prefer ripe fruits, feeding behavior varies both within and among genera, and species tend to utilize different resources as fallback foods (Harrison and Marshall, 2011). In *Pan*, bonobos (*P. paniscus*) have been documented to have a greater year-round reliance on piths and leaves of terrestrial herbaceous vegetation (THV) than chimpanzees (*P. troglodytes*), which tend to consume THV primarily during times of fruit scarcity (Badrian and Malenky, 1984; Malenky and Stiles, 1991; Malenky and Wrangham, 1994). However, work by Chapman et al. (1994) suggests this generalization may not hold true across all feeding sites and further data are necessary to characterize differences in feeding behavior between these species.

Like *Pan*, *Gorilla* species prefer fruit, but *G. gorilla* consumes more THV only when fruits are unavailable (Williamson et al., 1990; Tutin and Fernandez, 1993; Nishihara, 1995). Alternatively, *G. beringei* diet consists almost entirely of THV, including ground level leaves, stems, and shrubs, with flowers, pith, bark, and roots making up a small component of their diet (Watts, 1984).

Finally, Bornean (*Pongo pygmaeus*) and Sumatran (*P. abelii*) orangutans both prefer fruit, but tend to fall back on different food resources when fruit is scarce. *P. pygmaeus* tends to rely on small vines, insects, and young leaves during times of fruit scarcity, and has been noted to utilize bark heavily (e.g., 47% of foraging time for a single wet month) (Galdikas, 1988). In contrast, although *P. abelii* has been documented to consume similar quantities of fruit, fewer fluctuations in fruit availability on Sumatra allow *P. abelii* to rely on fruit throughout the year; bark and other plant parts therefore make up a very small percentage of their diet (2.7% vs. 9.3–14.2% for *P. pygmaeus*) (Rodman, 1988; Knott, 1998; Fox et al., 2004; Wich et al., 2006).

Data describing food material properties (FMPs) exists only for *G. beringei beringei* (Elgart-Berry, 2004), *P. pygmaeus wurmbii* (Vogel et al., 2008), and *P. troglodytes schweinfurthii* (Vogel et al., 2008). These data suggest that average fracture toughness (i.e., the energy required to generate a crack of a given area [Lucas, 2004]) is highest in *Pongo* and *Gorilla*, and lower in *Pan*. Maximum toughness values recorded for each species were very high in *Pongo* (e.g., 2,464 J m^{-2} for fruits) in comparison to both *Pan* and *Gorilla* (289 and 1,190 J m^{-2} for fruits, respectively) (Elgart-Berry, 2004; Vogel et al., 2008). No data on elastic modulus (i.e., Young's modulus, a measure of stiffness or rigidity, [Lucas, 2004]) are available for *Gorilla*, but data for *Pongo* and *Pan* follow this same trend, with *Pongo* consuming stiffer foods (both average and maximum values) than does *Pan*.

Food ingestion and processing behaviors also differ among the apes and likely influence maximum jaw gape. Both *Pongo* and *Pan* rely heavily on their anterior dentition for food processing (Ungar, 1994; Lambert, 1999); for example, orangutans have been documented to use their anterior teeth to strip bark directly from tree trunks (Rodman, 1988; Leighton, 1993). Members of both genera have been observed performing "wadging" behaviors, where fibrous foods are masticated into a pulp, the nutritious juices sucked out, and the remaining fibrous wadge spit out (e.g., Wrangham et al., 1991; Vogel et al., 2008). No such behaviors have been observed in *Gorilla*, although they utilize similarly fibrous foods. Orangutans have further been observed breaking into exceptionally resistant seeds using their premolars (Lucas et al., 1994); such behaviors presumably require both moderate jaw gapes (for positioning the food item) and high occlusal forces.

In sum, these data indicate variation in both diet and food processing behavior among great ape genera. On average, *Gorilla* and *Pongo* tend to consume more mechanically challenging foods than *Pan*, while *Pan* and *Pongo* likely tend to rely more on their anterior teeth for food processing than does *Gorilla*. Assuming these behaviors reflect variation in masticatory loading and movement, I therefore expect to observe morphological differences among these taxa linked to differences in load resistance and TMJ range of motion. These predictions are outlined below.

Although we lack detailed FMP data describing differences between species within these genera, these data further suggest substantial differences in the properties of foods consumed by each of these species, such that *P. paniscus*, *G. beringei*, and *P. pygmaeus* consume more resistant foods than their congeners. I therefore expect to observe differences in TMJ form among species within these genera, but until better comparative data are available the comparisons of taxa within each genus presented here should be considered preliminary.

Previous analyses linking masticatory function and great ape TMJ morphology

Although a number of researchers have previously examined the great ape TMJ (e.g., Weidenreich, 1943; Ashton and Zuckerman, 1954; Lockwood et al., 2002; Sherwood et al., 2002), only work by Taylor has specifically examined this morphology in the context of masticatory biomechanics. Taylor (2002, 2003, 2005) found that, despite documented differences in the degree of folivory, there were few ontogenetic or adult differences in condylar shape between *P. paniscus* and subspecies of *P. troglodytes* (Taylor, 2002, 2005, 2006a). However, she did observe that mountain gorillas had significantly wider condyles and TMJs situated higher above the occlusal plane (relative to mandible length) when compared to all other African apes, and all *Gorilla* species/subspecies were characterized by comparable distinctions relative to all other species/subspecies of *Pan*. Similarly, Taylor (2006b) found that Bornean orangutans (*Pongo p. morio* and *P. p. wurmbii*) exhibit greater mandibular load resistance abilities, including larger condylar areas, relative to Sumatran orangutans. This work functionally linked these features to a greater reliance by *P. p. morio* and *P. p. wurmbii* on tougher and more obdurate foods when compared to *P. abelii*.

Finally, Taylor et al. (2008) used FMPs to generate minimum estimates of average and maximum bite forces in *P. p. wurmbii*, *G. b. beringei*, and *P.t. schweinfurthii*. She incorporated these data in a test of the hypothesis that the capacity to resist condylar loads would be relatively greater in *Pongo* compared with the African apes, and in *Gorilla* compared to *Pan*. These expectations were met only when maximum fracture toughness values of nonfruit, nonleaf vegetation were used to estimate bite force. Results based on all other estimates of average and maximum bite force either did not systematically conform, or ran contrary to, their predictions.

Morphological predictions for the TMJ

This study extends these previous analyses to further address the functional link between great ape TMJ form and feeding behavior by examining additional aspects of condylar form, as well as variation in the cranial component of the TMJ. Based on theoretical and experimental analyses of masticatory biomechanics and previous analyses of TMJ morphology in other primate taxa, I formulate predictions (Table 1) related to two (nonmutually exclusive) research questions: (1) Can features of the TMJ be predictably linked to variation in joint load resistance? and (2) Can features of the TMJ be predictably linked to variation in joint range of motion?

Masticatory biomechanics and the TMJ. Theoretical (e.g., Greaves, 1978; Smith, 1978; Spencer, 1999) and experimental (e.g., Hylander, 1979; Hylander and Bays, 1979) studies of masticatory function indicate many factors determine the magnitude of the joint reaction force (JRF) including (among others) magnitude and position of the muscle resultant force; TMJ position in relation to the tooth row; position of the bite point; and geometry of the masticatory apparatus. For example, bite forces are determined (in part) by the amount of muscle force required to process the food, which, in turn, influences the magnitude of the TMJ JRF (e.g., Greaves, 1978; Hylander, 1979; Spencer, 1999). Furthermore, all other components being equal, anterior bite points produce relatively higher JRFs than do posterior bite points (e.g., Hylander, 1979; Hylander and Bays, 1979; Brehnan et al., 1981).

Many of these factors also limit condylar and mandibular range of motion (ROM). TMJ movements occur primarily in anteroposterior (AP) and mediolateral (ML) planes. Anteroposterior movements of the condyle relative to the mandibular fossa include rotation and translation. This AP movement (or sagittal sliding; Wall, 1999) is correlated with linear gape in cineradiographic analyses (Wall, 1995, 1999). Thus, increases in jaw gape may necessitate changes in ROM at the TMJ (e.g., Lucas, 1981, 1982; Wall, 1999; Vinyard et al., 2003). Behaviors that necessitate large gapes may include nonmasticatory behaviors such as canine displays, feeding behaviors such as the incision of relatively large food objects, or gouging. Wide jaw gapes may also be necessary for placing and crushing small resistant foods, such as seeds, on the premolars or molars (Lucas et al., 1994).

In contrast to incisal behaviors, mastication is characterized by both AP and ML deviation of the mandible and condyles. Analyses of masticatory movements suggest that lateral deviation increases as foods become more mechanically challenging (Byrd et al., 1978; Anderson et al., 2002; Komiyama et al., 2003; Wall et al., 2006; but see Reed and Ross, 2010).

Predictions for features linked to loading at the TMJ

Condylar surface area is relatively larger in taxa that experience high JRFs. Large joint surface areas allow forces to be distributed over larger areas, increasing joint load resistance capabilities. There are two ways high JRFs may be produced: high bite forces distributed along the posterior dentition and/or increased anterior tooth use. Smith et al. (1983) found that condylar area (relative to body mass) is larger in cercopithecines than colobines, and that increased condylar area may be linked to durophagy. In contrast, Bouvier (1986a,b) found no significant differences in condylar area relative to mandible length, and suggested that condylar morphology should be broken down into AP and ML dimensions

TABLE 1. Predicted variation in aspects of TMJ shape in each of the taxa examined

Prediction #	Variable	Hominids	*Pan*	*Gorilla*	*Pongo*
JRF 1a	Condylar area	*Gorilla* and *Pongo* > *Pan*	*P. paniscus* > *P. troglodytes*	*G. beringei* > *G. gorilla*	*P. pygmaeus* > *P. abelii*
JRF 1b	Condylar area	*Pongo* and *Pan* > *Gorilla*	*P. troglodytes* > *P. paniscus*	*G. gorilla* > *G. beringei*	*P. abelii* > *P. pygmaeus*
JRF 2	Condylar width	*Gorilla* and *Pongo* > *Pan*	*P. paniscus* > *P. troglodytes*	*G. beringei* > *G. gorilla*	*P. pygmaeus* > *P. abelii*
ROM 1a	Glenoid fossa length	*Pan* and *Pongo* > *Gorilla*	*P. troglodytes* > *P. paniscus*	*G. gorilla* > *G. beringei*	*P. abelii* > *P. pygmaeus*
	Preglenoid plane length	*Pan* and *Pongo* > *Gorilla*	*P. troglodytes* > *P. paniscus*	*G. gorilla* > *G. beringei*	*P. abelii* > *P. pygmaeus*
	PreGlLg/GlenLg ratio	*Pan* and *Pongo* > *Gorilla*	*P. troglodytes* > *P. paniscus*	*G. gorilla* > *G. beringei*	*P. abelii* > *P. pygmaeus*
ROM 1b	Condylar length	*Pan* and *Pongo* > *Gorilla*	*P. troglodytes* > *P. paniscus*	*G. gorilla* > *G. beringei*	*P. abelii* > *P. pygmaeus*
	Condylar AP curvature	*Pan* and *Pongo* > *Gorilla*	*P. troglodytes* > *P. paniscus*	*G. gorilla* > *G. beringei*	*P. abelii* > *P. pygmaeus*
ROM 1c	Glenlg/Condlg ratio	*Pan* and *Pongo* > *Gorilla*	*P. troglodytes* > *P. paniscus*	*G. gorilla* > *G. beringei*	*P. abelii* > *P. pygmaeus*
ROM 2	Entoglenoid process projection	*Gorilla* and *Pongo* > *Pan*	*P. paniscus* > *P. troglodytes*	*G. beringei* > *G. gorilla*	*P. pygmaeus* > *P. abelii*
ROM 3	Articular tubercle projection	*Gorilla* and *Pongo* > *Pan*	*P. paniscus* > *P. troglodytes*	*G. beringei* > *G. gorilla*	*P. pygmaeus* > *P. abelii*

and considered in the context of anterior vs. posterior tooth use. Taylor (2002, 2005) found significantly larger condylar area relative to mandible length in folivorous gorillas when compared to the more frugivorous *P. troglodytes*, but no other predicted differences among taxa were significant, leading her to conclude that there is no systematic relationship in African apes. Similar analyses of condylar area in *Pongo* (Taylor, 2006) did adhere to the expected pattern, however, with larger condylar areas (relative to mandible length) in *P. pygmaeus* compared to *P. abelii*.

These previous analyses present an inconsistent picture of the functional link between condylar area and feeding behavior. I therefore test two non-mutually exclusive scenarios for the great apes using three-dimensional condylar area (a measure which has not been used previously) and two load-arm estimates, one for incisal biting and one for postcanine mastication.

1.. If greater use of the posterior teeth is associated with relatively larger condylar areas, then *Gorilla* and *Pongo* will have larger mandibular condyles relative to a masticatory load-arm estimate than *Pan*, and within each genus species that masticate more mechanically challenging foods will have relatively larger condyles.
2.. If intensive use of the anterior dentition requires relatively larger condylar surface areas to improve TMJ load resistance, *Pongo* and *Pan*, which are documented to more frequently utilize their anterior dentition for food processing, should have larger condylar surface areas relative to an incisal load-arm estimate than *Gorilla*.

The condyle is relatively wider mediolaterally (ML) in taxa masticating resistant food objects. The lateral aspect of the TMJ has been suggested to experience higher stresses than other portions of this joint (Moffett et al., 1964; Hylander, 1979; Hylander and Bays, 1979; Hinton, 1981). Two mechanisms are proposed to explain this. First, during the opening stroke of mastication the working-side condyle shifts laterally, compressing the lateral aspect of the condyle against the lateral aspect of the glenoid. Second, this region of the working-side condyle is further compressed during the power stroke, when the mandibular corpus twists along its long axis (e.g., Hylander, 1979, 2006; Hylander and Bays, 1979). Previous comparative work has found that, relative to mandibular length, taxa that tend to rely on their posterior dentition have relatively wider condyles when compared to taxa that rely more on their anterior dentition (Bouvier, 1986; Taylor, 2005, 2006). Correspondingly, I predict that *Gorilla* and *Pongo,* which masticate more resistant food objects, should have ML wider condylar joint surfaces (measured relative to a masticatory load arm) when compared to *Pan*, and within each genus the more resistant object feeder will have relatively wider condyles.

Predictions for features linked to range of motion at the TMJ

The anteroposterior (AP) length of the TMJ articular surface varies in relation to frequency of ingestive behaviors. Relatively large maximum jaw gapes, as may be necessary during food processing, are in part facilitated by relative increases in the AP joint dimensions, which increase TMJ ROM (Wall, 1995, 1999; Vinyard et al., 2003). Work by Bouvier (1986a,b) found relatively AP longer condyles in cercopithecines compared to colobines (Bouvier, 1986a,b), suggesting a link between this feature and ingestive behaviors. Similarly, Vinyard et al. (2003) observed relatively longer cranial and condylar articular surfaces in tree-gouging primates when compared to closely related nongougers. However, Taylor (2005) found no differences in condylar length among the African Apes, perhaps indicating that this pattern does not hold across clades. All of these studies measured condylar length relative to an incisal load arm.

There are three ways in which TMJ form may be altered to increase ROM. First (a), the cranial articular surface may be elongated anteroposteriorly to allow for increased condylar translation. I measure elongation of the cranial articular surface as length of the glenoid and preglenoid plane; to assess the contribution of preglenoid plane length to overall glenoid length I further calculate a ratio between these variables. Second (b), the condylar articular surface may be relatively elongated anteroposteriorly to allow for increased condylar rotation. Condylar articular surface is approximated both via an AP chord length of the condyle and as a measure of condylar curvature. Last (c), the ratio between the cranial and condylar articular surfaces (e.g., glenoid length relative to condylar length) may be increased. Given the above-outlined observations of ingestive behaviors, I predict that *Pan* and *Pongo* will show features of the glenoid and condyle associated with relative increases in TMJ ROM compared with *Gorilla*.

The entoglenoid process is relatively more projecting in resistant object feeders. Cineradiographic analyses show that the condyle contacts the entoglenoid process during mastication, and that entoglenoid process width/projection, ML condylar curvature, and sagittal sliding are correlated (Wall, 1995, 1999). These data suggest that wide and projecting entoglenoids guide sagittal sliding and limit ML condylar movement during mastication (Wall, 1999).[2] Given these data and the correlation between dietary resistance and mandibular lateral deviation (see references above), I predict *Gorilla* and *Pongo*, which masticate more resistant foods, will have relatively more projecting entoglenoid processes than *Pan*, and within each genus the more resistant object feeder will have relatively more projecting entoglenoids (as scaled relative to a masticatory load arm).

Resistant object feeders have relatively more projecting articular tubercles. As the attachment site of the temporomandibular ligament (TML), the articular tubercle is likely correlated with TML size (Wall, 1995). This ligament has been suggested to resist tensile forces at the joint by maintaining contact between the condyle and articular eminence (Greaves, 1978; Hylander, 1979; Spencer, 1995; Wall, 1995). The TML may also stabilize the TMJ during lateral movements of the condyle, such as during lateral deviation (Sun et al., 2002). Since lateral deviation increases with dietary resistance (see references above), resistant object feeders should have relatively more projecting articular tubercles. I predict that this feature will be larger relative to a masticatory load arm in *Gorilla* and *Pongo* in comparison to *Pan,* and relatively larger in the more resistant object feeders in each genus.

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[2] Wall (1999) originally measured the entoglenoid process as a linear distance from the most superior point on the glenoid fossa to the most inferior point on the entoglenoid process and then divided this distance by glenoid width. This measure therefore includes components of ML entoglenoid width and entoglenoid projection.

TABLE 2. Comparative taxa used in this study

Species	Female	Male
Pan troglodytes schweinfurthii	12	12
Pan troglodytes troglodytes	7	9
Pan troglodytes verus	4	5
Pan paniscus	12	10
Gorilla beringei	8	10
Gorilla gorilla	12	12
Pongo abelii	9	10
Pongo pygmaeus	12	12

Comparing *Pongo* to *Gorilla* or *Pan*

Although the above sections outline my predictions regarding how *Pan* should compare to *Pongo* and *Gorilla* in features linked to masticatory behaviors, and how *Pongo* and *Pan* should compare to *Gorilla* in features linked to ingestive behaviors, it is unclear how we might expect all three of these genera to compare to one another in these features. Evaluating masticatory behaviors is particularly challenging because of the difficulty of determining the nature of the loading environment in these taxa, and especially the distinction between high frequency (but lower magnitude) and high magnitude (but lower frequency) stresses. For example, *Gorilla* is known to feed on large quantities of certain plant parts that require cyclical loading of the mandible to process (e.g., leaves, pith; Elgart-Berry, 2004), whereas *Pongo* has been documented to occasionally process exceptionally resistant foods (e.g., seeds and bark) that require high occlusal forces to breach and/or masticate (Vogel et al., 2008). Furthermore, previous analyses of masticatory morphology have found mixed results when comparing *Pongo* and *Gorilla* (Constantino, 2007; Taylor et al., 2008). In lieu of sufficient data on the loading environments experienced by *Gorilla* and *Pongo*, I have no *a priori* expectations for how these genera should compare to one another.

Similarly, behavioral data suggest that both *Pan* and *Pongo* rely on their anterior teeth for food processing (Ungar, 1994; Lambert, 1999), but whether or how these taxa differ in these behaviors is unclear. Furthermore, given the observation that orangutans exploit exceptionally resistant foods, it is possible that orangutans experience a functional trade-off in their ability to generate wide jaw gapes, in favor of the ability to produce high occlusal forces (e.g., Taylor and Vinyard, 2009). I therefore make no direct predictions for how *Pan* and *Pongo* differ in features linked to incisal behaviors.

MATERIALS AND METHODS

Samples and measurements

Data were collected for both sexes from eight great ape taxa (Table 2) using a Microscribe G2X digitizer; accuracy for this Microscribe is ±0.23 mm, and an intraobserver error analysis for the dataset from which these data were drawn found an average error of ~0.03 mm for the skull and ~0.04 mm for the mandible (Terhune, 2010). Renderings of the articular surfaces of the mandibular fossa and condyle were created by collecting a dense cloud of landmarks describing each of these surfaces in the program Rhino 3D (McNeel and Associates, 2008); joint surface areas were then calculated using these point clouds. Mandibular fossa and condylar shape were quantified using linear measurements extracted from these three-dimensional (3D) coordinate data (Supporting Information, Table 1). Variables that were analyzed and the predictions they are linked to are listed in Table 3. All variables (except dimensionless ratios) were adjusted relative to an appropriate biomechanical load-arm estimate for incision, mandibular length (Hylander, 1985; Bouvier, 1986a,b) and/or mastication, distance from condyle to M_1 (Vinyard, 2008).

Data analysis

Preliminary *t*-tests indicated that males and females of each species do not differ significantly in any TMJ shape variable. I therefore combined the sexes in all analyses. Additionally, in the absence of specific functional predictions, all subspecies of *P. troglodytes* were pooled. One-tailed student's *t*-tests were used to compare species within each genus (*P. pygmaeus* vs. *P. abelii*, *G. gorilla* vs. *G. beringei*, and *P. troglodytes* vs. *P. paniscus*). Where one-tailed tests failed to find significant differences in the predicted direction, two-tailed tests were performed to test for differences in the opposite direction than predicted. A critical $\alpha = 0.05$ was further adjusted for multiple comparisons using the sequential Bonferroni method (Rice, 1989); this adjustment was applied across all variables in each species comparison.

Generic comparisons were made using a one-way ANOVA with a Tukey's HSD test for multiple comparisons. Data for each of the species in *Gorilla* and *Pongo* were pooled because they differed in the same direction when compared with the other genera. However, *P. paniscus* and *P. troglodytes* were analyzed separately because of significant differences between these two species.[3] All analyses were performed in the program IBM SPSS (Version 19).

RESULTS

Comparisons within genera

When species within genera were compared *P. paniscus* and *P. troglodytes* differed most consistently (Table 4), and for most of the significant differences variation was in the predicted direction. *P. paniscus* has relatively larger condylar surface areas and relatively more AP curved condyles than *P. troglodytes*. *P. troglodytes* has relatively AP longer cranial articular surfaces (e.g., glenoid length, preglenoid plane length).

Fewer significant differences were found when *P. pygmaeus* and *P. abelii* were compared (Table 5). As predicted, *P. pygmaeus* has relatively larger condylar areas than *P. abelii* relative to TMJ-M_1 (JRF1a), but not relative to mandible length (JRF1b). In contrast, *P. pygmaeus* and *P. abelii* differed in the direction opposite of that predicted for several features related to range of motion at the joint. *P. pygmaeus* has a relatively AP longer preglenoid plane, and *P. abelii* has relatively more projecting entoglenoid process.

Finally, comparison of the two species of *Gorilla* (Table 6) revealed only a single significant difference: articular tubercle projection. However, this variable differed in the direction that was opposite my prediction. A number of other variables (relative condylar width, glenoid length, preglenoid plane length, and condylar curvature) approached statistical significance (e.g., $P < 0.05$) in the direction predicted, but did not reach significance after Bonferroni correction.

Comparisons among genera

Of the features linked to load resistance at the TMJ (Fig. 1, Table 7), relative condylar width did not differ

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[3] Analyses performed among all species (i.e., where species of *Gorilla* and *Pongo* were not pooled), and analyses where species in all three genera were pooled were very similar to the results reported here.

TABLE 3. Measurements included in the univariate analysis

Name	Abbreviation	Definition	Prediction #	Analyzed relative to
Condylar area	CondArea	Sum of the surface area of the polygons connecting a cloud of points covering the articular surface of the mandibular condyle	JRF 1a JRF 1b	TMJ-M$_1$ MandLg
Condylar width	CondWid	Distance between the most medial and most lateral points on the mandibular condyle (Ldmks 13 and 14)	JRF 2	TMJ-M$_1$
Glenoid fossa length	GlenLg	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)	ROM 1a	MandLg
Preglenoid plane length	PreGlenLg	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)	ROM 1a	MandLg
Preglenoid plane length-mandibular fossa length ratio	PreGlenLg/ GlenLg	Preglenoid plane length divided by mandibular fossa length	ROM 1a	n/a
Condylar length	CondLg	Distance between the most anterior and most posterior points on the mandibular condyle (Ldmks 16 and 17)	ROM 1b	MandLg
Condylar AP curvature	CondAPIndex	Sum of the distances between semilandmarks describing anteroposterior curvature of the mandibular condyle (arc length) divided by the distance between landmarks 16 to 17 (chord length)	ROM 1b	n/a
Mandibular fossa length-condyle length ratio	GlenLg/ CondLg	Glenoid length divided by condyle length	ROM 1c	n/a
Entoglenoid process projection	EntGl	Inferior projection of the entoglenoid process (Ldmk 1), as measured from Frankfurt Horizontal	ROM 2	TMJ-M$_1$
Articular tubercle projection	ArtTub	Inferior projection of the articular tubercle (Ldmk 2), as measured from Frankfurt Horizontal	ROM 3	TMJ-M$_1$
Mandible length	MandLg	Distance from the center of the mandibular condyle to infradentale	n/a	n/a
Distance from the condyle to M1	TMJ-M$_1$	Distance from the center of the mandibular condyle to the lateral alveolar margin of mandibular M1	n/a	n/a

See Table 1 in the Supporting Information for landmark definitions.

TABLE 4. Means, standard deviations (SD), and p-values for the Student's t-tests between P. troglodytes *and* P. paniscus

	P. paniscus		*P. troglodytes*				
Variable	Mean	SD	Mean	SD	One-tailed *P*-value	Two-tailed *P*-value	As predicted?
CondArea/ TMJ-M$_1$	0.230	0.019	0.209	0.016	**0.00002**	–	Yes
CondArea/ MandLg	0.153	0.014	0.143	0.011	NS	**0.004**	No
CondWid/ TMJ-M$_1$	0.272	0.021	0.262	0.021	NS (0.037)	-	No difference
GlenLg/ MandLg	0.217	0.013	0.230	0.014	**0.0001**	-	Yes
PreGlenLg/ MandLg	0.114	0.009	0.128	0.013	**0.00002**	-	Yes
PreGlenLg/GlenLg	0.526	0.034	0.555	0.037	**0.002**	-	Yes
CondLg/ MandLg	0.074	0.007	0.073	0.007	NS	NS	No difference
CondAPIndex	1.227	0.034	1.181	0.052	NS	**0.002**	No
GlenLg/CondLg	2.941	0.310	3.098	0.559	NS	NS	No difference
EntGl/ TMJ-M$_1$	0.218	0.026	0.221	0.030	NS	NS	No difference
ArtTub/ TMJ-M$_1$	0.158	0.020	0.147	0.022	NS (0.029)	-	No difference

Two-tailed *t*-tests were only performed if the one-tailed test failed to find a significant difference or where there were two opposite predictions (i.e., condylar area). 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.

significantly ($F = 1.204$, $P = 0.311$) for any pair of taxa. When scaled by a masticatory load arm, condylar area was relatively larger in *P. paniscus* and *Pongo* in comparison to *Gorilla,* and was relatively larger in *Pongo* when compared to *P. troglodytes*. However, when scaled by an incisal load arm condylar area was relatively larger in *Gorilla* and *Pongo* when compared to *P. troglodytes*, but not *P. paniscus*. Neither of these analyses of

TABLE 5. Means, standard deviations (SD), and p-values for the Student's t-tests between P. pygmaeus *and* P. abelii

	P. pygmaeus		*P. abelii*				
Variable	Mean	SD	Mean	SD	One-tailed p-value	Two-tailed p-value	As predicted?
CondArea/ TMJ-M$_1$	0.225	0.011	0.214	0.016	**0.007**	-	Yes
CondArea/ MandLg	0.158	0.009	0.151	0.014	NS	NS (0.034)	No difference
CondWid/ TMJ-M$_1$	0.263	0.021	0.262	0.024	NS	NS	No difference
GlenLg/ MandLg	0.218	0.015	0.203	0.024	NS	NS (0.022)	No difference
PreGlenLg/ MandLg	0.117	0.010	0.103	0.017	NS	**0.003**	No
PreGlenLg/GlenLg	0.535	0.026	0.507	0.057	NS	NS (0.042)	No difference
CondLg/ MandLg	0.078	0.007	0.076	0.008	NS	NS	No difference
CondAPIndex	1.241	0.056	1.258	0.048	NS	NS	No difference
GlenLg/CondLg	2.820	0.265	2.706	0.409	NS	NS	No difference
EntGl/ TMJ-M$_1$	0.210	0.023	0.253	0.028	NS	**<0.0001**	No
ArtTub/ TMJ-M$_1$	0.157	0.018	0.156	0.027	NS	NS	No difference

All results are presented as described in Table 4.

TABLE 6. Means, standard deviations (SD), and p-values for the Student's t-tests between G. beringei *and* G. gorilla

	G. beringei		*G. gorilla*				
Variable	Mean	SD	Mean	SD	One-tailed *P*-value	Two-tailed *P*-value	As predicted?
CondArea/ TMJ-M$_1$	0.205	0.017	0.206	0.015	NS	NS	No difference
CondArea/ MandLg	0.152	0.012	0.151	0.011	NS	NS	No difference
CondWid/ TMJ-M$_1$	0.272	0.023	0.260	0.016	NS (0.03)	–	No difference
GlenLg/ MandLg	0.220	0.017	0.232	0.014	NS (0.015)	–	No difference
PreGlenLg/ MandLg	0.098	0.011	0.104	0.008	NS (0.03)	–	No difference
PreGlenLg/GlenLg	0.445	0.050	0.448	0.029	NS	NS	No difference
CondAPIndex	1.222	0.099	1.267	0.056	NS (0.039)	–	No difference
CondLg/ MandLg	0.075	0.007	0.075	0.006	NS	NS	No difference
GlenLg/CondLg	2.965	0.328	3.112	0.253	NS	NS	No difference
EntGl/ TMJ-M$_1$	0.218	0.032	0.235	0.024	NS	NS	No difference
ArtTub/ TMJ-M$_1$	0.121	0.027	0.142	0.021	NS	**0.008**	No

All results are presented as described in Table 4.

relative condylar area conforms to my original predictions for variation in this feature.

In features linked to TMJ range of motion (Fig. 2), only two variables did *not* differ among taxa: relative condylar length (F = 2.025, P = 0.113) and relative entoglenoid process projection (F = 1.041, P = 0.376). Relative glenoid fossa length was largest in *Gorilla* and smallest in *Pongo*, and there were significant differences in this variable between *Gorilla* and *Pongo* and *P. troglodytes* and *Pongo*. Interestingly, this variation is opposite the predicted direction. However, another measure of translation potential at the TMJ is relative preglenoid plane length (as the primary surface upon which the condyle translates during jaw opening [Wall, 1999; Crompton et al., 2006]); this variable showed strong divergence among taxa and did vary as predicted. Together, these data indicate that, although *Gorilla* has the relatively longest mandibular fossa, they have the shortest relative preglenoid plane length. Thus, preglenoid plane length makes up a comparatively smaller percentage of overall glenoid length (PreGlenLg/GlenLg) in *Gorilla* (44%) when compared with *Pongo* (52%) and *Pan* (*P. paniscus* = 53%, *P. troglodytes*=55%) (F = 56.63, P < 0.001). In contrast, taxa do not differ strongly in relative AP condylar length, either as a chord distance or as a measure of curvature. The index of condylar curvature did find two significant differences among taxa, with *Gorilla* and *Pongo* having relatively more curved condyles than *Pan*. However, these data were in the direction opposite of my prediction. The glenoid length/condyle length ratios may explain this variation. These ratios, as well as the preglenoid plane and condylar data, suggest that *Pan* has the relatively longest preglenoid plane and AP shortest condyle, indicating that members of this genus have the greatest potential for condylar translation when compared with both *Pongo* and *Gorilla*.

Although relative articular tubercle projection was significantly larger in all taxa when compared with *Gorilla*, this variation was opposite the predicted direction.

DISCUSSION

Although some work has previously evaluated great ape TMJ form, these analyses have focused largely on the mandibular condyle. For example, condylar form has previously been investigated in all of these taxa (Taylor 2002, 2005, 2006); however, the data presented here are only partly consistent with prior findings. This may be in part for methodological reasons: I used a different scaling variable for some of my variables, I calculated 3D rather than 2D condylar areas, and I looked at condylar curvature in addition to AP chord length of the condyle. Like Taylor (2005), I found relatively larger condylar areas in *P. paniscus* than *P. troglodytes*, and

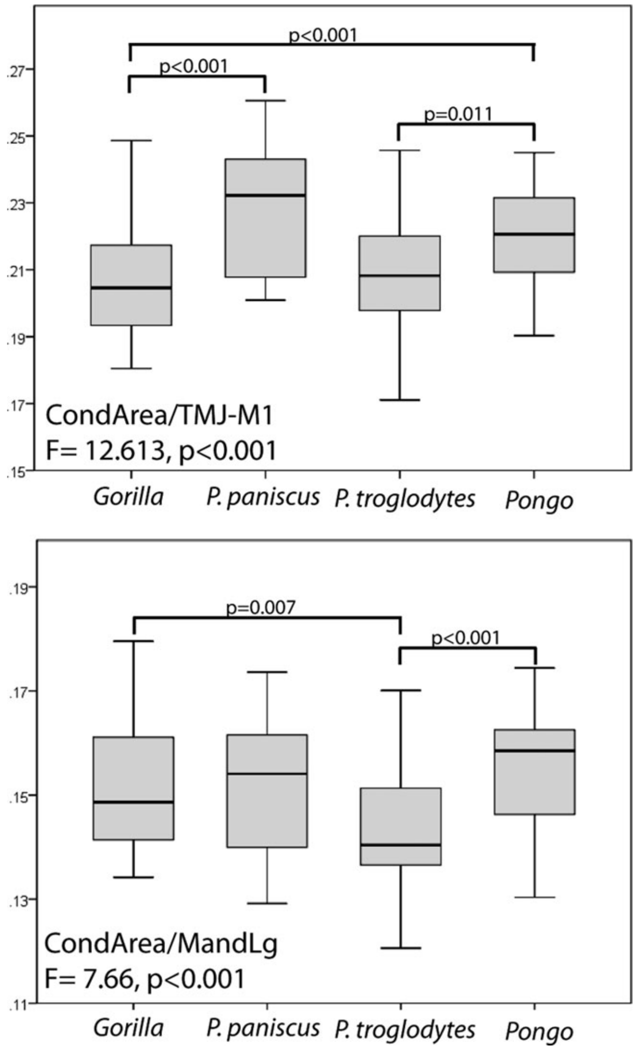

Fig. 1. Box plots of features linked to load resistance in the TMJ and corresponding ANOVA results with post-hoc *P*-values for multiple comparisons. Darkened bars represent the median value for each group, the boxes show the interquartile range (25th to 75th percentile), and the whiskers extend to 1.5 times the interquartile range. The distribution for condylar width is not shown ($F = 1.204$, $P = 0.311$).

relatively more curved condyles in *P. paniscus* when compared to *P. troglodytes*, though this was counter to my prediction. However, where Taylor (2005) found *Gorilla* to have larger condylar areas (relative to mandible length) than *Pan*, I found condylar area to be relatively larger in *P. paniscus* than *Gorilla*. Finally, while Taylor (2002, 2005) found relatively wider condyles in *G. beringei*, I did not identify any differences in relative condylar width among taxa.

Importantly, the additional evaluation of the cranial component of the TMJ provided here suggests more consistent differences among taxa in features linked to joint range of motion (ROM) than to features related to joint loading. This is not to say that other features of the masticatory apparatus not examined here are unrelated to generating and/or resisting higher masticatory forces (e.g., TMJ height, muscle architecture, etc.) but instead that inferred differences in joint loading are not strongly reflected in TMJ morphology. This finding mirrors other work that has failed to find strong differences in mandibular morphology related to the dissipation of masticatory loads in the great apes (Daegling, 1989, 2007; Taylor et al., 2008), despite FMP data demonstrating differences in food resources utilized by these species (Elgart-Berry, 2004; Vogel et al., 2008).

Variation within and among genera

Comparisons within genera. As predicted, *P. paniscus* displays features related to increased TMJ loading and lateral deviation, such as relatively larger condylar areas, whereas *P. troglodytes* exhibits features of the TMJ related to increased sagittal sliding. Thus, while some authors suggest that *P. paniscus* may not rely heavily on THV at all sites (Chapman et al., 1994) and that perhaps bonobos preferentially select younger, less mechanically challenging leaves, the morphological data presented here suggest improved load resistance capabilities in the bonobo TMJ that may be linked to increased THV consumption in this species (Badrian and Malenky, 1984; Malenky and Stiles, 1991).

In contrast to *Pan*, most significant differences in *Gorilla* and *Pongo* were counter to the predictions outlined for this study. For example, *P. pygmaeus* has a relatively AP longer preglenoid plane than *P. abelii*, suggesting that the capacity for condylar translation in *P. pygmaeus* is increased over that of *P. abelii*. Relative entoglenoid process projection also differed significantly in the opposite way than predicted. It is unclear why variation in *Pongo* ran counter to my expectations. One possibility is that these results indicate a lack of sufficient data regarding incisal behaviors in these species. For example, *P. pygmaeus* has been noted to feed extensively on bark during times of fruit scarcity, often gnawing directly on the trunk, using incisors to strip bark from the ends of twigs, or using their canines to split bark (Rodman, 1988; Leighton, 1993). Thus, it may be more appropriate to posit that, given these behaviors, it is necessary for *P. pygmaeus* to retain the ability to produce relatively wider jaw gapes while simultaneously increasing their ability to masticate very resistant food objects on their posterior dentition, as has been suggested recently for *C. apella* (Taylor and Vinyard, 2009). Interestingly, the entoglenoid process in *C. apella* is relatively less projecting than in other members of the genus *Cebus*, and both *C. apella* and *P. pygmaeus* are known to use their anterior dentition heavily for food processing, and have been documented to use their canines as a wedge to propagate cracks (e.g., Terborgh, 1983; Rodman, 1988; Leighton, 1993). This parallel may imply that, rather than limiting condylar movements as was predicted, less projecting entoglenoid processes may accommodate increased ML condylar movements during use of the canines and anterior dentition for food processing. Conversely, where resistant object feeders tend to rely more heavily on the posterior dentition for repetitive mastication of certain food items, the entoglenoid process may play a larger role in guiding movements of the condyle, acting to decrease TMJ range of motion. Admittedly, there are few experimental data with which to infer entoglenoid process function; as a result it is also possible that the entoglenoid process does not act to guide condylar movements as previously suggested (Wall, 1995, 1999) and that we should instead seek alternative explanations to explain entoglenoid process variation.

TABLE 7. Means and standard deviations (SD) for the combined Gorilla *and* Pongo *samples and two species of Pan, as well as the results of the analysis of variance*

Variable	*Gorilla* Mean	*Gorilla* SD	*Pongo* Mean	*Pongo* SD	*P. paniscus* Mean	*P. paniscus* SD	*P. troglodytes* Mean	*P. troglodytes* SD	ANOVA Results F	ANOVA Results *P*-value
CondArea/TMJ-M_1	0.206	0.016	0.220	0.015	0.230	0.019	0.209	0.016	12.61	<**0.001**
CondArea/MandLg	0.152	0.011	0.155	0.012	0.153	0.014	0.143	0.011	7.66	<**0.001**
CondWid/TMJ-M_1	0.265	0.020	0.263	0.022	0.272	0.021	0.262	0.021	1.204	0.311
GlenLg/MandLg	0.227	0.016	0.211	0.021	0.217	0.013	0.230	0.014	11.11	<**0.001**
PreGlenLg/MandLg	0.101	0.010	0.111	0.015	0.114	0.009	0.128	0.013	34.91	<**0.001**
PreGlenLg/GlenLg	0.447	0.039	0.522	0.045	0.526	0.034	0.555	0.037	56.63	<**0.001**
CondAPIndex	1.248	.080	1.249	.052	0.074	0.007	0.073	0.007	10.65	<**0.001**
CondLg/MandLg	0.075	0.006	0.077	0.007	1.227	0.034	1.181	0.052	2.025	0.113
GlenLg/CondLg	3.050	0.292	2.767	0.340	2.941	0.310	3.098	0.559	12.08	<**0.001**
EntGlHt/TMJ-M_1	0.228	0.028	0.230	0.033	0.218	0.026	0.221	0.030	1.041	0.376
ArtTub/TMJ-M_1	0.133	0.026	0.156	0.022	0.158	0.020	0.147	0.022	8.552	<**0.001**

Significant *P*-values are shown in bold.

Comparisons among genera. The majority of the significant differences in TMJ form found in this study were found when taxa from different genera were compared, and most of these differences were in features linked to range of motion at the TMJ. While variation in some of these features did not conform to my initial predictions, when combined with other features of the joint the overall picture produced is one of strong differences in AP range of motion at the joint. In particular, these data suggest that *Pan* likely experiences much greater translation at the joint (via a relatively long preglenoid plane and short condyle), whereas *Pongo* and *Gorilla* have comparatively less capacity for translation, but may experience more rotation at the TMJ (via relatively more AP curved condyles). Particularly in light of the very small preglenoid plane to overall glenoid fossa length ratio in *Gorilla*, these data suggest that much less translation occurs in this taxon even in comparison to *Pongo*. Since behavioral data would suggest that gorillas are likely repetitively loading the postcanine dentition at relatively small jaw gapes (i.e., when the condyle is situated on the posterior aspect of the articular eminence and in the mandibular fossa proper), this variation may be related to an emphasis on postcanine masticatory behaviors in this taxon.

These data imply differences in TMJ movement that may represent differences in relative gape, or that the same gapes are being achieved in different ways (Wall, 1999; Vinyard et al., 2003). Experimental data are necessary to confirm these findings, however, and other factors should be considered in order to correlate this observed variation to gape capacity. For example, height of the TMJ above the occlusal plane is negatively correlated with linear gape (Herring and Herring, 1974), and previous studies suggest *Gorilla* has a relatively higher TMJ than does *Pan* (Taylor, 2005). Muscle architecture and position may also significantly influence relative jaw gape (Taylor and Vinyard, 2004, 2009). Data describing linear gape in each of these taxa are therefore necessary before further conclusions can be drawn.

In all, these data suggest that, when specimens in these genera are compared the most consistent differences in TMJ shape are related to TMJ range of motion. However, variation in two features that were predicted to be associated with range of motion at the joint, the articular tubercle and entoglenoid process, did not conform to predictions. Articular tubercle projection in particular departed from expectations. In fact, *Gorilla* has the relatively least projecting articular tubercles. Further experimental and soft tissue data are necessary to fully determine the role of the temporomandibular ligament and articular tubercle in the function of the TMJ, as well as the role of the entoglenoid process in guiding condylar movements.

Where does Pongo fit in? Previous work by Taylor et al. (2008) and Constantino (2007) hypothesized that *Pongo* should be best able to resist high masticatory forces given that this genus has been documented to breach exceptionally tough and stiff foods (Vogel et al., 2008). However, the nature of any similarities or differences in the masticatory loading environment in *Pongo* and *Gorilla* are unclear. Behavioral data for *Pongo* indicate that orangutans can exploit food items that are exceptionally resistant (Vogel et al., 2008). Importantly, though, these foods items are commonly items such as seeds that, once breached, are quick to break down. In contrast, mountain gorillas in particular have been documented to habitually exploit food resources that are of low nutrient value and are consumed in large quantities (e.g., leaves, pith) (Watts, 1984). Gorillas therefore likely experience more frequent loading of the mandible, and tend to exploit food items that are resistant, but not exceptionally so in comparison to *Pongo* (Elgart-Berry, 2004; Vogel et al., 2008). Accurately determining the forces actually placed on the masticatory apparatus during these feeding behaviors is difficult, and will require further data regarding chewing cycles, FMPs, and food use.

For this study, I made no specific predictions for how *Gorilla* and *Pongo* should vary in relation to one another in features related to masticatory behaviors. If, as Taylor et al. (2008) and Constantino (2007) predicted, the masticatory morphology of *Pongo* is better adapted to dissipating high forces than *Gorilla*, I would have expected to see relatively larger condylar areas in *Pongo* than in *Gorilla* or *Pan*. However, although relative condylar area in *Pongo* does exceed *P. troglodytes*, it does not exceed *P. paniscus*, and *Pongo* only exceeds *Gorilla* in condylar area when scaled by a masticatory load arm. Thus, there is no clear pattern in this feature. Similarly, the lack of a significant difference between *Gorilla* and *Pongo* in relative condylar width further implies few differences in the ability of each of these taxa to dissipate reaction forces at the TMJ. This result may be related to previous findings that suggest the mandible is “over-designed” (Daegling, 2007; Taylor et al., 2008).

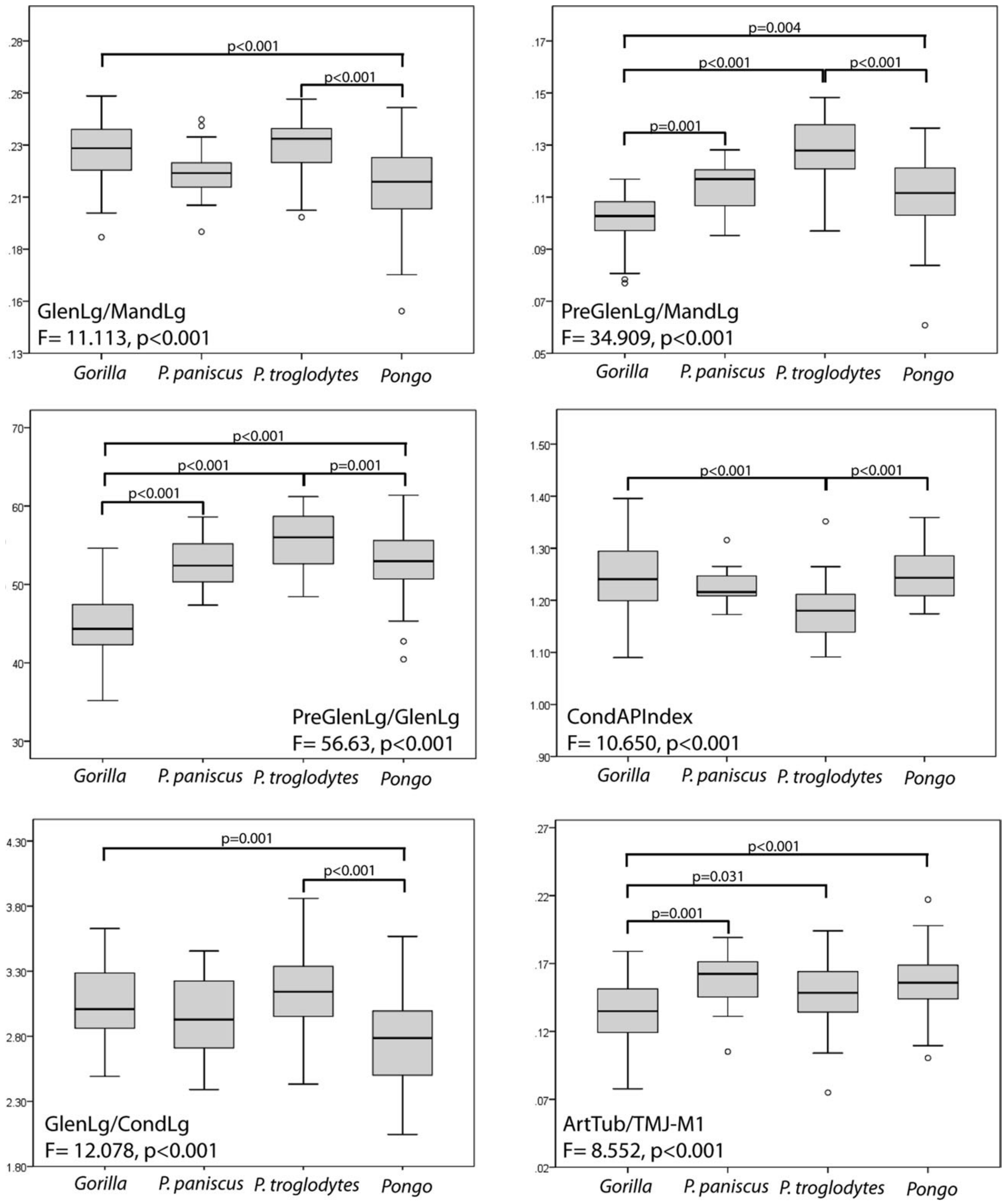

Fig. 2. Box plots of features linked to TMJ range of motion and corresponding ANOVA results with post-hoc P-values for multiple comparisons. Darkened bars represent the median value for each group, the boxes show the interquartile range (25th to 75th percentile), and the whiskers extent to 1.5 times the interquartile range. Outliers are designated by open circles. The distributions for condylar length ($F = 2.025$, $P = 0.113$) and entoglenoid process size ($F = 1.041$, $P = 0.376$) are not shown.

In contrast to features related to joint loading, features linked to range of motion do suggest differences in joint shape between *Gorilla* and *Pongo*, as predicted. As indicated above, *Pongo* appears to be intermediate in the capacity for translation and rotation at the TMJ when compared to *Gorilla* and *Pan*. This finding is consistent with expectations based on behavioral data that suggest *Pongo* and *Pan* tend to use their anterior dentition more frequently for ingestive behaviors than does *Gorilla*, and the intermediate position of *Pongo* perhaps indicates a trade-off between this taxon's ability to generate wide jaw gapes and their ability for generating large bite forces, which are difficult to maximize simultaneously (Taylor and Vinyard, 2004, 2009).

Comparisons to other primate taxa

The data presented here suggest that much of the observed variation in TMJ shape among great apes is related to the AP dimensions of the joint, and this variation may perhaps relate to differences in maximum gape capacity among taxa. Given the behavioral data for these species, it seems likely that these data reflect differences in ingestive behaviors, and particularly use of the anterior teeth during food processing or even for harvesting bark (as in *P. pygmaeus*). Previous work has identified similar variation in other primate clades (Bouvier, 1986a,b; Wall, 1999; Vinyard et al., 2003; Terhune, 2011a). Bouvier (1986a,b) first suggested a relationship between AP elongation of the condyle and reliance on the anterior dentition in cercopithecines. Subsequently, in vivo studies by Wall (1999) demonstrated a link between condylar form and sagittal sliding of the condyle. Finally, morphometric analyses have linked AP elongated TMJs to tree-gouging behaviors in marmosets and the fork-marked lemur (Vinyard et al., 2003); to vocal behaviors in *Alouatta* (Terhune, 2011a); and to seed predation in the pitheciines (Terhune, 2011a).

These data would seem to suggest a stronger link between mandibular range of motion and TMJ shape, with comparatively less support for a link between TMJ morphology and load resistance capabilities. However, previous analyses have successfully demonstrated a link between masticatory robusticity and dietary resistance (e.g., Anapol and Lee, 1994; Wright, 2005; Constantino, 2009; Norconk et al., 2009), and it is therefore clear that masticatory morphology must, at least in part, reflect variation in masticatory loading. One possible explanation for this disconnect is that differences in masticatory loading may not be reflected in ape TMJ morphology or that perhaps other features of the joint not examined here (e.g., the articular eminence) are acting to mediate joint forces (e.g., Terhune, 2011b). More likely, however, is that variation in masticatory and TMJ form as related to load resistance and range of motion presents in a mosaic fashion across primates. Thus, although features linked differences in joint range of motion appear to vary considerably in the great apes, this may not be true for all primate clades. Further analyses designed to examine the suite of features related to these two performance variables are necessary to fully evaluate the wide range of masticatory morphologies represented across primates.

CONCLUSIONS

While variation in some morphologies appear to reflect documented behavioral differences among taxa (e.g., AP dimensions of the joint linked to differences in food processing behaviors), other behaviors do not appear to be reliably reflected in the TMJ. In particular, different loading magnitudes in the masticatory apparatus as inferred from FMPs do not appear to have a straightforward relationship to bony masticatory morphology, as indicated by this and other studies (Daegling 2007; Taylor et al., 2008). However, whether this absence of evidence is in fact evidence of absence for the adaptive significance of particular morphologies related to differences in TMJ loading is unclear. This and other studies (Vinyard et al., 2003; Terhune, 2011a), appear to suggest that TMJ form can be more strongly linked to differences in joint range of motion at the TMJ. These findings do not preclude other features of the TMJ from being related to load resistance, however. For example, histological analyses may reveal differences in bone mineralization and articular cartilage (e.g., Ravosa et al., 2007), and further comparative and experimental analyses designed to identify the functional significance of other features of the TMJ (e.g., the entoglenoid process and articular tubercle) are warranted. Furthermore, as we continue to refine the behavioral and FMP data for primates, we may be better able to address the impact of fallback foods on masticatory morphology.

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