

## **Tooth Orientation during Occlusion and the Functional Significance of Condylar Translation in Primates and Herbivores**

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### **Introduction**

The temporomandibular joint (TMJ) in carnivores is a ginglymoid (hinge) joint in which the preglenoid and postglenoid processes limit anteroposterior movements of the mandibular condyle, permitting almost exclusively rotation around a transverse axis (Becht, 1953; Maynard Smith & Savage, 1959; Noble, 1973; Freeman, 1979; Crompton, 1981). In contrast, the TMJ in anthropoid primates and several orders of specialized herbivores (Perissodactyla and Artiodactyla) is a diarthroidal joint that permits the mandibular condyles not only to rotate around a transverse axis but also to slide anteroposteriorly (“translate”) relative to the glenoid fossa during jaw closure and opening. In a study on goats, De Vree and Gans (1975) pointed out that lateral shifts of the mandible in animals with a diarthroidal TMJ must occur by the translation of one condyle in its fossa coincident with rotation of the opposite condyle about a vertical axis through the second fossa. There is little precise information on how the active and balancing side condyles move relative to the glenoid fossae during a masticatory cycle. Weijs (1994) claimed that, during closing, medially directed movement of the working side mandible is essentially a pure rotation around the working side condyle, which is braced against the postglenoid flange. Extensive transverse jaw movements obviously require an anteroposteriorly long glenoid. However, it is not obvious why both condyles move anteriorly during opening and posteriorly (at different rates) during closing given that medial and lateral movement of the mandible can be accomplished by rotating the mandible about a stationary working side condyle that is buttressed against the postglenoid flange while translating the balancing side condyle. It is this aspect of condylar translation that we wish to discuss in this paper.

Several hypotheses have been proposed to explain anteroposterior condylar translation in the diarthroidal TMJ. First, Moss (1960, 1975, 1983) suggested that condylar translation is an adaptation to stabilize the axis of rotation of the mandible near the location of the mandibular

foramen. Second, following on Moss's observation, Carlson (1977), Hylander (1978, 1992), and Weijs et al. (1989) proposed that condylar translation is an adaptation to maximize the contractile force of the masseter and medial pterygoid muscles during jaw adduction by minimizing their stretching. The position of the masseter and medial pterygoid muscles relative to the TMJ and molar rows constrains not only how far the jaws can open but also the maximum gape at which effective force can be generated by the adductors. Muscle stretching is an important biomechanical consideration because the length-tension curve of sarcomeres becomes less efficient when muscles elongate beyond forty to fifty percent of their resting length (McMahon, 1984). Support for this hypothesis comes from several sources. Smith (1985) found that maximum jaw abduction without translation in humans would stretch the masseter by approximately forty-one percent, approximately twice the twenty-one percent stretching observed with translation. Wall (1995) found that condylar translation during mastication and incision in anthropoid primates moved the mandible's instantaneous center of rotation anteriorly, thereby minimizing stretching and maximizing bite force for the masseter, medial pterygoid, and anterior temporalis over a range of gapes. However, varying the orientation of fibers within different regions of individual muscles can partially compensate for different degrees of stretching and has been shown to characterize the masseter of many mammals with diarthroidal TMJs, including hippopotami, suids, and hyracoids (Herring, 1975, 1980; Herring et al., 1979; Janis, 1979, 1983). In addition, kinematic and electromyogram studies of human mastication indicate that the optimum lengths of the masseter and medial pterygoid occur near resting position at 10–20 mm of gape (Garrett et al., 1964; Manns et al., 1981; Rugh & Drago, 1981). In fact, peak contraction of the masseter in primates, goats, and other mammals occurs just before maximum intercuspsation, toward the end of the power stroke when stretching of the adductors would be minimal (De Vree & Gans, 1975; Hylander & Johnson, 1985, 1993; Hylander et al., 1992; Lieberman & Crompton, 2000).

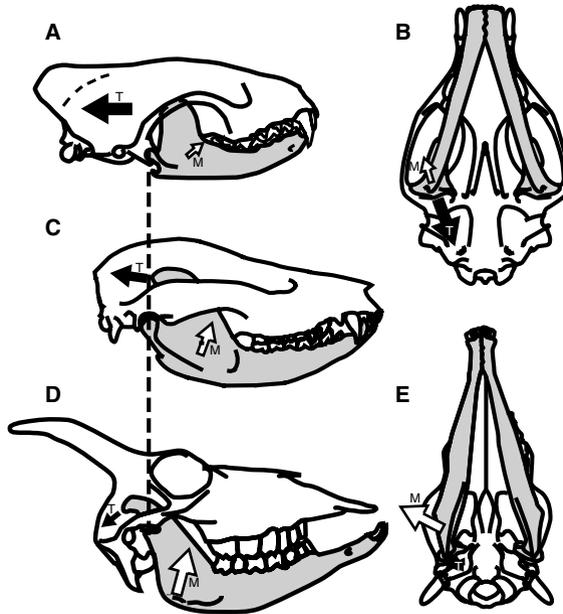
Another hypothesis, proposed by Smith (1985) and others (e.g., Craddock, 1948; DuBrul, 1964; Herring, 1975; Mack, 1984) is that condylar translation is an adaptation to prevent impingement of the esophagus, trachea, carotid sheath, and the larynx by the posterior margins of the mandible, tongue, and suprahyoid muscles during maximum gape. Impingement of these structures is an evident problem in humans in which upright posture, in combination with a descended larynx and a highly flexed cranial base, positions these structures within a few millimeters of

the posterior margin of the mandibular ramus at resting position (Smith, 1985). The impingement hypothesis, however, is an unlikely explanation for condylar translation in many quadrupedal mammals with highly extended (flat) cranial bases in which the pharynx is oriented craniocaudally away from the mandibular ramus (Smith, 1985; Hylander, 1992). There is no evidence that the deep mandibular angle and tongue impinge on the pharynx in these species during maximum gape.

### **Model (A)**

It is very likely that condylar translation serves more than one function. We propose here an additional hypothesis: that condylar translation is an adaptation for occlusion. In particular, we suggest that, in nonrodent mammals whose tall mandibular rami position the occlusal plane below the level of the TMJ, the working and balancing side condyles are retracted at slightly different rates from their protracted position at the end of opening to maintain a vertical trajectory of the working side lower molariform teeth relative to the upper molariform teeth during unilateral mastication.

To introduce the above hypothesis, it is useful to review variations in the anatomy of the TMJ in the context of the overall design of the mammalian masticatory system. One major difference between mammals with and without condylar translation is the position and orientation of the jaw adductors relative to the tooth row. In mammals with a ginglymoid (hinge) TMJ, the joint usually lies on or close to the same plane as that of the lower dentition (figs. 11.1A, 11.2A), whereas the diarthroidal TMJ (sliding hinge) usually occurs in association with a vertically tall mandibular ramus that positions the glenoid fossa well above the occlusal plane of the posterior dentition (figs. 11.1D, 11.2B). These differences relate partly to the pattern of molar occlusion. Mammalian carnivores, especially felids and mustelids, have molars designed for crushing and slicing (Mills, 1967; Crompton & Kielan-Jaworowska, 1978). Masticatory movements are primarily orthal, with only a small medially directed component (Mills, 1967; Crompton, 1981; Weijjs, 1994). The dentary condyle, which is cylindrically shaped and transversely oriented (fig. 11.1A, B), is tightly held within the temporal bone by postglenoid (also referred to as retroarticular) and preglenoid processes. These processes limit jaw movement to the sagittal plane, permitting only a slight amount of mediolateral shifting of the jaw as a whole. The dominant adductor muscle in mammals with ginglymoid TMJs is the temporalis. The moment arm of the posterior temporalis is a function of the distance of its insertion point on the coronoid process to the TMJ. The combination of a tall coronoid process and extension of the



**Figure 11.1.** Comparison of TMJ and cranial morphology in mammals with ginglymoid and diarthroidal TMJs. (A, B) Lateral and inferior views of a mustelid (*Martes pennanti*) with a ginglymoid TMJ.

Note the TMJ lies in the same plane as the postcanine occlusal plane; the dominant adductor is the temporalis, T; the superficial masseter, M, is small, in a parasagittal plane, and anteriorly oriented. The sizes of the arrows indicate schematically the relative size of the temporalis versus the masseter and medial pterygoid complex. (C) Lateral view of opossum (*Didelphis virginianus*) in which the short diarthroidal TMJ lies slightly above the occlusal plane; the temporalis and masseter muscles are roughly equivalent in size; the masseter is more laterally and dorsally oriented than in the carnivore. (D, E) Lateral and inferior views of a goat (*Capra hircus*). Note the tall ramus, which positions the occlusal plane well below the long diarthroidal TMJ; the temporalis is small relative to the size of the masseter. The masseter has a strong dorsal and lateral orientation, whereas the medial pterygoid has a dorsal and medial orientation.

skull posterior to the TMJ permits both a large gape and a powerful bite. The superficial masseter inserts close to the TMJ and therefore adds speed without restricting gape. The postglenoid processes resists the posteriorly directed force of the temporalis and the preglenoid process resists the anteriorly directed force of the superficial masseter. These two muscles acting synchronously on one side form a force couple that tends to move the jaw medially; the flanges prevent this movement.

In herbivores, the masseters and medial pterygoids tend to be the dominant adductor muscles, composing 50–80 percent of total adductor mass, whereas the temporalis composes twenty to thirty percent of

adductor mass (Janis, 1979; Weijs, 1994). Herbivores have a tall ascending ramus, which effectively positions the mandibular condyle high above the occlusal plane. A postglenoid flange resists the posteriorly directed force of the temporalis. The orientation of the fibers of the superficial masseter and medial pterygoid is more vertical than in typical mammalian carnivores and a preglenoid flange, which would limit condylar translation, is not present. In some cases (e.g., the pygmy hippopotamus), the mass of the masseter and medial pterygoid muscles is increased by positioning the posteroventral margin of the expanded mandibular angle considerably below the occlusal plane (Herring, 1975). Mammals with a diarthroidal TMJ also tend to have molars primarily designed for grinding (Becht, 1953; Kay & Hiiemae, 1974; Kay, 1978; Lucas, 1982; Janis, 1983; Herring, 1985; Hiiemae & Crompton, 1985; Weijs, 1994). In ungulates and primates, the lower molars and molariform premolars on the working side mandible are drawn transversely across the upper dentition to triturate material. The amount of dorsal movement that accompanies the transverse movement is highly variable: high in most artiodactyls and low in most perissodactyls (Becht, 1953). The flat condyle and long glenoid lacking preglenoid processes (fig. 11.1D) result in a highly mobile TMJ. Differential contraction of the jaw adductors on both sides can generate precisely controlled medially directed movements of the working side mandible (Becht, 1953; Crompton, 1981; Hiiemae & Crompton, 1985; Hylander et al., 1987; Hylander, 1992; Weijs, 1994).

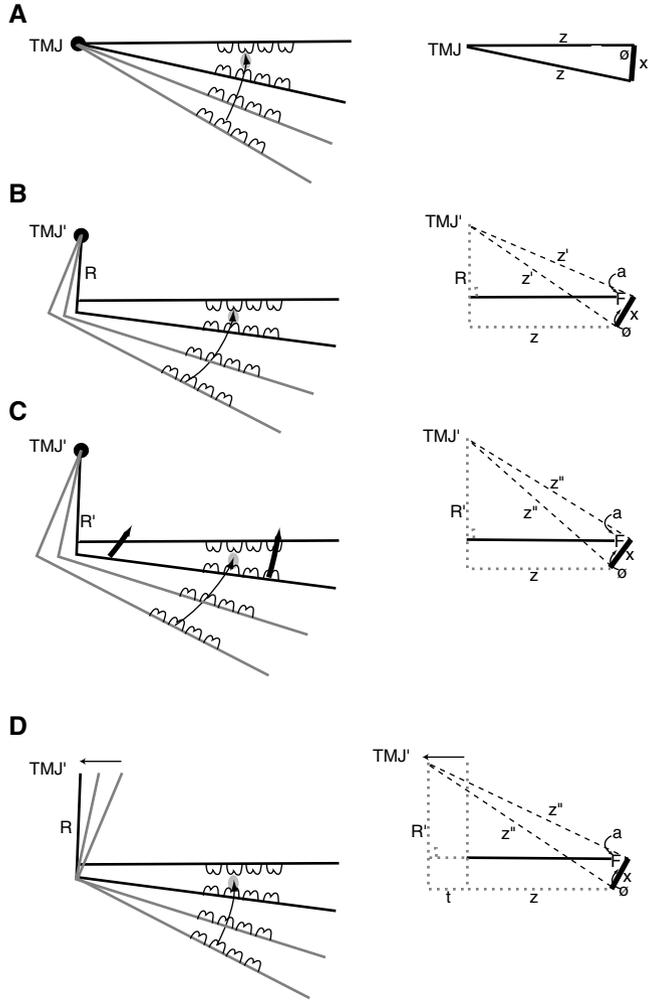
As noted previously (e.g., Osborn, 1987), positioning the TMJ well above the occlusal plane affects the parasagittal trajectory of the molariform teeth during jaw closure (fig. 11.2). In a masticatory system in which the plane of occlusion is in line with the glenoid fossa (fig. 11.2A), the distance between a given tooth and the center of rotation at the TMJ is the same for occluding teeth on the mandible and the maxilla. As a result, the trajectory of the lower tooth relative to the upper tooth in the sagittal plane,  $\emptyset$ , is a function of  $X$ , the distance between the two teeth, and  $Z$ , the distance to the TMJ:

$$\emptyset = \arccos(X/2Z)$$

so that  $\emptyset$  approaches  $90^\circ$  as  $X$  approaches 0. It is important to note, however, that tooth-food-tooth contact—when peak masticatory force is exerted—occurs before maximum intercuspatation (when  $X = 0$ ), so that  $\emptyset$  is always slightly less than  $90^\circ$ .

In mammals with diarthroidal TMJs (illustrated in fig. 11.2B), the occlusal plane is positioned below the glenoid fossa by a tall ascending

**Figure 11.2.** Geometric model of TMJ function in relation to occlusal plane position. (A) Ginglymoid TMJ in which the orientation of the mandibular tooth row relative to the maxillary tooth row,  $\phi$ , at any given gape,  $x$ , equals  $\arccos(X/2Z)$ . (B) Effect of positioning the occlusal plane below the TMJ by distance  $R$  so that  $\phi = \Phi - \alpha$  (see text for details), introducing an anterior component to the trajectory of the mandibular teeth relative to the maxillary postcanine occlusal plane. (C) Effect of increasing ramus height to  $R'$ , which makes  $\phi$  more acute relative to the postcanine maxillary occlusal plane (see text for details). Note also that  $\phi$  is more anteriorly oriented (thick arrows) for more posterior teeth that lie closer to the TMJ. (D) Effect of posterior translation on the orientation of the mandibular tooth row relative to the maxillary tooth row, making  $\phi$  more dorsally oriented.



ramus of length  $R$ , changing the center of rotation to  $TMJ'$ . Assuming the mandibular and maxillary planes of occlusion are perpendicular to the ascending ramus, this configuration increases the distance between occluding teeth and the center of rotation,  $Z'$ , in proportion to  $R$ :

$$Z' = (Z^2 + R^2)^{0.5}$$

so that

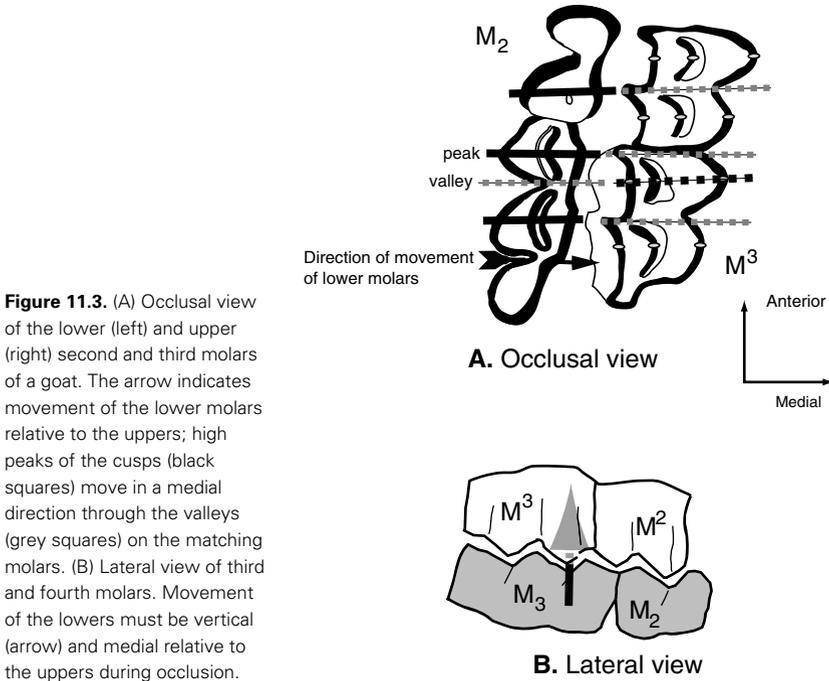
$$\Phi = \arccos[X/2 \cdot (Z^2 + R^2)^{0.5}].$$

It is important to note, however, that in this configuration  $\Phi$  does not describe the angle of the sagittal trajectory of a lower tooth relative to the maxillary tooth row,  $Z$ . This angle,  $\emptyset$ , is equal to  $\Phi - \alpha$ , where

$$\alpha = 90^\circ - [\arctan(Z/R) + (180^\circ - 2\Phi)]$$

As  $R$  gets larger,  $\emptyset$  becomes smaller for a given  $X$ , making the trajectory of a lower tooth relative to an upper tooth in the sagittal plane more acute. In other words, the taller the mandibular ramus, the more acute is the trajectory of the dentition during tooth-food-tooth contact. This effect of ramus length on  $\emptyset$  is illustrated in figure 11.2C. Note that the trajectory of  $\emptyset$  varies with position along the tooth row and is more acute for more posterior teeth that lie closer to the TMJ (see fig. 11.2C). In other words, the effect of positioning the tooth row below the TMJ on the anterior trajectory of the lower molars is greatest on the posterior teeth, which occlude at wider gapes than more anteriorly positioned teeth. Greaves (1974, 1978, 1980) has claimed that, in herbivores, because of the transverse movement of the jaw during the power stroke, it is important for the upper and lower molariform dentitions to occlude essentially simultaneously as food is ground. This can be true only of herbivores in which the occlusal surface of the molars is horizontal (i.e., at right angles to the sagittal plane). In this case all the teeth can come into occlusion before any transverse movement occurs. However, in most herbivores (especially artiodactyls), the occlusal plane of the molars relative to the sagittal plane is oblique and often as high as  $45^\circ$  (Becht, 1953). In this case, the posterior molars are the first to contact and the more anterior teeth occlude as the jaw moves mediodorsally.

Regardless of the angle of the occlusal plane of the molars relative to the sagittal plane, and the degree to which the jaw moves transversely and/or rotates longitudinally, the important point is that the lower teeth move dorsally and not anterodorsally during occlusion. Many lines of evidence support this point. For example, the pattern of wear of the molars in primates and ungulates indicates that, as the teeth come into occlusion, the lower molariform row moves dorsally and medially but not anteriorly relative to the upper row (fig. 11.3). Weijs (1994) recognized this feature when he pointed out that, at least in the rabbit, the lower tooth row approximates the upper in a vertical path, recognizing that the working side condyle must translate posteriorly as the teeth come into occlusion. It is unlikely, therefore, that the working side condyle is braced against the postglenoid flange before the working side jaw begins to move medially. Posterior translation of the mandibular condyle results in a more vertical trajectory for the



lower teeth. This effect (illustrated in fig. 11.2D) correctly aligns the lower molar shearing facets relative to those of the occluding upper molars.

We therefore predict that the amount of posterior translation of the working side condyle as the molars approach and enter into occlusion should vary as a function of the height of the TMJ above the postcanine occlusal plane ( $R$ , hereafter termed ramus height), independent of mandible length. In particular, the correlation between  $R$  and maximum anteroposterior translation distance (translation potential) of the working side condyle is predicted to be strong and independent of mandible length in both ungulate herbivores and primates. In addition, because the effects of positioning the occlusal plane below the TMJ on the orientation of tooth movement in the sagittal plane should be the same for all mammals with diarthroidal TMJs, the slope of the regression between ramus height and translation potential is predicted to be the same for primates, artiodactyls, and perissodactyls. In contrast, the anteroposterior length of the glenoid fossa in mammals with ginglymoid TMJs is expected to be independent of ramus height relative to mandibular length.

In short, condylar translation of the working side condyle during closing minimizes muscle stretching and also aligns the shearing surfaces on

occluding molars. We stress that, for the topography of the crowns of the occluding molars to “fit” one another as they come into occlusion, the working side lower jaw must move dorsally and medially but not anteriorly. Even in primitive mammals with tribosphenic molars such as the American opossum, where the lower tooth row is positioned slightly below the TMJ, the working side condyle translates during occlusion. Tribosphenic molars are characterized by embrasure shearing (Crompton & Kielan-Jaworowska, 1978), and, for the lower molars to move into occlusion, they must move vertically relative to the uppers. We suggest that the same constraint on occlusal trajectory was retained in ungulates and anthropoid primates and could have been maintained only if increasing amounts of condylar translation developed in parallel with the elevation of the TMJ above the occlusal surface.

## Materials and Methods

### Sample

Table 11.1 summarizes the sample studied. Measurements of mandibular and glenoid fossa size were taken on five males and five females from thirty-one mammalian species of various sizes with diarthroidal

**Table 11.1.** Sample studied (by order)

Primates	Artiodactyla + Perissodactyla	Carnivora
<i>Allouatta seniculus</i>	<i>Bison bison</i> (A)	<i>Canis latrans</i>
<i>Ateles paniscus</i>	<i>Bos taurus</i> (A)	<i>Canis lupus</i>
<i>Cebus olivaceus apiculatus</i>	<i>Camelus bactrianus</i> (A)	<i>Conepatus sonoriensis</i>
<i>Cercopithecus aethiops</i>	<i>Capra ibex</i> (A)	<i>Eira barbara</i>
<i>Colobus badius oustaleti</i>	<i>Madoqua kirki</i> (A)	<i>Felis catus</i>
<i>Gorilla gorilla gorilla</i>	<i>Equus burchelli boehmi</i> (P)	<i>Gulo gulo luscus</i>
<i>Homo sapiens</i>	<i>Equus caballus</i> (P)	<i>Mustela erminea kanel</i>
<i>Hylobates syndactylus</i>	<i>Equus zebra zebra</i> (P)	<i>Panthera leo</i>
<i>Lagothrix lagotricha cana</i>	<i>Giraffa camelopardalis</i> (A)	<i>Panthera tigris</i>
<i>Macaca fascicularis</i>	<i>Lama glama</i> (A)	<i>Ursus maritimus</i>
<i>Pan troglodytes schweinfurthii</i>	<i>Mazama americana</i> (A)	
<i>Papio hamadryas</i>	<i>Odocoileus virginianus</i> (A)	
<i>Pongo pygmaeus</i>	<i>Ovis ammon poli</i> (A)	
<i>Saguinus fuscicollis</i>	<i>Ovis canadensis canadensis</i> (A)	
<i>Saimiri sciureus oerstedii</i>	<i>Tapirus terrestris</i> (P)	

Note: Abbreviations: A, Artiodactyla; P, Perissodactyla.

TMJs from diverse families of primates ( $n = 15$ ), artiodactyls ( $n = 11$ ), and perissodactyls ( $n = 4$ ). In addition, as many of the same measurements as possible were taken on five males and five females from ten carnivoran species of various sizes with ginglymoid TMJs. All individuals were adults with all molars fully erupted and were sampled from the collections of the American Museum of Natural History (New York).

### **Measurements**

Measurements were taken with sliding digital calipers (accurate to 0.01 mm), with the exception of measurements greater than 200 mm, which were taken with plastic measuring tape (accurate to 1 mm). Whenever possible, measurements were taken on both sides of each individual and then averaged. The average standard error of measurement is estimated to be 0.36 mm on the basis of five sets of all measurements (see below) taken on the same individual.

Anteroposterior translation potential was measured in two ways. Maximum anteroposterior translation potential,  $TP_{\max}$ , was measured using the maximum anteroposterior length in the parasagittal plane between the postglenoid process and the anterior margin of the subcondral surface of the preglenoid plane. Note that  $TP_{\max}$  may overestimate the actual amount of translation that occurs because it estimates only the maximum amount of space available for anteroposterior translation of the condylar head relative to the articular surface of the glenoid fossa and preglenoid plane. A second estimate of translation,  $TP_{\min}$ , was therefore measured as the anteroposterior length in the parasagittal plane between the postglenoid process and the ventralmost point on the articular eminence in primates and between the postglenoid process and the midpoint of the articular plane in herbivores. In carnivores,  $TP_{\text{carn}}$  was measured as the maximum anteroposterior distance between the preglenoid and postglenoid processes. These estimates of anteroposterior translation need to be verified with kinematic studies (e.g., Wall, 1995), but there is some indication that  $TP_{\max}$  is a reasonably accurate predictor of actual translation potential. Cinefluorographic studies indicate that maximum anteroposterior translation in humans is 18–20 mm (Smith, 1985), which is almost the same as the  $TP_{\max}$  value reported here (21.2 mm).

The height of the postcanine occlusal plane below the glenoid fossa,  $R$ , was measured from the most dorsal point on the condyle perpendicular to the plane of occlusion of the mandibular molars (determined by placing a thin rod along the molar tooth row). Because  $R$  correlates strongly across species with mandibular length (Wall, 1995, 1999), the

total anteroposterior length of the mandible, ML, was measured in the midline from the gonial angle to the anteriormost point on the symphysis.

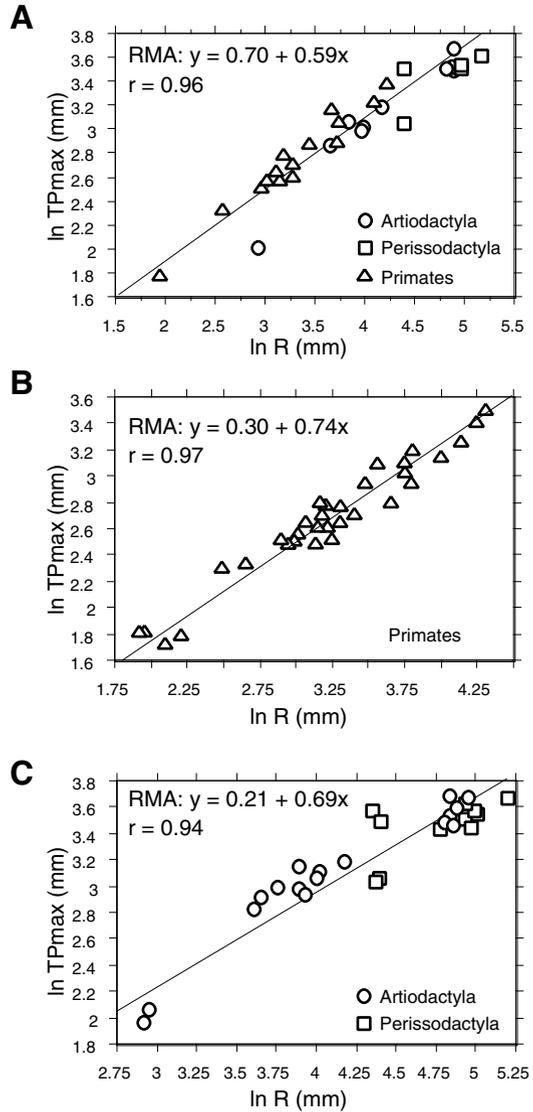
### **Analysis**

All measurements were entered into Statview 4.5 (Abacus Concepts, Berkeley) and mean values were determined for all species by sex. Several statistical tests were used to examine the hypothesized relationship between  $R$ , the height of the occlusal plane below the TMJ, and estimated anteroposterior translation ( $TP_{\max}$ ,  $TP_{\min}$ , and  $TP_{\text{carn}}$ ). Most importantly, reduced major axis (RMA) regression of logged measures of  $R$  versus TP was used to examine the correlation between and scaling of these variables (Sokal & Rohlf, 1995). Because of the strong correlation between ramus height and mandibular length (Wall, 1995, 1999), partial correlation analysis was used to estimate the strength of the correlation between  $R$  and the estimates of anteroposterior translation independent of mandibular length. Significance of Pearson correlation coefficients was determined by Fisher's  $r$ - $z$  test; significance of partial correlations was determined by using the significance of partial regression coefficients (Sokal & Rohlf, 1995). Finally, least-squares regressions were also computed for estimated anteroposterior translation versus  $R$  standardized by mandibular length as an alternative means of examining the strength of the relationship between translation potential and  $R$  independent of mandibular size.

### **Results**

Correlation and partial correlation coefficients for  $R$ , TP, and ML are summarized for the pooled sample of primates, perissodactyls, and artiodactyls in table 11.2, for primates in table 11.3, for perissodactyls and artiodactyls in table 11.4, and for carnivorans in table 11.5. Among the pooled sample of primates and ungulates (table 11.2A), there is a strongly correlated and highly significant ( $r = 0.927$ ;  $P < 0.001$ ) negative allometry ( $b = 0.594$ ) between  $TP_{\max}$  and  $R$  (fig. 11.4A). Because of the high correlation between mandibular length and ramus height ( $r = 0.927$ ), only a proportion of this relationship ( $r = 0.579$ ,  $P < 0.001$ ) is attributable to  $R$  independent of mandibular length as determined by partial correlation analysis. The relationship between  $TP_{\min}$ ,  $R$ , and ML is almost the same as that between  $TP_{\max}$ ,  $R$ , and ML (see table 11.2B, and fig. 11.5).

When these predicted relationships are examined for primates and the ungulate herbivores separately, several important patterns are evident. Among primates (table 11.3), there is a strongly correlated and highly significant ( $r = 0.974$ ;  $P < 0.001$ ) negative allometry ( $b = 0.74$ ) between



**Figure 11.4.** Reduced major axis regression of log-transformed  $R$  versus  $TP_{\max}$ . (A) Combined sample of primates and ungulate herbivores; (B) primates; (C) combined herbivore sample (artiodactyls and perissodactyls). The slopes of the primate and herbivore regressions are not significantly different from each other but both are significantly different from isometry ( $P < 0.001$ ).

$TP_{\max}$  and  $R$  (fig. 11.4B). While the Pearson correlation coefficient between  $R$  and  $TP_{\max}$  is high ( $r = 0.963$ ,  $P < 0.001$ ), mandibular length also correlates strongly with both  $R$  ( $r = 0.935$ ,  $P < 0.001$ ) and  $TP_{\max}$  ( $r = 0.972$ ,  $P < 0.001$ ), raising the possibility that any relationship between  $R$  and  $TP_{\max}$  may be an autocorrelation with mandibular length. Partial correlation analysis, however, indicates that, when the effects of mandibular

**Table 11.2.** Correlation (A) and partial correlation (B) coefficients for pooled primate, perissodactyl and artiodactyl sample

<b>A</b>			
Variable	<i>R</i>	TP <sub>max</sub>	ML
<i>R</i>	—	0.927***	0.927***
TP <sub>max</sub>	0.579***	—	0.896***
ML	0.580***	0.260 ns	—
<b>B</b>			
Variable	<i>R</i>	TP <sub>min</sub>	ML
<i>R</i>	—	0.938***	0.927***
TP <sub>min</sub>	0.614***	—	0.907***
ML	0.522***	0.291 ns	—

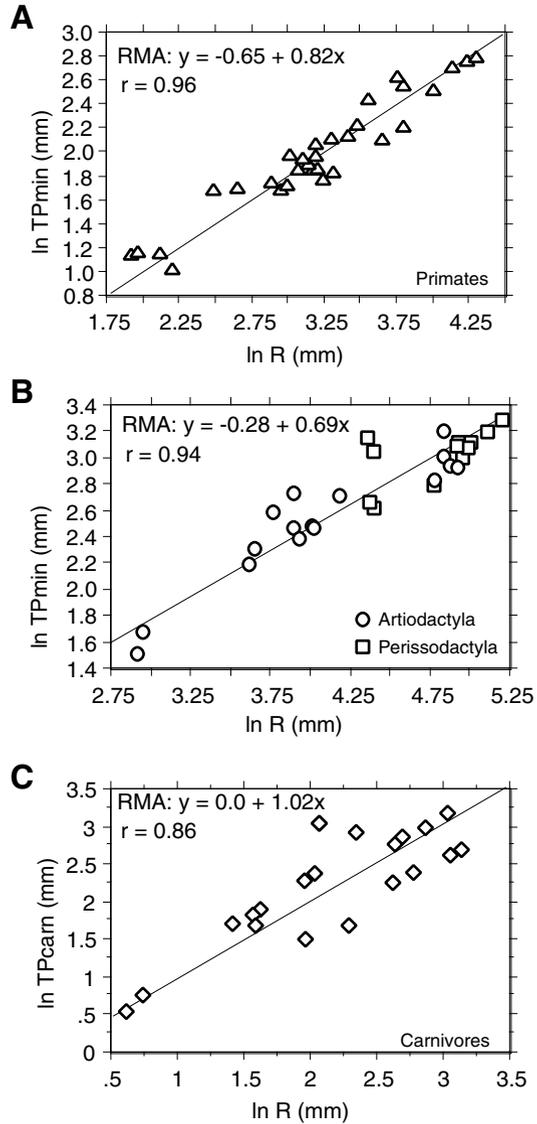
Note: Abbreviations: *R*, height of the TMJ above the occlusal plane; ML, distance between gonial angle and most anterior point on symphysis; TP<sub>max</sub>, maximum translation potential of the condyle estimated from the cranium (see Methods); TP<sub>min</sub>, minimum translation potential of the condyle estimated from the cranium (see Methods). Significance: \* =  $P < 0.05$ ; \*\* =  $P < 0.01$ ; \*\*\* =  $P < 0.001$ ; ns = not significant.

**Table 11.3.** Correlation (A) and partial correlation (B) coefficients for primate sample

<b>A</b>			
Variable	<i>R</i>	TP <sub>max</sub>	ML
<i>R</i>	—	0.963***	0.935***
TP <sub>max</sub>	0.649**	—	0.972***
ML	-0.20 ns	0.752***	—
<b>B</b>			
Variable	<i>R</i>	TP <sub>min</sub>	ML
<i>R</i>	—	0.941***	0.935***
TP <sub>min</sub>	0.612**	—	0.910***
ML	0.564***	0.249 ns	—

Note: Abbreviations as in Table 11.2.

length are held constant, the relationship among primates between *R* and TP<sub>max</sub> is moderately strong ( $r = 0.649$ ,  $P < 0.01$ ). The independence of this relationship is corroborated by the results shown in fig. 11.6A, which illustrates the moderately strong correlation ( $r = 0.733$ ,  $P < 0.001$ ) between translation potential and *R* standardized by mandibular length. Table 11.3B and figures 11.4B and 11.5A confirm that the correlation and



**Figure 11.5.** Reduced major axis regression of log-transformed  $R$  versus  $TP_{\min}$ . (A) Primates. (B) Combined herbivore sample (artiodactyls and perissodactyls). (C) Carnivores. The slopes of the primate and herbivore regressions but not the carnivores are significantly different from isometry ( $P < 0.001$ ).

strength of the relationship between  $R$  and  $ML$  with  $TP_{\min}$  are very similar to those between  $R$ ,  $ML$  and  $TP_{\max}$ .

As predicted by the above model, the ungulate herbivores exhibit a pattern similar to that in primates in which the coefficients of allometry between  $TP_{\max}$  and  $R$ , and between  $TP_{\min}$  and  $R$  (in both cases,  $b = 0.69$ ), are almost the same as in the primate sample (see table 11.4, figs. 11.4C,

**Table 11.4.** Correlation (A) and partial correlation (B) coefficients for the combined artiodactyl and perissodactyl sample

<b>A</b>			
Variable	<i>R</i>	TP <sub>max</sub>	ML
<i>R</i>	—	0.903***	0.878***
TP <sub>max</sub>	0.502**	—	0.923***
ML	0.267 ns	0.635***	—
<b>B</b>			
Variable	<i>R</i>	TP <sub>min</sub>	ML
<i>R</i>	—	0.894***	0.878***
TP <sub>min</sub>	0.568**	—	0.861***
ML	0.475**	0.354 ns	—

Note: Abbreviations as in Table 11.2.

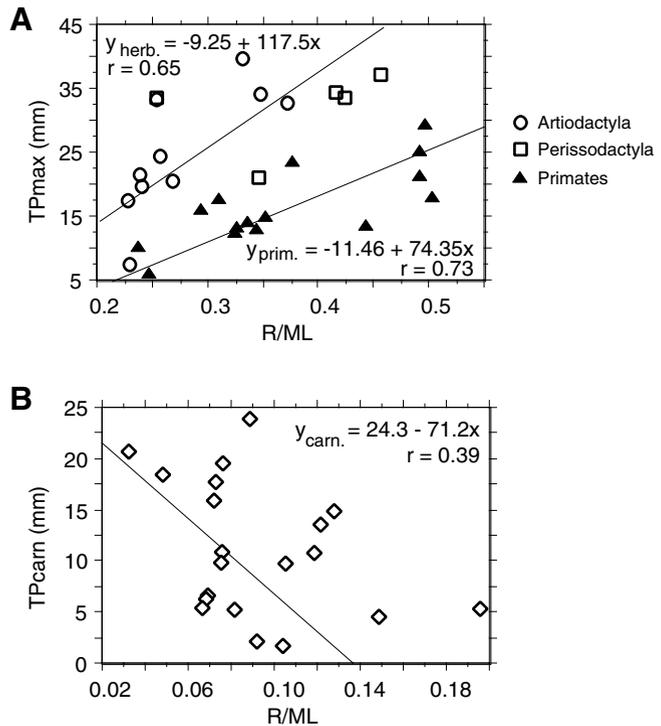
11.5B). As in primates, Pearson correlation coefficients between TP<sub>max</sub> and *R* ( $r = 0.903$ ;  $P < 0.001$ ) and between TP<sub>max</sub> and ML ( $r = 0.878$ ;  $P < 0.001$ ) are high, but when mandibular length is controlled for using partial correlation analysis, the relationship between *R* and TP<sub>max</sub> is moderate and highly significant ( $r = 0.502$ ;  $P < 0.01$ ) (table 11.4A). As figure 11.6 illustrates, this relationship is not as strong ( $r = 0.647$ ;  $P < 0.01$ ) and is significantly steeper than in the primate sample, presumably because total mandibular length relative to the position of the molar tooth row is much greater in most ungulate herbivores than in primates, which have shorter rostra relative to overall cranial size. Table 11.4 indicates that the correlation and partial correlation coefficients of *R*, ML, and TP<sub>min</sub> in the ungulate herbivore sample are almost identical to those between *R*, ML, and TP<sub>max</sub>.

The relationship between TP<sub>carn</sub>, *R*, and ML in the carnivorans with ginglymoid TMJs is quite different in several respects from that observed in primates, artiodactyls, and perissodactyls. First, the coefficient of allometry between *R* and TP<sub>carn</sub> is isometric ( $b = 1.02$ ,  $r = 0.857$ ) rather than negative (fig. 11.5C). In addition, while there is a moderately strong correlation between TP<sub>carn</sub> and *R* ( $r = 0.718$ ,  $P < 0.01$ ), the partial correlation between these dimensions is close to zero ( $r = -0.094$ , ns) when the effects of mandibular length are controlled for by partial correlation analysis (table 11.5). When TP<sub>carn</sub> is plotted against *R* standardized by mandibular length (fig. 11.6B), the correlation is both low ( $r = 0.392$ , ns) and negative ( $b = -71.17$ ), in contrast to the moderate and positive relationship

**Table 11.5.** Correlation coefficients for the carnivoran sample

Variable	<i>R</i>	TP <sub>carn</sub>	ML
<i>R</i>	—	0.718*	0.743***
TP <sub>carn</sub>	-0.094 ns	—	0.983***
ML	0.287 ns	0.964***	—

Note: Abbreviations as in Table 11.2; TP<sub>carn</sub>, maximum anteroposterior distance between pre- and postglenoid flanges.



**Figure 11.6.** Least squares regression plots of *R* standardized by mandibular length (ML) against (A) TP<sub>max</sub> in primates, perissodactyls, and artiodactyls; and (B) TP<sub>carn</sub> in carnivores.

between *R* and TP/ML in primates, artiodactyls, and perissodactyls with translating TMJs.

## Discussion

Condylar translation on the working side during postcanine mastication occurs in taxa whose masticatory systems are dominated by the masseter and medial pterygoid muscles and whose occlusal planes are

positioned below the plane of the TMJ by a tall mandibular ramus. Previous studies (e.g., Carlson, 1977; Hylander, 1978; Smith, 1985; Weijs et al., 1989) have focused on two disadvantages of this configuration: it limits gape, and it exacerbates muscle stretching during wide-gape positions. Although both problems are reduced and/or eliminated by condylar translation, there are several reasons to believe that condylar translation may have additional and possibly alternative evolutionary bases.

The above results provide preliminary support for the additional hypothesis, which is not mutually exclusive of those discussed above, that anteroposterior condylar translation is an adaptation to reduce the extent to which the lower postcanine teeth move anteriorly relative to the upper postcanine teeth during jaw closure in mammals whose tooth row lies below the plane of the TMJ. As shown above, in the absence of translation, anteriorly directed movements of the teeth are a direct, unavoidable trigonometric function of the depth of the tooth row below the glenoid fossa: the trajectory of the lower teeth relative to the upper teeth during the power stroke becomes more anteriorly oriented as a function of this distance. In addition, more posterior teeth have more anteriorly oriented trajectories than more anterior teeth. Anteriorly oriented occlusal trajectories are a significant problem, because mammal molars (with the exception of rodents) have morphologies and wear facets that indicate that the jaw moves dorsally, coupled with various amounts of medial movement during occlusion (fig. 11.3). Of course, molar wear can considerably modify the topography of the crowns of recently erupted molars. Given that condylar translation causes a vertical trajectory of the lower molars as they come into occlusion, it could be argued that the orientation of the matching wear facets on occluding molars is simply a by-product of condylar translation, which therefore would not be an adaptation for reorienting tooth movements during occlusion. We reject this view because of the topography of the crowns of unworn molars of primates and ungulates as well as mammals with tribosphenic molars. The unworn molars of these mammals can occlude correctly only if lower jaw movements are vertical and lack an anteriorly directed component. Consequently, changing the instantaneous center of rotation through condylar translation must compensate for the biomechanical advantages of dropping the tooth row below the TMJ.

The hypothesis that translation is an adaptation to reorient the trajectory of the postcanine mandibular teeth relative to maxillary teeth in mammals with occlusal planes below the TMJ specifically predicts a

strong correlation between translation potential and  $R$ , the height of the postcanine tooth row below the TMJ, independent of mandibular size. As shown above, this prediction is supported by regression analysis and partial correlation analysis for perissodactyls, artiodactyls, and primates, but not for carnivores. Wall (1999) also found a strong relationship between ramus height and the degree of translation in anthropoid primates. In addition, because the trigonometric relationship between  $R$  and the sagittal trajectory of the lower teeth relative to the upper teeth must be the same for all mammals, the coefficient of allometry between translation potential and the height of the postcanine tooth row below the TMJ is predicted to be the same in primates and ungulate herbivores. This prediction is also supported by the results presented above for the relationship between  $R$  and  $TP_{\max}$ , which is not significantly different in ungulates and primates but is less strong for the relationship between  $R$  and  $TP_{\min}$ . Negative allometry in this case makes sense because the relationship between the angle of the lower-to-upper molariform teeth ( $\emptyset$ ) is a nonlinear cosine function (see above). Thus, the scaling relationship between anteroposterior linear translation ("t" in fig. 11.2) and  $R$  should scale with negative allometry to maintain a constant  $\emptyset$  (the slope varying depending on the value of  $\emptyset$ ). In contrast, the length of the glenoid fossa in which any translation can occur in carnivores is isometric with the height of the postcanine tooth row below the TMJ. In other words, glenoid fossa length in carnivores scales with jaw size. In fact, the length of the glenoid fossa in carnivores is essentially equal to the anteroposterior length of the condyle (the slope of the least squares regression of condyle length against  $TP_{\max}$  is 1.2;  $r = 0.98$ ). In addition, the relationship between translation potential and ramus height in carnivores is not statistically significant and is also negative when one factors out the effects of variation in mandibular size. The slightly different results in primates and ungulates for regressions between  $R$  versus  $TP_{\max}$  and  $TP_{\min}$  probably reflect differences in how these two measurements estimate translation but need to be verified with *in vivo* kinematic studies.

Given the complexity of condylar translation, better kinematic data are needed to test further the hypothesis that posterior translation of the working side condyle during closing renders the trajectory of the lower molars more vertical than would be the case if the mandible merely rotated around a nontranslating condyle. Except for well-documented evidence (discussed above) that the jaw as a whole is drawn anteriorly during opening and posteriorly during closing, there is little information that precisely correlates the movements of the working and balancing side

condyles with the trajectory of the lower molars during jaw closure (Gibbs et al., 1971). Our model assumes that the working side condyle moves posteriorly during most if not all of the closing phase (fast close and the power stroke).

Once again, we stress that the results presented here are not mutually exclusive of hypotheses that condylar translation reduces muscle stretching and/or prevents impingement of the pharynx. In fact, the above predictions and results are reasonably compatible with the impingement hypothesis with one exception. Because many primates, especially humans, tend to be more orthograde than perissodactyls and artiodactyls, one might expect a different allometric relationship between condylar translation and ramus height in these taxa. In particular, impingement should be more problematic, and hence translation potential should be proportionately greater in orthograde mammals in which the pharynx is not directed caudally away from the posterior margin of the ramus. Yet humans, gibbons, chimpanzees, and other highly orthograde primates all fall closely along the same line as more pronograde primates (e.g., macaques, baboons) and ungulate herbivores. The fact that humans exhibit the same relationship between translation potential and  $R$  is especially significant because humans have a flexed cranial base that further exacerbates the potential for the posterior margin of the mandible to impinge on crucial pharyngeal structures.

Condylar translation is clearly a complex phenomenon, and it probably evolved because it is adaptive for several reasons. However, any satisfactory understanding of the evolutionary basis for translation probably needs to include some consideration of occlusal function as well as gape and muscle efficiency. Further testing of the hypothesis proposed here as well as previous hypotheses regarding the evolution and functional basis for condylar translation will require comparative, *in vivo* kinematic data on translational movements in a variety of species in conjunction with data on cranial, mandibular, and dental morphology. Kinematic data are also necessary to test the accuracy of any estimates of translation potential based on measurements of the glenoid fossa.

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