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ARTICLE

What Does Feeding System Morphology Tell Us About Feeding?

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Feeding is the set of behaviors whereby organisms acquire and process the energy required for survival and reproduction. Thus, feeding system morphology is presumably subject to selection to maintain or improve feeding performance. Relationships among feeding system morphology, feeding behavior, and diet not only explain the morphological diversity of extant primates, but can also be used to reconstruct feeding behavior and diet in fossil taxa. Dental morphology has long been known to reflect aspects of feeding behavior and diet but strong relationships of craniomandibular morphology to feeding behavior and diet have yet to be defined.

To understand why this might be, we review here the field of primate feeding biomechanics. Biomechanics develops and tests hypotheses relating morphological to behavioral variation (diversity) using physical principles such as Newton's Laws applied through mathematical models of biological systems. Biomechanists use a wide range of techniques, including morphometric measurements of museum collections and living animals, kinematic and physiological recordings of feeding behavior in laboratory and wild primates, and mathematical modeling of feeding system function and evolution. In feeding biomechanics, biomechanical analysis relates variation in feeding system morphology (size and shape of muscles, bones, teeth, tongues, joints) to variation in how animals feed (feeding behavior) and what they feed on (diet). It assumes that the abilities of organisms to exert forces on food items in the environment and to resist and dissipate the associated reaction forces are measures of feeding performance that are important determinants of survival and relative fitness. Feeding biomechanics characterizes different feeding behaviors by quantifying not only muscle activity and, dynamics, and jaw and tongue movements (kinematics), but also models and measures the relative and absolute magnitudes of muscle, bite, and joint reaction forces generated during those behaviors (kinetics). Feeding biomechanics also measures local stress and strains, as well as overall deformation regimes (*sensu Ross and coworkers*[8]) of the musculoskeletal system produced by these forces during these behaviors and evaluates whether feeding system morphology varies with behavior in such a way as to improve feeding performance. The premise of biomechanical analysis is that the design of biological systems by natural selection, with design meaning a match of form and function,[13] can be understood by assessing the mechanical performance of biological systems in interactions with the environment. When biomechanics fails to identify clear relationships between morphology and function, it may be that our biomechanical analyses are flawed or incomplete, or that nonmechanical factors are more important determinants of morphology.

This review synthesizes the current state of knowledge of primate feeding biomechanics by addressing a series of questions regarding primate feeding system morphological design and examines the evidence linking behavioral to morphological variation. We also comment on other likely determinants of feeding system design such as phylogenetic relatedness in living primates. We focus on feeding, excluding foraging (the search for and location of food items) and digestion (the breakdown of food in the gastrointestinal tract for assimilation into the bloodstream) except to point out where answers to our questions lie with regard to these processes. The mechanics of food fracture and their relationships to dental morphology are reviewed elsewhere.[14–16] Our focus here is craniomandibular morphology. A glossary of terms in primate feeding biomechanics is provided. We begin by reviewing terminology used to describe primate feeding behavior.

PRIMATE FEEDING BEHAVIOR

The daily feeding time of individual primates is divided into feeding

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Glossary of Terms Used in Studies of Primate Feeding Behavior

Anisodontic — lower teeth with different width (usually narrower) than upper teeth.[93]

Anisognathous — lower tooth rows with (e.g., bi-molar) width different (usually narrower) than upper tooth rows. See isognathy.[93]

Centric occlusion — position of the teeth when the protocone tips are firmly locked in the talonid basins.[20]

Centric relation — midline position of the lower jaw.[20]

Chewing — breakdown of food in the oral cavity using cyclic (repetitive) movements of jaw and tongue and cyclic application of bite forces.

Cyclic behavior or movement — a behavior, such as a gape or tongue movement cycle, that occurs more than once.

Daily feeding time — amount of time spent feeding expressed as a percentage of daily activity budget.[70,71] Feeding time should be distinguished from foraging time, when animals are actively searching for food.

Deformation regime — pattern of deformation such as twisting or bending associated with a loading regime. Deformation regimes are intuitive short-hand descriptions of shape changes in skeletal elements when external forces are applied to them.

Feeding bout — Nonhomogeneous distribution of food and the effects of gut-filling mean that wild primates feed in bouts. At the group level, a feeding bout begins when a group enters a tree or area and ends when the group leaves.[139] For an individual primate, a feeding bout begins when it starts processing food and ends when it stops processing a specific item within a given feeding tree or area. If they switch items or leave the tree or area, a new feeding bout begins.

Feeding sequence — In the laboratory, feeding data are collected during experimental sessions. During experiments, feeding occurs in feeding sequences, from ingestion to final swallow. When primates use multiple swallows within a sequence or obviously extract a new bolus of food from the vestibule or cheek pouch for processing, these cycles separate the sequence into subsequences.

Gape cycles — the cyclic elevation or depression and medial or lateral movements of the jaw, defined here from maximum gape to maximum gape.

Gape cycle types — Gape cycles are assigned to different categories to reflect variation in an animal's behavior across feeding sequences. These categories include ingestion, manipulation, stage 1 transport, mastication, and swallowing cycles. Stage 1 transport is the movement of food items from the ingestion point to the molars for mastication. Stage 2 transport is the movement of the food bolus past the palatoglossal arch (pillars of the fauces) and thereby out of the oral cavity *sensu stricto* and into the oropharynx. Stage 2 transport occurs during a swallow, as well as during cycles when food is accumulated in the valleculae between the back of the tongue and the epiglottis.

Gape cycle phases — Each gape cycle is made up of gape cycle phase*s* (FC, SC, SO, FO) that mark key jaw kinematic events (described in Fig. 1). These occur when the upward movement of the mandible slows due to the teeth contacting the food (FC-SC transition); when the upward movement of the jaw ends (minimum gape = SC-SO transition); when the jaw starts opening quickly after the tongue has coupled to the food item sufficiently for it to be ready for transport (SO-FO transition); and when the jaw changes from opening to closing (maximum gape = FO-FC transition). These jaw kinematic events are associated with transitions in sensory afferent input and are key events in sensorimotor control.[140]

Ingestion — In feeding biomechanics, ingestion cycles are those in which food is passed through the oral fissure into the oral vestibule or cavity. The primate behavior and ecology literature sometimes uses ingestion as a synonym for feeding or as a lumped reference to getting food from the environment into the body.

Isodontic — upper and lower teeth of the same width.

Isognathous — upper and lower tooth rows of the same width.

Loading regime — combination of external forces acting on a skeletal element.[8]

Mastication — the type of chewing characteristic of extant mammals, inferred for many stem mammals and synapomorphic of mammals. Primitively, mastication was characterized by upward, medial, and anterior movement of the lower teeth relative to the upper teeth during the power stroke, a jaw kinematic pattern retained in all primates studied to date.

Recruitment — in motor control literature, recruitment specifically refers to enlistment of new muscle motor units to generate more muscle force. At low force levels, motor unit recruitment is the primary means of increasing force; at higher forces, increases in muscle force are achieved by increasing the rate at which action potentials arrive at the muscle. In the primate chewing literature, recruitment is also used to refer to the patterns of firing of whole muscles, as estimated from EMG data.

Rhythmic chewing — degree of variation in chew cycle durations, quantified as the coefficient of variation of cycle duration. Mammals chew (and locomote) more rhythmically than do lizards or fish.[26,77,78,141]

Stress — force per unit area (F/L^2; N/m^2)

Stress regime — pattern of internal forces associated with a loading regime.[8]

Strain — deformation at a point; change in length over the original length (L/L; dismensionless).

Strain regime — patterns of internal strains associated with a loading regime.[8]

Triangle of support — triangle defined by bite point and two jaw joints. When the resultant vector of the jaw elevator muscle forces passes through this triangle during biting, both TMJs are in compression. It is hypothesized that primates recruit their jaw muscles to keep muscle resultant within this triangle to prevent TMJs being put into tension (that is, pulled apart).

Working and balancing side — like most mammals,[29] primates usually chew on only one side at a time. The biting side is the working side; the nonbiting side is the balancing side. Ingestion can also be sided, particularly if the animal ingests by biting something with the premolars or canines on one side.

bouts during which they process specific items within a given feeding tree or area. Feeding bouts in the wild and in many feeding experiments in the laboratory are divided into sequences starting with ingestion of a piece of food and ending in a final swallow (Fig. 1) (see Vinyard and coworkers,[17] Fig. 12). The sequence consists of a series of gape and tongue movement cycles, a gape cycle being defined by the cyclic elevation and depression of the mandible. Gape cycles are of different types: ingestion cycles, in which food is passed through the oral fissure into the oral vestibule or oral cavity; stage 1 transport cycles, when food is moved from the ingestion point to the molars for mastication; and stage 2 transport cycles, when the food bolus is moved out of the oral cavity *sensu stricto* and into the oropharynx. Stage 2 transport can occur as the oral phase of a swallow cycle, or during mastication cycles, when food is accumulated in the valleculae

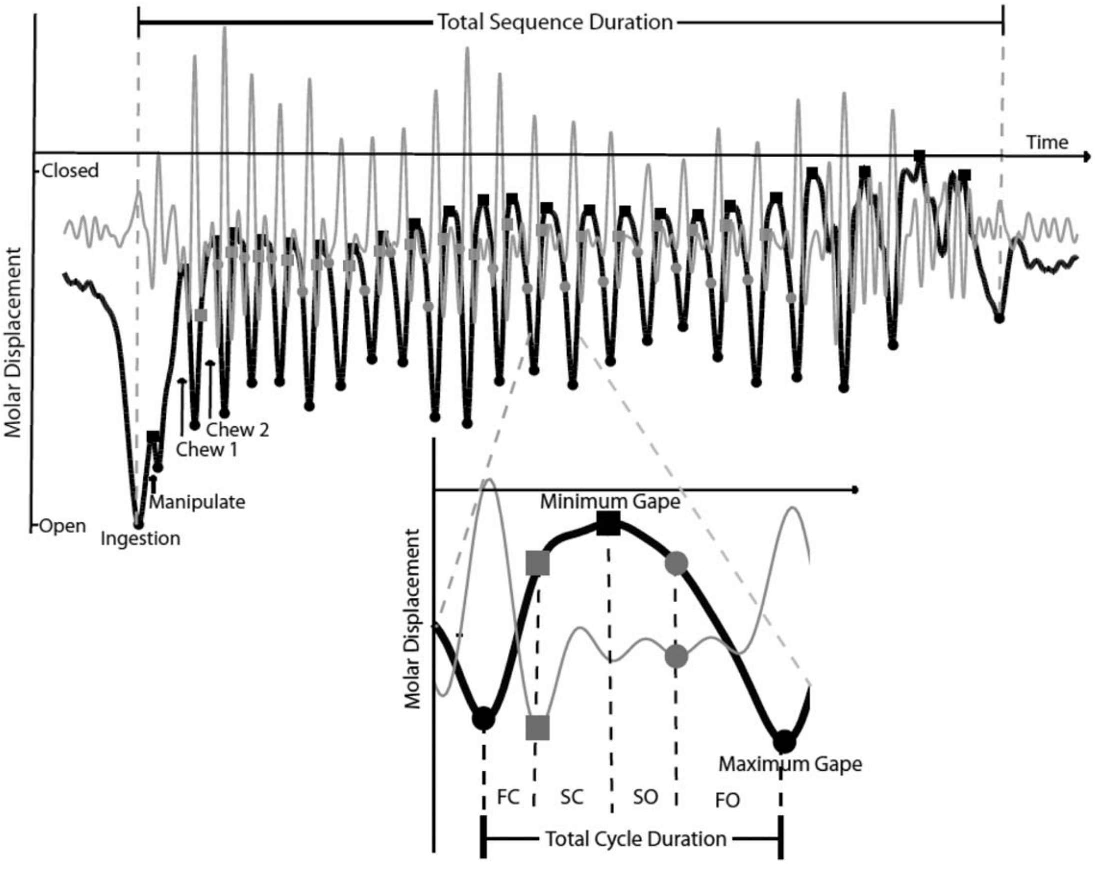


Figure 1. Definitions of feeding sequence, gape cycle, and gape-cycle phases. The upper graph plots, the black line, open-close displacements (gape) of the lower jaw during a complete feeding sequence from ingestion to final swallow. The second derivative of the displacement, the grey line, is used to define the four chew-cycle phases. Most chewing gape cycles are made up of Hiiemae's four gape-cycle phases: fast close, FC; slow close, SC; slow open, SO; fast open, FO.[137] The four gape-cycle phases are delineated by jaw and tongue kinematic events associated with changes in sensory afferent input that are key events in sensorimotor control.[138] SC starts when the teeth contact the food and mandibular closing movements slow; SC ends and SO begins when the mandible stops moving upward and begins moving downward (minimum gape); SO ends when the mandible starts depressing quickly (SO-FO transition, in theory when the tongue has captured the food item ready for transport); and FO ends when the mandible changes from depression to elevation (maximum gape).

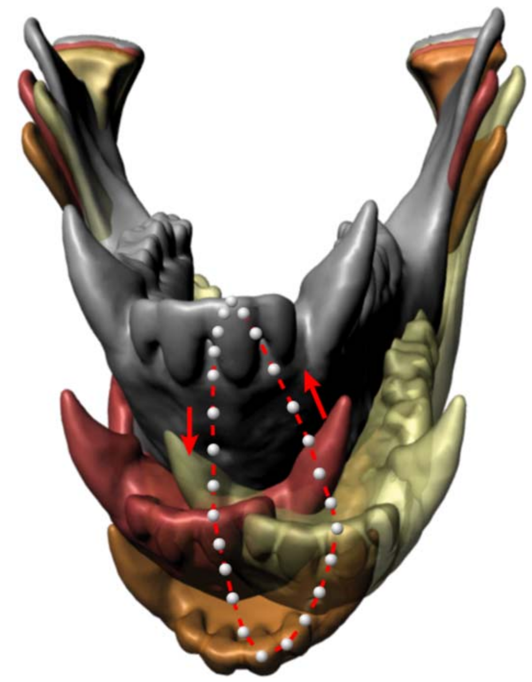


Figure 2. Diagram illustrating the three-dimensional position of the mandible through a gape cycle of a macaque (*Macaca mulatta*). Gray points represent the consecutive positions of the left lower lateral incisor through the cycle; red arrows indicate the direction of displacement. The mandibles in gray and brown respectively represent the mandible at maximum occlusion and maximum gape. The red and yellow mandibles respectively represent the mandible position midway through the opening and closing phases. Mandible displacements have been exaggerated for clarity. Actual displacements can be seen in a movie in the online Supporting Information. (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

between the back of the tongue and the epiglottis. Gape cycles when food is broken down between the teeth are puncture crushing cycles, when the mandible moves relatively vertically and the teeth do not contact each other, and mastication cycles, characterized by more transversely oriented jaw and tooth movements while the teeth are in occlusion.[18]

Chewing (cyclic breakdown of food in the oral cavity) has evolved multiple times in fishes, lizards, and dinosaurs.[19] The particular type of chewing practiced by stem mammals and most extant ones is mastication. Mastication primitively and in primates involves lateral to medial movements of the lower teeth relative to the uppers during the power stroke of the gape cycle[20] (Fig. 2). When combined with precise occlusion, mastication improves chewing efficiency, making it possible to increase digestive performance without increasing food intake rate or decreasing gut passage time.[21] Developmentally, precise occlusion in primates, as in all eutherian mammals, is achieved through determinate skull growth,[22] limited replacement of postcanine teeth,[22,23] development of the appropriate occlusal morphology on the teeth prior to eruption[23] and via post-eruption tooth wear, and plasticity in the positions and orientations of the teeth via remodeling of alveolar bone. Neurologically, precise occlusion is facilitated by sensory feedback from nerves in the periodontal ligament signaling the magnitude and orientation of bite forces, presumably reducing tooth wear and the probability of tooth breakage.[24–26] This periodontal sensory information, combined with sensory feedback from jaw muscle spindles, perhaps in the cerebellum,[27] is used to estimate and control the location of the jaw elevator muscle resultant and the magnitude and orientation of jaw joint reaction forces.[24,28]

Like most mammals,[29] primates usually chew on only one side at a time. The biting side is the working side; the nonbiting side is the balancing side. Ingestion can also be sided, particularly if the animal ingests by biting with the premolars or canines. A cineradiographic (x-ray movie) and dental occlusal study of one individual each of *Tupaia*, *Otolemur*, *Saimiri,* and *Ateles*[18,30,31] revealed that all four species resemble *Didelphis* and primitive mammals in exhibiting upward, medial, and forward movement of the working side mandible and teeth during the power stroke (Fig. 2).[32] This has also been demonstrated in *Homo,*[33,34] *Papio,*[35] *Macaca,*[36] and *Cebus*.[37] (The online Supporting Information includes movies of jaw movements in one individual from each of *Papio, Macaca,* and *Cebus*.) To achieve this movement, the mandible must rotate about an axis that is not orthogonal to the mid-sagittal plane (Fig. 3). Rather, the axis of rotation is tilted in both frontal and transverse planes. Projection of this axis onto an orthogonal axis system centered on the cranium allows jaw movements during feeding to be expressed as rotations about transverse, vertical, and rostrocaudal axes. Rotations about the transverse axis produce jaw depression and elevation movements (mouth opening and closing); rotations about the vertical axis produce mediolateral movements of the teeth and anteroposterior movements of the mandibular condyles; and the small rotations that occur about the rostrocaudal axis are caused by asymmetric movements of the condyles up and down the articular eminence of the temporomandibular joint (TMJ) (Fig. 3).

WHAT DRIVES VARIATION IN JAW KINEMATICS AMONG PRIMATES?

Jaw kinematics (movement) is one determinant of the orientation of the bite and joint reaction forces acting on the mandible during feeding and of stress and strain regimes in the skull and, therefore, presumably of feeding system skeletal design. Jaw

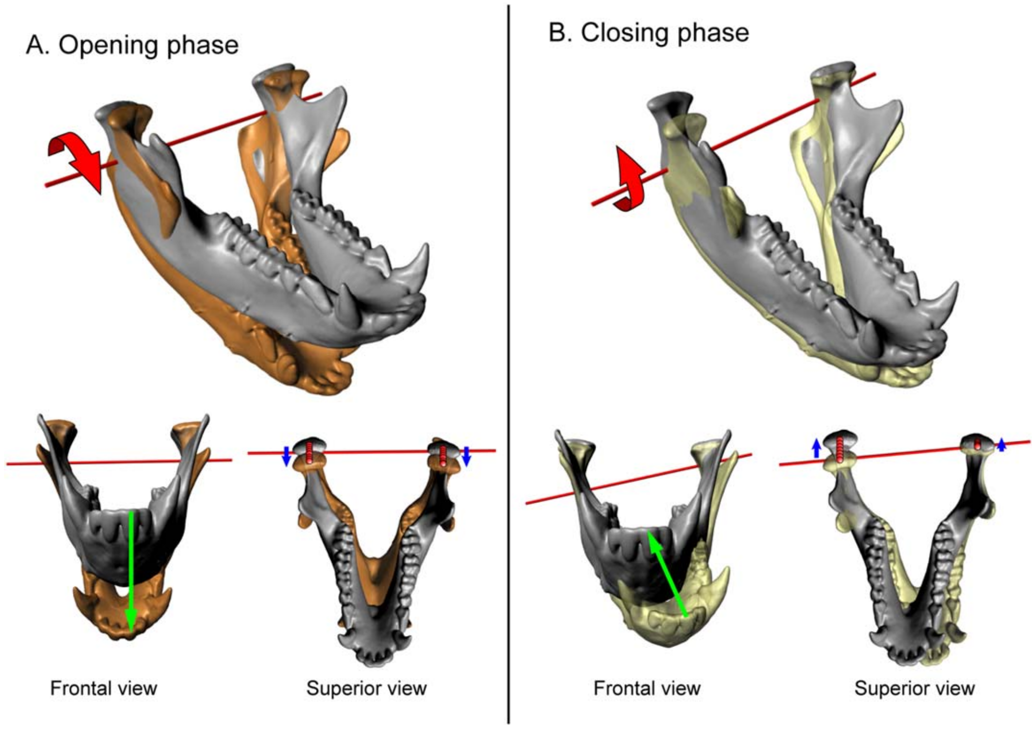


Figure 3. Mandible displacement during chewing by a macaque (*Macaca mulatta*) during the opening (A) and closing phases (B) of the gape cycle. Mandible positions are color coded according to Figure 1. The red stick represents the position of the helical axis of rotation; the red arrow indicates the direction of rotation. The green arrow in the frontal view indicates the displacement of the left mesial incisor. The red circles in the superior view represent the consecutive positions of the mandibular condyles during the sequence. The blue arrows indicate the directions and relative magnitudes of displacement. Mandible displacements, based on data collected from our lab, have been exaggerated for clarity. Actual displacements can be seen in movies in the Supporting Information. (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

kinematics could be influenced by species-specific and individual variation in muscle, tooth, and jaw joint morphology; material properties of food items, which vary between feeding sequences on different foods; and bolus size and shape, which vary between cycles within sequences. Hiiemae and Kay[30] showed that the relative durations of the four phases of the gape cycle (defined in Fig. 1) are very similar from one species to another. They found that puncture crushing and chewing cycles are distinguished by differences in the relative proportions of the gape cycle phases and identified species-specific effects on how this was achieved. Extending their analysis to vertical and lateral displacements of the mandible,[37,38] the majority of the variance is found between gape cycles within feeding sequences (Fig. 4). This suggests that the effects of feeding on foods with different material properties (at the feeding sequence level) are smaller than the effects of changes in bolus properties between cycles within sequences. Primates have the ability to modulate their jaw movements in response to changing bolus properties, but the basic patterns of jaw kinematics are shared by different species. Notably, species effects on jaw kinematics during SC are only evident for hard, brittle foods such as nuts. These effects are due to species-specific variation in muscle forces or morphology of occlusal surfaces, TMJs, and/or craniomandibular ligaments,[39–44] with occlusal morphology probably being an important determinant of jaw movement during SC.[45] These results support Hiiemae and Kay's hypothesis that: "changes in the morphology of the masticatory apparatus in general, and of the cheek teeth in particular, have not involved any significant change in the pattern of mastication as expressed by absolute cycle times or the percentage duration of each of the strokes".[30,50] Whether this reflects conservation of an inherited central motor pattern across generations and lineages and/or geometric constraints imposed by the functional requirements of mastication remains to be determined.[46]

STRUCTURE AND FUNCTION OF JAW ELEVATOR MUSCLES

The forces generated by the jaw elevator and depressor muscles are the primary determinants of mandibular kinematics, stress, strain, and deformation. The basic morphological plan seen in primate jaw muscles — masseter, temporalis, medial pterygoid, lateral pterygoid, and digastric (Fig. 5) — is common to most mammals. In addition, primates share with "generalized" mammals (such as insectivores and *Didelphis*) a relatively large temporalis muscle.[47,48] Within primates, muscle architecture (pinnation angle, fiber/fascicle length, and tendon size and shape) shows relationships to feeding

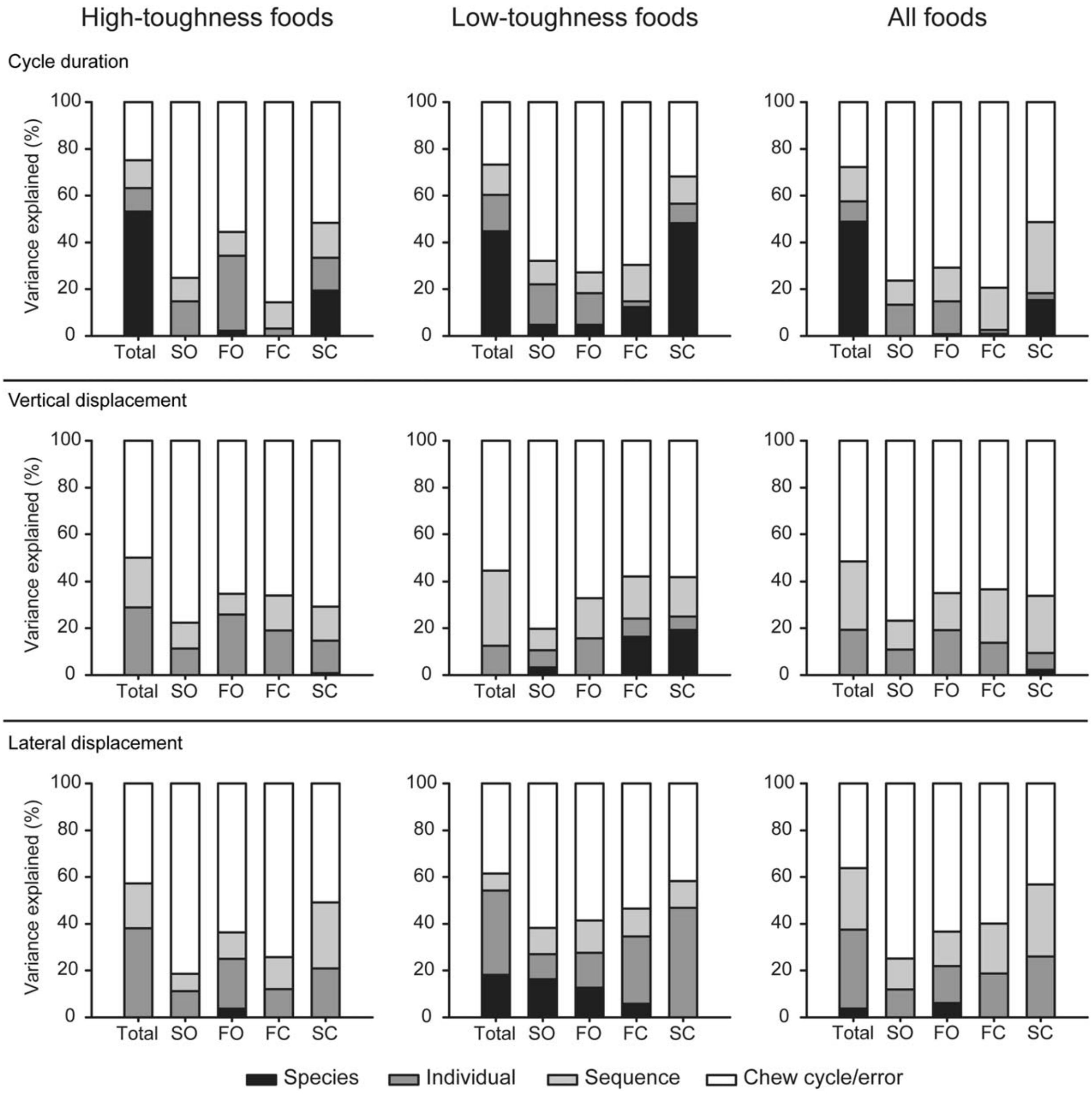


Figure 4. The percentage of variance in temporal and spatial variables of jaw kinematics in primates explained by each hierarchical factor in a nested ANOVA analysis.[38] Factors assessed were species (*Cebus, Macaca, Papio*), individual (3 *Cebus*, 2 *Macaca, 2 Papio*), feeding sequence (n = 817) (where food material properties are nested), and chewing cycles (n = 7,436) (where variance in bolus properties is nested). Data included were the first 10 chewing cycles (*Cebus*, n = 2,036 cycles; *Macaca*, n = 1,767; *Papio*, n = 3,633). To control differences in body size, spatial variables were standardized by the individual's jaw length. Displacement and temporal variables were calculated for the whole chew cycle (Total), and the slow-open (SO), fast-open (FO), fast-close (FC), and slow-close (SC) phases of the chewing cycle. The phases of the gape cycle were expressed as a percentage of total cycle duration.

behavior. For example, tree-gouging marmosets have longer muscle fibers in masseter and temporalis and lower physiological cross-sectional areas than their nongouging close relatives (tamarins), reflecting the fact that they do not need to generate relatively high forces at large gapes during gouging[49,50] (Box 1). In contrast, *Cebus apella* have larger masseter and temporalis muscles than congenerics, reflecting the fact that they also appear to generate larger forces at large gapes.[51]

Morphological subdivisions within the masseter and temporalis muscles are well documented,[47,52–55] but the relationships between this morphological diversity and functional diversity (electromyographic activity) has focused almost exclusively, but not entirely,[56] on anterior and posterior temporalis and superficial and deep masseter.[2,6,57–61] Subtle differences in relative timing of activity between the subdivisions and left versus right sides of the jaw elevator muscles[62] produce the 3-D movements of the primate mandible. Jaw rotations about a transverse axis (depression or

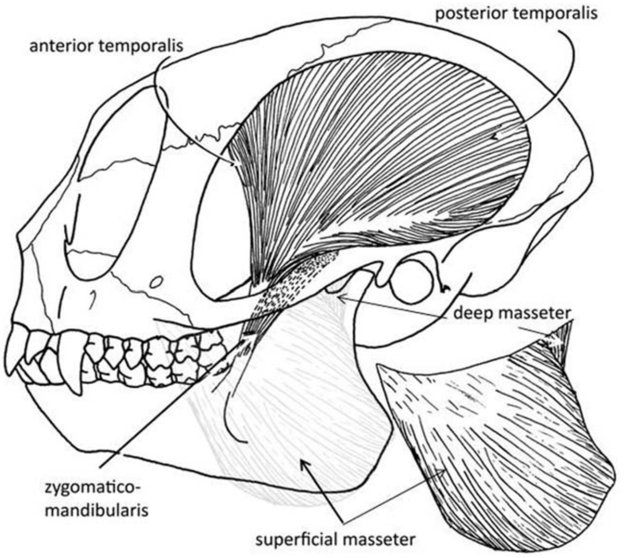


Figure 5. Diagram of the head of *Aotus* showing the jaw elevator muscles. The locations of the superficial and deep masseters are shown as transparent on the mandible. The medial pterygoid muscle is not shown: its line of action is parallel with that of the superficial masseter in lateral view, but it lies medial to the ramus of the mandible. Zygomatico-mandibularis is one of the subdivisions of the jaw elevators, the function of which is unknown.

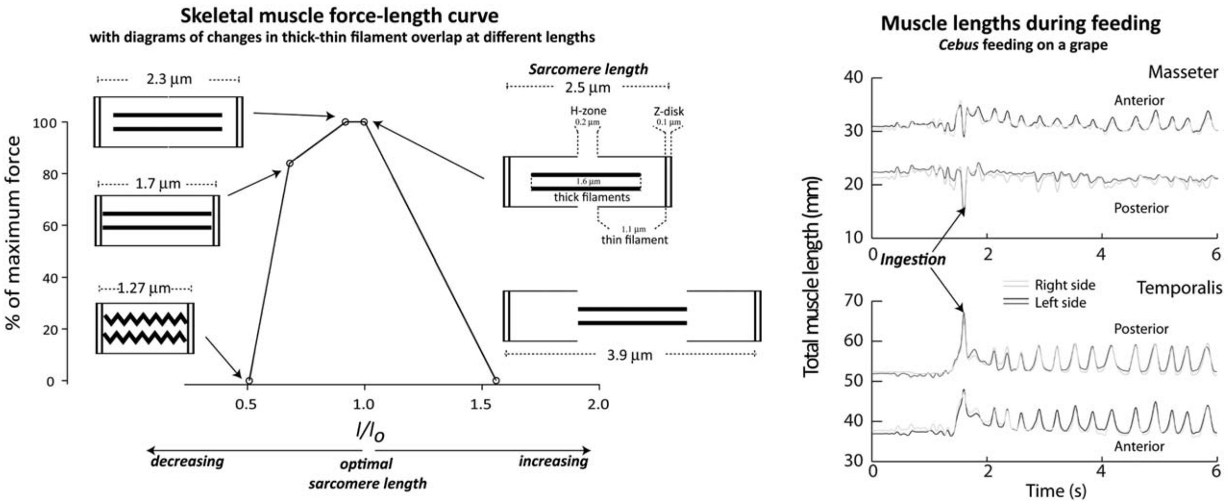
elevation of the jaw) are produced by muscles with components of force acting orthogonal to the transverse axis (that is, vertical and anteroposterior), whereas jaw rotations about the vertical axis are produced by muscles with anteroposterior and mediolateral components. The relative timing of jaw elevator muscle activity in primates has been summarized using Weijs'[62] concept of muscle "triplets," adapted to primates by Hylander and colleagues.[59,61,63,64] According to this model, primates achieve transverse movements of the tooth row during closing by sequential activity of two muscle triplets (Fig. 6). Triplet I, consisting of the working-side temporalis and the balancing-side superficial masseter and medial pterygoid, is recruited first during FC; its activity continues into SC. Triplet II, consisting of the balancing-side temporalis and the working-side superficial masseter and medial pterygoid muscles, is then active during SC, with extensive overlap with Triplet I.[59] This muscle activity pattern, which characterizes *Lemur*, *Otolemur*, and *Tupaia*, is reasonably hypothesized to represent the primitive condition for primates. Nonhuman anthropoid muscle activity patterns (represented by *Macaca, Papio*, and *Aotus*) differ from those of strepsirrhines and tree shrews in showing early activity of the working-side deep masseter muscle and late activity of the balancing-side posterior temporalis and deep masseter muscles.[57–59,61,64,65] (Humans differ from other anthropoids in not showing late activity in the balancing-side deep masseter.[66]) Although these muscle "triplets" are a useful heuristic device for understanding the muscles that generate transverse movements of the mandible during closing, there is considerable variation between individuals and species in their relative timing.[60]

The amount of force that a muscle generates at any time during chewing cycles is a function of its length, its shortening velocity, and its activity level (Box 1), which biomechanists estimate using electromyogram (EMG) amplitudes (Box 2). Jaw muscle EMG amplitudes are often presented as the ratio of amplitudes in the homologous muscle on working and balancing sides — that is, working-balancing side (W/B) ratios[57,59,63,65] — which vary across taxonomic groups. Tree shrews show relatively high levels of asymmetry in anterior temporalis amplitudes, with more working-side than balancing-side activity, whereas W/B ratios for the anterior temporalis and superficial masseter are not significantly different between anthropoids and strepsirrhines. This suggests that they recruit similar relative amounts of working- and balancing-side muscle force. In contrast, anthropoids show significantly higher amplitudes of EMG activity in the balancing side deep masseter and posterior temporalis muscles than do tree shrews and strepsirrhines.[59,61,64]

Differences in these ratios between muscles and species are important for understanding differences in loading, stress, and strain regimes, and hence, the morphology, of primate mandibles. The relatively greater activity in anthropoid balancing-side deep masseter and posterior temporalis muscles is functionally related to the presence of symphyseal fusion in extant anthropoids. Symphyseal fusion strengthens the symphysis against muscle force being transferred from the balancing to the working side, especially transversely directed muscle forces generated by the balancing-side deep masseter late in the power stroke.[57,59,61,63,64,67,68] Recent support for this hypothesis comes from the observation that adult *Propithecus verreauxi*, which have convergently evolved a nearly completely fused mandibular symphysis, also resemble anthropoids in displaying relatively high EMG amplitudes in the balancing-side deep masseter and posterior temporalis, which also peak late in the power stroke.[58] Thus, differences between anthropoids and most strepsirrhines in how jaw movements are produced and how working and balancing muscles are recruited have consequences for mandibular design.[46] Indeed, balancing-side deep masseter amplitudes and timing appear to be linked to symphyseal morphology across other mammals that display transverse movements of the mandible during the power stroke of mastication.[46]

Consideration of the distribution of variance in jaw muscle EMG activity patterns provides further

Box 1. Muscle Structure and Function



The left diagram illustrates relationships between length-related changes in overlap of thick and thin filaments in the sarcomeres of skeletal muscles and the associated length-related changes in force generation potential (redrawn from,[5] based on[4]). Force is expressed as a % of maximum. l/l_o = sarcomere length as a proportion of optimal. There is an optimal length for muscle force generation capability: stretching or shortening jaw muscles away from this optimal part of the length-force curve decreases their force generation potential.[9,10] Because of these length-force properties of the sarcomeres, jaw gape affects the amount of force that the jaw muscles can produce. The diagram on the right plots changes in muscle length during a feeding sequence calculated from 3-D jaw kinematic data. Note how different parts of the masseter and temporalis change length to different degrees during different behaviors.

insight into principles of primate feeding system design. Analysis of the effects of species, individual, experimental session, feeding sequence, and chew cycle on variance in EMG amplitudes and relative timing during mastication of a range of foods in one species of tree shrew and fourteen species of primates reveals, as with the jaw kinematic results reported earlier, that most of the variance in relative timing of jaw muscle peak activity is nested between chewing cycles in feeding sequences.[60] This suggests that variation in food bolus properties within sequences elicits greater variation in jaw kinematics via modulation of jaw muscle relative timing than does variation in food material properties associated with different foods. In contrast, variation in relative EMG amplitudes is more equally distributed both between and within feeding sequences. This reflects the well-documented fact that different foods require different amounts of force to process and that the amount of force needed to process the bolus changes through the chewing sequence (mostly decreasing). Given that combinations of external muscle forces and reaction forces at joints and at the bite point produce internal stresses and strains on the mandible during chewing, kinematic and EMG results suggest that there is more variance in mandibular stress and strain regimes between different cycles within sequences than there is between sequences of chewing on different foods. This calls into question attempts to link variation in mandibular corpus morphology to variation in patterns of stress and strain during mastication of different foods.[38] Links between variation in mandibular morphology and in other feeding behaviors require more attention.

ARE ENERGETICS IMPORTANT IN FEEDING SYSTEM DESIGN?

It is almost axiomatic in biomechanics to assess the performance of musculoskeletal systems by estimating their energetic consumption. While energetic constraints on system design are certainly important in musculoskeletal systems that consume a large proportion of an animal's overall energy budget, as do locomotion and digestion, it seems unlikely that energetic considerations are important for systems in which total energy consumption is relatively low. In the hearing system, for example, as long as energy can be delivered to the tensor tympani and stapedius muscles at a high enough rate, it seems unlikely that selection acts on organisms in which total energy consumption by these muscles is high. Therefore, in order to know whether feeding system design reflects selection to minimize its energy consumption, either because of constraints on the rate at which energy can be supplied to the system or the total amount of energy the system uses, it is important to know the proportion of the overall energy budget consumed by the

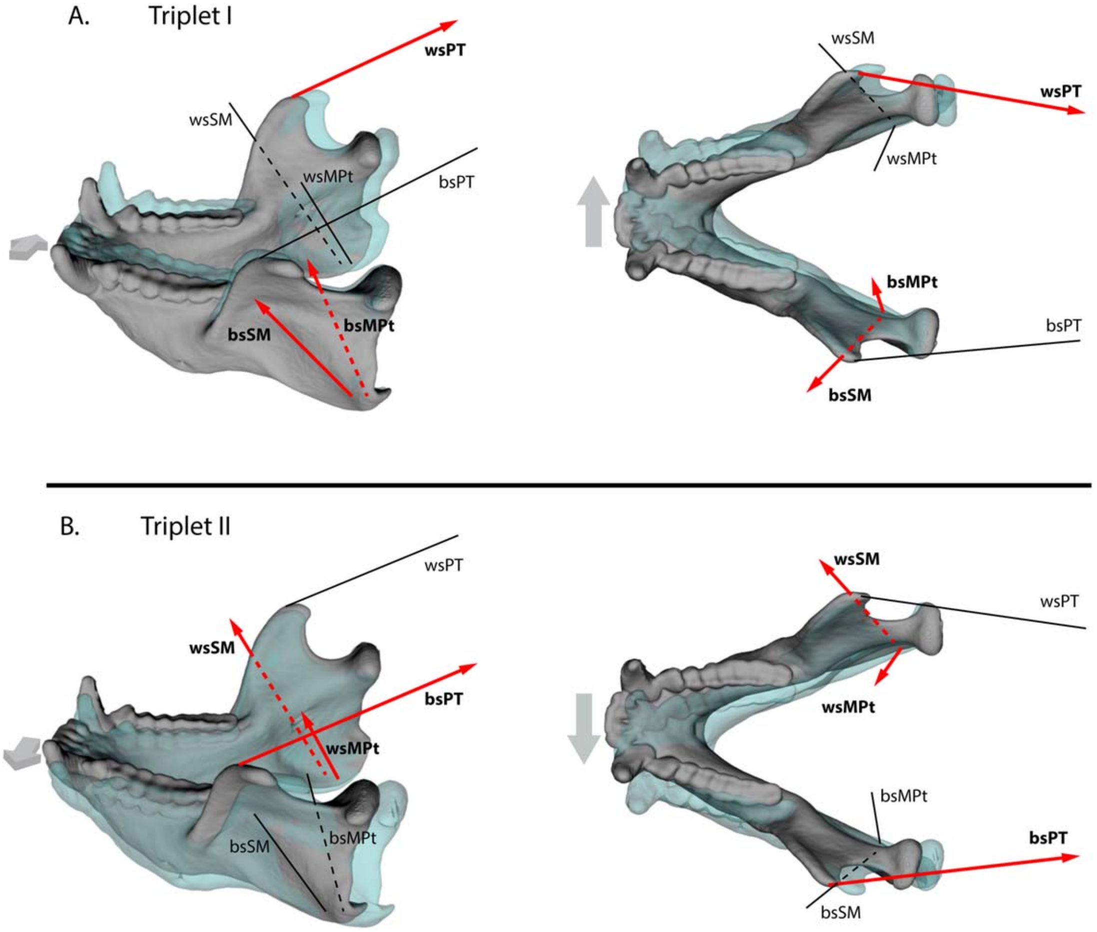


Figure 6. Jaw-closing muscle firing patterns for a right chew according to the "triplet" model. In both A and B, the left pane depicts the mandible in oblique view and the right panel in superior view. Each line represents the line of action of a jaw-closing muscle. Red arrows represent the more active triplet and black lines the less active triplet. Muscles names in bold also indicate the active triplet set of muscles. ws and bs respectively indicate the working-side and balancing-side muscles. SM, superficial masseter; PT, posterior temporalis; MPt, medial pterygoid. In each panel, the blue transparent mandible represents the end position of the mandible produced by the action of a triplet. (A) Triplet I. During the first part of closing, triplet I, consisting of the ws posterior temporalis (wsPT), the balancing-side superficial masseter (bsSM), and balancing-side medial petrygoid (bsMPt), fires first, moving the mandible toward the working side. (B) Triplet II. Composed of the balancing-side posterior temporalis (bsPT), the working-side superficial masseter (wsSM), and working-side medial pterygoid (wsMPt), triplet II fires second, moving the front of the mandible toward the balancing side. (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

orofacial components of the feeding system and whether there are design constraints on the rate at which energy is delivered to it. Data on the energetics of feeding behavior are scant. Ongoing work on this question by Wall, Hanna, and O'Neill[69] will be extremely valuable.

PRIMATES ARE NOT OPTIMIZED TO EAT FAST

In primates, daily feeding time, or the proportion of the daily activity budget spent ingesting and chewing food, ranges from 0.1% in *Loris*, 7% in *Tarsius spectrum,* to over 80% in some female mountain gorillas.[70] Larger primates spend more time feeding than smaller primates, but they also chew more slowly than smaller primates,[71,72] accounting for some of this body-mass-related increase in feeding time. When this effect is quantified by dividing daily feeding time by chew cycle time, generating an estimate of the number of chews per day, body mass explains only 2.2% of the variance in number of chews per day; the scaling exponent is very low (number of chews per day scales to body mass$^{0.06}$). Hence, body mass is not a strong determinant of daily feeding time in primates.[38] Indeed, if ingested bolus size (the amount of food that primates put in their mouths) increases isometrically with body mass,[73] and the number of chews per bolus does not change with size, then primates have ample time during the day for feeding.[70] Of course this may not always be true, especially in times of hardship, but the available evidence does not support the hypothesis that primate feeding systems are optimized for maximizing short-term food intake rate by minimizing chew cycle time; that is, primates could chew more slowly than they currently do and

Box 2. Electromyography

Jaw muscle activity during feeding is measured using indwelling or surface EMG electrodes. EMG activity recorded from an electrode is the sum of all action potentials within the recording range of that electrode. Because relatively larger potentials can be due to large muscle motor units and/or motor endplates close to the electrode, increases in EMG signal amplitude can be due to increases in the size of motor units being activated, the number of motor units being activated (motor unit recruitment), or to increases in firing rate of individual motor units.[1] Consequently, relative differences in EMG amplitudes between muscles can only be made with standardized data.[2–4] The relative timing of muscle activity is less affected by these issues, although the delay between the muscle activity recorded with an EMG electrode and force generation by the host muscle needs to be considered.[6,7] Although it is often assumed that this delay is constant across feeding muscles and primate species,[11] there are reasons to think otherwise.[12]

still meet their metabolic needs. This is probably because primates cannot feed faster than their gasrointestinal tracts digest and pass food, so that digestive strategy (fast passage and inefficient extraction versus slow passage and efficient extraction) may be the limiting factor of daily feeding time.[74–76] Thus, unlike the locomotor system, where the ability to move the musculoskeletal components at a range of frequencies is an important aspect of system performance, primate feeding systems appear to be optimized to operate within a relatively narrow frequency band.[77,78] Indeed, they may even modulate the ingested bite size with food type so they can operate within this frequency band, thereby avoiding fatigue.[17,37]

Dividing daily feeding time by chew cycle time provides a rough approximation of the number of jaw movement cycles in a day, but primate feeding involves more than just chewing. Other feeding behaviors, such as incisor biting, gouging, and premolar biting, not only have cycle times that differ from those of chewing, but probably are also associated with different muscle activity patterns, different patterns of stress and strain in the bones, muscles, and ligaments, and different energetics.[69] There has been some work on bone strain, muscle activity, and feeding muscle design associated with incisor biting and gouging,[2,49,51,79–85] and some work on energetics of feeding in primates.[69] However, a complete understanding of the relationship between feeding system morphology and feeding behavior requires better estimates of the relative importance (time spent) of different behaviors in the wild, as well as better *in vivo* data on their biomechanics from both laboratory and wild primates.[86–90]

ARE PRIMATE FEEDING SYSTEMS DESIGNED TO RESIST FATIGUE LOADING?

It has been hypothesized that larger primates chew more than smaller ones, making the mandibles of larger animals more prone to fatigue damage, which is produced by repeatedly applied loads.[40,58,91–93] The scaling of the number of chews per day presented earlier suggests that although larger primates do chew more than smaller ones, the body size effect is subtle. To estimate whether the magnitude of this effect would produce size-related changes in the probability of fatigue damage in primate mandibles, we used regression equations relating the number of cycles to failure to strain magnitude in human bone.[94] Assuming a tensile strain magnitude of 3,000 $\mu\varepsilon$ (greater than that routinely recorded from the mandible), we estimated that 10^{10} cycles are needed to produce fracture of the mandible, an order of magnitude more cycles than the largest primates could generate if they chewed 24 hrs a day for their entire lives. Thus, it is not clear that primate mandibles are likely to fracture from fatigue damage within a primate's lifetime, calling into question the hypothesis that size-related changes in primate mandible design reflect adaptations to decrease the risk of fatigue fracture. If this is correct, it predicts no differences in bony morphology of feeding systems designed to withstand large forces from those designed to withstand many repetitive loading events.[95]

CRANIA ARE NOT OPTIMIZED FOR DISSIPATING FEEDING FORCES (MINIMIZING STRESS)

External forces during feeding result in stress, strain, and deformation of the mandible and cranium. Are the size and shape of skull bones adapted to minimize stresses and strains associated with different deformation regimes (bending, twisting, shearing)? One clue to the strength of the relationship between skull shapes and deformation regimes comes from the magnitude of the strains associated with that deformation: that is, bone strain magnitudes provide clues to the relative importance of strain in skull design. For example, low strain magnitudes in the supraorbital region during feeding reveal that these areas are not optimized for maximizing strength with minimal material during feeding; that is, bone could be removed or rearranged without significantly impacting feeding performance and cranial strength and integrity.[96] Hylander, Picq, and Johnson[96] and Ravosa, Johnson, and Hylander[97] hypothesized that bone in these areas instead functions to protect the brain and eyes against "relatively infrequent non-masticatory external forces associated with highly active primates (e.g., traumatic accidental forces applied to the orbits and neurocranium)". Subsequently it was shown that very low strains also

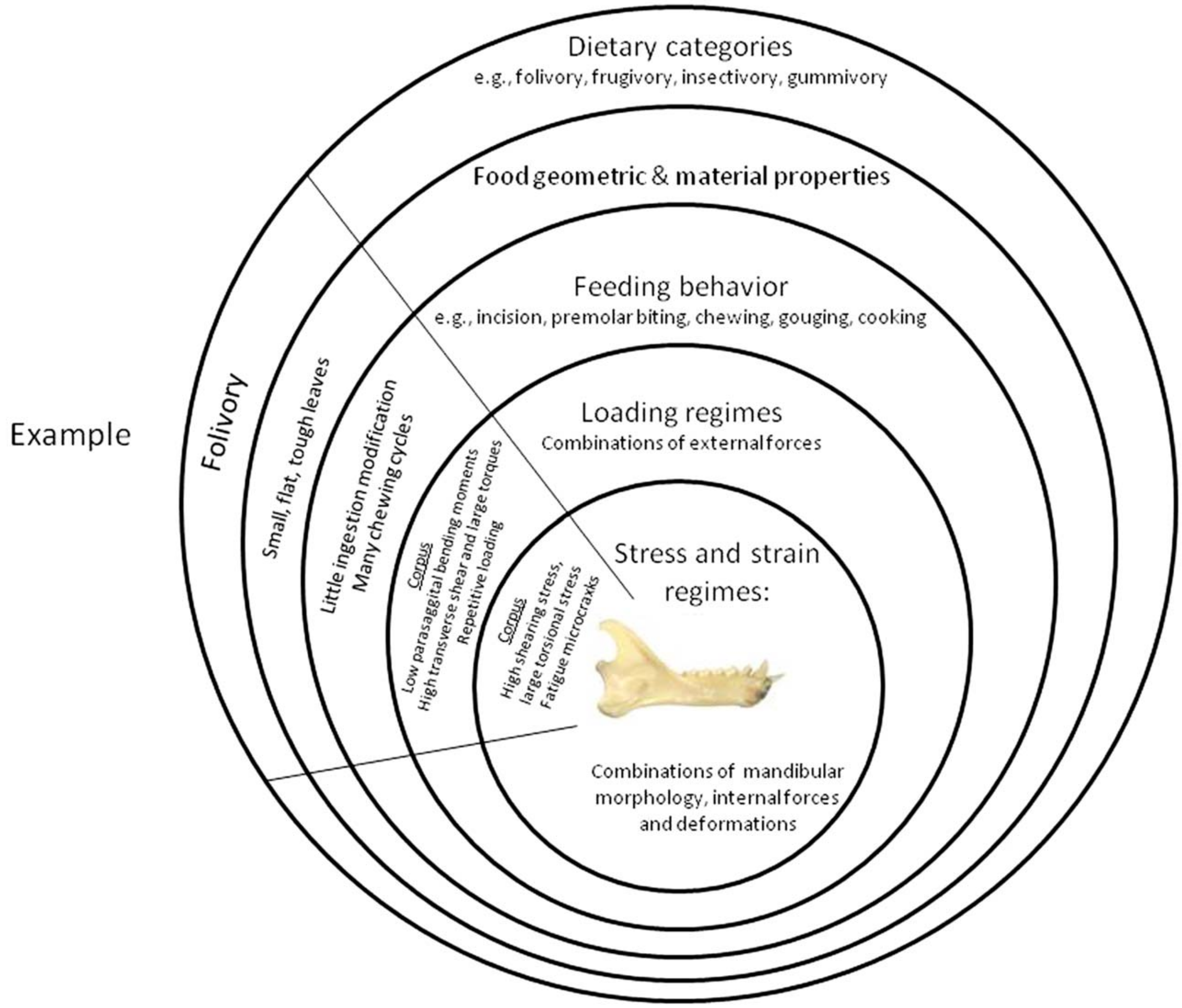


Figure 7. Diagram of conceptual relationships between mandibular morphology (center) and, from outside in, dietary categories, food geometric and material properties, feeding behavior, mandibular loading regimes (combinations of external forces), and mandibular stress and strain regimes (combinations of internal forces and deformation regimes).[8] Dietary categories will map exclusively and consistently to mandibular morphology if: (a) there are exclusive and consistent associations between dietary categories, food geometric and material properties, feeding behavior, loading regimes, and stress and strain regimes; (b) natural selection selects for these features of mandibular morphology because they improve feeding performance and fitness; and (c) these selective forces act in the same morphological and behavioral context, in part defined by phylogenetic history. One example is given, for folivory. From Ross, Iriarte, and Nunn.[38]. (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

characterize the intraorbital surfaces of the brow ridge (orbital roof), postorbital septum, medial orbital wall, and orbital floor (roof of maxillary sinus).[8,142] Variation in bone size and shape in these areas is unlikely to be related to feeding behavior because areas of the cranium that experience bone strain of low magnitudes during feeding are not optimized for resisting feeding forces. Finite-element models of extant and fossil hominid crania confirm that supraorbital and calvarial strains are or were also very low during feeding in these taxa,[98–100] arguing against hypotheses linking their supraorbital morphology to feeding behavior. Subsequent arguments against these interpretations of the strain magnitude data[101] have been effectively refuted.[102]

In contrast, some areas of the skull experience relatively high strain and stress magnitudes during feeding. These include the buccal aspect of the mandibular corpus below the molars, the mandibular symphysis, the zygomatic arch, the anterior root of the zygoma, and, if finite-element analyses are correct, the anterior pillar of *Australopithecus africanus*.[98–100] The mandibular symphysis, condyle, and corpus also show adaptive plasticity associated with differences in food material properties (FMPs).[103–106] In these areas, one might expect that the amount and distribution of bone (size and shape) and/or plastic responsiveness are under selection for feeding performance and that variation in morphology is associated with variations in feeding behavior that are also associated with variation in patterns of stress and strain.

The interspecific differences in primate mandibular morphology predicted to be associated with this behavioral variation derive from Hylander's model of mandibular deformation regimes in primates.[40,41,79,81] This model posits that during unilateral mastication the most important deformation regimes in the balancing-side mandibular corpus are sagittal bending (that is, bending in sagittal planes), dorsoventral shear (in sagittal planes), and torsion about its long axis. On the working side, unilateral mastication is associated with torsion of the corpus about its long axis, dorsoventral shear and, to a lesser extent, bending in sagittal and transverse planes. The mandibular symphysis experiences dorsoventral shear, bending in coronal planes due to twisting of the mandibular corpora and "wishboning" caused by lateral transverse bending of the mandibular corpora. In anthropoids, wishboning is the dominant deformation regime during unilateral mastication; during unilateral biting, the most important deformation regimes are twisting about a transverse axis and bending in coronal planes.

Invoking this model, various workers have related external (depth and width)[40,41,107,108] or internal (cortical bone distribution)[84,109–114] dimensions of the corpus and symphysis to variation in diet. Review of these studies does not reveal a convincing relationship between mandible morphology and either dietary category or FMPs.[38,107,108,115–118] We suggest that this is because of our incomplete understanding of the relationships between variation in feeding behavior and variation in strain, stress, and deformation regimes in primate mandibles (Fig. 7). For example, jaw kinematic data reveal that, contrary to predictions,[40,41] tougher foods do not elicit more transverse jaw movements[37,41,119] and therefore probably are not chewed with more laterally directed bite reaction forces nor greater mandibular torsion or transverse bending. External measures of mandibular morphology may also primarily capture variation in the ability of the feeding system to generate force and transmit it to the bite point, rather than its ability to resist these forces internally.

IS SKULL MORPHOLOGY OPTIMIZED FOR GENERATION AND TRANSMISSION OF FORCES TO THE BITE POINT?

Although it is difficult to marshal a convincing case for strong and pervasive covariation between skull morphology and the ability to resist internal forces acting in the skull during feeding on different diets, a strong case can be made for covariation between skull morphology and the ability to generate and transmit force*s* during feeding on different diets. This has also recently been shown to be the case in bats.[143] This principle is manifest through variation in muscle mechanical advantage, the ratio of the lever arm of a muscle to the lever arm of the bite point. Mechanical advantage is an important determinant of both the total amount of force that can be generated by a given amount of muscle and the efficiency with which muscle force is converted into force. Colobines have a greater mechanical advantage of the masseter and larger attachment areas for masseter and medial pterygoid muscles than do cercopithecines and are more folivorous.[68,120] *Macaca fuscata* has a more anteriorly placed masseter muscle than other macaques and probably a tougher, harder diet.[121] Asian colobines that eat more seeds (*Presbytis rubicunda* and *Trachypithecus phayrei*) have better mechanical advantage of the jaw muscles than species that rarely exploit seeds (*Presbytis comata, Trachypithecus obscurus*, and *Semnopithecus vetulus*).[122] Inuit generate relatively high bite forces and have enlarged muscle attachment areas and better jaw mechanical advantage than other native Americans.[123] Tufted capuchins have jaw muscles that are relatively larger and have better leverage than those of other capuchins, facilitating feeding on large, hard objects.[51,124] Moreover, the most often cited explanations for variation in fossil hominin cranial form focus on variation in hominin ability to generate force, not to resist it.[125,126]

Covariation between skull morphology and the ability to generate and transmit force to the bite point is also reflected in aspects of feeding system design related to gape. Anteroposteriorly long TMJs are linked to wide gape behaviors, such as tree-gouging in callitrichids and *Phaner,*[85] vocalization in *Alouatta*, seed predation in pitheciines,[39] and adaptations to gape in great apes.[39] Adaptations in callitrichid mandibles for resisting stresses associated with gouging are unremarkable,[84,85,127] but their mandible shapes do facilitate large gapes and their jaw muscles are designed for the extensive excursion required for large gape gouging.[49,83] Because the jaw elevator muscles need to be stretched during jaw opening, the maximum possible gape is determined, all else being equal, by the maximum amount of possible muscle stretch. For a given amount of muscle stretch, the farther forward the masseter is positioned, the smaller the maximum possible gape distance. In addition, as discussed in Box 1, muscle stretch can decrease the amount of force a muscle can generate. Thus, when mechanical advantage is improved through rostral displacement of the jaw elevator muscles, there are trade-offs in maximum possible gape distance. The importance of this design constraint is revealed by the observation that variation in relative jaw gape is related to relative canine height.[128] Thus, selection for improved mechanical advantage has to trade off with large gape requirements imposed by feeding behaviors, such as gouging, and social behaviors, such as threat displays. One way to minimize the detrimental effects of muscle stretch during jaw depression is by locating the axis of rotation of the mandible below, rather than at, the TMJ.[10,129,130]

Another trade-off in feeding system design is the constraint on bite force magnitudes at nonmidline bite points enforced by the requirement that the TMJs not be subjected to tensile (distractive) forces.[131] This constraint has been conceptualized using the "triangle of support," with vertices at the two TMJs and the bite point. For all three vertices to be under compression during biting, the resultant of the jaw elevator muscle forces must lie within this "triangle of support." The trade-off arises when the bite point is located off the midline, the triangle is reduced in size, and its anterior edge is displaced posteriorly. In order to maintain the jaw elevator muscle resultant within the "triangle of support," the balancing or nonbiting side muscle force amplitudes must be reduced. This moves the muscle resultant toward the working side and into the "triangle of support," but reduces the maximum bite force that can be generated at nonmidline bite points. Morphological and experimental evidence corroborates the hypothesis that it is important to maintain compressive forces at the TMJs during biting and chewing off the midline.[132,133] This is another way in which feeding system design reflects selection for generation and transmission of bite forces. Presumably, the control mechanisms for maintaining the muscle resultant in the "triangle of support" use feedback from the periodontal afferents and muscle spindles described earlier, along with stretch receptors in the ligaments around the TMJ.

CONCLUSIONS

Why are relationships of craniomandibular morphology with feeding behavior and diet so weak? For example, why does variation in the percentage of time spent feeding within dietary categories — folivory, frugivory and insectivory — map nicely onto some aspects of dental occlusal morphology[134] but not onto variation in mandibular and cranial morphology?[38] Why has incorporation of data on FMPs not improved the mapping of mandible form to diet?[38] Our review of the literature suggests that the lack of strong relationships between craniomandibular morphology and either feeding behavior or diet is in part real: It reflects trade-offs in primate feeding system design enforced by the multiple performance criteria that the feeding system must meet.

One source of trade-offs is the wide range of behaviors used in feeding, such as preingestive food preparation; ingestive biting with incisors, canines, premolars or molars; and chewing, swallowing, and digestion. What is good for one behavior might not be good for another. Chewing food a lot certainly increases bolus' surface area and aids digestion, but it makes the food bolus unsafe to swallow.[135] Long muscle fibers facilitate wide gape behaviors for food acquisition, but they compromise the ability of those muscles to generate high forces at smaller gapes.

Why are relationships of craniomandibular morphology with feeding behavior and diet so weak? For example, why does variation in the percentage of time spent feeding within dietary categories — folivory, frugivory and insectivory — map nicely onto some aspects of dental occlusal morphology[134] but not onto variation in mandibular and cranial morphology?

Another source of trade-offs in feeding system design is the nonfeeding behaviors that the system is used for, such as vocalizing, fighting, and threat displays. These impose functional requirements on craniomandibular morphology that do not facilitate feeding performance, resulting in features such as brow ridges and large canines that are not optimized for feeding functions.[96,128] These trade-offs highlight the need for biomechanical analysis not only of all aspects of primate feeding behavior, but also of the role of the feeding system in nonfeeding behaviors. Better data are needed on the relative importance (in time and number of cycles) of feeding behaviors employed in wild primates and their biomechanical correlates (muscle activity, kinematics, strain).

Another reason for the lack of strong relationships between craniomandibular morphology and either feeding behavior or diet may be the influence of phylogenetic history on primate feeding system design. When analyses have been done in a phylogenetic context, they have revealed important patterns: very weak scaling of daily feeding time with body size;[38] no relationship between gut mean retention time and body size;[75] no relationship between working or balancing jaw elevator EMG amplitude ratios and jaw robusticity;[46] and no relationship between superficial masseter W/B ratios and mandibular corpus area;[46] but a relationship between balancing-side deep masseter timing and symphyseal cross-sectional area.[46] Many of the biomechanical studies of the last few decades have not used phylogenetic techniques. The distribution of variance in feeding system morphology and behavior across primate phylogeny needs to be better documented. As more data on jaw kinematics and jaw muscle EMG patterns accumulate, it will be interesting to see whether the conserved primate jaw kinematic patterns reflect conservation of an inherited central motor pattern and/or geometric constraints imposed by the functional requirements of mastication.[46]

Despite the confounding influences of functional trade-offs and phylogenetic inertia, morphometric analyses have established relationships between the external morphology of primate feeding systems and the ability of the system to generate and transmit forces to the bite point. This suggests that the weak and inconsistent relationships between external morphology and internal force resistance may also be real. One possibility is that variation in internal force resistance is more highly correlated with internal than external morphology of the mandible. Evaluating this hypothesis will require better data on internal morphology of the skull, especially the mandible, and how this is related to patterns of stress and strain during different feeding behaviors.[112,113] However, it is possible that even internal mandible morphology is not strongly and directly related to specific feeding behaviors and diets. Some strain regimes, particularly shear, do not make strong predictions as to exactly how bone is distributed within mandible, only that there is enough bone. The fact that primate mandibles are so short relative to their depth means that shear could well be their dominant strain regime, predicting no relationships of internal and external mandible shape to feeding behavior and diet.

At this time we cannot confidently use skull morphology to reconstruct diet and feeding behavior in fossil primates. Dental morphology has proven useful in the past, probably because it is directly at the interface between organism and food, and will probably continue to dominate in this domain. However, it has its limitations.[136] Continued research on relationships among skull morphology, diet, and feeding behavior in living primates promises to reveal new insights into feeding in fossil primates.

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CORRIGENDUM

In the recently published news article “Upholding the Legacy: East African Association for Paleoanthropology and Paleontology Held Its 4th Biennial Meeting in Kenya” by Emmanuel Ndiema and Amanuel Beyin (Evolutionary Anthropology 23:41–43), sponsors for the conference were inadvertently omitted.

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