SYMPOSIUM

The Instantaneous Center of Rotation of the Mandible in Nonhuman Primates

Claire E. Terhune,[1,*] José Iriarte-Díaz,[†] Andrea B. Taylor[*,‡] and Callum F. Ross[†]

*Department of Community and Family Medicine, Duke University School of Medicine, Durham, NC, USA;
[†]Department of Organismal Biology and Anatomy, University of Chicago, Chicago, IL, USA; [‡]Department of Evolutionary Anthropology, Duke University, Durham, NC, USA

[1]Email: claire.terhune@duke.edu

Synopsis Kinematic analyses of mandibular movement in humans demonstrate that the mandibular instantaneous center of rotation (ICoR) is commonly located near the level of the occlusal plane and varies in its position during a chewing sequence. Few data are available regarding the location of the ICoR in nonhuman primates and it remains unclear how the position of the ICoR varies in association with mastication and/or gape behaviors. ICoR was quantified throughout the gape cycle in five species of nonhuman primates (*Macaca mulatta*, *Cebus apella*, *Chlorocebus aethiops*, *Eulemur fulvus*, and *Varecia variegata*). The ICoR is commonly located below the mandibular condyle close to the occlusal plane and varies considerably both superoinferiorly and anteroposteriorly through the gape cycle. The path of the ICoR, and by inference condylar movement, in *Macaca* and *Chlorocebus* differs from humans whereas movement in *Cebus* resembles that of humans. Similarities between humans and *Cebus* in articular eminence and occlusal morphology may explain these resemblances. Food material properties had little influence on ICoR movement parameters.

Introduction and background

The primate temporomandibular joint (TMJ) is a complex synovial joint with a moveable socket formed by the condylar head of the mandible and the mandibular fossa of the squamous temporal bone (Hylander 2006). During feeding the condyle of primates experiences large amounts of anteroposterior (AP) translation, similar to those seen in many nonprimate omnivores and herbivores (Noble 1973; Aiello and Dean 1990; Wall 1995; Crompton et al. 2006). High degrees of mobility in the TMJ mean high mobility of the mandible during mastication (Crompton et al. 2006; Hylander 2006). In contrast, the TMJ of many carnivores is shaped in such a way as to make the joint more stable; the postglenoid and preglenoid processes are enlarged and wrap around the mandibular condyle, prohibiting mandibular translation (Noble 1973; DuBrul 1974). This increased stability is thought to minimize the risk of TMJ dislocation associated with the use of the

masticatory apparatus in capturing and subduing struggling prey (Maynard Smith and Savage 1959).

Differences in the degree of condylar translation during feeding are associated with differences in the location of the center of rotation (CoR). In carnivores, the CoR is hypothesized to pass through the mandibular condyle and 100% of jaw gape is achieved via condylar rotation. In contrast, in primates, the CoR does not pass through the condyle and, instead, the condyle translates during jaw opening and closing and some amount of jaw gape is achieved through condylar translation (approximately 23% of jaw gape as measured in humans [Ferrario et al. 2005]). Thus, the location of the CoR provides an indirect measure of condylar movements during feeding.

Many authors have attempted to quantify the location of the CoR of the mandible. As early as 1908, Bennett (1908: 92) suggested that both angular rotation and translation occur at the TMJ during

opening and closing of the jaw in humans, the combination of which results in a constantly changing instantaneous CoR (ICoR) that is commonly located "behind and below the condyle." Further analyses have confirmed this finding in humans, rabbits, and pigs (Grant 1973; Weijs et al. 1989; Lindauer et al. 1995; Wall and Hylander 1999; Sun et al. 2002). These data further suggest that there is considerable variation in the position of the ICoR both among and within subjects (Lindauer et al. 1995). Most commonly, the path of the ICoR in humans has been described as lying just posterior and inferior to the mandibular condyle at the start of jaw opening, traveling inferiorly and anteriorly during jaw opening (Bennet 1908; Grant 1973), to lie slightly anterior to the TMJ prior to maximum gape. During jaw closing, the ICoR reverses along this path, coming to lie just posterior and inferior to the condyle prior to minimum gape.

More recently, Gallo et al. (1997, 2000, 2006) calculated the finite helical axis (FHA) of the mandible in humans. This axis summarizes movements of the mandible in three-dimensions (3D) and can therefore be used to evaluate differences in working side versus balancing side condylar movements. Gallo et al. (1997) found that the FHA position shifts considerably during opening and closing of the jaw, and on average is positioned ∼50 mm from the condyle (usually inferior and posterior to the TMJ, often outside of the mandible). Gallo et al.'s data further suggest that mandibular and condylar movements differ on the working and balancing sides, with more movement of the balancing side condyle in association with lateral deviation of the mandible toward the working side. Furthermore, these researchers found that the path of the FHA during jaw closing is more variable than the path during jaw opening and that movements of the FHA are highly variable within and among subjects (Gallo et al. 2000, 2006).

Several investigators have proposed explanations for the functional significance of the location of the ICoR, and more generally why condylar translation occurs at all. Moss (1959) suggested that the location of the ICoR is coincident with the mandibular foramen thereby reducing stretch of the inferior alveolar neurovascular bundle. Later analyses have not refuted this hypothesis, but instead found stronger support for alternative hypotheses (Smith 1985; Weijs et al. 1989). For example, the airway-impingement hypothesis (DuBrul 1964; Smith 1984, 1985) suggests that if the mandible rotated about a CoR running through the condyles then the increased height of the TMJ above the occlusal plane (hereafter referred to simply as TMJ height) would cause the mandible to

impinge on the airway during opening of the jaw. Anterior translation of the condyle during opening avoids this impingement. However, this hypothesis cannot explain why condylar translation occurs in mammals with TMJs at or near the occlusal plane, and there is no convincing evidence in humans that the airway would be obstructed in the absence of translation (Hylander 1992, 2006). Alternatively, Hylander (1978, 2006) and Carlson (1977) proposed that condylar translation minimizes changes in the length of sarcomeres in the masseter and medial pterygoid muscles at wide gapes. By having the CoR positioned below the condyle, the mandibular condyle translates forward and/or down onto the articular eminence (AE), and the masseter and medial pterygoid are stretched less than would be the case if the CoR lay in the condyles. As the force output of muscle fibers is inversely proportional to the amount they are stretched once they are beyond their optimal length on the length tension curve, this decreased stretch during translation allows for increased force output at a wider variety of gapes. Support for this hypothesis was subsequently found in rabbits (Weijs et al. 1989). However, this hypothesis does not explain the presence of condylar translation at low gape angles, when the masseter and medial pterygoid are likely to be at or near the optimal part of their length tension curves (Anapol and Herring 1989). One explanation for condylar translation at low gape angles is Crompton et al.'s (2006) proposal that, in animals with the condyle positioned above the occlusal plane, condylar translation maximizes simultaneous occlusal contact during jaw closing by allowing the lower teeth to move vertically into occlusion.

It is notable from this review of previous calculations of the ICoR and FHA that few published data regarding either of these variables exist for nonhuman primates. It is therefore unclear how mandibular and condylar movements compare across primates. However, kinematic and behavioral data suggest that chew cycle and sequence duration, chewing frequency, volume of food processed, and daily feeding time (among other variables) vary considerably across primates, mammals, and vertebrates (e.g., Hiiemae 1978; Herrel et al. 1996; Buschang et al. 2000; Throckmorton et al. 2001; Wainwright, 2006; Ross et al. 2009a, 2009b, 2010; Reed and Ross 2010). Some of this variation may be related to food material properties (FMPs) and/or body size of the organism in question (Anderson et al. 2002; Meyers et al. 2002; Bhatka et al. 2004; Wall et al. 2006; Wintergerst et al. 2008; Ross et al. 2009b). In turn, these kinematic differences have important implications for variation in feeding behavior and a major

goal of every living organism: meeting their metabolic needs (e.g. Ross et al. 2009b).

A major goal of this study, therefore, is to present some of the first data for ICoR position in nonhuman primates. Building on previous work (Grant 1973; Hylander et al. 1987; Weijs et al. 1989; Wall 1995; Vinyard 1999; Sun et al. 2002), we predicted that the ICoR would be located well inferior to the mandibular condyle, and its position would vary throughout opening and closing of the jaw. We further hypothesized that, as was found by Lindauer et al. (1995) and Gallo et al. (1997, 2000, 2006), a large portion of variation in ICoR position would be among gape cycles within a particular chewing sequence. While the location of the ICoR doubtlessly has functional significance, we hypothesize that it is not a kinematic variable that animals or humans actively control. Rather, active control is more likely exerted over variables such as position, velocity, and acceleration of specific points (i.e., the occlusal surfaces of the teeth); the magnitude and orientation of joint reaction, bite, and muscle forces; and the length, and rate of change in length of chewing muscles. Passive control is exerted by the stiffness of the jaw muscles (Ostry and Munhall 1994) and bony morphology of the temporomandibular joint (Wall 1995; Vinyard 1999). The location of the ICoR is of interest to the extent that it reflects or summarizes control over these kinematic or kinetic variables. By summarizing masticatory movements in this way, we can then begin to generate hypotheses for how and why jaw kinematics vary across primates, mammals, and vertebrates.

Materials and methods

Subjects

We quantifed ICoR throughout the gape cycle in five species of nonhuman primates: *Chlorocebus aethiops*, *Macaca mulatta*, *Cebus apella*, *Eulemur fulvus*, and *Varecia variegata* (Table 1). Animals were housed

and studied at Stony Brook University and University of Chicago in accordance with relevant Federal regulations and approved IACUC protocols.

Data collection

Data for *Chlorocebus*, *Eulemur*, and *Varecia* were collected using digital videofluoroscopic methods described by Ross et al. (2010). Briefly, radio-opaque markers were fixed to the mandibles and teeth and lateral view videofluoroscopy was used to track their movements during chewing. Marker positions were digitized using MiDAS motion analysis software (Xcitex, Boston MA, USA). Data for *Macaca* and *Cebus* were collected using 3D motion-capture methods described by Reed and Ross (2010). Reflective markers were coupled to the mandible and cranium using bone screws, their positions relative to the teeth measured with a 3D digitizer (Immersion, Microscribe G2), and their movements measured in 3D using 6-camera and 10-camera Vicon systems. The 3D movements of the mandible were calculated in the local coordinate system of the cranium using methods described in Iriarte-Díaz et al. (2011). Briefly, the position of the cranial markers at minimum gape was defined as the reference position and the displacement of the mandibular markers was calculated with respect to the fixed-cranium coordinate system. The XY plane of the cranial coordinate system corresponds to the sagittal plane of the cranium, so that the X- and Y-coordinates correspond to a lateral view of the marker's displacement. These data represent what would be obtained in an exactly lateral X-ray video and are therefore comparable to the data for *Chlorocebus*, *Eulemur*, and *Varecia*. Finally, the XY data were centered at the TMJ by matching the position of the teeth from the 3D digitizer with the position of the teeth from 3D models for *Cebus* and X-rays for *Macaca*.

Preliminary calculations of ICoR position demonstrated considerable variance, some of which is attributable to sources of error: (1) errors in

Table 1 Data set used in this study

Species	Experiments/individuals[a]	Sequences	Cycles	Food items
Chlorocebus aethiops	2 (1 male, 1 female)	9	80	Apple, almond, prune, grape
Eulemur fulvus	1 (female)	3	24	Apple, raisin
Varecia varecia[b]	1 (male)	3	14	Apple, raisin
Macaca mulatta	2 (females)	15	419	Potato, kiwi, almond, zucchini, yam, apple, blueberry, carrot
Cebus apella	1 (male)	8	149	Hazelnut, almond, grape, apple, walnut

[a]Each experiment involved a separate individual; therefore, in this instance individual and experiment are synonymous. All individuals were adults.
[b]No data on timing of the gape phase were available for *Varecia*; these data were only included in the qualitative analyses.

measurement of markers' locations during data collection (e.g., error inherent in the Vicon and cineradiographic equipment); (2) digitizing error (e.g., how reliably are landmarks identified during digitization); (3) rotation of the sagittal planes of the animals away from a position parallel to the image-intensifier screen (Wall 1995); and (4) instability of the ICoR at low angular velocities (Gallo et al. 1997). Error in data collection cannot be eliminated: for the 3D capture of motion, markers' positions were precise to ~40 μm (Reed and Ross 2010), and for the 2D videofluoroscopic data precision was ~200 μm. Errors arising from the collection and digitizing of data were reduced by filtering the data prior to analysis (low-pass Butterworth filters with cutoff frequencies of 11 and 15 Hz for the 2D and 3D data, respectively). To minimize effects of out-of-plane rotation in the 2D data, we eliminated all frames in which the head was rotated greater than $15°$ out of plane (Miller and Petak 1973). Error due to low angular velocity was minimized by calculating ICoR across large windows in time (a minimum of every 20 ms [e.g., 5 frames at 250 frames/s]), and by excluding from analysis data in which angular velocities of the mandible were $<75°/s$ (Gallo et al. 1997, 2000, 2006). We also defined an envelope of interest for our analyses at ~100 mm from the TMJ in all directions; this envelope encompasses the skull and mandible as well as the upper cervical vertebrae, and is what we consider to be the biologically relevant region for analysis of this kinematic variable.

Data analysis

The position of the ICoR was calculated in IGOR Pro 4.0 (WaveMetrics, Inc.) from the Cartesian coordinates of the maxillary and mandibular markers using the method of Bennett (1908) and Weijs et al. (1989). All data were transformed into a coordinate system centered at the top of the mandibular condyle at rest, with the occlusal plane parallel to the X-axis and the rostrum of each animal oriented to the left (Fig. 1). Gape angle, angular velocity of the mandible, and out-of-plane rotation angle (for the 2D data only) were calculated to define gape cycles and minimize error. Plots of the mandibular markers and ICoR coordinates during each chewing sequence were visually inspected; then the average position of the ICoR during the four phases of the gape cycle [fast close (FC), slow close (SC), slow open (SO), and fast open (FO) (Hiiemae 1978)] was calculated. Plots of these averaged coordinates were used to qualitatively describe the path of
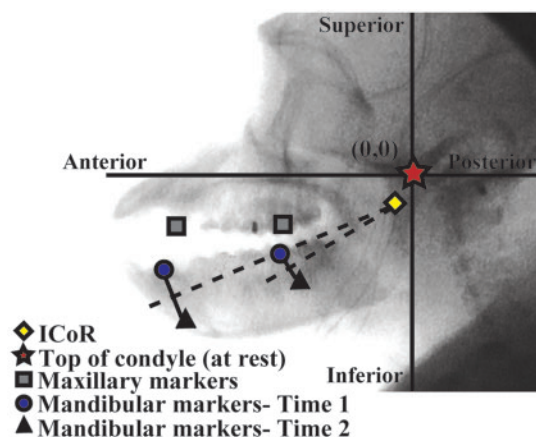

Fig. 1 Method of calculation for ICoR used in this study. ICoR was calculated as the intersection of the lines perpendicular to the vectors between each mandibular marker in two successive frames.

the ICoR during the phases of the gape cycle. These observations were then quantified by calculating the number of times the ICoR shifted anteriorly/posteriorly and superiorly/inferiorly from one phase to another (e.g., the percentage of cycles in which the average vertical position of SC is lower than in FC).

To identify sources of variance in ICoR, variance in phase-averaged ICoR positions was analyzed using a series of random effects (Model II) hierarchical ANOVAs (Vinyard et al. 2008). Five hierarchical categories were used: suborder, species, experiment/individual, chewing sequence, and chewing cycle/error (Table 1). Note that error is contained within the between-cycle variance. Each of these experimental factors was nested within another, such that the lowest level, chewing cycle/error, was nested in all other levels. This ANOVA design is unbalanced for a number of reasons (e.g., unequal numbers of experiments, sequences, and cycles), preventing exact tests of significance (Sokal and Rohlf 1995; Searle et al. 2006). Thus, here we examine overall patterns of variance attributed to different experimental factors (Vinyard et al. 2008).

Separate ANOVAs were performed for the X (AP) and Y [superoinferior (SI)] coordinates of ICoR during each of the phases of the gape cycle (xFC, xSC, xSO, xFO, yFC, ySC, ySO, and yFO). The effects of FMPs on ICoR position were assessed by performing these ANOVAs for all food items, and also separately for more resistant (which included carrot, potato, almond, yam, and hazelnut) and less resistant (which included apple, raisin, prune, grape, kiwi, zucchini, and blueberry) food items. (Not all animals were willing to eat all food items, resulting in an unbalanced distribution of these food items

across experiments and species. Specifically, strepsirrhines were unwilling to eat more resistant foods. Thus, we ran separate hierarchical ANOVAs for more and less resistant foods, thereby eliminating the suborder level from these analyses.) Attribution of food items to these two categories was based on FMPs calculated by Williams et al. (2005) (although FMPs for all of these food items are not yet documented). All of the nested ANOVAs were performed in the program StatGraphics (version 16.1, Statpoint Technologies, Inc.).

Results

As predicted, the ICoR in our primate sample was distributed inferior to the TMJ, close to the level of the occlusal plane. In few instances was the ICoR positioned at the TMJ, suggesting that the condyle translates AP during the gape cycle in all species studied. There was considerable variation in the AP and SI positions of the ICoR among gape cycles and chewing sequences, although to different extents in different species. In both of the macaque experiments, the X- and Y-coordinates of the ICoR were strongly linearly correlated, such that ICoR position was oriented along an oblique axis just below the TMJ and crossing the occlusal plane (Fig. 2) (this correlation was also present in the other species examined, but to a lesser degree). In both of the macaque experiments, there is considerable AP and SI variance in ICoR position. In contrast, the position of the ICoR in *Cebus* was more constrained, lying mostly within a ~15–20 mm region just inferior to the TMJ (and above the occlusal plane) (Fig. 2). Further differences in the position of the ICoR are apparent in *Chlorocebus*, *Eulemur*, and *Varecia*. In *Chlorocebus*, as in macaques, the ICoR is arrayed along the occlusal plane just inferior to the TMJ; however, ICoR position in *Chlorocebus* tends to be more anterior than in macaques. Similarly, the ICoR is also more anteriorly positioned in *Eulemur* and *Varecia* than in *Chlorocebus*. Furthermore, ICoR position in the strepsirrhines (and especially *Eulemur*) is superoinferiorly constrained, with most of the variation in ICoR position occurring in the AP direction.

The path of the ICoR during opening and closing of the jaw also varies among taxa. In *Macaca* and *Chlorocebus* (Table 2) the ICoR moves anteriorly (~56% of the cycles) and superiorly (70% of the cycles) from FC to SC. Between SC and SO the ICoR moves anteriorly in 61% of the cycles, and in all but one experiment (*Chlorocebus* 2) the ICoR

consistently (80% of cycles) moves inferiorly. During jaw opening the pattern of ICoR movement in *Macaca* and *Chlorocebus* is more consistent than during jaw closing (Gallo et al. 2000): from SO to FO the ICoR position moves posteriorly (~77% of cycles) and superiorly (81% of cycles). Thus, in *Macaca* and *Chlorocebus* the ICoR moves superiorly during jaw closing, shifts inferiorly and sometimes anteriorly from SC to SO, then moves posteriorly and superiorly from SO to FO (Fig. 3).

The pattern of movement of the ICoR in *Cebus* and *Eulemur* differs considerably from the pattern described for *Macaca* and *Chlorocebus*. In *Cebus*, the pattern is opposite of that found in *Macaca* and *Chlorocebus*, with ICoR position in SC rarely being anterior to the ICoR during FC (e.g., only in 24% of cycles). As the gape cycle shifts from SC to SO, the ICoR shifts further anteriorly and inferiorly (78 and 82% of cycles, respectively). From SO to FO the ICoR moves anteriorly in only 53% of the cycles but consistently superiorly (83% of cycles). This results in the ICoR most commonly moving posteriorly and superiorly during jaw closing, shifting anteriorly and inferiorly from SC to SO, and then moving further superiorly during jaw opening (Fig. 3). In contrast, in *Eulemur* the ICoR moves superiorly during jaw closing (90% of cycles), shifts inferiorly from SC to SO (80% of cycles), and then inferiorly and anteriorly (70% and 85% of cycles, respectively) during jaw opening (Table 3).

Hierarchical ANOVA across all food items (Fig. 4) reveals more variance in AP position than in SI position of the ICoR at the cycle level. The AP position of the ICoR during FO (xFO) is the only variable showing any variance at the level of suborder or species, which is consistent with the marked difference in ICoR movement during jaw opening for *Eulemur* and *Cebus* described above. In contrast, the SI position of the ICoR shows more variance at the experiment level suggesting relatively strong differences in ICoR position among individuals of the same species. While all portions of the gape cycle show some variance at the suborder and/or species level, the SI position of the ICoR during SO shows considerably more variance at each of these levels.

ANOVA reveals that FMPs have little effect on the distribution of variance (Fig. 4). With more resistant foods, relatively more variance in AP position is concentrated at the cycle level, and there is more variance at the sequence level in the AP position of ICoR during FC. In contrast, with less resistant foods a larger percentage of variance occurs at the species level.
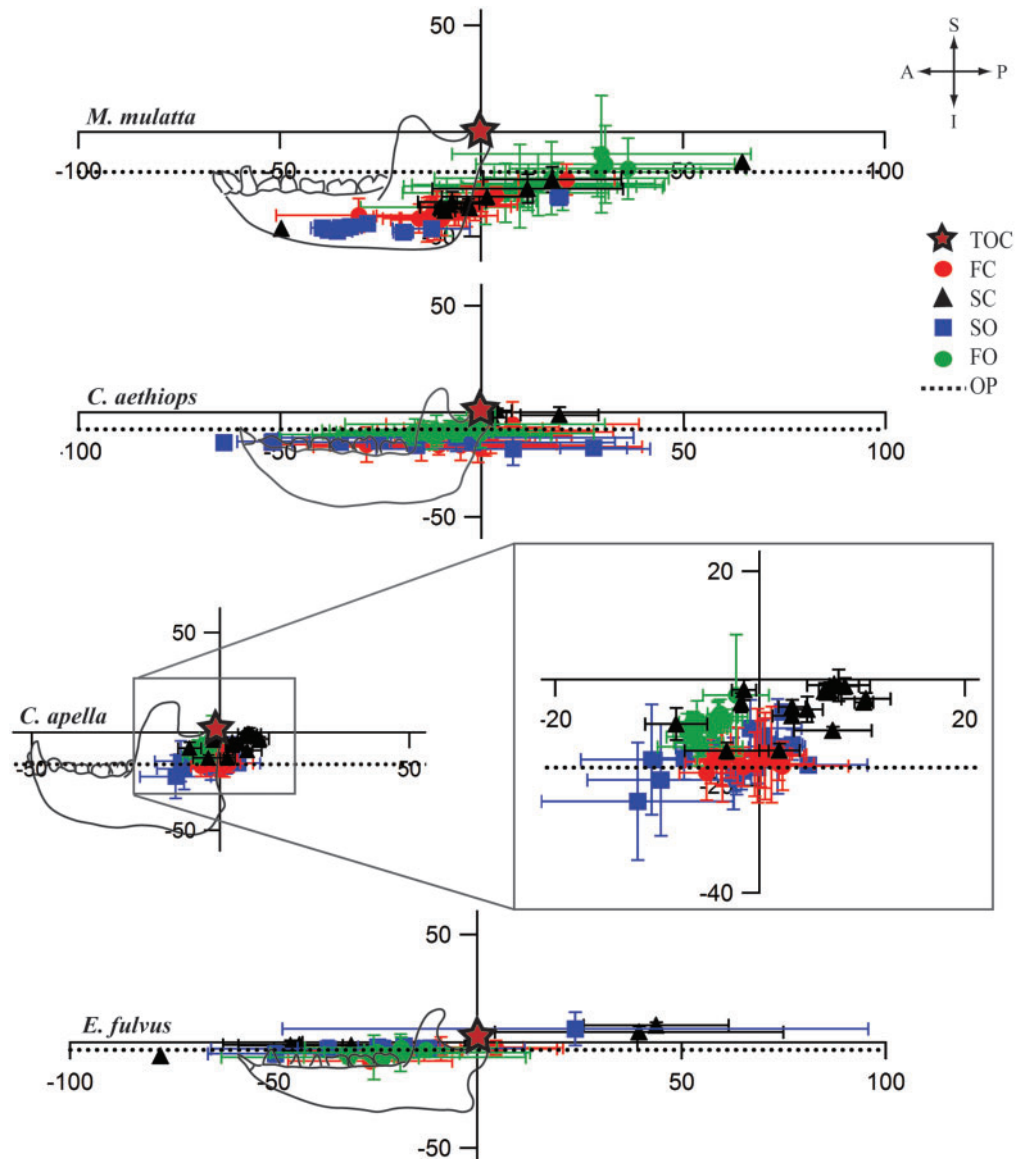
Fig. 2 Illustration of ICoR position throughout a single chewing sequence for *Macaca* (upper left), *Chlorocebus* (upper right), *Cebus* (lower left), and *Eulemur* (lower right). Values presented are the average ICoR coordinate for each phase of the gape cycle. Symbols represent the position of the top of the condyle (TOC = star), the phases of the gape cycle (fast close[FC] = red circle, slow close[SC] = triangle, slow open[SO] = square, fast open[FO] = green circle), and the occlusal plane (OP = dotted line). Error bars represent ±1 SD. A = anterior, S = superior, P = posterior, I = inferior. Scale is in millimeters (mm).

Table 2 Results of the sign test of the consistency of ICoR movement from FC to SC, SC to SO and SO to FO[a]

	xFC>xSC	yFC>ySC	xSC>xSO	ySC>ySO	xSO<xFO	ySO<yFO
Macaca 1	70	53	80	87	90	94
Macaca 2	50	22	50	86	80	93
Chlorocebus 1	50	21	45	82	54	85
Chlorocebus 2	55	23	67	44	85	54
Macaca/ Chlorocebus Average	56	30	61	75	77	81
Cebus	24	21	78	82	47	83
Eulemur	50	10	50	80	31	15
Entire sample	50	32	55	65	75	88

[a]X- and Y-coordinates were tested separately. Values presented are percentage of cycles in which the greater than statement in the column header is true. Greater than symbol (>) indicates anterior (X-coordinate) or inferior (Y-coordinate) movement between phases, less than symbol (<) indicates posterior (X-coordinate) or superior (Y-coordinate) movement between phases.
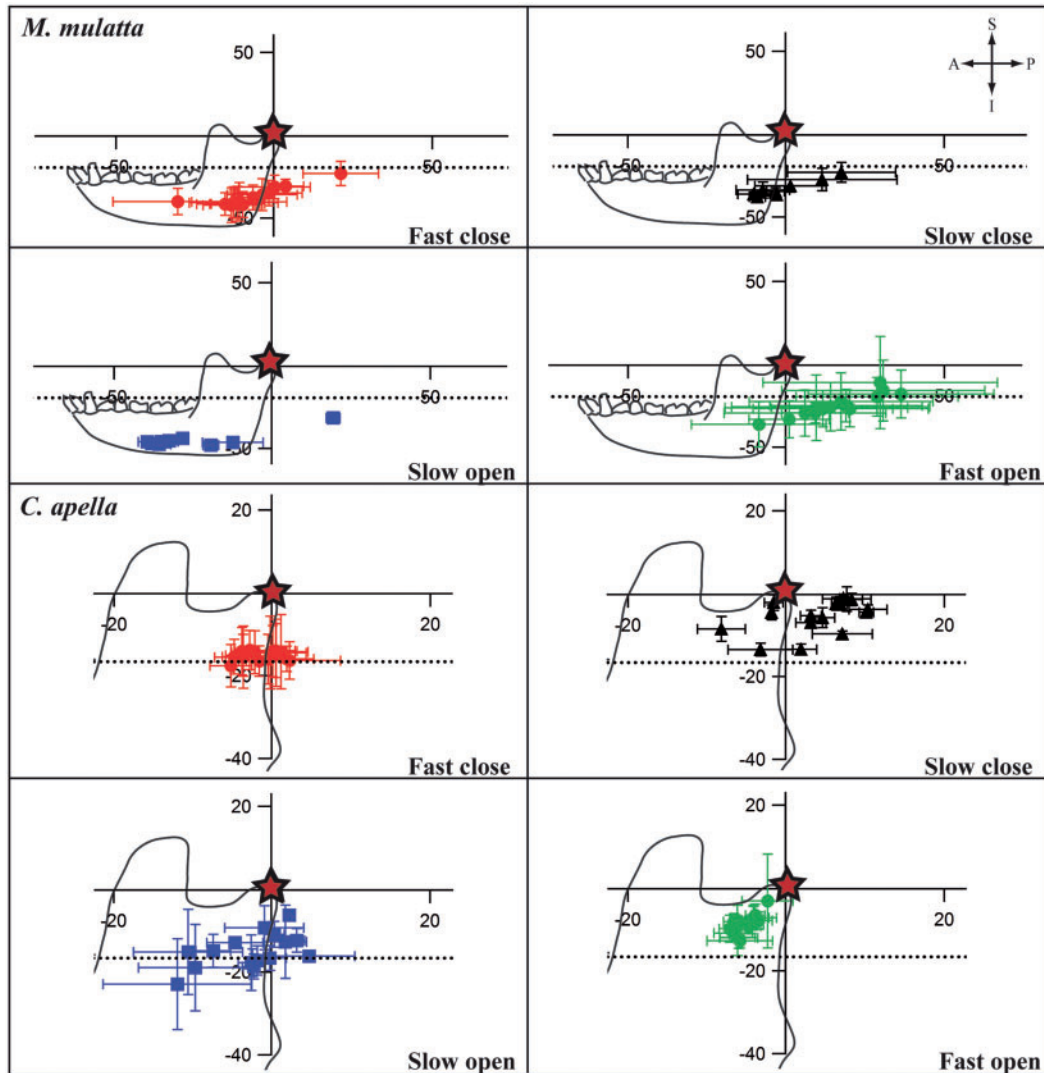
Fig. 3 Plots of ICoR position during each phase of the gape cycle for *Macaca* (above) and *Cebus* (below). Scale is in millimeters (mm). Note differences in scale between *Cebus* and *Macaca* plots. Symbols are as in Fig. 2.

Discussion

Previous analyses of the ICoR in humans, rabbits, and pigs have found the ICoR to lie well inferior to the TMJ, approximately at the level of the tooth row (Bennett 1908; Grant 1973; Weijs et al. 1989; Sun et al. 2002; Gallo et al. 1997, 2000, 2006). This ICoR position is consistent with the observation that these taxa exhibit relatively large degrees of condylar translation, since an ICoR situated close to the mandibular condyle would be indicative of increased rotation (rather than translation) of the condyle (i.e. less translation per unit of rotation). Less consideration has been given to the AP placement of the ICoR, but this position is important for identifying exactly how the condyle moves during opening and closing of the jaw. If the ICoR lies in front of the condyle during opening, the condyle must be moving

superiorly. Conversely, if the ICoR is located posterior to the condyle during opening, the condyle must be moving inferiorly. The reverse is true during closing. Thus, AP and SI variation in the position of the ICoR will be indicative of both AP and SI movements of the condyle. For example, an ICoR situated inferior and posterior to the TMJ during opening will be associated with inferior and anterior movement of the condyle.

Patterns of condylar movement in humans and nonhuman primates

The ICoR in humans is located posterior and inferior to the mandibular condyle at the beginning of jaw opening, then shifts anteriorly and inferiorly during opening to lie in the region of the intersection of the occlusal plane and the ascending ramus of the

Table 3 Summary of ICoR movements during jaw closing, occlusion, and jaw opening for *Macaca* and *Chlorocebus*, *Cebus*, and *Eulemur*

	Jaw closing (FC to SC)	Occlusion (SC to SO)	Jaw opening (SO to FO)
Macaca/ Chlorocebus[a]	ICoR can move anteriorly or posteriorly, but usually moves superiorly (70%)	ICoR moves anteriorly (61%) and inferiorly (75%)	ICoR moves posteriorly (77%) and superiorly (81%)
Cebus	ICoR moves posteriorly (75%) and superiorly (79%)	ICoR moves anteriorly (78%) and inferiorly (82%)	ICoR can move anteriorly or posteriorly, but consistently moves superiorly (83%)
Eulemur	ICoR can move anteriorly or posteriorly, but consistently moves superiorly (90%)	ICoR can move anteriorly or posteriorly, but consistently moves inferiorly (80%)	ICoR moves anteriorly (69%) and inferiorly (85%)

[a]Values for *Macaca/Chlorocebus* represent the average for all four experiments.
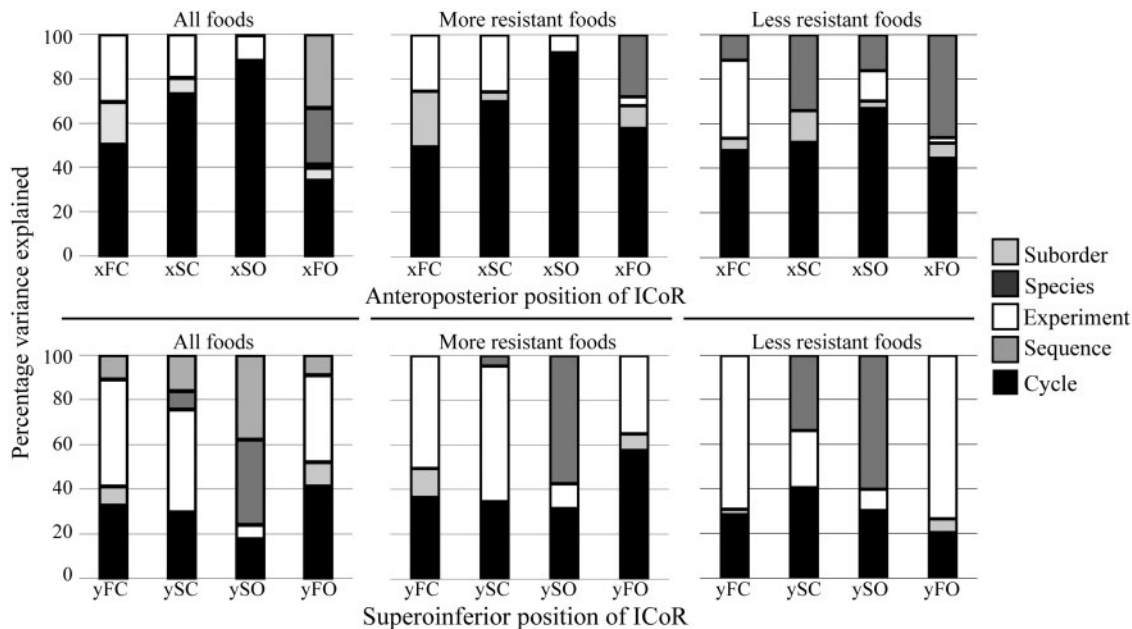

Fig. 4 Bar charts showing the percentage variance attributed to each of the experimental levels in the ANOVAs performed for data from all food types (left), only more resistant foods (middle), and less resistant foods (right). Note that the ANOVAs broken down by food resistance do not include a suborder level due to a lack of data for more resistant foods for *Eulemur* and *Varecia*. Anteroposterior movement of the ICoR is shown on the top (X-coordinate) and SI movement of the ICoR is shown on the bottom (Y-coordinate).

mandible prior to maximum gape (Bennett 1908; Grant 1973; Lindauer et al. 1995; Gallo et al. 1997, 2000). This path of ICoR movement indicates that the human condyle first moves inferiorly and then anteriorly during jaw opening.

The data presented here suggest that the pattern of condylar movements varies across primates (Fig. 5). In *Macaca* and *Chlorocebus*, the condyle first moves anteriorly and then inferiorly during jaw opening. In contrast, *C. apella* shows a more human-like pattern of condylar movement during jaw opening. This pattern is characterized by initial inferior and anterior displacement of the condyle, followed by slight anterior movement of the condyle as the ICoR approaches the mandibular condyle (Fig. 5).

The estimated position of the ICoR in *Eulemur* is difficult to explain, since its relatively anterior and superior position suggests movement of the condyle superiorly into the mandibular fossa (Fig. 5), a movement that is biologically implausible (Wall and Hylander 1999). We can note that comparison of the velocity of the X- and Y- coordinates of the ICoR across all taxa indicates that the rate of change in the X-coordinate is extremely high in *Eulemur* (e.g., the ratio of change in the X versus Y ICoR coordinate for *Eulemur* is approximately 8 times that of *Chlorocebus* and *Varecia* and approximately 18 times the values for *Macaca* and *Cebus*). Thus, the ICoR only resides at the calculated ICoR position for a fraction of a second; as a result, condylar movements at these points in the gape cycle are likely to
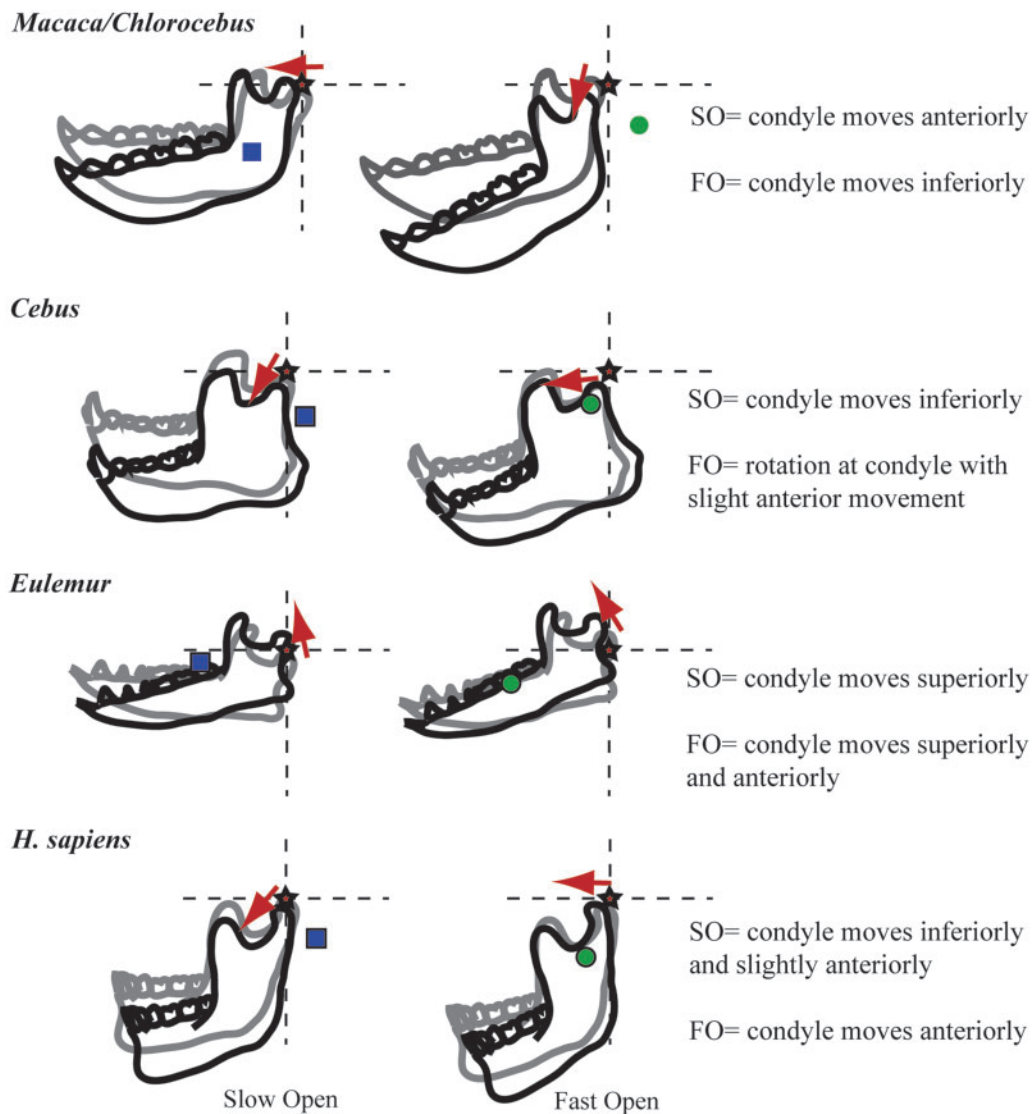
Fig. 5 Simulated mandibular movements during jaw opening for the nonhuman primate taxa included in this analysis as well as for humans [based on previous research by Bennett (1908), Grant (1973) and Gallo et al. (1997, 2000)]. Illustrations on the left show movement from the beginning of SO (gray mandibular outline) to the end of SO (black mandibular outline) based on the position of the ICoR as illustrated (squares). Illustrations on the right show movement from the beginning of FO (gray mandibular outline) to the end of FO (black mandibular outline) based on the position of the ICoR as illustrated (circles). Arrows indicate the approximate direction of condylar movements. A star indicates the origin of the coordinate system at the top of the condyle during maximum occlusion. Not to scale.

be very small. Additional data for *Eulemur* and other strepsirrhines are necessary to fully evaluate this pattern of movement.

We hypothesize at least four plausible explanations for why we observe these differences in ICoR path and, by inference, condylar movements: AE morphology and height of the TMJ above the occlusal plane, occlusal morphology, and muscle firing patterns; these are not mutually exclusive. Inclination of the AE probably constrains condylar movements during opening and closing of the jaw. In humans,

the AE is markedly more inferiorly inclined (i.e., the face of the AE is directed posteriorly) than in many other primate species (Terhune, 2010). As a result, this strong inclination could act to limit the extent to which the condyle can move anteriorly, at least until the condyle has moved out of the mandibular fossa. The AE of *Macaca* and *Chlorocebus*, in contrast, is relatively flat, and would therefore be less likely to constrain anterior condylar movements.

The position of the ICoR and inclination of the AE are also related to height of the TMJ above the

occlusal plane (Wall 1995, 1999; Terhune 2010). With increased height of the TMJ, AP movements of the condyle (or bony measures of translation potential) increase (Wall 1995, 1999; Crompton et al. 2006). By inference, these data imply that increased height of the TMJ results in an ICoR positioned further away from the TMJ. Our observations of an ICoR generally situated at, or near, the level of the occlusal plane support this inference. Furthermore, height of the TMJ may be linked to inclination of the AE, such that as the TMJ becomes more superiorly positioned the AE becomes more inclined, thereby maintaining the same spatial relationships among the components of the masticatory apparatus and/or resisting nonnormal forces at the TMJ (Spencer 1995; Osborn 1996; Terhune 2010).

Although the AE of *C. apella* is not as strongly inclined as in humans, it is relatively more inclined compared to some other primates (including *M. fascicularis*) (Terhune 2010), and the TMJ in *C. apella* is raised well above the occlusal plane. These morphological similarities between *C. apella* and humans could partially account for the observed similarity in their condylar movements. Likewise, occlusal morphology in *Cebus* and *Homo* is similar in that both taxa have relatively bunodont teeth that appear adapted to distributing bite forces over a larger occlusal area (Rosenberger and Kinzey 1976; Anapol and Lee 1994; Swindler 2002; Lucas 2004; Hillson 2005). The teeth of *Macaca*, *Chlorocebus*, and *Eulemur*, in contrast, are higher cusped (Kay 1975; Hillson 2005). Thus, it is also possible that variation in occlusal morphology is driving these observed differences in ICoR position and corresponding condylar movements, particularly during the SO phase of the gape cycle when the teeth are coming out of occlusion.

Lastly, electromyographic studies of masticatory muscle activity in primates have demonstrated different patterns of firing in strepsirrhines and haplorhines (Hylander et al. 1992, 2002, 2000, 2005; Vinyard et al. 2007). Muscle firing patterns directly influence mandibular movements and therefore could also be related to the observed differences in ICoR position between these suborders.

Future analyses of the FHA in *Macaca* and *Cebus* will allow us to further evaluate links between 3D mandibular movements, occlusal morphology, and inclination of the AE. If occlusal morphology and TMJ height are important determinants of ICoR location, *Homo* and *Cebus* should resemble each other most closely, especially during SC. If the morphology of the AE is important, then *Macaca* and *Cebus* should be most similar, or *Cebus* should be

intermediate to *Macaca* and *Homo*. Finally, if *Macaca* and *Homo* share some phylogenetically related aspect of feeding system function relevant to ICoR location, they will most closely resemble each other. This work is in progress.

Variance components and FMPs

The results of the hierarchical ANOVA are consistent with the differences in the path of the ICoR as described above. In particular, the partitioning of variance across the hierarchical levels suggests important differences in ICoR movement at the suborder, which are consistent with the unique pattern of movement observed for *Eulemur*. This analysis is also consistent with findings from previous analyses of the ICoR and EMG activity in the masticatory muscles. Lindauer et al. (1995) and Gallo et al. (1997, 2000, 2006) observed high levels of variance among and within subjects in the position of the ICoR and FHA, respectively. Our results are similar, although they do further indicate that the AP position of the ICoR is more variable than is the SI position. Similarly, data presented by Vinyard et al. (2008) found high levels of between-cycle variance in EMG activity and timing across primates. These results could reflect changes in FMPs between chewing cycles, as well as changes in the location of the bite point or in muscle firing patterns.

Food material properties have been shown to influence mandibular movements (Byrd et al. 1978; Anderson et al. 2002; Komiyama et al. 2003; Wall et al. 2006; Reed and Ross 2010; Iriarte Díaz et al. 2011), and by proxy, the position of the ICoR. However, we did not observe a large influence of FMPs. For example, if FMPs contributed significantly to variance in ICoR position, we should have observed an increase in the percent of variance attributed to the chewing-sequence level of the analysis, since each sequence represents a different food item. The only portion of the gape cycle for which this holds is FC (and particularly the AP position of ICoR during FC). This may reflect initial differences in the size of food objects and/or the material properties of food.

The ANOVAs performed for more resistant versus less resistant foods also found few differences in how variance was partitioned across taxa. This finding is consistent with Vinyard et al.'s (2008) analysis of variance in EMG patterns. However, the increased variance in AP position of the ICoR at the cycle level in the ANOVAs for more resistant foods could be indicative of stronger changes in FMPs during a chewing sequence (Reed and Ross 2010).

Conversely, the increased variance observed at the species level for AP position of the ICoR could reflect a released constraint on mandibular movements during the mastication of less resistant foods (e.g., with weaker foods, species are free to vary more in how they go about masticating those foods).

Conclusions

The data presented here represent the first quantification of the ICoR in nonhuman primates and suggest intriguing differences in patterns of mandibular movements across primates and between nonhuman primates and humans. These results imply that these differences in movement may bring the mandible into occlusion during the power stroke in subtly different, but perhaps meaningful, ways. One drawback of the technique employed here is that we have no ability to discern mediolateral movements of the mandible during masticatory behaviors. It is, therefore, unclear exactly how the teeth are coming into occlusion in these taxa and what the magnitude of the transverse movement of the powerstroke may be. We are currently quantifying mandibular movements in two of these taxa using methods similar to those employed by Gallo et al. (1997, 2000, 2006) on humans, enabling us to quantify differences in 3D movement and the extent to which they are linked to bony morphology or to firing patterns in the jaw muscles.

The fact that the ICoR is not static during chewing in primates, but moves throughout the gape cycle, including during opening, calls into question Moss' (1959) hypothesis that the location of the ICoR is coincident with the mandibular foramen and thereby reduces stretch of the inferior alveolar neurovascular bundle during opening of the jaw. Clearly a mobile ICoR during opening cannot prevent stretch of the neurovascular bundle in the way proposed by Moss. Additionally, if the sarcomere-length hypothesis is valid, we would predict an ICoR situated more inferiorly (e.g., below the occlusal plane) during wide gapes, particularly in taxa that have been hypothesized to generate relatively large muscle forces and bite forces at wide gapes, as is the case for *C. apella* (Taylor and Vinyard 2009). Thus, additional evaluation of this hypothesis in light of these results may be warranted.

Acknowledgments

Thanks to Susan Williams, Chris Wall, Rebecca German, and Chris Vinyard for inviting the authors to participate in the symposium, "Synthesis of Physiologic Data from the Mammalian Feeding Apparatus using FEED, the Feeding Experiments End-User Database" and for their valuable feedback on this study.

References

Aiello L, Dean C. 1990. An introduction to human evolutionary anatomy. London: Academic Press.

Anapol F, Herring SW. 1989. Length-tension relationships of masseter and digastric muscle of miniature swine during ontogeny. J Exp Biol 143:1–16.

Anapol F, Lee S. 1994. Morphological adaptation to diet in platyrrhine primates. Am J Phys Anthropol 94:239–61.

Anderson K, Throckmorton GS, Buschang PH, Hayasaki H. 2002. The effects of bolus hardness on masticatory kinematics. J Oral Rehabil 29:689–96.

Bennett NG. 1908. Contribution to the study of the movements of the mandible. J Prosthet Dent 8:41–54.

Bhatka R, Throckmorton GS, Wintergerst AM, Hutchins B, Buschang PH. 2004. Bolus size and unilateral chewing cycle kinematics. Arch Oral Biol 49:559–66.

Buschang PH, Hayasaki H, Throckmorton GS. 2000. Quantification of human chewing-cycle kinematics. Arch Oral Biol 45:461–74.

Byrd KE, Milberg DJ, Luschei ES. 1978. Human and macaque mastication: a quantitative study. J Dent Res 57:834–43.

Carlson DS. 1977. Condylar translation and the function of the superficial masseter muscle in the rhesus monkey (*M mulatta*). Am J Phys Anthropol 47:53–63.

Crompton AW, Lieberman DE, Aboelela S. 2006. Tooth orientation during occlusion and the functional significance of condylar translation in primates and herbivores. In: Carrano MT, Gaudin TJ, Blob RW, Wible JR, editors. Amniote paleobiology: perspectives on the evolution of mammals, birds, and reptiles: a volume honoring James Allen Hopson. Chicago: University of Chicago Press. p. 367–88.

DuBrul EL. 1974. Origin and evolution of the oral apparatus. Front Oral Physiol 1:1–30.

Ferrario VF, Sforza C, Lovecchio N, Mian F. 2005. Quantification of translational and gliding components in human temporomandibular joint during mouth opening. Arch Oral Biol 50:507–15.

Gallo LM, Airoldi GB, Airoldi RL, Palla S. 1997. Description of mandibular finite helical axis pathways in asymptomatic subjects. J Dent Res 76:704–13.

Gallo LM, Brasi M, Ernst B, Palla S. 2006. Relevance of mandibular helical axis analysis in functional and dysfunctional TMJs. J Biomech 39:1716–25.

Gallo LM, Fushima K, Palla S. 2000. Mandibular helical axis pathways during mastication. J Dent Res 79:1566–72.

Grant PG. 1973. Biomechanical significance of the instantaneous center of rotation: the human temporomandibular joint. J Biomech 6:109–113.

Herrel A, Cleuren J, De Vree F. 1996. Kinematics of feeding in the lizard *Agama stellio*. J Exp Biol 199:1727–42.

Hiiemae KM. 1978. Mammalian mastication: a review of the activity of the jaw muscles and the movements they produce in chewing. In: Butler PM, Joysey KA, editors. Development, function and evolution of teeth. London: Academic Press. p. 361–98.

Hillson S. 2005. Teeth. Cambridge: Cambridge University Press.

Hylander WL. 1978. Incisal bite force direction in humans and the functional significance of mammalian mandibular translation. Am J Phys Anthropol 47:53–63.

Hylander WL. 2006. Functional anatomy and biomechanics of the masticatory apparatus. In: Laskin JL, Greene CS, Hylander WL, editors. Temporomandibular disorders: an evidenced approach to diagnosis and treatment. New York: Quintessence Pub Co.

Hylander WL, Johnson KR, Crompton AW. 1987. Loading patterns and jaw movements during mastication in *Macaca fascicularis*: a bone-strain, electromyographic, and cineradiographic analysis. Am J Phys Anthropol 72:287–314.

Hylander WL, Johnson KR, Crompton AW. 1992. Muscle force recruitment and biomechanical modeling: an analysis of masseter muscle function in *Macaca fascicularis*. Am J Phys Anthrop 88:365–387.

Hylander WL, Ravosa MJ, Ross CF, Wall CE, Johnson KR. 2000. Symphyseal fusion and jaw-adductor muscle force: an EMG study. Am J Phys Anthropol 112:469–92.

Hylander WL, Vinyard CJ, Wall CE, Williams SH, Johnson KR. 2002. Recruitment and firing patterns of jaw muscles during mastication in ring-tailed lemurs. Am J Phys Anthropol 34(Suppl):88.

Hylander WL, Wall CE, Vinyard CJ, Ross C, Ravosa M, Williams SH, Johnson KR. 2005. Temporalis function in Anthropoids and Strepsirrhines: an EMG study. Am J Phys Anthropol 128:35–56.

Iriarte-Díaz J, Reed DA, Ross CF. 2011. Sources of variance in temporal and spatial aspects of jaw kinematics in two species of primates feeding on foods of different properties. Integr Comp Biol 51:307–19.

Kay RF. 1975. The functional adaptation of primate molar teeth. Am J Phys Anthropol 43:195–216.

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

Lindauer SJ, Sabol G, Isaacson RJ, Davidovitch M. 1995. Condylar movment and mandibular rotation during jaw opening. Am J Orthodon Dentofac Ortho 107:573–77.

Lucas PW. 2004. Dental functional morphology: how teeth work. New York: Cambridge University Press.

Maynard Smith J, Savage RJG. 1959. The mechanics of mammalian jaws. School Sci Rev 141:289–301.

Meyers JJ, Herrel A, Birch J. 2002. Scaling of morphology, bite force and feeding kinematics in an iguanian and a scleroglossan lizard. In: Aerts P, D'Aout K, Herrel A, Van Damme R, editors. Topics in functional and ecological vertebrate morphology. Maastrich: Shaker Publishing. p. 47–62.

Miller DI, Petak KL. 1973. Three-dimensional cinematographphy. Kinesiology 3:14–19.

Moss M. 1959. Functional anatomy of the temporomandibular joint. In: Schwartz L, editor. Disorders of the temporomandibular joint: diagnosis, management, relation to occlusion of teeth. Philadelphia: WB Saunders Co.

Noble HW. 1973. Comparative functional anatomy of temporomandibular joint. Oral Sci Rev 2:3–28.

Osborn JW. 1996. Features of the human jaw design which maximize the bite force. J Biomech 29:589–95.

Ostry DJ, Munhall KG. 1994. Control of jaw orientation and position in mastication and speech. J Neurophysiol 71:1528–45.

Reed DA, Ross CF. 2010. The influence of food material properties on jaw kinematics in the primate, *Cebus*. Arch Oral Biol 55:946–62.

Rosenberger AL, Kinzey WG. 1976. Functional patterns of molar occlusion in platyrrhine primates. Am J Phys Anthropol 45:281–98.

Ross CF, Baden AL, Georgi J, Herrel A, Metzger KA, Reed DA, Schaerlaeken V, Wolff MS. 2010. Chewing variation in lepidosaurs and primates. J Exp Biol 213:572–94.

Ross CF, Reed DA, Washington RL, Eckhardt A, Anapol F, Shahnoor N. 2009a. Scaling of chew cycle duration in primates. Am J Phys Anthropol 138:30–44.

Ross CF, Washington RL, Eckhardt A, Reed DA, Vogel E, Dominy NJ, Machanda Z. 2009b. Ecological consequences of scaling of chew cycle duration and daily feeding time in Primates. J Hum Evol 56:570–85.

Searle SR, Casella G, McCulloch CE. 2006. Variance components. New York: Wiley.

Smith RJ. 1984. Comparative functional morphology of maximum mandibular opening (gape) in primates. In: Chivers DJ, Wood BA, Bilsborough A, editors. Food acquisition and processing in primates. New York: Plenum Press. p. 231–55.

Smith RJ. 1985. Functions of condylar translation in human mandibular movement. Am J Orthod 88:191–202.

Sokal RR, Rohlf FJ. 1995. Biometry: the principles and practice of statistics in biological research. 3rd ed. New York: W. H. Freeman and Co.

Spencer MA. 1995. Masticatory system configuration and diet in anthropoid primates [dissertation]. [Stony Brook (NY)]: State University of New York.

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

Swindler DR. 2002. Primate dentition: an introduction to the teeth of non-human primates. Cambridge: Cambridge University Press.

Taylor AB, Vinyard CJ. 2009. Jaw-muscle fiber architecture in tufted capuchins favor generating relatively large muscle forces without compromising jaw gape. J Hum Evol 57:710–20.

Terhune CE. 2010. The temporomandibular joint in anthropoid primates; functional, allometric, and phylogenetic influences [dissertation]. [Phoenix (AZ)]: Arizona State University.

Throckmorton GS, Buschang BH, Hayasaki H, Phelan T. 2001. The effects of chewing rates on mandibular kinematics. J Oral Rehab 28:328–34.

Vinyard CJ. 1999. Temporomandibular joint morphology and function in Strepsirrhine and Eocene primates [dissertation]. [Evanston (IL)]: Northwestern University.

Vinyard CJ, Wall CE, Williams SH, Johnson KR, Hylander WL. 2007. Masseter electromyography during chewing in ring-tailed lemurs (*Lemur catta*). Am J Phys Anthropol 130:85–95.

Vinyard CJ, Wall CE, Williams SH, Hylander WL. 2008. Patterns of variation across primates in jaw-muscle electromyography during mastication. Integr Comp Biol 48:294–311.

Wainwright PC. 2006. Functional morphology of the pharyngeal jaw apparatus. Fish Biomech 23:77–101.

Wall CE. 1995. Form and function of the temporomandibular joint in anthropoid primates [dissertation]. [Stony Brook (NY)]: State University of New York.

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

Wall CE, Hylander WL. 1999. A comment on: the instantaneous center of rotation during human jaw opening and its significance in interpreting the functional meaning of condylar translation (Chen X. 1998. Am J Phys Anthropol 106:35–46). Am J Phys Anthropol 110:105–7.

Wall CE, Vinyard CJ, Johnson KR, Williams SH, Hylander WL. 2006. Phase II jaw movements and masseter muscle activity during chewing in *Papio anubis*. Am J Phys Anthropol 129:215–24.

Weijs WA, Korfage JAM, Langenbach GJ. 1989. The functional significance of the position of the centre of rotation for jaw opening and closing in the rabbit. J Anat 162:133–48.

Williams SH, Wright BW, Truong VD, Daubert CR, Vinyard CJ. 2005. Mechanical properties of foods used in experimental studies of primate masticatory function. Am J Prim 67:329–46.

Wintergerst AM, Throckmorton GS, Buschang PH. 2008. Effects of bolus size and hardness on within-subject variability of chewing cycle kinematics. Arch Oral Biol 53:369–75.