

## Why Fuse the Mandibular Symphysis? A Comparative Analysis

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**KEY WORDS** symphysis; mammals; primates; electromyograms; mandible; mastication

**ABSTRACT** Fused symphyses, which evolved independently in several mammalian taxa, including anthropoids, are stiffer and stronger than unfused symphyses. This paper tests the hypothesis that orientations of tooth movements during occlusion are the primary basis for variations in symphyseal fusion. Mammals whose teeth have primarily dorsally oriented occlusal trajectories and/or rotate their mandibles during occlusion will not benefit from symphyseal fusion because it prevents independent mandibular movements and because unfused symphyses transfer dorsally oriented forces with equal efficiency; mammals with predominantly transverse power strokes are predicted to benefit from symphyseal fusion or greatly restricted mediolateral movement at the symphysis in order to increase force transfer efficiency across the symphysis in the transverse plane. These hypotheses are tested with comparative data on symphyseal and occlusal morphology in several mammals, and with kinematic and EMG analyses of mastication in opossums (*Didelphis virginiana*) and goats (*Capra hircus*) that are compared with published data on chewing in primates. Among mammals, symphyseal fusion or a morphology that greatly restricts movement correlates significantly with occlusal orientation: species with more transversely oriented occlusal planes tend to have fused symphyses. The ratio of working- to balancing-side adductor muscle force in goats and opossums is close to 1:1, as in macaques, but goats and opossums have mandibles that rotate independently during occlusion, and have predominantly vertically oriented tooth movements during the power stroke. Symphyseal fusion is therefore most likely an adaptation for increasing the efficiency of transfer of transversely oriented occlusal forces in mammals whose mandibles do not rotate independently during the power stroke. *Am J Phys Anthropol* 112:517-540, 2000. © 2000 Wiley-Liss, Inc.

During early development, all mammals have a chondrogenic, fibrocartilagenous symphysis between the two mandibles in which lateral growth occurs (de Beer, 1937; Moore, 1981; Enlow, 1990). The mandibular symphysis remains unfused throughout life in most mammalian species, but in several taxa, including anthropoid primates, most perissodactyls, hyracoids, vombatidae, some

edentates (e.g., Bradypodidae), and many artiodactyls (Camelidae, Hippopotamidae, Suidae, and Tayassuidae), the symphysis

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Grant sponsor: National Science Foundation; Grant number: IBN 96-03833.

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Received 19 May 1998; accepted 22 November 1999.

fuses prior to or roughly at the time that occlusion commences. In addition, partial-to-complete fusion occurs late in postnatal development in some species in which juveniles typically have unfused symphyses (Beecher, 1977a; Scapino, 1965, 1981; Ravosa and Simons, 1994).

There is general agreement that the principal advantage of an unfused mandibular symphysis is to allow independent or semi-independent movement of the two mandibles during occlusion (Kallen and Gans, 1972; Hylander, 1979b; Scapino, 1981). There is less consensus, however, about why mandibular fusion evolved convergently in certain taxa. Two general types of arguments have been proposed. The most common is that symphyseal fusion is an adaptation to *strengthen* the mandible in the symphyseal region. Strength, defined here as the ability to resist structural failure in response to applied forces, is an important adaptation in bone tissue that helps to maintain structural integrity so that a bone can remain stiff (Currey, 1984; see below). Arguments about the adaptive basis for symphyseal strength have been proposed primarily for primates. DuBrul and Sicher (1954) and Tattersall (1973, 1974) suggested that fusion was an adaptation in higher primates to resist large medial and lateral transverse bending forces caused by adductor muscles. Beecher (1977a,b, 1979), noting partial fusion of the symphysis in many prosimians, proposed that the fused symphysis in higher primates helps to resist elevated magnitudes of dorso-ventral shear generated by larger bite forces associated with anthropoid primate diets. Analyses of in vivo strain and muscle function (Hylander, 1977, 1979a, 1984, 1986; Hylander and Johnson, 1985, 1994; Hylander et al., 1987, 1992) demonstrated that during mastication, anthropoid primates not only generate high magnitudes of twisting strain and lateral transverse bending (known as "wishboning") during the power stroke, but also experience similar strain magnitudes on the balancing-side and working-side mandibular corpora. According to Hylander (1979a), the ratio of working-side to balancing-side strain (W/B) in the mandible is approximately 1.5:1 in the crab-eating ma-

caque (*Macaca fascicularis*) but is about 3.5:1 in the thick-tailed bushbaby galago (*Otolemur crassicaudatus*). Given the high correlation between adductor muscle contractile activity and strain magnitudes, Hylander (1986, 1979a,b) and Ravosa and Hylander (1993, 1994) interpreted the W/B strain ratios that approach 1:1 in the macaque as evidence for the recruitment of more dorsally oriented force from the balancing-side adductor muscles to generate occlusal force on the working side during unilateral mastication and biting. Ravosa and Hylander (1993, 1994) therefore suggested that a fused symphysis may be an adaptation to prevent structural failure from the repeated high magnitudes of strain that these transferred forces generate.

A second, complementary hypothesis is that symphyseal fusion is an adaptation to *stiffen* the mandible in the symphyseal region. Stiffness, defined here as the ability to resist deformation in response to applied forces,<sup>1</sup> is the primary mechanical property of bones which enables them to transfer force (Currey, 1984, p. 3–4). Several types of arguments have been made that the fused symphysis evolved as an adaptation for stiffness. In the case of primates, Kay and Hiiemae (1974a,b) and more recently Greaves (1988, 1993) suggested that symphyseal fusion stiffens the symphysis during incisal biting of hard objects, thereby preventing any potentially inefficient dissipation of dorsally-directed force across the symphysis. Ravosa and Hylander (1993, 1994), however, rejected this hypothesis by noting that primates with fused symphyses rarely if ever use their incisors to crush hard objects. In a more general argument based on a comparative analysis of the structure of unfused symphyses in carnivores, Scapino (1981) suggested that symphyseal fusion is an adaptation for transferring proportionately higher occlusal forces from the balancing- to working-side mandibular corpora. According to this hy-

<sup>1</sup>Note that strength and stiffness are different properties. Many stiff substances such as glass have little strength because they are brittle, and relatively elastic tissues such as muscle or tendon are strong because they are not stiff. In addition, strength and stiffness are planar. Tendon is strongest along its long axis, the plane in which it has some elasticity.

pothesis, mammals with unfused symphyses generate proportionately lower forces when they chew than mammals with fused symphyses. However, Dessem (1985) showed that fused and unfused symphyses transfer dorsally oriented forces with equal efficiency<sup>2</sup> from the balancing to working sides. In mammals with unfused symphyses, rapid and complete force transfer occurs because cruciate ligaments and/or interdigitating rugosities (see below) create sufficient stiffness in the sagittal plane to resist dorso-ventral shearing movements between the two mandibles.

### AN ALTERNATIVE HYPOTHESIS ON THE ADAPTIVE BASIS OF SYMPHYSEAL FUSION

This paper tests an alternative hypothesis (see also Hylander et al., 2000) related to the idea that symphyseal fusion is an adaptation to stiffen the mandible. We propose that the orientations of the movements of the lower teeth relative to the upper teeth during occlusion are the primary basis for variations in symphyseal fusion.<sup>3</sup> Although unfused symphyses appear to be as effective as fused symphyses in transferring dorsally oriented force (see above), the fused symphysis, by virtue of its stiffness in all planes, is likely to be more effective transferring force in the *transverse plane*. As a result, it is predicted that mammals with a strong transverse component of intercuspal movement during occlusion will benefit from a fused symphysis or from other adaptations that restrict medio-lateral movement in the symphysis. However, mammals whose teeth require some degree of rotation during occlusion and/or who have primarily dorsally oriented occlusal trajectories will not benefit from symphyseal fusion and are predicted to retain an unfused symphysis.

Several observations underlie this hypothesis. First, although there is compelling

evidence that fusion is correlated with a stronger mandibular symphysis in higher primates, it is not evident that fusion per se is a means of strengthening rather than stiffening the symphysis. Given the essential adaptation of bone tissue is to be stiff, it follows that bones require strength primarily in those planes in which they resist deformation (Wainright et al., 1976; Currey, 1984). As noted above, both unfused and fused symphyses efficiently transfer force in the sagittal plane because they remain stiff in this plane. As a result, both types of symphyses must counteract high strains in the sagittal plane solely by adding mass in the same plane. This principle may explain why, with the important exception of prosimian primates and some carnivorans (Scapino, 1981; Ravosa, 1991, 1996; Ravosa and Hylander, 1994), there is no apparent relationship between mandibular size and symphyseal fusion in most mammalian taxa. Because of the negative allometry between cranial size and jaw muscle size, larger mammals have proportionately smaller cross-sectional areas of their adductor muscles, and therefore might be expected to recruit more balancing-side muscle force to generate equivalent working-side bite forces (Ravosa, 1991, 1996). Symphyseal fusion, however, does not appear to be correlated with body-size variation within nonprimate mammal and some carnivoran lineages. For example, all Bovidae, from dik-diks to water buffalo, have unfused symphyses, whereas the paenungulata, from small hyraxes to large elephants, have fused symphyses. Thus, while the high W/B strain ratios in galagos with unfused symphyses suggest that they recruit less balancing-side force than macaques with fused symphyses (Hylander, 1979a), this pattern may not be generally characteristic for other mammals with unfused symphyses (Crompton, 1995; see below).

A second observation is that force transfer is a function of stiffness. The anatomy of the cruciate ligaments and rugosities of the symphysis stiffen the unfused symphysis in the sagittal plane in order to transfer dorsally oriented force efficiently and also to resist antero-posterior forces (Scapino, 1981), but these structures clearly allow

<sup>2</sup>The term efficiency here is used in this paper in the context of the timing and degree of force transfer. Stiffness increases the efficiency of force transfer between two objects because no force is stored elastically, or dissipated through movement or the generation of heat.

<sup>3</sup>We assume here that the movements of the lower and upper teeth relative to each other during the power stroke reflect to some extent the orientation of intercuspal force that is generated.

some degree of independent movement of the two mandibles in terms of lateral transverse bending and twisting (Oron and Crompton, 1985). These independent movements can occur because the symphyseal ligaments (which are stiff only along their long axis) are predominantly oriented vertically and obliquely (Beecher, 1977a; Scapino, 1981; see below).<sup>4</sup> If the two mandibles can twist and wishbone independently to some extent in an unfused symphysis, then such movements must generate less strain in the symphyseal margins of an unfused than a fused symphysis. These strains presumably dissipate in the ligaments that connect the symphyses, just as Herring and Mucci (1991) showed to occur in the zygomatic suture. In other words, fused symphyses are predicted to lay down bone in order to resist high twisting and wishboning strains because they are stiff in all planes, whereas unfused symphyses of noncarnivoran mammals are predicted to experience high strains primarily from dorso-ventral shearing because they are stiff in just the sagittal plane. It follows that a likely explanation for symphyseal fusion in most taxa is to increase the efficiency of force transfer in the transverse plane in order to generate high forces in this plane during occlusion. Because fusion is probably the most effective means of stiffening the symphysis in the transverse plane, fused symphyses may require additional mass in the transverse plane in order to counteract high wishboning and twisting strains that would result from any stiffness that fusion creates (Hylander, 1988; Hylander et al., 1987; Hylander and Johnson, 1994; Ravosa and Hylander, 1994). As noted above, unfused symphyses can vary in their degree of stiffness in the transverse plane, depending

on the degree to which the ligaments are oriented transversely.

A final indication of the importance of transversely directed forces for symphyseal fusion is provided by the experimental studies by Hylander and Crompton (1986) and Hylander and Johnson (1994) of the relationship between jaw adductor muscle force, mandibular movements, and mandibular strain in macaques. Hylander and Crompton (1986) and Hylander and Johnson (1994) showed that lateral transverse movement during the power stroke in macaques occurs because maximum contraction of the working-side (W) medial pterygoid and the balancing-side (B) deep masseter occur significantly later (by 26 msec on average) than the balancing-side medial pterygoid and the working-side deep masseter. The former muscles not only adduct but also pull the mandible medially, and these transverse movements correlate strongly with peak wishboning strains in the symphysis. In addition, Hylander et al. (1992) demonstrated that as macaques chew harder food, they tend to (but do not always) recruit more balancing-side masseter force (approaching 1:1 ratios), generating significantly higher wishboning strains in the symphyseal region. These data, therefore, indicate that wishboning in the macaque is primarily a function of the recruitment of high levels of balancing-side muscle force whose primary function is to pull the mandible medially. In other words, mammals in which more medial movement of the teeth of the working side occurs *during the power stroke* are predicted to transfer proportionately more *transversely oriented* balancing-side muscle force across the symphysis. Therefore, wishboning strains within the mandible on either side of the ligamentous region of the symphysis are predicted to be lower than in forms with a fused symphysis because of more rapid and complete force transfer in the transverse plane.

### Hypotheses to be tested

Comparative morphological and kinematic data are used to test four general hypotheses predicted by the above model.

<sup>4</sup>The structure and loading of the mandibular symphysis in carnivorans is very complex and this group will not be discussed in this paper. It should, however, be pointed out that the symphysis of this group vary from unfused to interdigitating rugosities to complete fusion. The carnivoran symphysis is designed not only to transmit forces with varying directions from the balancing- to working-side, but also to resist the high forces generated by bilateral or unilateral canine use. In the dog, for example, the cruciate ligaments between the central parts of the symphyseal plates have a predominantly antero-posterior orientation, although there are some transversely and obliquely oriented ligaments (Scapino, 1981). This arrangement suggests that resisting antero-posteriorly directed forces is important.

**Hypothesis 1.** Mammal species (with the exception of carnivorans) with a strong transverse component of intercusp movement during the power stroke are predicted to have fused symphyses. Because the orientation of wear facets reflects the direction of tooth and jaw movements during occlusion (e.g., Smith and Savage, 1959; Mills, 1967; Crompton and Kielan-Jaworowska, 1978; Janis, 1979b; Oron and Crompton, 1985), this hypothesis can be tested by comparing symphyseal morphology with measurements of the orientation of the occlusal wear facets of the molars relative to the transverse plane. In particular, the hypothesis predicts a significantly more transverse orientation of some of the upper and lower molar wear facets in mammals with fused rather than unfused symphyses, tested against the null hypothesis that there is no significant difference between these groups.

**Hypothesis 2.** Since the unfused symphysis transfers dorsally oriented forces effectively (Dessem, 1985), the pattern documented by Hylander (1979a) for galagos, in which the W/B ratio of mandibular strain was roughly 3.5:1, is not predicted to be characteristic of other mammalian taxa with unfused symphyses. This study, however, uses electromyogram (EMG) data rather than mandibular strain data to examine directly the ratio of W/B force in the jaw adductor muscles, because EMG potentials provide a more direct test of the hypothesis that mammals with fused symphyses recruit more balancing-side force than mammals with unfused symphyses. Another reason to focus on EMG data is that strain magnitudes have the potential to reflect aspects of masticatory kinematics and mandibular corpus shape that do not correlate directly with muscle force recruitment (Daegling, 1993). Therefore, the specific hypothesis to be tested here is that the ratio of W/B muscle force generated in mammals with unfused symphyses while chewing hard or resistant food should be roughly comparable to that of mammals with fused symphyses (i.e., close to 1:1). In particular, we examine combined activity levels of all the major jaw adductors (deep masseter, superficial masseter, medial pterygoid, and

temporalis) as well as combined ratios for just the superficial and deep masseters. We focus on the masseter ratios, in part, because the study by Hylander et al. (1987) of W/B ratios in the macaque measured just the deep and superficial masseters. If this specific hypothesis is not rejected, then the more general hypothesis that symphyseal fusion is an adaptation to strengthen the mandible in response to proportionately higher forces that transfer across symphysis may not be true of all mammals, but instead may be a specific explanation for the evolution of symphyseal fusion in primates.

**Hypothesis 3.** Mammals with unfused symphyses are predicted to have some degree of independent rotation (inversion and eversion) of the mandibles, presumably to match the steep occlusal planes of occluding teeth (Oron and Crompton, 1985). The study by Oron and Crompton (1985) of the tenrec, which has a highly mobile symphysis, demonstrated that the ventral margin of the mandible inverts prior to the power stroke and then everts during the power stroke, thereby moving the lower trigonid in a dorsal and lingual direction during occlusion into and out of the embrasure between the upper trigons. The marked rotation observed in the tenrec is associated with the virtual absence of a deep masseter that stabilizes the mandible. A similar though less marked degree of rotation is expected in the goat and the opossum, both of which have well-developed deep masseters. In addition, the pattern of medial pterygoid activity is expected to differ in mammals with unfused symphyses whose mandibles rotate around their long axes during unilateral mastication. The medial pterygoid is the only major adductor which causes the ventral margin of the mandible to invert, counteracting the everting tendency of the masseter. Therefore, these muscles are predicted to have different patterns of activity in mammals with fused and unfused symphyses. The medial pterygoid is predicted to contract biphasically in the goat and the opossum, presumably to invert the mandible prior to occlusion, and then to help control the tendency of the masseter and temporalis mus-

cles to evert the mandible during the power stroke.

**Hypothesis 4.** Finally, the above-described hypotheses concerning differences in masticatory kinematics are predicted to correlate with differences in the cross-sectional morphology of the symphysis between species with fused and unfused symphyses. In contrast to the fused symphysis in species such as the crab-eating macaque which is stiff in all planes, the structure of the unfused symphysis is predicted to ensure stiffness in the sagittal plane but to allow some degree of independent movement in other planes.

#### Hypothesis testing

To test hypothesis 1, we compare the orientation of occlusal wear facets in a comparative sample of herbivorous mammals with fused and unfused symphyses. Hypotheses 2–4 are tested with data on symphyseal morphology, and on the kinematics and EMG patterns of muscle activity during mastication in the goat (*Capra hircus*) and the American opossum (*Didelphis virginiana*), which we compare with previously published data on these aspects of mastication in the macaque (*Macaca fascicularis*) from Crompton and Hylander (1986), Hylander and Crompton (1986), and Hylander et al. (1987, 1992).

As a caveat, we stress that hypotheses 2–4 are tested here with only a small number of taxa. Integrated kinematic, EMG, and histological data are needed on more taxa with fused and unfused symphyses to determine the extent to which galagos are representative of prosimians, macaques are representative of mammals with fused symphyses, and goats and opossums are representative of mammals with unfused symphyses. However, the differences between opossums, goats, and macaques in terms of symphyseal structure and occlusal kinematics make them especially useful for an initial attempt to test hypotheses about the relationship between symphyseal fusion and chewing. Mammals such as the opossum and several insectivores possess tribosphenic molars, and thus have a very generalized, primitive pattern of occlusion (for

details, see Crompton and Hiiemae, 1970; Crompton and Kielan-Jaworowska, 1978; Hiiemae and Crompton, 1985). Molars of this type are characterized by embrasure shearing in which the tall trigonid of the lower molar fits precisely and tightly into a V-shaped embrasure between two upper molars. Shearing takes place between the leading edges of the crests connecting the main cusps. The occlusal angle is steep, and little transverse movement occurs during occlusion: dorsally oriented jaw movement (about 80° relative to the transverse plane of the tooth row) stops when the protocone fits into the talonid basin; movement of the lower molars out of occlusion is directed almost entirely ventrally, although with a slight degree of mandibular rotation (Crompton and Hiiemae, 1970; see also below).

In goats, the molars are also designed to shear food, but in contrast to mammals with a tribosphenic molar, shearing surfaces in the goat are aligned parallel to the longitudinal axis of the tooth row; shearing involves extensive movement of the lower jaw in a medial direction. Artiodactyl molars are selenodont, with two sets of “selenes” or half-moon-shaped lophs, each with a labial and lingual loph (Janis, 1979a). Food is subjected to a “double chop” as the antero-posteriorly aligned lophs of the lower molars are drawn across those of the uppers at an angle of approximately 45–50° relative to the horizontal plane. Occlusion is therefore characterized by a single stroke that combines both vertical and transverse movement (de Vree and Gans, 1976).

In macaques, as in most anthropoids, the lower molars initially move into occlusion at a steep angle. However, the power stroke in anthropoids, including humans, tends to be predominantly transverse, typically within 30° of the horizontal plane (Kay and Hiiemae, 1974b; Proschel, 1987; Wong, 1989; Miller, 1991). In contrast to tribosphenic molars, the crushing surfaces of opposing molars are relatively larger. Crushing occurs between the hypocone and protocone of the upper molars and the trigonid basin and talonid of the lower molars. Although it was originally believed that the primate power stroke was divided into distinct dorsal (phase I) and lingual (phase II) components

(Kay and Hiiemae, 1974a,b), it is now evident that there is no clear distinction between these phases, and that the power stroke occurs during predominantly transversely oriented movements of the lower teeth relative to the upper teeth (Hylander et al., 1987; Hylander and Johnson, 1994). Phase II, if it exists, occurs as occlusal forces decline (Hylander et al., 1987).

## MATERIALS AND METHODS

### Comparative occlusal morphology

To test the hypothesis that mammals with fused symphyses tend to have a more transversely oriented component of movement during the power stroke than those with unfused symphyses, the orientation of the occlusal planes of the upper and lower second permanent molars was measured relative to the plane of the tooth row on pooled-sex samples of 4 adult skulls from 12 diverse species of herbivorous mammals from the Museum of Comparative Zoology (Harvard University). These mammals were chosen because they sample a wide range of sizes and families. Mammals with fused symphyses include *Camelus dromedarius*, *Rhinoceros unicornis*, *Equus caballus*, *Lama huanachus*, *Macaca fascicularis*, *Procapra capensis*, and *Sus scrofa*. Mammals with unfused symphyses include *Didelphis virginiana*, *Capra hircus*, *Cervus elaphus*, *Gazella gazella*, *Lemur fulvus*, and *Odocoileus virginiana*. In all species, we measured the angle formed by the apices of the entoconid and hypoconid wear facets of the  $M_2$  and the angle formed by the apices of the metacone and hypocone wear facets of the  $M^2$  relative to the transverse plane of the tooth row. The transverse plane of the tooth row was determined by placing an index card across the deepest point of the left and right second molars. Wear facet angles in all species were measured by affixing a thin rod of graphite (0.5-mm diameter) with cyanoacrylate glue to each wear facet under a dissecting microscope. The angle of the graphite rod relative to the transverse plane was recorded on an index card (see above) and measured with a protractor accurate to 1°. Following this procedure, the glue was removed with acetone. Repeated measures on

the same individual indicate that these wear facet angles are accurate to within a few degrees.

A Mann-Whitney U-test was used to test if upper and lower wear facet angles are more horizontal in species with fused than unfused symphyses against the null hypotheses that they do not differ significantly.

### Comparative symphyseal morphology

The histology and structure of the mandibular symphysis were examined in specimens of the three species for which we present experimental data: *C. hircus*, *M. fascicularis*, and *D. virginiana*. Mandibles of adult *C. hircus* and *D. virginiana* were defleshed, fixed in formaldehyde, cleared with xylene, dehydrated in ethanol, and then embedded in Osteobed™. A mandible of a juvenile macaque (permanent incisors and canines had not yet erupted) was embedded in Castrolite™. Serial ground sections were cut in the coronal plane (transverse to the longitudinal axis) of the jaw at 1-mm intervals with an Isomet™ diamond saw, mounted to glass slides with Epotek™ 310 epoxy, and ground and polished to a thickness of approximately 100 µm. Sections were examined in plain and cross-polarized transmitted light, and photographed with Kodak Ektachrome™ slide film (Kodak, Rochester, NY). The resultant color slide was scanned with a Polaroid Sprint-Scan35 connected to a Power Macintosh 8500/120 and printed on a Tektronix Phaser 560.

### Experimental subjects

We report the results of experiments in opossums (*Didelphis virginiana*) and goats (*Capra hircus*; breed: Nubian). Three opossum adults (O1, O2, and O3) were recorded while masticating different foods during each experiment. We report here the results when O1 was fed cooked beef, O2 was fed bone, and O3 was fed both apple and bone. Raw EMGs for O2 when it was chewing chicken flesh were published by Crompton and Hylander (1986). The two goats (G1, G2) were both Nubian goats: G1 was an 18-month-old female adult; G2 was a 4-month-old male. In all experiments, the goats were fed dry hay.

### EMG electrodes and recording procedure

**Opossums.** Simultaneous electromyographic (EMG) measurements of jaw adductor activity were recorded in O1–O3 using bipolar fine-wire electrodes inserted into left and right sides of the following muscles. To place the electrodes, each animal was anaesthetized using halothane. Electrodes were made from 0.002-inch coated steel wire (J. Wilbur and Driver Co., Newark, NJ) and inserted into the muscles using a hypodermic needle (for protocol, see Gans, 1992). EMG potentials were amplified between 2,000–10,000 times, with a low-frequency cutoff at 300 Hz, filtered at 60 Hz, and recorded on a Bell and Howell (Pasadena, CA) CPR 4010™ magnetic tape recorder at 15 inches/sec. In O1, electrodes were inserted into the posterior and anterior compartments of the temporalis, the deep masseter, the superficial masseter, the medial pterygoid, and the digastric. In O2, electrodes were inserted into the posterior, middle, and anterior compartments of the temporalis, the deep masseter, and the superficial masseter. In O3, electrodes were inserted into the deep masseter, the superficial masseter, and the medial pterygoid. Recordings of chewing sequences for each animal were made over 3 days following surgical implantation of electrodes. Verification of electrode placement was made by manual dissection after the animals were euthanized with an intracardial injection of sodium pentobarbital.

**Goats.** Electrodes were made from 0.004-inch coated silver wire (California Fine Wire Co., Grover Beach, CA). Electrodes were inserted during an aseptic surgical procedure in which strain gauges were also attached to the mandibles (the strain data are not reported here). A surgical plane of anesthesia was induced by ketamine (20.0 mg/kg) and atropine (0.04 mg/kg) and maintained with halothane (Muir and Hubbell, 1989). A single incision was made between the ventral margins of the two mandibles. In G1, electrodes were inserted using a hypodermic needle into the left and right deep masseters, superficial masseters, anterior compartments of the temporalis, and medial

pterygoids. In G2, electrodes were inserted into the left and right deep masseters, superficial masseters, and medial pterygoids. EMG potentials were amplified between 2,000–10,000 times, with a low-frequency cutoff at 300 Hz, filtered at 60 Hz, and recorded on a TEAC RD 145T DAT recorder (TEAC America, Inc., Montebello, CA). Recordings of chewing sequences for each experiment were made over 2 days following surgical implantation of electrodes. After each experiment, still radiographs were taken to verify electrode position.

### Cineradiographic recording

In order to correlate EMG activity with jaw movement and to determine balancing and working sides, the animals were filmed in several projections using normal light and X-rays. There were some differences between experiments in terms of the projections used because of differences in the experimental setup and whether strain-gauge data (not reported here) were also being acquired.

**Opossums.** Radiopaque metallic fillings were placed in the upper and lower canines and third molars of all animals. O1 and O3 were filmed synchronously in frontal view with a Photosonics 16-mm 1PL camera and in lateral view with an Eclair GV-16 camera attached to a Siemens image intensifier (exposure 65 kV, 120 mA). All filming during mastication was recorded at 100 frames/sec with Kodak 16-mm Plus-X reversal film (no. 7276). O2 was filmed with the above cineradiographic equipment in both dorso-ventral and lateral view at 100 frames/sec. Voltage pulses triggered by the camera shutters were recorded by the tape recorder, allowing precise synchronization of frames from the two sets of the film with the EMG data.

**Goats.** G1 and G2 were both filmed in dorso-ventral projection at 100 frames/sec using a GV 16 Photosonics cine camera attached to a Siemens image intensifier (exposure 65 kV, 120 mA). Radiopaque metallic fillings were placed in the lower first and fourth incisors in G1. G2 was also filmed in lateral projection with Kodak 16-mm Plus-X reversal film (no. 7276). Voltage pulses trig-

gered by the camera shutter were recorded on the tape recorder.

### Kinematic analysis

Movements of the mandibles relative to each other and to the maxilla (gape, transverse movement, and rotation) were measured from the X-ray film. The film was projected on a Vanguard Motion Analyzer (Model M160W, Vanguard Instrument Corp.) so that selected points could be digitized with a Graph/Pen Sonic Digitizer (Model C-P-6/50, Science Accessories Corporation). Kinematic data were recorded only from sequences in which there was minimal head movement during the chewing cycle and in which the subject's head was neither tilted nor flexed. A BASIC software program developed by J. McGarrick (St. Thomas' Hospital, United Medical Schools, London, UK) was used to calculate the position of marker points relative to the projected transverse (X) and mid-sagittal (Y) planes. The transverse plane is defined here as the plane of occlusion of the postcanine teeth. Gape was measured directly (as the distance from the upper central to lower central incisors) in films taken in lateral view; in dorso-ventral films, gape was estimated by measuring the relative change in distance between the front of the symphysis and the back of the palate as seen in dorso-ventral view. This distance decreases as the jaw opens and increases as the jaw closes, but it only approximates gape, since head movements during feeding can also affect this projected distance. As measured here, presumptive gape tends to be a more accurate estimator of maximum gape than minimum gape. Transverse movements of the mandible in O2 were calculated by plotting the transverse movement of a lower canine marker relative to the mid-sagittal plane. Transverse movements of the mandible in the goat (G2) were calculated by plotting the transverse movement of the left and right fourth mandibular incisors relative to the mid-sagittal plane.

Rotation of the mandible can be observed in dorso-ventral projection, but it is difficult to quantify the degree of rotation about the mandibular axis (symphysis to condyle). In the opossum (O2), rotation was measured by plotting the medio-lateral distance be-

tween the lateral edge of the ventral surface of the mandible below the ascending process and the medial surface of the dorsal margin of the ascending process. The latter lies medial to the former; consequently, a decrease in this distance indicates inversion of the ventral margin of the mandible. This technique cannot be used in the goat because the ventral margin of the ramus is not always visible in dorso-ventral view. Instead, the apparent rotation of the goat symphysis around the mandibular axis was estimated in G1 by measuring the differences in the transverse movement of  $I_1$  and  $I_4$  relative to the mid-sagittal plane. Estimating rotation is possible because, in dorso-ventral projection, the horizontal distance between  $I_1$  and  $I_4$  will decrease when the ventral margin of the mandible either inverts or everts (see Fig. 7); if no rotation occurs, this distance remains constant. The distance between  $I_1$  and  $I_4$  decreases during rotation because the center of rotation of the symphysis, the fibrocartilagenous pad (see below), lies close to  $I_1$  when the ventral margin of the mandible inverts or everts, so  $I_4$  tends to move more medially than  $I_1$  when the whole jaw shifts medially and everts, and  $I_4$  tends to move more laterally than  $I_1$  when the whole jaw shifts laterally and inverts.

### EMG analysis

Selected portions of the EMG data for which kinematic sequences were also available (see above) were played through an A-D converter into a Macintosh computer at 10,000 points/sec. Data from O1-O3 were analyzed using a Labview™ II virtual instrument (written by K. Johnson, Duke University); data from experiments G1-G2 were analyzed using a Superscope™ II virtual instrument (written by D. Lieberman and D. Sadowsky, Rutgers University). Following Hylander and Johnson (1993), EMG data were integrated over a 1-msec interval with a window of 20 msec, filtered using a root-mean-squares (RMS) function, and then normalized so that the peak values during each chewing sequence were 1.0 for each muscle across one or more documented side-shifts. Normalizing the RMS waveform across documented side-shifts allows quantitative comparison between the activity of a

single muscle when it is on the balancing vs. working side (Gorniak and Gans, 1980). Final analysis of all data was done on Igor Pro™ 2.01 (WaveMetrics, Inc., Lake Oswego, OR). Using Igor, onset and offset of the power stroke were defined as the points at which the wave began to rise or fall steeply from adjacent regions of inactivity. For each power stroke, the area under the normalized RMS curve was collected for each muscle (calculated as the average amplitude of the wave times the number of points).

As noted above, determination of balancing side and working side (hence side-shifts) was made in three ways. In sequences with cine data (O1, O2, O3, G1, G2), identification of balancing and working side was made by visual examination of the masticatory cycle. For O1 and O3, synchronized anterior and lateral views of jaw movement were available. For O2, G1, and G2, side-shifts were clearly visible in dorso-ventral cineradiographic films. In O3, determination of side was also confirmed using single-element strain gauges (see Crompton, 1995 for details) bonded to the lateral surface of the mandible near the ventral margin just posterior to the symphysis (i.e., anterior to the bite point). Gauges in this location register tensile strain on the working side and compressive strain on the balancing side (Crompton, 1995). Determination of balancing and working sides was also confirmed in the goats, using the differential timing of the deep and superficial masseters (see Results). During the power stroke in goats as in many other mammals (see Hylander et al., 1987), the working-side deep masseter and the balancing-side superficial masseter consistently fire prior to the balancing-side deep masseter and the working-side superficial masseter. This pattern was consistently observed in the goats, using sequences with dorso-ventral cineradiographic data (see Fig. 4).

**RESULTS**

**Occlusal angle and symphyseal morphology**

Hypothesis 1 predicts that fused symphyses evolved convergently in mammals with

TABLE 1. Occlusal wear facet orientations relative to the transverse plane

Species	Upper second molar			Lower second molar		
	Mean	SD	n	Mean	SD	n
<i>Camelus dromedarius</i>	163.5	4.36	4	158.8	2.87	4
<i>Capra hircus</i>	155.8	3.78	4	149.8	5.25	4
<i>Didelphis virginiana</i>	118.5	8.70	4	106.3	6.95	4
<i>Equus caballus</i>	157.3	4.50	4	158.3	4.27	4
<i>Gazella gazella</i>	153.8	6.13	4	142.8	6.75	4
<i>Lama huanachus</i>	153.0	2.45	4	161.3	8.02	4
<i>Lemur fulvus</i>	121.8	1.71	4	117.5	9.04	4
<i>Macaca fascicularis</i>	154.3	4.65	4	156.3	5.68	4
<i>Odocoileus virginiana</i>	153.8	3.95	4	151.0	4.90	4
<i>Procavia capensis</i>	130.5	5.26	4	131.5	4.44	4
<i>Rhinceros unicornis</i>	155.3	2.52	3	144.3	12.90	3
<i>Sus scrofa</i>	172.0	3.46	4	173.5	3.70	4
Mean unfused	155.11	12.74	27	155.2	13.84	27
Mean unfused	140.7	17.94	20	133.5	19.60	20

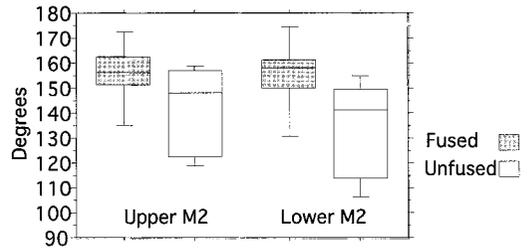


Figure 1. Box-and-whisker plot (showing mean, standard error, and standard deviation) comparing the orientation of occlusal wear facets of M<sub>2</sub> and M<sup>2</sup> relative to the transverse plane of occlusion for five species of mammals with unfused symphyses and eight species with fused symphyses. See text for details of measurements and species included. Although there is more variation in occlusal angles among mammals with fused symphyses, a Mann-Whitney U-test indicates that the wear facets are significantly ( $P < 0.01$ ) more transversely oriented in both the upper and lower molars in species with fused than unfused symphyses.

low-cusped teeth in which grinding occurs with the lower jaw moving primarily medio-laterally in the transverse (horizontal) plane against the upper teeth. An analysis of variation in the occlusal angles in herbivores provides general support for this hypothesis. Table 1 and Figure 1 provide summary data on the mean orientations of the occlusal wear facets of the upper and lower second molars relative to the transverse axis of the tooth row for the comparative sample of adult herbivores with fused and unfused symphyses. A Mann-Whitney U-test indicates that the orientation of occlusal wear facets on the lower molars is on average 20.3° ( $P < 0.005$ ) more transversely

TABLE 2. Estimated W/B ratios in *Didelphis* during mastication of hard foods, with standard deviations in parentheses<sup>1</sup>

Subject	Food	Cycles	Posterior temporalis	Middle temporalis	Anterior temporalis	Combined temporalis	Deep masseter	Superficial masseter	Combined masseter	Medial pterygoid	All
O1	Beef	9	3.56 (2.06)		1.36 (0.32)	1.97 (1.03)	2.74 (1.79)	0.94 (0.09)	1.34 (0.32)	1.19 (0.32)	1.41 (0.35)
O2	Bone	10	1.40 (0.28)	1.32 (0.38)	1.60 (0.60)	1.39 (0.19)	1.69 (0.49)	1.27 (0.19)	1.42 (0.20)		1.37 (0.13)
O3	Bone	10					1.14 (0.26)	1.14 (0.16)	1.14 (0.20)	1.03 (0.27)	1.08 (0.20)
O3	Apple	13					1.29 (0.63)	1.44 (1.00)	1.34 (0.77)	0.90 (0.23)	1.07 (0.25)
Grand mean			2.48	1.32	1.48	1.68	1.72	1.20	1.31	1.04	1.23

<sup>1</sup> W, working-side; B, Balancing-side.

oriented in mammals with fused than unfused symphyses; similarly, the orientation of upper occlusal wear facets is on average 12.6° ( $P < 0.0001$ ) more transversely oriented in mammals with fused than unfused symphyses. However, it is important to note from Table 1 that while all species with unfused symphyses have fairly steep occlusal angles, there is more variation among the species with fused symphyses.

#### W/B EMG adductor ratios

Hypothesis 2 predicts that the results of Hylander (1979a), in which strain data were used to infer that primates with an unfused symphysis such as the galago recruit proportionately less balancing-side than working-side adductor muscle force than macaques, are not expected to characterize most nonprimate mammals with unfused symphyses during mastication of hard food. This hypothesis is tested with EMG data on goats and opossums, and compared with previously published data on macaques from Hylander et al. (1992).

**Opossums.** Table 2 summarizes descriptive statistics for W/B ratios of the summed areas under the normalized EMG waves for each muscle and for all working-side and balancing-side muscles from four separate sequences of chews with side shifts from O1—O3 (see above). In addition, Figures 2 and 3 present side-shift sequences with EMG and gape profiles from O1 and O3. O1<sub>beef</sub> comprises 2 side shifts with 4 left-side chews and 5 right-side chews; O2<sub>bone</sub> comprises 2 side shifts with 7 left-side chews and 3 right-side chews; O3<sub>bone</sub> comprises 2 side shifts with 4 left-side chews and 6

right-side chews; O3<sub>apple</sub> comprises 3 side shifts with 6 left-side chews and 7 right-side chews. The number of cycles analyzed in each sequence is limited because the analysis is restricted to chewing cycles in which we were able to verify accurately with cineradiography and strain gauges the side on which the animal was chewing. Figures 2 and 3 and Table 2 show that the combined W/B ratios in the opossum are close to equal, ranging from 1.07–1.41, and averaging 1.23. There is, however, some variation in the W/B ratios among the different adductor muscles and between subjects that is probably related to differences in food hardness and bolus position in the oral cavity. In O1<sub>beef</sub>, for example, the posterior temporalis has the highest average W/B ratio (3.56), considerably higher than in O2<sub>bone</sub> (1.40), but in some of the individual cycles the ratios are close to 1:1. In addition, W/B ratios are slightly higher in the deep masseter than the superficial masseter in all experiments, with the exception of O3<sub>apple</sub>. Medial pterygoid activity during the power stroke is the least differential in all experiments, averaging 1.04. The combined W/B ratios of the deep and superficial masseters are very similar to the overall W/B ratios for all subjects.

**Goats.** Table 3 summarizes descriptive statistics for the summed areas under the normalized EMG waves for each muscle and for summed values of all working-side and balancing-side muscles from two separate sequences of chews with side-shifts from each goat. The first G1 sequence includes one side shift in which the animal first chewed on the right side for 12 cycles and

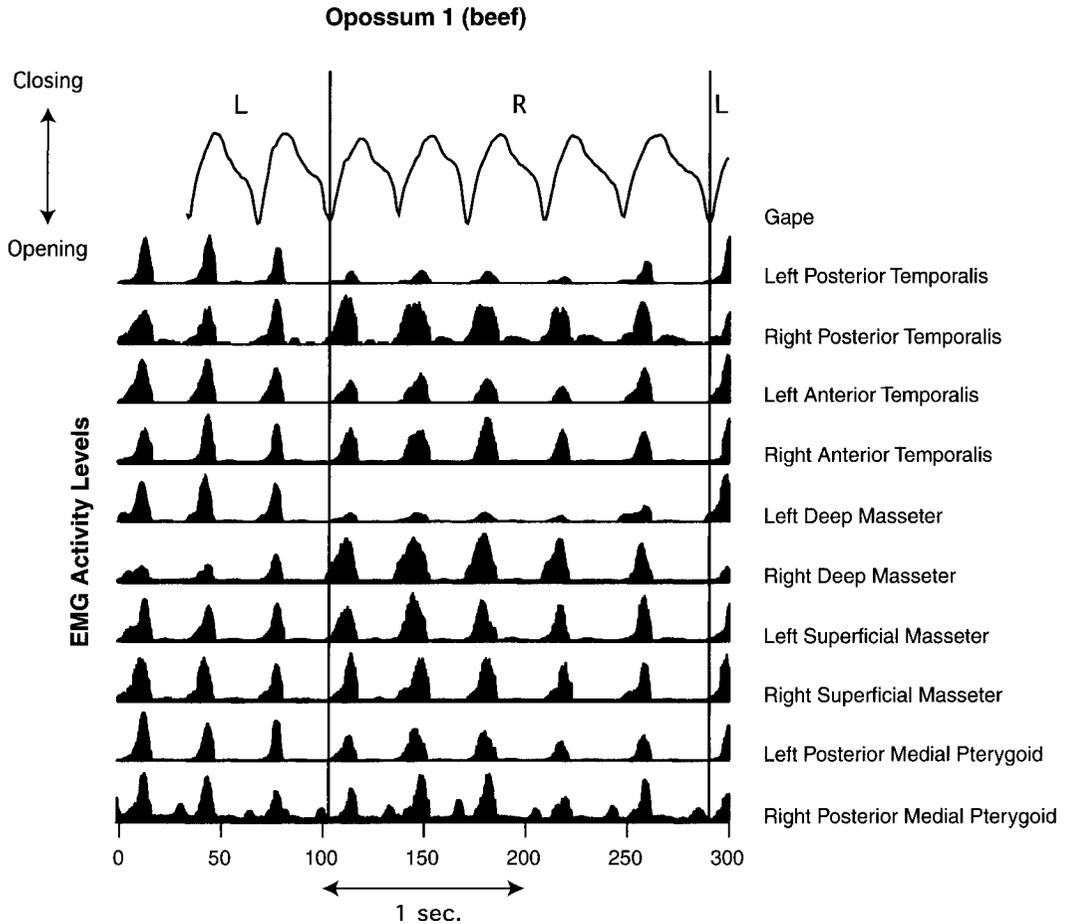


Figure 2. Jaw movements and muscle activity during a sequence of side-shifts from opossum 1 (O1) while chewing beef chunks. Side-shifts and gape determined by film (see Materials and Methods). Left- and right-side chews denoted as L and R, respectively, at top; vertical lines denote side-shifts. Plotted are gape and

the normalized root-mean squared EMG values for the temporalis (anterior and posterior compartments), masseter (deep and superficial compartments), and medial pterygoid. Note that differential working- vs. balancing-side muscle activity occurs mostly in the deep masseter and posterior temporalis.

then switched to the left side for 12 cycles. The second G1 sequence, however, is a synthesized side-shift in which the goat first chewed on the left side for 13 cycles, was fed more hay, and then chewed on the right side for 16 cycles. The first sequence for G2, illustrated in Figure 4, comprises two side-shifts with 13 left-side chews and 8 right-side chews; the second G2 sequence comprises one side-shift with 9 left-side chews and 8 right-side chews. In both goats, total W/B ratios for the adductor muscles sampled range between 1.10–1.37, with a grand mean of 1.23. Combined superficial and deep masseter W/B ratios are quite sim-

ilar, averaging 1.32, with the deep masseter showing slightly higher W/B ratios than the superficial masseter. As in the opossum, the temporalis appears to have the highest W/B ratios (2.22 and 1.42), but these data come from only G1, and need to be verified with additional studies.

**Comparison with macaques.** Figure 5 plots the W/B ratios for just the combined superficial and deep masseters in the goats and opossums with the same type of data reported by Hylander et al. (1992) for macaques. Because W/B masseter ratios in the macaque are proportional to food hardness,

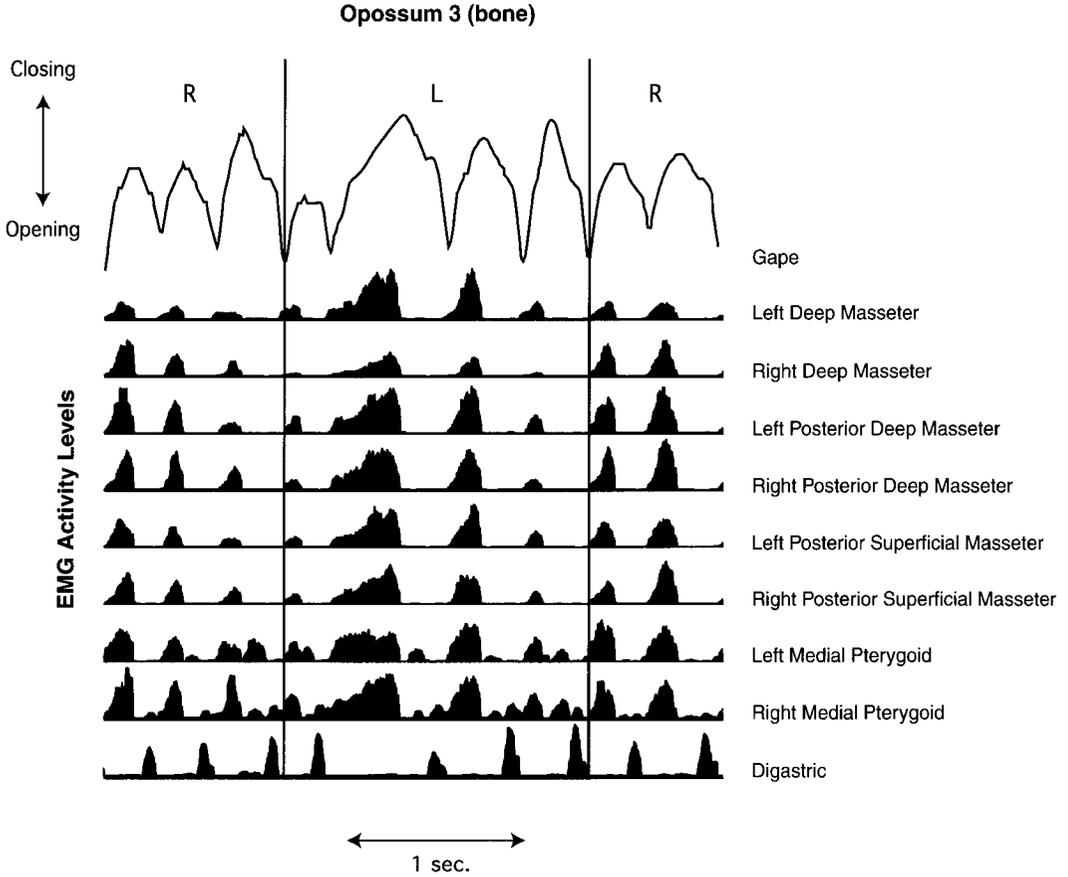


Figure 3. Jaw movements and muscle activity during a sequence of side-shifts from opossum 3 (O3) while chewing chicken bone. Side-shifts and gape determined by film (see Materials and Methods). Left- and right-side chews denoted as L and R, respectively, at top; vertical lines denote side-shifts. Plotted are gape and

the normalized root-mean squared EMG values for the masseter (posterior deep, anterior deep, and superficial compartments) and the medial pterygoid; EMG data were also collected for the digastric and are included here to illustrate abductor muscle activity during the opening stroke.

TABLE 3. Estimated W/B ratios in *Capra* during mastication of hard foods, with standard deviations in parentheses<sup>1</sup>

Subject	Food	Cycles	Anterior temporalis	Deep masseter	Superficial masseter	Combined masseter	Medial pterygoid	All
G1	Hay	20	2.22 (2.65)	1.70 (0.62)	1.22 (0.45)	1.34 (0.35)	1.17 (1.08)	1.10 (0.32)
G1	Hay	29	1.42 (0.54)	1.17 (0.25)	1.39 (0.42)	1.24 (0.20)	1.19 (0.47)	1.22 (0.20)
G2	Hay	21		1.23 (0.13)	1.26 (0.18)	1.24 (0.10)	1.33 (0.49)	1.24 (0.13)
G2	Hay	17		1.67 (0.31)	1.20 (0.21)	1.45 (0.27)	1.35 (0.38)	1.37 (0.21)
Grand mean			1.82	1.44	1.27	1.32	1.26	1.23

<sup>1</sup> W, working-side; B, balancing-side.

we plot only the mean W/B ratios for the higher force levels (4–6) reported by Hylander et al. (1992; their Table 3) to make

the data comparable with the goat and opossum W/B ratios reported here, which come from sequences in which hard food was

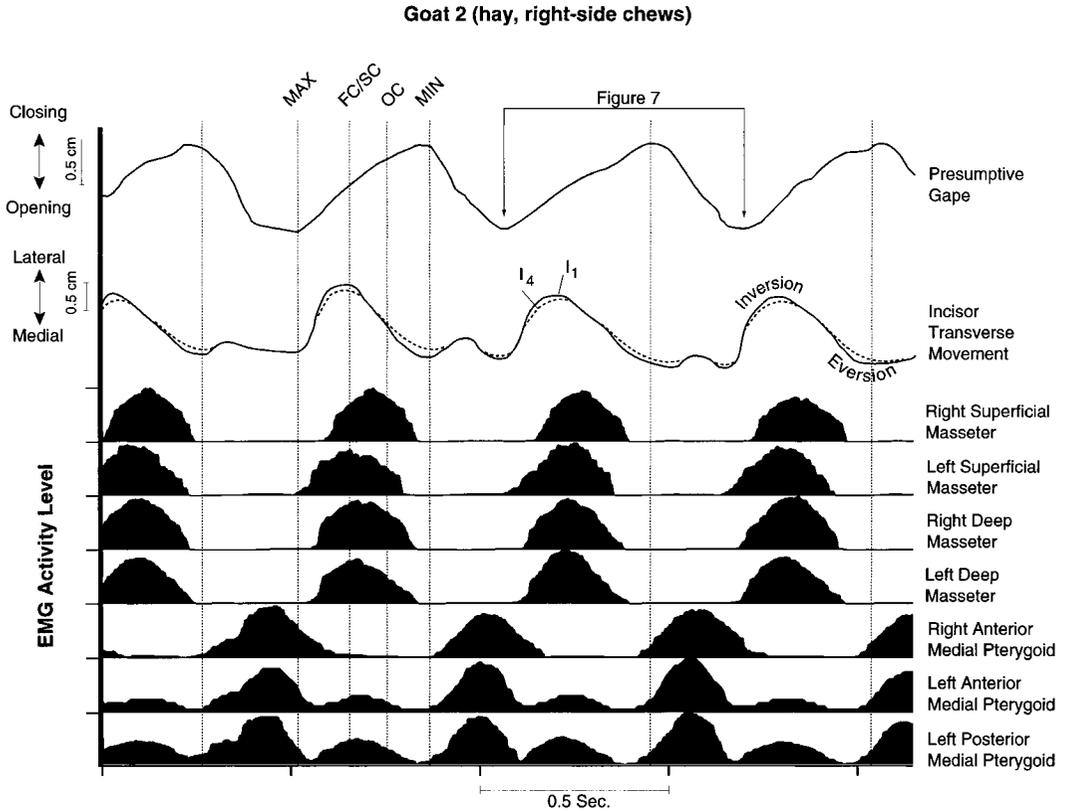


Figure 4. Jaw movements and muscle activity during a sequence of right-side chews from goat 2 (G2) while chewing dry hay. Side-shifts and gape determined by film (see Materials and Methods). Plotted are presumptive gape, transverse movement, and inversion and eversion of the symphysis, and normalized root-mean squared EMG values for the masseter (deep and superficial) and medial pterygoid muscles. Inversion

and eversion are estimated from differential transverse movement of the medial (solid lines) and lateral (dashed line) incisors, as explained in Materials and Methods. Four points during the chewing cycle are highlighted: MAX, maximum gape; FC/SC, the transition between fast and slow close; OC, the temporal midpoint of the slow close phase; and MIN, minimum gape.

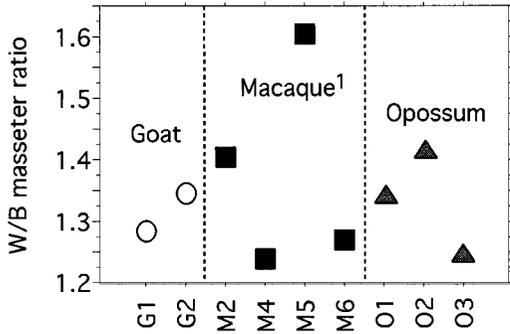
chewed. As Figure 5 shows, the W/B ratios for the goat and the opossum fall within the range of the W/B ratios reported for the macaque, with no statistically significant differences between any of the species.

**Mandibular rotation**

Hypothesis 3 predicts that mammals with unfused symphyses tend to rotate their mandibles independently during occlusion, unlike mammals with fused symphyses. In addition, the medial pterygoid is predicted to contract biphasically in the goat and the opossum, presumably to invert the mandible prior to occlusion, and then to help control the tendency of the masseter and tem-

poralis muscles to evert the mandible during the power stroke.

**Opossum.** Figure 6 plots gape and rotation of the left and right mandibles around their longitudinal axes in O2 during a side-shift while chewing on a chicken bone. Figure 6B exaggerates the changing orientation of the vertical axis of the mandible (from the mandibular condyle to the ventral margin of the ascending ramus). Note that the ventral margin of the working-side mandible tends to evert during the fast close phase prior to the power stroke and then invert slightly during the power stroke. In contrast, the ventral margin of the balanc-



<sup>1</sup>Data from Hylander et al., 1992

Figure 5. Comparison of W/B masseter (combined deep and superficial) ratios from O1–O3 and G1–G2 with published hard food (levels 4–6) W/B masseter ratios from Hylander et al. (1992). An ANOVA finds no significant differences between the fused and unfused species.

ing-side mandible inverts during fast close and everts considerably during the power stroke, presumably because the teeth do not restrict this rotation. Unfortunately, it is not possible to calculate absolute degrees of rotation from the film. These data derive from a single experiment, and thus need to be tested using additional subjects, but they correspond to the predicted biphasic activity of the medial pterygoid activity that is documented in Figure 2 (O1<sub>beef</sub>), Figure 3 (O3<sub>bone</sub>), and numerous other sequences (not shown here) in which the medial pterygoid fires during both the opening and closing strokes. Similar biphasic medial pterygoid activity was previously documented in O2 by Hylander and Crompton (1986, their Fig. 4).

**Goat.** As noted above, it is more difficult to measure mandibular rotation in vivo in the goat because it is not possible to see the lateral border of the mandible in dorso-ventral view. Nevertheless, preliminary evidence for independent rotation of the mandibles in G2 is provided by Figure 4, which plots the transverse movement of the inner and outer incisors along with gape, and EMGs from the left and right side deep and superficial compartments of the masseter, and from the anterior and posterior compartments of the medial pterygoids on both

sides during a sequence of right-side chews (immediately followed by a side-shift) (see methods for details). Figure 7 is a schematic of the movements of the symphysis in frontal view based on the chewing sequence illustrated in Figure 4. In this sequence (not shown in full), the projected transverse distance between the left I<sub>1</sub> and I<sub>4</sub> relative to the distance between these teeth during the end of the opening stroke decreased by 0.15 mm (SD 0.06 mm, n = 8), with I<sub>4</sub> moving less laterally than I<sub>1</sub>, which is consistent with inversion of the ventral margin of the mandible. In addition, during the end of the power stroke, between the point of maximum intercuspation (OC) and minimum gape (MIN), the projected distance between the left I<sub>1</sub> and I<sub>4</sub> decreased by 0.37 mm (SD 0.12 mm, n = 8), with I<sub>4</sub> moving less medially than I<sub>1</sub>, which is consistent with eversion of the ventral margin of the mandible. Although these data derive from a single experiment, and thus need to be tested using additional subjects, they correlate well with the differential activity of the medial pterygoid and masseter muscles also shown in Figure 4 and documented in the other experimental subjects. As in the opossum, the combined activity of the temporalis and masseter muscles during the power stroke not only adducts and shifts the mandibles transversely but, because of their insertion sites laterad to each mandible, also rotates them around their longitudinal axes. This rotation everts the ventral margin of each mandible. Activity in the medial pterygoids would tend to counteract this rotation, but medial pterygoid levels are relatively low during slow close (Fig. 4), with the possible exception of the working-side posterior medial pterygoid.

Note from the sequence of chews illustrated in Figure 4 that activity in the balancing-side superficial masseter consistently precedes that on the working side. This activity tends to move the mandible laterally during fast close, to bring the lower molars into the correct position to engage the upper molars. Moreover, activity in the working-side superficial masseter consistently continues beyond that of the balancing-side masseter, helping to move the mandible medially during the power stroke.

**Opossum 2 (bone)**

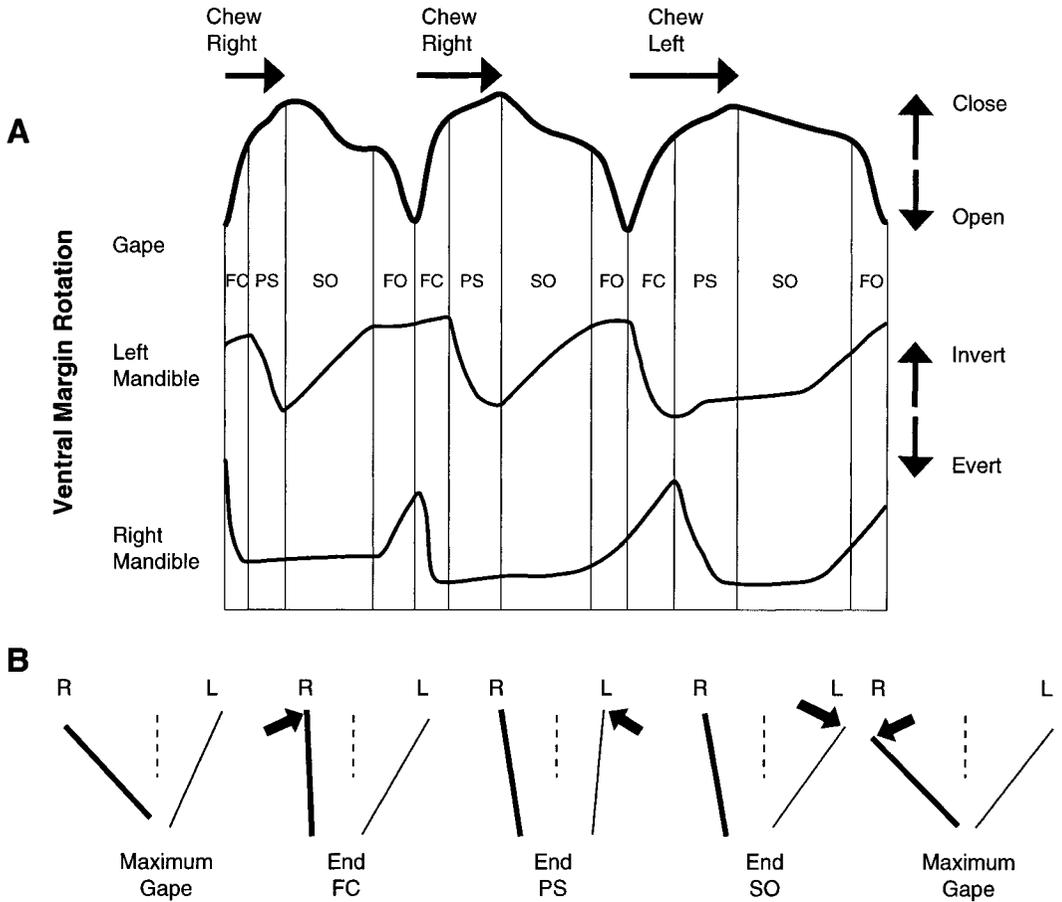


Figure 6. Mandibular rotation in the opossum 2 (O2) while chewing chicken bone. **A:** Gape and rotation (inversion vs. eversion) of the ventral margin of the mandible during a side-shift. Four phases of the chewing cycle are highlighted: FC, fast close; PS, power

stroke (slow close); FO, fast open; SO, slow open. **B:** Summary schematic of orientations of left and right mandibles during a left-side chew, with phases of the chewing cycle as noted above. Note how working- and balancing-side mandibles rotate independently.

Figure 4 also shows that there is no significant differential timing in the goat between the working- and balancing-side deep masseters. Apparently, the working-side superficial masseter pulls the working-side mandible medially, whereas the balancing-side deep masseter does little to pull the balancing-side mandible laterally and help in the side-shift. This pattern differs significantly from that of the macaque, in which the balancing-side deep masseter continues to contract for at least 26 msec after the working-side deep masseter, contributing to wishboning (Hylander and Johnson, 1994).

**Comparative symphyseal morphology**

Hypothesis 4 predicts that the cross-sectional morphology of the unfused symphysis restricts movement in the sagittal plane, to allow rapid and complete transfer of dorsally oriented forces, but should allow some degree of independent movement in other planes to accommodate the tendency of the mandibles to wishbone and rotate around their longitudinal axes as documented above. Figure 8 illustrates representative transverse sections through an anterior and posterior region of the mandible of an adult

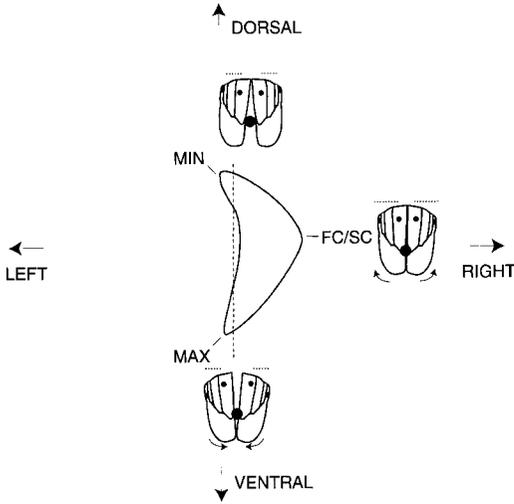


Figure 7. Schematic anterior view of mandibular and symphyseal movement in a goat during one chewing cycle (noted in Fig. 4). Small black dots are radiopaque fillings placed in the first and fourth incisors; large black dot represents the dorsal margin of the fibrocartilagenous pad, which acts as a center of rotation. The dashed line is the mid-sagittal plane. MIN, minimum gape; MAX, maximum gape; FC/SC, transition between fast close and slow close, which is the onset of the power stroke. Note that at both maximum and minimum gape the twisting of the goat symphysis decreases the projected (dotted) horizontal distance between the inner and outer incisors. See text for further details.

opossum, an adult goat, and a juvenile macaque. Within each species, little variation was observed between transverse sections from the same region of the mandible and symphysis.

**Opossum.** As Figure 8a shows, the opossum has a typical class I symphysis (as defined by Scapino, 1981). A fibrocartilagenous pad lies in the antero-dorsal region of the symphysis, widely separating the two mandibles and acting as a center of rotation. Ventral to this pad, the two symphyseal plates are joined by cruciate ligaments, the majority of which are dorso-ventrally oriented. Posterior to the pad (Fig. 8b), the symphyseal plates in the opossum are also linked almost entirely by dorso-ventrally oriented cruciate ligaments. Because ligaments are stiff and strong only in their long axis, this orientation ensures stiffness in the sagittal plane, thereby ensuring that dorsally oriented forces will transfer effi-

ciently from one mandible to the other, but allowing rotation of each mandible around its longitudinal axis.

**Goat.** The goat has a typical class III symphysis (as defined by Scapino, 1981) in which the symphyseal plates are characterized by interdigitating rugosities. As Figure 8c,d shows, there are significant differences in structure between the anterior, posterior, dorsal, and ventral regions of the symphysis in the goat. A small fibrocartilagenous pad between the two mandibles is present dorsally at the anterior end of the symphysis (Fig. 8c). This pad acts as the center or rotation for both the twisting of the mandibles around their longitudinal axis (condyle to cartilage pad) and independent medio-lateral transverse movements of the mandibles. At the anterior end of the symphysis, the medial surfaces of the mandible are roughly parallel to each other and are firmly connected by the fibrocartilagenous pad and by numerous densely interlaced cruciate ligaments below. The posterior region of the symphysis (Fig. 8d) is dominated by robust processes (interdigitating rugosities) arranged to form horizontal ridges which project laterally from each symphyseal plate and which interdigitate with depressions in the opposite side. These ridges consist of heavily vascularized, remodeled bone. The space in between the two symphyseal margins, therefore, forms a sigmoid-shaped interface in transverse section. The opposing symphyseal plates and their processes are bound together by ligaments that are oriented in a variety of directions, often at right angles to one another (see below).

As one proceeds posteriorly and ventrally in the goat symphysis, the distance between the mandibles widens and the processes of the symphyseal plates become increasingly thicker and more projecting. The orientation of the ligamentous fibers in between the rugosities is mostly dorso-ventral; towards the ventral margin, however, they tend to run antero-posteriorly through the symphysis, oriented approximately  $45^\circ$  to either side of the sagittal plane. At the postero-ventral margin of the symphysis, the two plates are separated by mostly vascular tissue with a much lower density of randomly

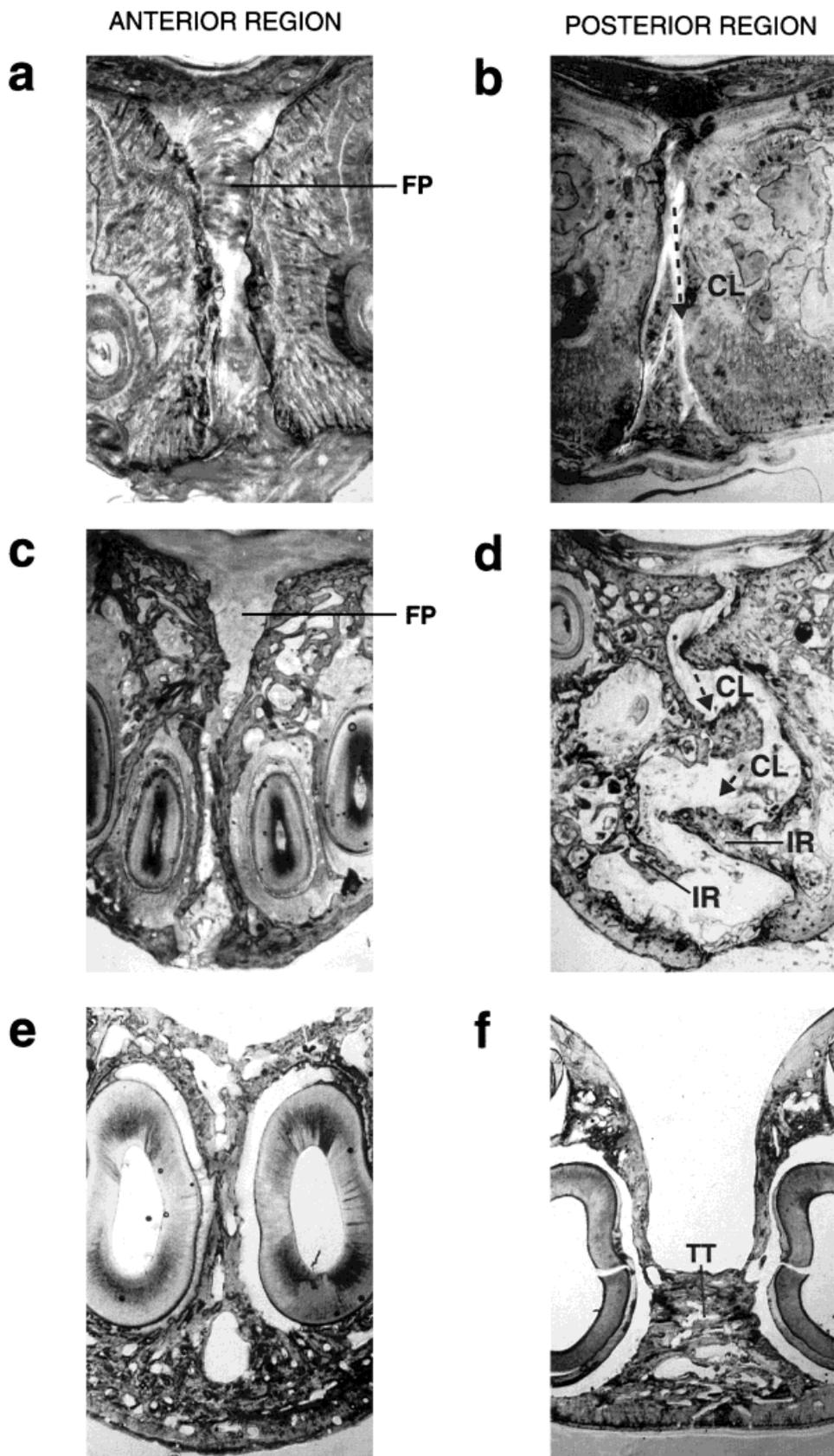


Fig. 8.

oriented ligaments. The space between the symphyseal plates, in other words, becomes wider and less fixed along an axis from the antero-dorsal to postero-ventral ends. At the ventral and dorsal margins of the anterior end of the symphysis, the two plates are less than 2 mm apart; the symphyseal space is increasingly wider postero-ventrally, but remains narrow close to the dorsal margin.

The orientation of the ligaments and interdigitating rugosities of the goat symphysis described above limits sagittal-plane movement between the two mandibles, thereby permitting the transfer of dorsally oriented forces, but these structures permit some independent twisting and medio-lateral movements of the mandibles relative to each other (wishboning). However, if the vertically and obliquely oriented ligaments between the interdigitating rugosities become taut during the power stroke, then it is likely that they stiffen the symphysis in the transverse plane, helping to transfer horizontally oriented force from balancing-side to working-side mandibles, dragging the working-side mandible medially.

**Macaque.** The macaque has a typical class IV symphysis (as defined by Scapino, 1981). Although the symphysis illustrated in Figure 8e,f is a juvenile, the two symphyseal plates are entirely fused with each other, preventing any independent movement of the hemimandibles in any plane. Note that in the posterior end of the symphysis (Fig. 8f), the two mandibles are fused solely by an inferior transverse torus, which Hylander (1988) has shown to be a likely adaptation to resist wishboning and twisting strains.

## DISCUSSION

An unfused symphysis is primitive for Mammalia and is present in all Mesozoic mammals. These are predominately insectivorous or small herbivorous, multituber-

culate species. In the larger herbivorous forms that were present in the early Tertiary and underwent a subsequent adaptive radiation, there is a tendency to either completely fuse the symphysis or increase the area of contact (e.g., through interdigitating rugosities) between the mandibles at the symphysis. In most mammals (see below for discussion of anthropoids and hyracoids) there appears to be a good predictive relationship between the presence of mandibular fusion and the movement of the lower jaw during occlusion. As shown above, mammals with unfused symphyses tend to have occlusal morphologies with steeply (dorso-ventrally) oriented shearing facets, which correspond to the primarily dorsally oriented movement of the jaw and molars during the power stroke. In contrast, most mammals with fused symphyses have significantly more horizontally oriented occlusal wear facets, reflecting a greater degree of transverse movement of the jaw and teeth during the power stroke.

In addition, there is evidence that most mammals with unfused symphyses have mandibles that rotate independently during mastication, in marked contrast to taxa with fused symphyses in which such movements cannot occur. Independent rotations of the mandible are documented here for the goat and the opossum, and have also been documented in carnivorans (Scapino, 1981), insectivorans (Kallen and Gans, 1974; Oron and Crompton, 1985), and galagos (Beecher, 1977b). These data therefore support the hypothesis that, in many mammals, the unfused symphysis is primarily an adaptation (or retention) to allow independent movements of the mandibles during mastication. As discussed above, mandibular rotation helps to align the cusps of the lower teeth relative to the upper teeth as they move into and out of occlusion. In mammals such as the opossum with tribosphenic molars which have embrasure shearing, the movement of the lower molars relative to the upper molars during occlusion is determined by the angles of the shearing facets, which define the orientation of the embrasures into which the molars fit. The ability to control mandibular rotation may therefore be necessary to ensure correct orienta-

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Figure 8. Comparison of coronal sections through respective anterior and posterior regions of opossum (a, b), goat (b, c), and macaque (d, e). FP, fibrocartilagenous pad; CL, cruciate ligaments; IR, interdigitating rugosity; TT, transverse torus. See text for detailed descriptions and discussion.

tion of the lower molars relative to the upper molars in order to move into the embrasures. The slightest misalignment might result in damage to the molar crowns. In the goat, controlled inversion of the mandibles around their longitudinal axes prior to the power stroke is probably a mechanism for orienting the occlusal plane of the lower molars parallel with that of the upper molars.

Independent rotations of the mandibles in mammals with unfused symphyses are partly controlled by the activity of the medial pterygoid. The data presented above for goats and opossums suggest that the medial pterygoid (perhaps only certain compartments) tends to fire biphasically in mammals with unfused symphyses, in contrast to its more typical adductor-like pattern in mammals with fused symphyses. Future research, however, is necessary to determine exactly how much mandibular rotation occurs in goats and opossums, and how these rotations are controlled by the medial pterygoid and other muscles such as the lateral pterygoid, the masseter, and the temporalis.

The proposed relationship between symphyseal morphology and tooth movements during the power stroke is supported by detailed kinematic work on occlusion in a variety of mammal taxa, including the taxa studied here. The opossum, for example, has typical tribosphenic molars in which shearing occurs as the trigonid fits tightly into a V-shaped embrasure between two upper molars, with only a small crushing area between the protocone and talonid. Therefore, the lower molars move into and out of occlusion at a very steep angle (about 80° relative to the transverse plane) and there is no evidence of any phase II power stroke (Crompton and Hiiemae, 1970; Crompton and Kielan-Jaworowska, 1978). A less steep orientation of occlusion characterizes the goat, in which a double set of antero-posteriorly aligned lophs on the lower molars shears past a similar double set on the upper molars as the working-side mandible moves medio-dorsally during occlusion (Smith and Savage, 1959). Occlusion occurs as the high points of the cusps on the lower molars shear down the transversely oriented valleys formed between the cusps of

the upper molars and vice versa. The angle of occlusion in the goat is between 45–50° relative to the transverse plane, as the lower molars move dorso-medially relative to the upper molars (de Vree and Gans, 1976).

Occlusion in taxa with fused symphyses (including anthropoid primates) differs from occlusion in taxa with unfused symphyses in a number of important respects. First, taxa with fused symphyses cannot rotate their mandibles independently, even though the tendency of the adductors to rotate (twist) the mandibular corpora around their long axes generates high symphyseal strains (Hylander and Johnson, 1994). In addition, as shown above, most taxa with fused symphyses tend to have relatively horizontally oriented wear facets, which reflect a more horizontally oriented power stroke. Medial movement of the jaw on the working side during occlusion in primates and hyracoids is closer to the horizontal plane than in the goat or other herbivores that have an unfused symphysis (Janis, 1979a,b; Lucas, 1982). In horses, for example, occlusion takes place through shearing in a single, medially oriented chewing stroke (Lieberman and Crompton, unpublished data).

Viewed in this light, the independent evolution of the fused symphysis in those mammal taxa with primarily transversely oriented power strokes appears to relate to the combined function of providing stiffness in order to transfer force from the balancing-to working-side mandibles as well as providing strength to resist the strains that such forces generate. As shown in Figure 8 and as noted by previous researchers (Beecher, 1977a, 1979, 1983; Scapino, 1981; Dessem, 1985; Ravosa and Hylander, 1994), the generally vertical arrangement of the cruciate ligaments (and, when present, the interdigitating rugosities) that bind the unfused symphyseal plates, clearly creates stiffness in the sagittal plane by restricting dorso-ventral shearing movements, but allows some degree of lateral transverse bending and twisting around the long axes of the mandibles. Fusion is an obvious "solution" to the problem of how to transfer medially directed forces rapidly and completely

across the symphysis. Fusion prevents transverse bending and independent rotation of the mandibles, but perhaps generates higher wishboning and twisting stresses. Increased symphyseal mass will reduce the strains generated in all planes (Ravosa and Hylander, 1994). This principle may explain why, in carnivores, there is a tendency for larger-bodied species (especially felids and ursids) to have more rigid or "partially fused" symphyses than smaller-bodied species (Scapino, 1981). Ravosa (1991) documented a similar trend among prosimians in which longer-jawed species have wider, more rigid symphyses than shorter-jawed species. It is important to note, however, that such size-related trends appear to be lineage-specific. There is no evidence, for example, for any size-related effects on symphyseal fusion in bovids, probably because of the importance of mandibular rotation during occlusion (see above).

It seems likely that the unfused symphysis can be quite stiff in the sagittal plane: in the goat this stiffness is provided by interdigitating rugosities; in the opossum this stiffness is mostly a function of the arrangement of the cruciate ligaments. Since the unfused symphysis probably transfers dorsally oriented force as completely as the fused symphysis (see Dessem, 1985), it follows that mammals with unfused and fused symphyses are expected to have similar overall W/B adductor ratios as measured by EMGs. Gorniak and Gans (1980) showed that EMG levels normalized across side-shifts are reasonable indicators of the force generated by the adductor muscles. Therefore, equal activity in the same muscle when chewing on the balancing and working side means they are generating the same contractile force. To date, most of the direct EMG data on W/B adductor force ratios in mammals with fused symphyses come from macaques and humans, in which masseter W/B ratios tend to approach 1:1, depending on food hardness and bite location (Hylander et al., 1987; Spencer, 1995, 1998). The data presented above from goats and opossums indicate that, in these species, W/B ratios for the combined adductor muscles as well as the combined deep and su-

perficial masseters are not significantly different from those of the macaque. In the goat and the opossum, combined adductor W/B ratios average about 1.2:1; combined W/B ratios for the deep and superficial masseters average about 1.3:1. Weijs and Dantuma (1981) found that W/B adductor ratios in lagomorphs that have an unfused symphysis are also close to 1:1. Hylander et al. (2000), however, showed that W/B ratios in the galago for the combined masseters is 3.3:1, but almost all of this difference is caused by an extremely high W/B ratio (4.4:1) for the deep masseter. The EMG data presented here, therefore, do not support the hypothesis that, as a rule, mammals with unfused symphyses recruit proportionately less adductor force from balancing-side muscles than mammals with fused symphyses. The only major difference may be in those muscles that play a major role in generating transverse force (see below).

Based on the experimental data presented here, we predict that, as a general rule, most mammals with fused and unfused symphyses recruit equal amounts of dorsally oriented balancing-side and working-side adductor force, at least when chewing hard food. However, hypotheses 2–4 are tested here with only a small number of taxa. We stress that more experimental data on mastication are needed for more taxa with fused and unfused symphyses. In particular, additional EMG data from prosimians are needed to test more completely the hypothesis that anthropoids recruit more balancing-side force during mastication than prosimians. As noted above, Hylander et al. (2000) showed that W/B ratios in the galago are higher than those reported for other anthropoid primates for the superficial masseter, primarily because of differential activity in the deep masseter. Given the importance of the deep masseter in primates for generating transverse movement during the power stroke, these data therefore support the hypothesis that symphyseal fusion is an adaptation for generating transverse movement in anthropoids (Hylander et al., 2000). Along this vein, EMG data from nonprimates with fused symphyses are necessary to determine if these taxa

have higher W/B ratios than goats or opossums.

These interpretations raise some interesting questions regarding the evolution of symphyseal fusion in primates and hyraxes, and the hypothesis that symphyseal fusion in anthropoids is an adaptation to strengthen as well as stiffen the symphysis (see Ravosa and Hylander, 1994). As noted above, W/B strain ratios in the galago average 3.5:1 in the mandibular corpus, whereas W/B strain ratios are roughly 1.5:1 in the macaque, suggesting that galagos recruit less balancing-side adductor force than macaques (Hylander 1979a,b; Ravosa and Hylander, 1994). If strain ratios are representative of muscle force ratios, then one would expect the pattern of muscle recruitment and/or force transfer across the symphysis to be different in prosimians than in the other mammals with unfused symphyses. The EMG data reported above for galagos (Hylander et al., 2000), in which galagos have a significantly higher W/B ratio for the deep masseter compared not only with anthropoids but also with the goat and the opossum, suggest this to be the case. It is therefore possible that the pattern of balancing-side adductor muscle recruitment and force transfer across the symphysis is different in primates, especially prosimians, than in many mammalian taxa. As suggested by Hylander (1979a) and Ravosa and Hylander (1994), prosimians such as the galago may not recruit as much balancing-side adductor force as higher primates or other mammals with unfused symphyses for reasons that relate to differences in diet. In addition, if prosimians, like some carnivores, have little mandibular rotation and thus have no need to maintain an unfused symphysis, then a fused symphysis in primates may have evolved as an adaptation "to resist structural failure from the increased symphyseal stress resulting from increased recruitment of balancing-side jaw-muscle force during mastication" (Ravosa and Hylander, 1994, p. 451). Such a scenario accords well with the strong positive allometry between mandibular fusion and jaw size documented among primates (Ravosa, 1991; Ravosa and Hylander, 1994) and some carnivores (Scapino, 1981), but

not among other taxa in which mandibular rotation is known to occur during the power stroke. To test this hypothesis more fully, however, more data are needed on W/B EMG adductor ratios and the extent to which the mandibles rotate independently during the power stroke in prosimians.

## CONCLUSIONS

Fusion of the mandibular symphysis appears to be a function primarily of the movements of the teeth during occlusion. Mammals with predominantly vertically oriented occlusal wear facets on their teeth tend to have unfused mandibular symphyses, in which the two mandibles rotate independently of one another during the power stroke. Since an unfused symphysis probably transfers dorsally directed force as well as a fused symphysis, most mammals with unfused symphyses appear to have similar levels of adductor activity on their working- and balancing-side muscles, as documented here for the goat and the opossum. In this respect, there appears to be no difference in balancing-side to working-side adductor muscle ratios between nonprimates with unfused symphyses and the macaque, which has a fused symphysis.

Mammals such as anthropoids with transversely oriented occlusal wear facets on their teeth tend to have fused mandibular symphyses, which restrict transverse bending. These mammals also tend to have power strokes in which there is little independent movement (especially rotation) allowed between the working- and balancing-side mandibles, in spite of the tendency of many of the adductor muscles to evert the ventral margin of the mandible during the power stroke. Mandibular fusion in these taxa is probably an adaptation primarily to increase the speed and completeness with which transverse force transfers across the symphysis. Mandibular fusion also helps to strengthen the mandibular symphysis, perhaps because higher wishboning and twisting stresses are generated in the symphyseal region as a result of this force transfer.

## ACKNOWLEDGMENTS

We are grateful to R. Harb, C. Musinsky, K. Mowbray, T. Owerkowitz, A. Prescott,

and D. Sadowsky for their assistance with the experiments and in the preparation of the manuscript. We also thank W. Hylander, M. Spencer, M. Ravosa, C. Ross, and four anonymous reviewers for their comments on the manuscript, and C. Ross and C. Wall for their invitation to contribute to the symposium which generated this paper. This work was supported by NSF IBN 96-03833 to D.E.L.

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