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Modeling the biomechanics of articular eminence function in anthropoid primates

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Abstract

One of the most prominent features of the cranial component of the temporomandibular joint (TMJ) is the articular eminence (AE). This bar of bone is the primary surface upon which the condyle translates and rotates during movements of the mandible, and is therefore the primary point at which forces are transmitted from the mandible to the cranium during loading of the masticatory apparatus. The shape of the AE is highly variable across primates, and the raised eminence of humans has often been considered a defining feature of the human TMJ, yet few data exist to address whether this variation is functionally significant. This study used a broad interspecific sample of anthropoid primates to elaborate upon and test the predictions of a previously proposed model of AE function. This model suggests that AE inclination acts to resist non-normal forces at the TMJ, thereby maximizing bite forces (BFs). AE inclination was predicted to covary with two specific features of the masticatory apparatus: height of the TMJ above the occlusal plane; and inclination of the masticatory muscles. A correlate of this model is that taxa utilizing more resistant food objects should also exhibit relatively more inclined AEs. Results of the correlation analyses found that AE inclination is strongly correlated with height of the TMJ above the occlusal plane, but less so with inclination of the masticatory muscles. Furthermore, pairwise comparisons of closely related taxa with documented dietary differences found that the AE is consistently more inclined in taxa that utilize more resistant food items. These data preliminarily suggest that variation in AE morphology across anthropoid primates is functionally related to maximizing BFs, and add to the growing dataset of masticatory morphologies linked to feeding behavior.

Key words: human evolution; masticatory biomechanics; temporomandibular joint.

Introduction

There is considerable variation in the form of the temporomandibular joint (TMJ) across primate and mammalian taxa. One major feature of the cranial component of this joint is the articular eminence (AE), a transverse bar of bone that forms the anterior boundary of the concave mandibular (also known as the glenoid) fossa. Anteriorly, the AE blends with the flat preglenoid plane, which forms the anterior margin of the cranial component of the TMJ. Understanding variation in the shape of the AE is of importance in studies of living and fossil taxa because the AE is the primary articular surface upon which the mandibular condyle (via the articular disc) rotates and translates during movements of the mandible. Dissections, TMJ histology and experimental analyses indicate that, when the mandible is at rest, the head of the condyle directly abuts the posterior slope of the AE rather than lying in the depth of the fossa, while during jaw opening the condyle translates anteriorly onto the AE and preglenoid plane (Moffet et al. 1964; Wall, 1995, 1999; Hylander, 2006).

In humans, the AE is a raised bar that is convex anteroposteriorly and slightly concave mediolaterally. In contrast, in many other primates the AE is relatively flat and undefined, resulting in a gradually sloping anterior border to the glenoid fossa. The density of the bone that forms the AE is likely to vary across primates, although this remains to be quantified in taxa other than humans and macaques (Moffet et al. 1964; Hinton & Carlson, 1983).

Several functional reasons have been proposed to account for the unique form of the AE in humans. In an analysis of a growth series of human crania, Nickel et al. (1988a,b) found that the inclination of the AE increases during ontogeny (i.e. the surface of the AE gradually becomes directed more postero-inferiorly or posteriorly), and that this increasing inclination corresponds to an increasingly anteriorly directed joint reaction force (JRF; which was calculated mathematically). This result was interpreted to

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mean that the AE forms as a response to joint loading; however, this hypothesis does not explain why the AE is not raised and bar-like in all primate taxa, as JRFs are not exclusive to humans. Furthermore, several analyses have shown that increased loading causes the cartilage cells located in the proliferative zones along the mandibular fossa and condyle to form mesenchymal precursor cells, which inhibit osteogenesis (Petrovic, 1972; Hall, 1979; Hinton, 1981); thus, increased loading at the TMJ, in contrast to many other joints, results in regressive remodeling of bone rather than progressive remodeling.

More recently, Iwasaki et al. (2010) built on Nickel's initial work to develop a model of joint load minimization, which hypothesizes that the AE is inclined such that it acts to minimize the JRF. This study found that when the condyle is protruded anteriorly during joint loading the form of the eminence appears unable to minimize joint loads; this could therefore explain why the first signs of joint degeneration in the TMJ cartilage occur at the peak of the AE (Moffet et al. 1964). This 'load minimization' model is very similar to work by Osborn (1989, 1996) and Spencer (1995), who previously proposed that an inferiorly inclined AE acts to maximize the bite force (BF) by resisting the translatory component of an anteriorly directed muscle resultant force. The study presented here expands upon this previous work by laying out a comprehensive model describing the biomechanics of the AE, which is then tested by evaluating AE morphology across anthropoid primates.

Biomechanical model

The masticatory apparatus is commonly modeled as a third-class lever (Gysi, 1921; Hylander, 1975, 1979a,b, 2006; Greaves, 1978; Smith, 1978; Hylander & Crompton, 1980; Hylander et al. 1992). This model often sums the force vectors of the adducting masticatory muscles (e.g. masseter, medial pterygoid, temporalis) to produce a single muscle resultant force, the magnitude and direction of which must be equally opposed by the JRF and BF in order to maintain static equilibrium. Forces in this model are also often considered to be normal (or perpendicular) to the reference plane. In the simplest version of this model of masticatory function, the JRF is translated to the occlusal plane, which is frequently considered to be the plane of interest (i.e. reference plane, or plane between the JRF and BF; Hylander, 1975; Walker, 1978; Spencer, 1995). In such a configuration, and assuming that all of the forces in the model are normal (or perpendicular) to the reference plane, there need not be a non-normal component of the JRF that must be resisted by the AE in order to maintain static equilibrium (similarly, there is no non-normal component of the BF). As a consequence, the AE would be expected to be relatively flat, as all forces will be vertical and normal (Fig. 1a). However, a TMJ level with the occlusal plane is observed in very few primate taxa (e.g. some strepsirrhines, patas monkeys), and in most primate species the TMJ is raised well above the occlusal plane. In such an instance, and assuming that the forces acting upon the joint remain normal, the slope of the AE might be expected to covary with the height of the TMJ above the occlusal plane (hereafter referred to also as TMJ height), simply to maintain the same spatial relationships of the components of the masticatory apparatus (Fig. 1b). Alternatively, where the muscle resultant force is non-normal (regardless of TMJ height), we must expect these non-normal forces to be resisted either by non-normal forces at the TMJ or at the bite point (or some combination of the two). Changes in the orientation of the JRF or the BF could therefore necessitate bony or dental morphologies that help resist the translatory component of the non-normal muscle resultant. In the TMJ, this resistance is most likely to be supplied by an inclined AE, which should be oriented

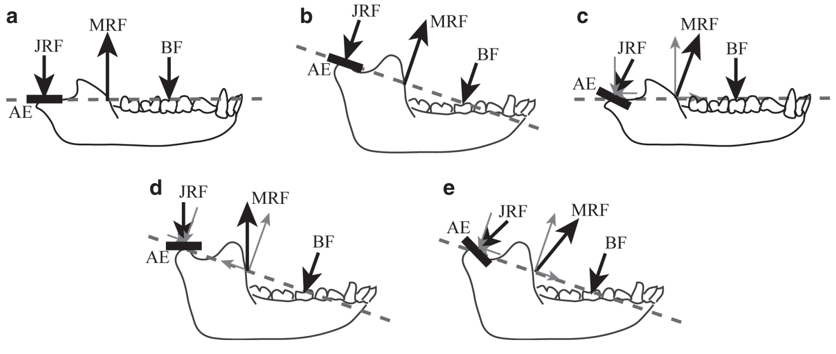

Fig. 1 Simplified 2D biomechanical models of the components of the masticatory apparatus showing: (a) the TMJ level with the occlusal plane and the force vectors normal to the reference plane (dashed line); (b) the TMJ raised above the occlusal plane and the force vectors normal; (c) the TMJ level with the occlusal plane and the force vectors non-normal; (d) the TMJ raised above the occlusal plane and the muscle resultant force more vertically oriented; and (e) the TMJ raised above the occlusal plane and the muscle resultant force more anteriorly oriented. Note that in (c–e), all of the non-normal forces of the inclined muscle resultant are opposed at the TMJ rather than the bite point. AE, articular eminence; BF, bite force; JRF, joint reaction force; MRF, muscle resultant force.

perpendicular to the primary axis of the JRF in order to maintain stability in the joint (Hylander, 1978; Osborn & Baragar, 1992; Fig. 1c). Resisting these non-normal forces primarily at the TMJ could then assist in maximizing the normal component of the BF, which may or may not be perpendicular to the occlusal plane.

Although the JRF in this model represents both the working- and balancing-side TMJs, the position of the working- and balancing-side condyles in relation to the AE vary during mastication. Experimental analyses of mandibular movement suggest that, during lateral deviation of the mandible, the working-side condyle does not move far from its starting position (at rest on the posterior slope of the AE), whereas the balancing-side condyle shifts downward (and slightly medially) along the AE (Miyawaki et al. 2000, 2001; Komiyama et al. 2003). Thus, during mastication the position of the two condyles will vary slightly depending upon the magnitude of the lateral deviation that occurs. However, it is probable that the condyle only translates anteriorly onto the preglenoid plane during wide jaw gapes (Wall, 1995, 1999); thus, the majority of the JRFs incurred during the power stroke of rhythmic chewing (which occurs as the balancing-side condyle is translating posteriorly into the rest position) are likely to take place on the posterior edge ⁄ or peak of the AE. For this reason, this model does not explicitly consider differences in the position of the working- and balancing-side condyles. However, further data are necessary to validate this assertion; in particular, experimental analyses coupling kinematic, electromyographic and bone strain data should help to further our understanding of the exact position of the working- and balancing-side condyles during mastication.

Model predictions

Given the model described above, we can therefore identify two potential factors that may covary with the slope of the AE: first, height of the TMJ above the occlusal plane; and second, orientation of the muscle resultant. These two factors could also be expected to work in conjunction with one another (Fig. 1d,e), such that a TMJ raised well above the occlusal plane but with a primarily vertical muscle resultant force should be expected to have a relatively flat AE (Fig. 1d). However, as discussed by Spencer (1995), increased TMJ height without a corresponding increase in anterior orientation of the muscle resultant should act to reduce forces at both the bite point and at the TMJ. Conversely, if the TMJ is raised above the occlusal plane and the muscle resultant force is significantly anteriorly oriented, the AE would be predicted to have an increased slope so that the JRF is normalized (Fig. 1e). Changes in the orientation of the AE in both of these scenarios (although perhaps more so for a raised TMJ with an anteriorly inclined muscle resultant) would assist in counteracting the bulk of the non-normal forces at the TMJ rather than the bite point, and would therefore function to maximize the BF (and especially the normal component of this force) during mastication (Spencer, 1995; Osborn, 1996).

There are several reasons why these two features of the masticatory apparatus may vary across species. The position of the TMJ above the occlusal plane has been demonstrated in a number of taxonomic groups to be relatively higher in species that eat more resistant (i.e. stiff or tough) foods (Kinzey, 1974; Rosenberger & Kinzey, 1976; Rosenberger & Strier, 1989; Jablonski, 1993; Spencer, 1995; Antón, 1996; Taylor, 2002; Constantino, 2007). Biomechanically, raising the TMJ above the occlusal plane is advantageous because it may act to increase attachment area for the medial pterygoid and masseter muscles (Freeman, 1988), increase the moment arms of the masseter and temporalis muscles (Maynard & Savage, 1959; Greaves, 1974; Dubrul, 1977; Spencer, 1995), and ⁄ or more evenly distribute occlusal loads along the postcanine dentition (Herring & Herring, 1974; Greaves, 1980; Ward & Molnar, 1980; Spencer, 1995). Similarly, anteriorly inclining the muscle resultant force vector has the effect of increasing the length of the muscle force moment arm as well as increasing the magnitude of the normal component of the muscle resultant force vector when the TMJ is raised and the plane of interest is the plane connecting the BF and the JRF (Fig. 1e). Both of these consequences of muscle resultant reorientation therefore act to increase BFs and decrease JRFs, as would be advantageous in resistant object feeders (Spencer, 1995). This configuration also has implications for the directionality of the BF. Assuming that the BFs are normal to the reference plane (again, the plane between the JRF and BF), BFs would become more anteroposteriorly angled, which may be advantageous in certain taxa (Rak & Hylander, 2008). Changes in muscle resultant orientation have also been documented in taxa that tend to utilize more resistant foods, although considerably less consistently than TMJ height (Spencer, 1995; Wright, 2005).

The purpose of this study is to test this biomechanical model across a broad, interspecific sample of anthropoid primates. Based on this model, I predict that height of the TMJ above the occlusal plane and ⁄ or masticatory muscle inclination is significantly correlated with AE inclination. Finding a significant correlation between either of these factors and AE morphology would support the validity of this model, and suggest that AE form varies primarily in response to and ⁄ or in association with changes in configuration of the masticatory apparatus as is related to force production along the postcanine dentition. Furthermore, the previous analyses outlined above also suggest that, not only should AE inclination be correlated with TMJ height above the occlusal plane and ⁄ or masticatory muscle orientation, but the AE should also be relatively more inclined in taxa that utilize more resistant food objects.

Materials and methods

Data collection

Data describing AE inclination, masticatory muscle orientation and height of the TMJ above the occlusal plane were collected for 1023 specimens from 48 primate taxa (Table 1). Taxa were chosen to represent all major clades of anthropoid primates, as well as a range of body sizes and diets. Only adult specimens with all permanent teeth erupted were included in the analysis, although no special effort was made to exclude specimens with unfused sphenoccipital synchondroses. Specimens displaying any pathological changes to the skull were excluded and specimens with extensive dental attrition were generally avoided, although this was difficult for some taxa, particularly the hominoid and human samples.

Data were originally collected as 3D landmarks using a Microscribe G2X digitizer (Immersion; Table 2). 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). The landmark data were then used to calculate the variables of interest in Excel and the program MacMorph (Spencer & Spencer, 1993; refer to Table 3 and Fig. 2 for descriptions of how these variables were defined. AE inclination was measured as the angle between a line describing the slope of the AE and a line describing the occlusal plane (Fig. 2); thus, this measure of AE inclination is functional (rather than solely topographic), and varies depending on both the topography of the joint and the orientation of the occlusal plane in relation to the basicranium. Standardization for variation in size for the single non-angular variable (TMJ height above the occlusal plane) was performed by dividing TMJ height by mandibular length. Mandibular length was chosen as the scaling variable because of its biomechanical relevance (Hylander, 1985; Vinyard et al. 2008), although analyses where TMJ height was scaled by a geometric mean of cranial size (not presented) were very similar.

Orientation of the anterior temporalis, superficial masseter and medial pterygoid muscles was quantified to assess correlations between muscle orientation and AE inclination. This was done by estimating the centroid of the muscle scar for the origin and insertion of each of these muscles separately, and calculating a 2D angle between a line connecting these centroids and a line representing the occlusal plane (Fig. 3). The quantification of muscle orientation involves multiple assumptions regarding the position of the muscle force vector and the magnitude of muscle force produced during mastication. In particular, the method of quantification here assumes that all of the muscle fibers of a given muscle are firing equally and therefore the orientation of the muscle force vector corresponds to the centroid of the muscle scar. Experimental data suggest that this is unlikely to occur on a regular basis during mastication, however (Blanksma & van Eijden, 1990; Blanksma et al. 1992; Herring, 1992; van Eijden et al. 1997; Spencer, 1998; Murray et al. 1999). Intrinsic aspects of muscle architecture such as fiber number, direction and pinnation; location and number of intramuscular tendons; and sarcomere length have also been documented to vary among species of primates (Cachel, 1984; Lovejoy & Ferrini, 1987; Hannam & Wood, 1989; Koolstra et al. 1990; Antón, 1994, 1999, 2000; Taylor & Vinyard, 2004, 2009; Perry, 2008). As a result, these measurements represent

Table 1 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
Cercocebus torquatus	4	5
Cercopithecus mitis	12	12
Cercopithecus nictitans	10	12
Chiropotes satanas	12	12
Colobus polykomos	12	12
Erythrocebus patas	7	12
Gorilla beringei	8	10
Gorilla gorilla	12	12
Homo sapiens	31	30
Hylobates agilis	9	12
Hylobates klossi	10	8
Hylobates lar	10	12
Lagothrix lagothrica	11	12
Lophocebus albigena	12	12
Macaca fascicularis	12	12
Macaca fuscata	12	9
Macaca nemestrina	11	12
Macaca sylvanus	9	4
Macaca thibetana	3	7
Mandrillus sphinx	5	9
Miopithecus talapoin	5	9
Nasalis larvatus	12	12
Pan paniscus	12	10
Pan troglodytes schweinfurthii	12	12
Pan troglodytes troglodytes	7	9
Pan troglodytes verus	4	5
Papio anubis	9	12
Papio cynocephalus	9	12
Papio ursinus	3	11
Pithecia pithecia	11	12
Pongo abelii	9	10
Pongo pygmaeus	12	12
Procolobus badius	12	12
Procolobus verus	11	12
Saimiri sciurius	10	10
Semnopithecus entellus	12	11
Symphalangus syndactylus	10	12
Theropithecus gelada	3	10
Trachypithecus obscurus	10	10

*Data were collected from the National Museum of Natural History, Washington, DC; American Museum of Natural History, New York, NY; Field Museum, Chicago, IL; Royal Museum for Central Africa, Tervuren, Belgium; and the Department of Primatology at the State Collection of Anthropology and Palaeoanatomy, Munich, Germany.

Table 2 Definitions of the 3D landmarks digitized for this study.

Landmark number	Landmark description
Mandibular landmarks	
1	Infradentale
2	Centroid of masseteric scar on mandible
3	Centroid of medial pterygoid scar on medial surface of angle of ascending ramus
4	Coronion
5	Tip of central incisor
6	Center of occlusal surface of mandibular M3
7	Center of occlusal surface of mandibular M3 (contralateral side)
8	Midpoint of line connecting the medial and lateral poles of the mandibular condyle
Cranial landmarks	
9	Prosthion
10	Point on alveolar margin of maxillary fourth premolar
11	Point on alveolar margin of maxillary second molar
12	Midpoint of cranial masseteric scar
13	Deepest and most superior point in the pterygoid fossa
14	Point on the ectocranial surface of the sphenoid at maximum postorbital constriction
15	Midpoint of the crest of the AE
16	Point on the posterior edge of the AE along a line perpendicular to the long axis of the AE
17	Anterior-most point on the articular surface of the cranial component of the TMJ
18	Most inferior point on the postglenoid process

AE, articular eminence; TMJ, temporomandibular joint.

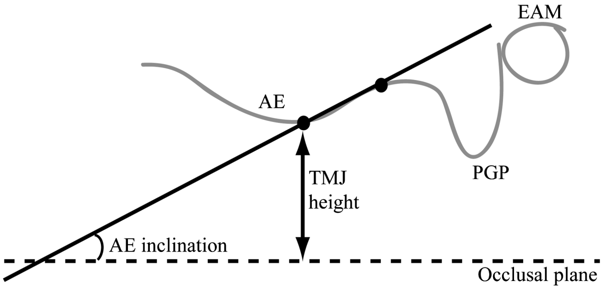

Fig. 2 Schematic illustration of a sagittal section through the articular eminence (AE), showing the methods by which AE inclination and temporomandibular joint (TMJ) height above the occlusal plane were calculated. EAM, external auditory meatus; PGP, postglenoid process. Not to scale.

reasonable approximations of the directionality of the force exerted by each of these masticatory muscles, but should be considered a rough estimate only as the orientation of the muscle force vector is likely variable within and among species. Furthermore, this analysis only incorporates estimates of the orientation of the anterior temporalis and superficial masseter, but not the posterior temporalis, deep masseter or lateral pterygoid muscles, as bony markings of these muscles are poorly defined and often difficult to locate.

Statistical analyses

Correlation analyses were performed to test for associations between AE orientation, muscle resultant orientation and TMJ height. For each of these sets of data, Pearson product-moment correlations (*r*) and *P*-values were calculated using species means, which were separated by sex. Based on the model outlined above, I predicted a positive correlation between TMJ height and AE inclination, but a negative correlation between AE inclination and masticatory muscle inclination (e.g. as the muscle becomes more anteriorly inclined, AE inclination increases). Because it is possible that TMJ height and

Table 3 Definitions of linear measurements used in this analysis.

Measurement	Abbreviation	Definition
AE inclination	AEIncl	Angle between the line connecting points 15 and 16, and the occlusal plane (9–10–11)
TMJ height above the occlusal plane	TMJHt	Perpendicular distance from the center of the mandibular condyle (8) to the occlusal plane of the mandibular dentition (5–6–7)
Masseter muscle orientation	MassAngle	Angle between the line connecting the origin (12) and insertion (2) of the masseter and a line describing the occlusal plane (10–11)
Medial pterygoid muscle orientation	MPAngle	Angle between the line connecting the origin (13) and insertion (3) of the medial pterygoid and a line describing the occlusal plane (10–11)
Temporalis muscle orientation	TempAngle	Angle between the line connecting the origin (14) and insertion (4) of the temporalis and a line describing the occlusal plane (10–11)
Mandibular length	MandLg	Distance from the midpoint of the mandibular condyle (10) to infradentale (1)
Glenoid length	GlenLg	Distance from the tip of the postglenoid process (18) to the anterior-most point on the articular surface of the TMJ (17)

AE, articular eminence; TMJ, temporomandibular joint.

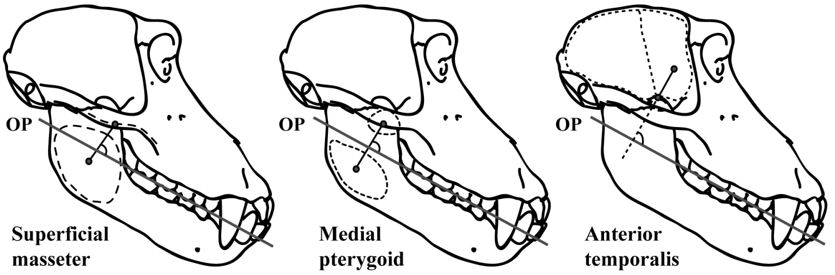

Fig. 3 Lateral views of a *Papio* cranium showing approximate areas of attachment (dashed lines) for the superficial masseter, medial pterygoid and anterior temporalis muscles. Dots indicate the centroids of these muscle attachments. Orientations of each of these muscles were measured as a 2D angle between a line connecting the centroids of the origin and insertion and the occlusal plane (OP).

masticatory muscle orientation are correlated with one another, partial correlations were examined controlling for TMJ height, mandible length (as a proxy for size) and muscle orientation. Furthermore, because previous work by Crompton et al. (2006) found a correlation between TMJ height and anteroposterior glenoid length across mammals with diarthrodial TMJs, I also calculated correlations between TMJ height and AE inclination while holding glenoid length and size constant, as well as between AE inclination and glenoid length while holding TMJ height and size constant.

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

I further hypothesized that taxa exploiting more resistant food items would have relatively more inclined AEs in association with increased height of the TMJ above the occlusal plane and/or increased anterior inclination of the muscle resultant force. Predicted variation in each of these comparative groups was based on documented differences in feeding ecology outlined in Terhune (2010); these expected relationships are summarized in Table 4. Pairwise comparisons of AE inclination, masticatory muscle orientation and TMJ height above the occlusal plane in closely related taxa with documented dietary differences were performed. Differences in these univariate measurements were analyzed using one-tailed Mann–Whitney *U*-tests. Where these tests failed to find significant differences among the taxa, a two-tailed test was subsequently performed to assess whether there were differences in the direction opposite than predicted. Critical alpha was set at 0.05 and was further adjusted for multiple comparisons using the Bonferroni method (Bonferroni, 1936). The Mann–Whitney *U*-tests were calculated using the program IBM SPSS Statistics (Version 19).

Table 4 Predicted variation in AE inclination for each of the comparative groups examined in this analysis.

Comparative group	Predicted variation
Atelines	*Alouatta seniculus* > *Ateles geoffroyi* & *Lagothrix lagothrica*
Cebines	*Cebus apella* > *Cebus capucinus* & *Cebus albifrons*
Macaques	*Macaca fuscata* & *Macaca sylvanus* > *Macaca fascicularis* & *Macaca nemestrina*
Papionins	*Theropithecus gelada* > *Papio anubis* & *Papio cynocephalus*
Hominids	*Gorilla gorilla* & *Pongo pygmaeus* > *Pan troglodytes*

Predicted differences for TMJ height above the occlusal plane will be identical, while predicted differences for muscle orientation will be opposite.

Results

Results of the correlation analyses for the entire dataset found significant relationships between AE inclination and orientation of the temporalis (but only in males), and orientation of the medial pterygoid muscle (in both males and females; Table 5). As predicted, significant correlations between the inclination of the masticatory muscles and the AE were negative, indicating that as the AE becomes more inclined, the medial pterygoid and (to a lesser extent) the temporalis muscles become more anteriorly inclined. The strongest correlations were between AE inclination and TMJ height in both males and females (Fig. 4). In both sexes, this correlation was positive, again as predicted. Results of the partial correlation analysis revealed a

Table 5 Results of the correlation and partial correlation analyses showing the Pearson product-moment correlation (*r*) and *P*-value for the contrast data, separated by sex.

		Females		Males	
	AEIncl vs.	*r*	*P*-value	*r*	*P*-value
Correlations	MassAngle	−0.039	0.798	−0.047	0.768
	MPAngle	**−0.413**	**0.004**	**−0.608**	**< 0.001**
	TempAngle	−0.233	0.115	**−0.427**	**0.005**
	TMJHt⁄ MandLg	**0.847**	**< 0.001**	**0.847**	**< 0.001**
Partial correlations	MassAngle*	0.065	0.674	0.218	0.177
	MPAngle*	0.050	0.745	0.005	0.975
	TempAngle*	−0.352	0.018	−0.125	0.442
	TMJHt**	**0.6290**	**< 0.001**	**0.5550**	**< 0.001**
	TMJHt***	**0.7310**	**< 0.001**	**0.6110**	**< 0.001**
	GlenLg‡	−0.094	0.539	−0.002	0.989

Critical alpha was set at 0.05⁄4 = 0.0125 for the correlation analysis, and 0.05⁄6 = 0.008 for the partial correlation analysis. Significant results are shown in bold.
*Controlling for TMJHt and MandLg.
**Controlling for MandLg, MassAngle, MPAngle and TempAngle°.
***Controlling for MandLg and GlenLg.
‡Controlling for MandLg and TMJHt.
AE, articular eminence; TMJ, temporomandibular joint.

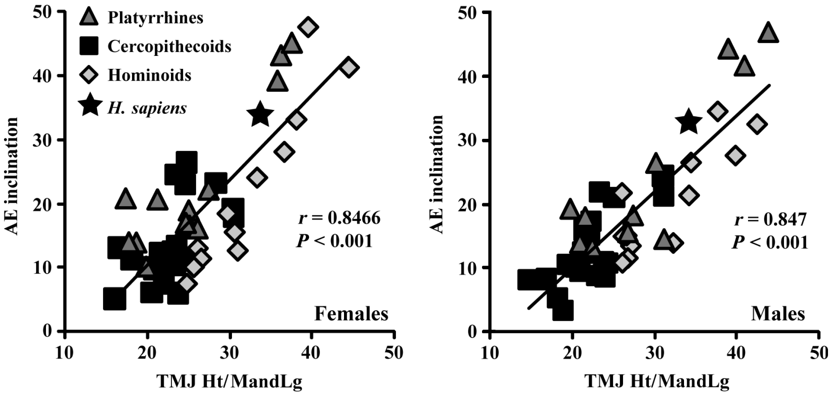

Fig. 4 Bivariate plots and correlations of articular eminence (AE) inclination (*y*-axis) and temporomandibular joint (TMJ) height above the occlusal plane (standardized by mandible length; *x*-axis) for the female and male samples. Note that the *r*- and *P*-values shown are for the data after correction for phylogenetic codependence.

significant correlation between AE inclination and TMJ height above the occlusal plane (when controlling for muscle orientation as well as when controlling for glenoid length), but not between AE inclination and muscle orientation (when controlling for TMJ height). Again, these correlations were positive, as predicted based on the biomechanical model outlined above. No significant correlation was found between AE inclination and glenoid length.

One very interesting result of this analysis was the relative inclination of the AE in humans when compared with other primate taxa (Table 6; Fig. 4). While inclination of the AE relative to the occlusal plane is very high in humans (~33 °), this inclination is matched or exceeded in several other taxa: all three species of *Alouatta* and both species of *Gorilla.* In general, AE inclination is much lower in cercopithecoids (13 °) and the remaining platyrrhine taxa (17 °) and, on average, the great apes have the most inclined AE (26 °).

The pairwise analyses suggest that the AE is most inclined in taxa with relatively more resistant diets, as predicted (Tables 6 and 7). Mean values for AE inclination are larger in taxa with more resistant diets in all of the comparative groups examined, and in both sexes. The Mann–Whitney *U*-tests further support this finding, although not all comparisons were statistically significant after Bonferroni correction. Similarly, TMJ height tends to show the same pattern of variation in the comparative groups examined; mean values are relatively higher in taxa that masticate more resistant foods and the Mann–Whitney *U*-tests found significant differences in TMJ height between taxa in most (but not all) comparisons. However, failure to find significant differences in this variable may be a result of smaller sample sizes for this variable in some groups. No consistent pattern of differences in muscle orientation could be identified in the dataset, and in several cases the opposite of the predicted pattern was observed (Table 7).

Discussion

The model of AE function presented here posits that AE form varies in association with the direction of the JRF and

Table 6 Means and standard deviations of the variables of interest for taxa in each of the comparative groups examined, as well as for humans.

		AE Inclination		TempAngle		MassAngle		MPAngle		TMJ Height/MandLg*100	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Females	*Ateles geoffroyi*	19.03	8.48	67.19	8.52	62.73	4.82	80.31	5.89	24.76	
	Lagothrix lagothrica	22.22	7.44	67.25	10.93	62.18	7.99	78.60	5.47	27.12	1.68
	*Alouatta seniculus**	44.80	5.41	64.14	10.81	60.89	5.53	68.05	3.49	37.04	1.42
	Cebus capucinus	14.13	5.17	78.51	8.13	50.15	3.98	85.97	2.65	17.61	1.92
	Cebus albifrons	14.10	7.83	76.50	6.53	49.50	7.35	90.38	4.64	18.51	3.26
	*Cebus apella**	20.72	5.75	66.10	7.59	56.49	4.84	86.27	6.23	21.03	
	Macaca fascicularis	12.61	7.03	83.71	6.97	55.16	6.59	82.76	5.10	21.33	1.07
	Macaca nemestrina	12.34	8.47	87.55	7.73	63.48	6.22	87.19	3.85	22.54	3.54
	*Macaca sylvanus**	18.19	3.95	61.84	10.82	57.71	5.45	85.42	4.06	30.15	3.57
	*Macaca fuscata**	23.25	10.74	82.10	9.56	63.22	6.94	85.85	5.44	27.99	2.44
	Papio anubis	7.76	7.48	96.14	5.14	75.67	6.90	96.47	4.92	21.73	4.41
	Papio cynocephalus	10.70	9.40	96.34	8.08	72.56	8.45	91.97	5.60	23.15	3.45
	*Theropithecus gelada**	19.38	4.53	100.38	3.88	77.03	3.74	94.57	2.83	30.03	
	Pan troglodytes	12.93	8.28	91.78	7.38	67.77	4.12	82.34	3.12	30.59	4.37
	*Pongo pygmaeus**	28.15	8.47	95.19	6.21	61.44	4.14	80.15	4.63	36.19	3.97
	*Gorilla gorilla**	41.15	6.79	85.29	7.79	59.71	4.11	73.62	5.89	43.95	3.73
	Homo sapiens	33.67	11.00	91.39	5.37	62.40	4.71	83.21	5.02	33.44	5.90
Males	*Ateles geoffroyi*	18.76	6.40	71.64	7.54	62.76	4.77	80.86	6.74		
	Lagothrix lagothrica	26.32	7.84	66.87	9.95	63.39	6.84	77.33	4.42	30.02	3.48
	*Alouatta seniculus**	46.76	5.91	58.13	14.41	65.51	7.16	70.69	5.39	43.80	1.15
	Cebus capucinus	17.86	8.21	73.68	8.63	50.34	6.32	85.75	7.11	21.35	2.55
	Cebus albifrons	13.12	6.07	74.88	8.08	47.70	5.29	86.03	5.39	22.22	2.84
	*Cebus apella**	22.67	4.40	65.16	7.47	55.91	6.61	83.22	4.16		
	Macaca fascicularis	9.33	9.66	92.87	6.33	61.33	5.46	86.88	5.62		
	Macaca nemestrina	3.18	2.93	95.23	4.09	64.48	7.78	89.95	3.62	18.75	3.06
	*Macaca sylvanus**	10.34	5.56	84.39	6.22	63.97	7.27	89.60	3.44		
	*Macaca fuscata**	24.27	8.37	85.38	7.33	60.44	5.54	84.59	6.51	30.88	1.33
	Papio anubis	5.12	2.90	106.00	6.72	77.42	2.84	98.80	3.58	18.05	2.55
	Papio cynocephalus	10.03	6.42	103.94	14.49	73.05	6.33	94.81	7.39	20.25	3.27
	*Theropithecus gelada**	21.06	6.21	95.23	5.55	78.19	2.03	93.82	2.91	30.95	2.59
	Pan troglodytes	13.70	9.83	95.17	7.73	69.46	7.27	84.16	6.68	32.19	3.22
	*Pongo pygmaeus**	27.44	7.97	94.60	6.64	61.05	3.99	78.96	3.82	39.80	4.65
	*Gorilla gorilla**	32.36	11.38	71.23	14.56	58.59	4.30	77.04	7.33	42.45	3.78
	Homo sapiens	32.69	9.51	88.88	6.53	63.91	5.39	83.22	5.10	34.20	7.77

*More resistant object feeders in each group.
**Angles are reported in degrees.
AE, articular eminence; TMJ, temporomandibular joint.

is optimized to resist translatory forces at the TMJ, thereby maximizing normal BFs and minimizing JRFs. This could be accomplished in two non-mutually exclusive ways: first, the AE maintains the same spatial relationships with other components of the masticatory apparatus by covarying with the height of the TMJ above the occlusal plane; and/or

Table 7 Results of the Mann–Whitney *U*-tests for significant differences between taxa in each of the comparative groups.

	Females					Males				
	AEIncl	Temp Angle	Mass Angle	MPAngle	TMJHt⁄ MandLg	AEIncl	Temp Angle	Mass Angle	MPAngle	TMJHt⁄ MandLg
Alouatta seniculus vs. *Ateles geoffroyi*	**< 0.001**	**< 0.001**	0.263	0.243	**< 0.001**	**< 0.001**	**0.006**	0.141	**0.001**	IS
Alouatta seniculus vs. *Lagothrix lagothrica*	**< 0.001**	**< 0.001**	0.234	0.327	**< 0.001**	**< 0.001**	0.054	0.291	**0.004**	0.013**
Cebus apella vs. *Cebus albifrons*	0.022	0.026	**0.003**	0.022	0.072	**0.001**	**0.002**	**0.003***	0.070	IS
Cebus apella vs. *Cebus capucinus*	**0.003**	**0.004**	**0.003**	**0.002***	0.324	0.085	**0.009**	0.044*	0.207	IS
Macaca fuscata vs. *Macaca fascicularis*	**0.004**	**0.004**	0.281	0.014	0.150	**0.002**	0.017	0.330	0.158	IS
Macaca fuscata vs. *Macaca nemestrina*	0.016	0.016	0.086	0.474	0.326	**< 0.001**	**0.005**	0.147	**0.006**	**< 0.001**
Macaca sylvanus vs. *Macaca fascicularis*	**0.005**	**0.005**	**< 0.001**	0.484	0.136	0.223	0.018	0.318	0.187	IS
Macaca sylvanus vs. *Macaca nemestrina*	0.040	0.040	**< 0.001**	0.025	0.272	0.015	**0.001**	0.500	0.330	IS
Theropithecus gelada vs. *Papio anubis*	0.018**	0.018**	0.139**	0.461	0.248**	**< 0.001**	**0.001**	0.300	**0.003**	**< 0.001**
Theropithecus gelada vs. *Papio cynocephalus*	0.073**	0.073**	0.105**	0.364	0.186	**< 0.001**	0.018	0.046*	0.336	**< 0.001**
Gorilla gorilla vs. *Pan troglodytes*	**< 0.001**	**< 0.001**	0.039	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	0.018	**< 0.001**
Pongo pygmaeus vs. *Pan troglodytes*	**< 0.001**	**< 0.001**	0.158	**0.001**	0.225	**0.002**	0.452	0.014	0.067	**0.001**

Critical alpha was set at 0.05⁄5 = 0.01. Significant results are shown in bold (and unless otherwise specified are one-tailed *P*-values).
*Difference is in opposite direction than predicted; *P*-values shown are for two-tailed test.
**Comparisons may be marginally significant due to reduced sample sizes ($n < 3$ for at least one group).
AE, articular eminence; IS, insufficient samples of this variable for analysis; TMJ, temporomandibular joint.

second, the AE covaries with the orientation of the masticatory musculature so as to counteract non-normal forces produced by the muscle resultant force. Furthermore, as TMJ height and muscle orientation have been linked to variation in feeding behavior (Kinzey, 1974; Rosenberger & Kinzey, 1976; Rosenberger & Strier, 1989; Jablonski, 1993; Spencer, 1995; Antón, 1996; Taylor, 2002; Constantino, 2007), a correlate of this model is that taxa utilizing relatively more resistant food objects should have a relatively more inclined AE.

The analyses presented here provide support for this model. Height of the TMJ above the occlusal plane covaries significantly with inclination of the AE, and inclination of the AE was consistently larger on average (often significantly so) in taxa that exploit more resistant foods than in closely related taxa with less resistant diets. This finding suggests that the maintenance of spatial relationships among the various components of the masticatory apparatus, and particularly maintaining the relationship between the inclination of the AE and the reference plane, is important for masticatory function and the maximization of BF. This is particularly true for taxa that have been documented to utilize more resistant diets, in which increased height of the TMJ may assist in increasing attachment area and moment arms of several of the masticatory muscles (Maynard & Savage, 1959; Greaves, 1974; Dubrul, 1977; Freeman, 1988; Spencer, 1995), and⁄or more evenly distribute occlusal loads along the postcanine dentition (Herring & Herring, 1974; Greaves, 1980; Ward & Molnar, 1980; Spencer, 1995). Interestingly, AE inclination was found to be the highest in several taxa (*Alouatta* and *Gorilla*) that have been identified to be relatively highly folivorous in comparison to closely related taxa of the same clade (Gaulin & Gaulin, 1982; Watts, 1984; Williamson et al. 1990; Tutin & Fernandez, 1993; Nishihara, 1995; Julliot, 1996).

While some correlations between masticatory muscle orientation and AE inclination were found (particularly for the inclination of the temporalis and medial pterygoid muscles), partial correlation analysis suggests that these correlations are most likely a function of covariance between muscle orientation and TMJ height. Additionally, few consistent patterns of muscle orientation were found in the comparative samples examined here. Thus, relatively less support was found for the prediction that AE inclination covaries with muscle orientation. This result could suggest two possible interpretations. First, this portion of the model may be invalid, and the observed lack of a correlation between muscle orientation and AE inclination may indicate that orientation of the muscle resultant is not a reliable enough indicator of the direction of the JRF. In other words, variation in the extent to which particular portions of each of the masticatory muscles function during chewing (Vinyard et al. 2008) could result in so much variation in the orientation and position of the muscle resultant force that a straightforward correlation between AE inclination and the orientation of the muscle resultant force is unlikely.

Second, the lack of strong correlations between muscle resultant orientation and AE inclination could be due to problems with the calculation of muscle resultant angulation. In this study, 2D angles between the three muscles of mastication (the medial pterygoid, superficial masseter and anterior temporalis) and the occlusal plane were calculated, and their individual correlations with AE inclination calculated. To some extent, the aforementioned difficulties in accurately calculating the orientation of the force vector of the masticatory muscles based on bony markings could account for the lack of support for this portion of the proposed model. The orientations of the three muscles examined were estimated based on methods developed and used by Spencer (1995). But, as he acknowledges, these estimates are far from perfect in that they make a number of assumptions regarding the mean position of the muscle force vector (based on the centroid of the muscle scar) and for determining the distribution of a muscle over the entire area of its attachment (which is particularly difficult for the temporalis muscle). The magnitude and orientation of the force vector may differ considerably depending upon which muscles are recruited during mastication, as well as which portions of those muscles are recruited; this method therefore estimates only the mean force assuming that all fibers of the muscle (as well as all muscles) are firing equally. This is, however, highly unlikely to occur on a regular basis during mastication of food objects. Furthermore, although there is little documentation in this regard, there are many factors regarding intrinsic muscle architecture that can vary among individuals and among species, including fiber direction and muscle pinnation, location and number of intramuscular tendons, sarcomere length and muscle attachment area (Cachel, 1984; Lovejoy & Ferrini, 1987; Hannam & Wood, 1989; Koolstra et al. 1990; Antón, 1994, 1999, 2000; Taylor & Vinyard, 2004, 2009; Perry, 2008).

Even given these difficulties, the analyses presented here still identified correlations between AE inclination and muscle orientation; this result suggests that, despite the considerations outlined above, the methodology employed here does reflect biological differences in muscle inclination that themselves may be associated with raising the TMJ above the occlusal plane, at least in some species. Thus, the ultimate cause of a more inclined AE may be selection for a TMJ situated high above the occlusal plane, which is advantageous for exploiting (and particularly masticating on the posterior dentition) relatively more resistant food objects (Kinzey, 1974; Rosenberger & Kinzey, 1976; Rosenberger & Strier, 1989; Jablonski, 1993; Spencer, 1995; Antón, 1996; Taylor, 2002; Constantino, 2007). These results are consistent with previous analyses that have linked aspects of feeding behavior to variation in TMJ morphology (Wall, 1995, 1999; Vinyard, 1999; Vinyard et al. 2003; Taylor, 2005; Terhune, 2010). The lack of a correlation between AE inclination and glenoid length when controlling for TMJ height also suggests that perhaps the covariance between glenoid length and TMJ height documented by Crompton et al. (2006) is a function of increased translation of the condyle during wide jaw gapes rather than during the powerstroke (i.e. when the AE is loaded), or that the majority of translation during the powerstroke is taking place on the posterior slope of the AE.

The AE is of course also a load-bearing structure in the TMJ. As a result, some component of the observed variation in AE morphology may be a result of variation in the loads routinely experienced by different taxa at the TMJ. The model outlined here makes no explicit predictions regarding how AE morphology might vary with joint loads in the absence of changes in TMJ height or muscle orientation. However, taxa that utilize more resistant food items likely also experience relatively higher JRFs than closely related taxa that exploit less resistant foods (Hylander, 1979a,b; Smith et al. 1983; Bouvier, 1986a,b). Therefore, I cannot exclude the possibility that these taxa have relatively more inclined AEs because of this increased joint loading (which is likely coupled with TMJs raised farther above the occlusal plane and/or a more anteriorly inclined muscle resultant force).

Biomechanical implications of this model

Whether this model is applicable both during rhythmic chewing (when the condyle is more likely to be on the posterior slope of the AE) and when forces are applied at wide jaw gapes is debatable. During wide jaw gapes, the mandibular condyles (both working- and balancing-sides) translate anteriorly past the peak of the AE onto the preglenoid plane (Wall, 1995, 1999). BFs that are generated at these wide gapes are relatively low, as the sarcomeres making up the masticatory muscles will likely be stretched beyond their resting length (Dechow & Carlson, 1982, 1990; Lindauer et al. 1993; Paphangkorakit & Osborn, 1997). Furthermore, theoretical and experimental data indicate that as the bite point moves more anteriorly, the BF decreases and the JRF increases (Hylander, 1979a; Hylander & Bays, 1979). Thus, activities where the bite point is relatively anteriorly situated (and particularly where large BFs are generated) will result in increased stresses being placed on the TMJ at the same time that the condyle is translated anteriorly. In such an instance, the AE is unable to function as outlined in the model here. Such a loading regime may help explain why the incidence of condylar remodeling and TMJ joint degeneration is particularly high in populations that habitually use their anterior teeth (Merbs, 1983; Richards, 1990), as well as why muscle stretch receptors are most sensitive at wide jaw gapes (i.e. to more carefully modulate BFs in an unstable loading environment; Wang et al. 2007).

In addition to helping minimize joint forces and maximize BFs, orientation of the AE could also be an important influence over movements of the mandible. Recent analyses of the instantaneous center of rotation (ICoR) and finite helical axis of the mandible in humans and non-human primates suggest intriguing differences in mandibular movements during jaw opening that may be linked to AE morphology (Bennett, 1908; Grant, 1973; Gallo et al. 1997, 2000, 2006; Terhune et al. 2011). Analyses of the path of the ICoR during the gape cycle (i.e. a complete circuit of jaw movement from maximum opening to maximal occlusion back to maximum opening; Hiiemae, 1978) suggest that the mandibular condyle first rotates inferiorly and then translates anteriorly in *C. apella*, whereas *Macaca mulatta* displays the opposite pattern of condylar movement (anterior translation followed by inferior rotation of the condyle). Based on data for human ICoR position and thus condylar movements (Bennett, 1908; Grant, 1973; Gallo et al. 1997, 2000), the *Cebus* pattern is considerably more similar to humans than is the macaque pattern of condylar movement. Similarly, inclination of the AE in *Cebus* (~21 °) is more comparable to AE inclination in *H. sapiens* (33 °) than either is to gracile macaques (*M. fascicularis* = 11 °; *M. nemestrina* = 8 °). Thus, AE inclination could be associated with these different kinematic patterns, as could differences in occlusal morphology and/or firing patterns of the masticatory muscles (Terhune et al. 2011). Further data are necessary to fully link these patterns of mandibular movement to differences in bony or soft tissue morphology and behavior.

Although few experimental data regarding the directionality of the BF exist (Hylander, 1978; Dechow & Carlson, 1983; Mao & Osborn, 1994), this model suggests that the orientation of the AE has implications for the direction of the BF. Even assuming that all forces are normal with respect to the reference line and that the JRF is primarily normal with respect to the AE, then as the AE becomes more inclined (as a consequence of increased TMJ height) it is less and less likely that the BF is vertically oriented (Fig. 1b). Thus, with increased height of the TMJ above the occlusal plane, the BF should become more posteriorly directed. This could suggest that these forces are less likely to be crushing forces (i.e. perpendicular to the occlusal surface), and are instead oriented obliquely in relation to the occlusal surface (i.e. shearing forces). Such a configuration may be advantageous for processing certain food items, as has been suggested recently for *Paranthropus* by Rak & Hylander (2008). Alternatively, this model may help explain the variable presence of the curve of Spee in certain primate taxa; this concavity in the occlusal plane could assist in making these posteriorly directed BFs more perpendicular to the occlusal surfaces of the dentition (Osborn, 1993). If this is the case, one would predict a correlation between the height of the TMJ and the presence and/or convexity of the curve of Spee. However, as it is likely that different diets necessitate different amounts of crushing and shearing forces, this relationship may vary across taxa.

Considerable variation in the form of the AE exists in fossil hominin taxa (Weidenreich, 1943; DuBrul, 1974, Dubrul, 1977; Kimbel et al. 1988, 2004; Martinez & Arsuaga, 1997). Geologically older taxa such as *Australopithecus afarensis* tend to have a very primitive TMJ that includes a relatively flat AE (Kimbel et al. 2004; Kimbel & Delezene, 2009). Conversely, the slightly younger robust australopiths (i.e. *Paranthropus*) have been documented to have a very human-like TMJ with a more inclined AE (DuBrul, 1974; Kimbel et al. 2004). This study suggests that at least some of this variation is likely to be a consequence of the increased height of the TMJ above the occlusal plane in *Paranthropus* (Rak & Hylander, 2008). Whether this relationship is valid across hominin taxa will require further evaluation.

Finally, an important result of this analysis is that AE inclination in humans is less unique than we may believe. This is not to say that other aspects of TMJ form in humans are not distinctive, but these data do imply that the function of the AE in humans does not differ from that of other primates. Calculated as it has been here (i.e. in relation to the occlusal plane), AE inclination in humans falls solidly within the range of variation observed in the great apes. As there are clearly substantial dietary differences between humans and the great apes, this similarity may be explained by phylogenetic inertia, but may also be related to the height of the TMJ relative to the shortened and retracted human mandible. For example, with the reorientation of the face in relation to the neurocranium, the reference plane between the TMJ and the bite point (M1 for example) shifts posteriorly, necessitating increased inclination of the AE simply to maintain the same geometric relationships among the components of the masticatory apparatus. Thus, although this biomechanical model applies to humans, there may be additional causal factors (e.g. decreased facial prognathism and reorientation of the occlusal plane in relation to the basicranium) that influence AE inclination in humans.

Concluding remarks

This study sought to test the validity of the preliminary biomechanical model of AE function first proposed by Spencer (1995) and Osborn (1996). The analyses presented here suggest that this model is valid, and that AE morphology most likely varies as a geometric correlate of height of the TMJ above the occlusal plane, which has been linked to more resistant diets. By inclining the AE when the TMJ is situated above the occlusal plane, the AE acts to resist non-normal forces at the TMJ, therefore maximizing forces at the bite point during rhythmic chewing. Resistance to these non-normal forces need not occur only at the TMJ, however. Non-normal forces could also be opposed by occlusal topography, and loading of the joint itself is likely to be mediated by soft tissue structures in the joint, particularly the articular disc. This model consequently serves as a starting point for further evaluation of the biomechanical consequences of increased height of the TMJ above the occlusal plane and the resultant non-normal forces in the masticatory apparatus. Furthermore, these data add to the growing body of literature that link differences in the bony morphology of the masticatory apparatus to variation in either feeding or social display behaviors.

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