Mandibular Corpus Strain in Primates: Further Evidence for a Functional Link Between Symphyseal Fusion and Jaw-Adductor Muscle Force

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ABSTRACT   Previous work indicates that compared to adult thick-tailed
galagos, adult long-tailed macaques have much more bone strain on the
balancing-side mandibular corpus during unilateral isometric molar biting
(Hylander [1979a] J. Morphol. *159:*253–296). Recently we have confirmed in
these same two species the presence of similar differences in bone-strain
patterns during forceful mastication. Moreover, we have also recorded
mandibular bone strain patterns in adult owl monkeys, which are slightly
smaller than the galago subjects. The owl monkey data indicate the presence
of a strain pattern very similar to that recorded for macaques, and quite
unlike that recorded for galagos. We interpret these bone-strain pattern
differences to be importantly related to differences in balancing-side jaw-
adductor muscle force recruitment patterns. That is, compared to galagos,
macaques and owl monkeys recruit relatively more balancing-side jaw-
adductor muscle force during forceful mastication.

Unlike an earlier study (Hylander [1979b] J. Morphol. *160:*223–240), we are
unable to estimate the actual amount of working-side muscle force relative to
balancing-side muscle force (i.e., the W/B muscle force ratio) in these species
because we have no reliable estimate of magnitude, direction, and precise
location of the bite force during mastication. A comparison of the mastication
data with the earlier data recorded during isometric molar biting, however,
supports the hypothesis that the two anthropoids have a small W/B jaw-
adductor muscle force ratio in comparison to thick-tailed galagos. These data
also support the hypothesis that increased recruitment of balancing-side
jaw-adductor muscle force in anthropoids is functionally linked to the
evolution of symphyseal fusion or strengthening. Moreover, these data refute
the hypothesis that the recruitment pattern differences between macaques
and thick-tailed galagos are due to allometric factors. Finally, although the
evolution of symphyseal fusion in primates may be linked to increased stress
associated with increased balancing-side muscle force, it is currently unclear
as to whether the increased force is predominately vertically directed,

transversely directed, or is a near equal combination of these two force components (cf. Ravosa and Hylander [1994] In Fleagle and Kay [eds.]: Anthropoid Origins. New York: Plenum, pp. 447–468). Am J Phys Anthropol 107:257-271, 1998.

The evolution of symphyseal fusion in mammals, i.e., the complete or partial ossification of the left and right dentaries, has occurred independently in many mammalian lineages (cf. Beecher, 1977). Furthermore, symphyseal fusion has also evolved numerous times in various primate lineages, and the functional significance of this trait is a much debated topic.

In 1975 it was suggested that in primates symphyseal fusion and increased amounts of balancing-side jaw-adductor muscle force are functionally linked (Hylander, 1975). That is, symphyseal fusion functions to prevent structural failure of the symphysis by strengthening it so as to more effectively counter increased amounts of symphyseal stress caused by increased recruitment of balancing-side jaw-adductor muscle force during unilateral mastication and biting (cf. Hylander, 1977; Ravosa and Hylander, 1994).

A few years after hypothesizing that symphyseal fusion and balancing-side jaw adductor muscle force are linked, it was discovered that long-tailed macaques (*Macaca fascicularis*) have about 1.5 to two times more bone strain along the working-side corpus than along the balancing-side corpus, whereas thick-tailed galagos (*Otolemur crassicaudatus*) have about seven times more strain along the working side corpus (Hylander, 1979a). It was also demonstrated during the late 1970s that the unfused symphysis of thick-tailed galagos is highly mobile with a relatively low concentration of supportive connective tissues, and therefore structurally is much weaker than the completely fused symphysis found in all extant anthropoids[1] (Beecher, 1977, 1979).

The differences in strain patterns between macaques and galagos were interpreted to indicate that compared to those prosimian

primates with unfused and structurally weaker symphyses, anthropoid primates recruit relatively more balancing-side jaw-adductor muscle force during unilateral molar biting. These data in and of themselves, however, provided no clue as to the actual amount of working-side adductor muscle force relative to balancing-side adductor muscle force (i.e., the W/B muscle force ratio) for these species. In that same year an analysis of bending moments combined with simultaneous transducer biting data and mandibular bone strain data recorded from the lower border of the mandible was used to calculate a first-approximation of the W/B ratio for *vertically directed* adductor muscle force during isometric molar biting (Hylander, 1979b). The data indicated that for macaques this ratio is about 1.4 whereas for galagos it is about 3.0. These data provided further support for the hypothesis that compared to those prosimians with highly mobile, unfused, and structurally weaker symphyses, extant anthropoids recruit relatively more balancing-side jaw-adductor muscle force during unilateral isometric biting.

Although the mandibular bone strain data provide support for the argument that symphyseal fusion and increased balancing-side jaw-adductor muscle recruitment patterns are functionally linked, there are at least two problems with this line of support. First, since the galago subjects were very reluctant to chew various food items, this argument is based on data recorded during episodes of isometric molar biting on a force transducer, rather than during mastication. As primate jaw-adductor muscle recruitment patterns during mastication differ considerably from episodes of isometric unilateral molar biting, and as data recorded during mastication are arguably more functionally relevant, a better (or at least additional) test of what we will refer to as the *symphyseal fusion-muscle recruitment hy-*

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[1]Some extant prosimians have rather robust partially-fused symphyses (Beecher, 1977, 1979) and there may not be major differences in strength between these symphyses and the completely fused symphysis of anthropoids (Ravosa and Hylander, 1994).

pothesis involves analyzing mandibular bone strain patterns recorded during mastication. Second, and more importantly, allometric factors may influence jaw-adductor muscle recruitment patterns, and therefore perhaps the correlation between symphyseal morphology and the relative amount of balancing-side muscle force in macaques and galagos is a spurious one. The rationale for the allometric argument is as follows.

Larger mammals may have proportionally less total physiological cross-sectional area to their jaw-adductor muscles and therefore relatively less capability to generate adductor muscle force (cf. Scapino, 1981). If so, perhaps larger mammals recruit more balancing-side jaw-adductor muscle force so as to develop equivalent amounts of bite force (Scapino, 1981; Hylander, 1985; Ravosa, 1991, 1996). Thus, long-tailed macaques, which are two to four times larger than thick-tailed galagos, may simply recruit more balancing-side muscle force because of allometric constraints, and if so, symphyseal fusion or strengthening in primates may not be functionally linked to an increase in balancing-side jaw-adductor muscle force during mastication, but instead to some other mechanical requirement (cf. Hylander and Johnson, 1997).

The purpose of this paper is to test further the symphyseal fusion-muscle recruitment hypothesis. We propose to address the apparent problems in the earlier study by analyzing mandibular mid-corpus strains recorded from long-tailed macaques and thick-tailed galagos during *mastication*, because, as already noted, this behavior is arguably more functionally relevant than isometric molar biting on a force transducer. We also propose to test the competing and what we will refer to as the *allometric constraint-muscle recruitment hypothesis*. This hypothesis can be tested by analyzing jaw-adductor muscle recruitment patterns in the above macaques, galagos, and a third primate species that has a relatively weak, highly mobile unfused symphysis and whose body size is equal to or greater than *Macaca fascicularis*. Alternatively, this hypothesis can be tested by analyzing jaw-adductor muscle recruitment patterns in macaques and gala-gos and a primate species that has a completely fused symphysis and whose body size is equal to or smaller than adult *Otolemur crassicaudatus*.

There are no known extant primate species that are as large as (or larger than) adult long-tailed macaques *and* have relatively weak, highly mobile unfused symphyses.[2] There are, however, numerous anthropoid species that have fused mandibular symphyses and are as small as (or smaller than) adult thick-tailed galagos. We have selected adult owl monkeys (*Aotus trivirgatus*), which are slightly smaller than thick-tailed galagos, to serve as experimental subjects.

The symphyseal fusion-muscle recruitment hypothesis predicts that the two primates with fused symphyses (macaques and owl monkeys) will have relatively high levels of balancing-side mid-corpus mandibular bone strain, whereas the greater galagos will have relatively low levels of balancing-side mid-corpus bone strain. Therefore, this hypothesis predicts that the W/B ratio for mandibular strain values are relatively small in macaques and owl monkeys, and relatively large in galagos. In contrast, the allometric constraint-muscle recruitment hypothesis predicts that the largest species, long-tailed macaques, will have the highest levels of balancing-side bone strain, the intermediate-sized species, thick-tailed galagos, will have intermediate levels of balancing-side bone strain, and the smallest species, owl monkeys, will have the lowest levels of balancing-side bone strain. Therefore, the allometric hypothesis predicts that the W/B ratio for mandibular strain values are relatively small in macaques, intermediate in galagos, and relatively large in owl monkeys.

MATERIALS AND METHODS
Subjects

The following primates served as subjects: four adult female (macaques 1, 2, 3, and 5)

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[2]Although some adult indriids are as large as an adult long-tailed macaque, their unfused (or partially fused) symphyses are very well buttressed (Ravosa, 1991) with a dense concentration of fibrous connective tissue, some of which is either calcified, ossified, or chondrified (Beecher, 1977).
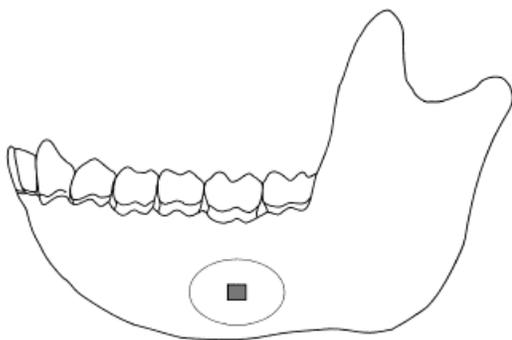
Fig. 1. Drawing of a macaque mandible indicating the approximate location of the rosettes. For each macaque experiment the rosette was positioned within the perimeter of the oval located below the postcanine teeth along the lower half of the mandible. Rosette position for the galagos and owl monkeys was confined, due to size considerations, to the second-molar mid-corpus region. See text for discussion.

and one adult male (macaque 4) *Macaca fascicularis*; four adult male (galagos 3, 5, 6, and 7) *Otolemur crassicaudatus*; and one adult female (owl monkey 2) and one adult male (owl monkey 1) *Aotus trivirgatus*.

Experiments

No new experiments were initiated for this study. Instead, this study is based on a recent analysis of data originally derived from a large and diverse series of experiments that were designed for other purposes. For macaques, the data are derived from studies described in Hylander (1979a, 1986), Hylander and Crompton (1986), and Hylander et al.(1987). For owl monkeys, the data are derived from studies described in Ross (1993) and Ross and Hylander (1996). For galagos, the data are derived from experiments described in Hylander (1979a) and Ravosa and Hylander (1993). In one experiment rosette strain gages were bonded *bilaterally*, i.e., one rosette on the left and one on the right side of the mandible (macaque 4, exp. E). In the remaining experiments the rosette strain gages were bonded *unilaterally* (Fig. 1). In four experiments two rosettes (rosette 1 and rosette 2) were bonded *unilaterally* along the macaque mandibular corpus immediately adjacent to one another (macaque 2, exps. A and B; macaque 3, exp. A; macaque 4, exp. A). With the exception of macaque 2, Exp. C, all rosettes in all sub-

jects were bonded along the upper or middle portion of the lower half of the mandibular corpus, i.e., at or slightly below the mid-corpus level. In this exception, the rosette was bonded very close to the lower border of the mandible. Rosette alignment and position was determined from radiographs and/or direct measurements during the bonding procedure.

Rosette bonding and bone strain recording procedures

The procedures and apparatus for bonding miniature 120-ohm stacked rosettes to cortical bone with a cyanoacrylate adhesive are described elsewhere (Hylander, 1979a, 1984, 1986; Hylander and Johnson, 1989). These procedures were performed with the subjects under general anesthesia using either fluothane or a combination of nitrous oxide and methoxyflurane (Hylander, 1979a), or the subjects were heavily sedated with a combination of acepromazine and ketamine (Connolly and Quimby, 1978). In all instances the surgical site was infiltrated subcutaneously with a local anesthetic (lidocaine HCl) containing epinephrine (1:100,000) so as to provide both profound anesthesia and adequate hemostasis.

Recording procedure

Each of the strain-gage elements of each rosette formed one arm of a Wheatstone bridge. Bridge excitation for each element was 1 volt. The voltage output from each of the strain-gage elements was first conditioned and amplified and then ordinarily recorded at 15 inches per second with a multiple-channel FM tape recorder. In several instances, however, the data were recorded on a six-channel chart recorder (Hylander, 1979a).

Prior to recovery from the general anesthesia or sedation, the subject was placed in a restraining chair (macaques) or restraining sling-suit (galagos and owl monkeys) especially designed to permit normal head, neck, and jaw movements during mastication (Hylander, 1979a; Ross and Hylander, 1996). Once the animal was fully alert, usually 3–6 hours later, it was fed pieces of apple skin and hard or tough foods, i.e., monkey chow,

dried apricot, popcorn kernels, dried gelatin candy (dried gummy bears) and prune seeds.

Immediately before and after each sequence of mastication the zero level of strain was determined when the subject's mandible was at rest. The subject was fed various foods in an intermittent and random fashion and data were recorded until either sufficient data were obtained or the animal refused to eat any additional food. During the recording sessions we noted directly on the voice track of the tape recorder what foods were eaten and whether the subject chewed on the left or right side (cf. Hylander, 1979a and Ross and Hylander, 1996). Chewing side identification was accomplished primarily by noting the position of the tongue and food bolus during jaw opening, i.e., noting whether the food was placed on the left or right side prior to the next power stroke. Macaques typically chewed on only one side throughout an entire sequence. In contrast, owl monkeys and galagos typically engaged in three or four power strokes on one side of the jaw, then shifted to the opposite side for a similar number of power strokes, and they continued to repeat this pattern throughout the chewing sequence. At the conclusion of the recording session the animal was sedated, each rosette was removed, the surgical incision was resutured, an antibiotic was administered, and the animal was returned to its cage. Healing of the surgical site was uneventful in all subjects.

Strain analysis

With the exception of data drawn directly from Tables 8 and 9 in Hylander (1979a), which were not recorded on a FM tape recorder, all bone strain recordings were reproduced for visual examination by playing the raw strain data from the tape recorder into a six-channel chart recorder. As described elsewhere (Hylander and Johnson, 1997), the raw strains of all chewing cycles for each selected sequence were played simultaneously from the tape recorder into a 16-channel analog-to-digital converter, and the digitized values were written to the hard disk of a microcomputer. Each channel was sampled and digitized at a rate of 500 Hz with a channel separation time of 0.125 ms. The digitized data files were used for subsequent strain calculations and analysis. For each food and subject we selected two chewing sequences for analysis. For macaques this consisted of one sequence of chewing on the left and one of chewing on the right. For galagos and owl monkeys, however, most sequences contained both left and right chews. Therefore, when possible, we selected one sequence that began with chews on the left and one that began with chews on the right.

The digitized raw strain values were filtered at 40 Hz using a digital low-pass Butterworth filter. The magnitude of the maximum and minimum principal strains (ϵ_1 and ϵ_2) and maximum shear strains (γmax) and the direction of ϵ_1 were calculated in 2 ms intervals. For purposes of analysis, γmax was used as an indicator of peak strain (Hylander and Johnson, 1989). Descriptive statistics of ϵ_1, ϵ_2, and γmax were calculated for peak strain, and for the 25%, 50% and 75% level of peak strain for both loading and unloading of each power stroke of mastication and incision. We also calculated the ratio of working-side γmax values/balancing-side γmax values (W/B strain) from the peak mean values. For this study we will only report on the descriptive statistics for the magnitude of γmax and the W/B γmax ratios at peak strain during mastication.

RESULTS

Typically, some subjects simply refused to eat certain foods. With the exception of one galago (galago 5) and one macaque (macaque 1), all subjects chewed at least one of the hard or tough foods. Furthermore, the macaques and owl monkeys readily chewed apple skin. In contrast, none of the galagos chewed apple skin, although they all readily chewed apple pulp. As the only food that galago 5 chewed was apple pulp, we will present the strain data recorded from this subject during the chewing of this food. Data recorded from the other primates during the chewing of apple pulp, however, will not be presented. As in our most recent studies, we

TABLE 1. Descriptive statistics of working- and balancing-side mandibular corpus shear strain magnitudes and W/B shear strain ratios for macaques during mastication

Subject/experiment	Food	Working-side shear					Balancing-side shear					W/B ratio shear
		N	Mean	Largest	SD	CV	N	Mean	Largest	SD	CV	
Macaque 1												
Exp. A	Apple skin	41	716	982	(100)	14	35	446	538	(71)	16	1.61
Exp. B	Apple skin	41	455	595	(70)	15	32	245	401	(77)	31	1.86
Mean[1]	Apple skin		586		(85)	15		346		(74)	24	1.73
Macaque 2												
Exp. A												
Ros. 1	Apple skin	33	531	708	(93)	18	31	464	782	(130)	28	1.14
Ros. 2	Apple skin	33	823	1093	(145)	18	31	391	673	(117)	30	2.10
Exp. B												
Ros. 1	Apple skin	32	607	748	(98)	16	26	277	369	(66)	24	2.19
Ros. 2	Apple skin	32	538	628	(70)	13	26	262	397	(69)	26	2.05
Exp. B												
Ros. 1	Chow	50	653	973	(136)	21	50	366	561	(88)	24	1.78
Ros. 2	Chow	50	735	1196	(188)	26	50	524	859	(148)	28	1.40
Exp. C	Apple skin	45	516	851	(152)	29	29	580	882	(187)	32	0.89
Exp. D	Apple skin	37	536	670	(81)	15	43	226	311	(27)	12	2.37
Exp. E	Apple skin	31	682	974	(166)	24	21	555	684	(90)	16	1.23
Mean[1]	Apple skin		605		(110)	19		394		(95)	24	1.71
	Chow		694		(162)	23		445		(118)	26	1.59
Macaque 3												
Exp. A												
Ros. 1	Apple skin	26	658	855	(128)	19	23	330	437	(60)	18	1.99
Ros. 2	Apple skin	26	376	483	(65)	17	23	250	320	(41)	16	1.50
Exp. A												
Ros. 1	Chow	30	1125	1679	(238)	21	37	413	568	(100)	24	2.72
Ros. 2	Chow	30	585	896	(129)	22	37	314	442	(72)	23	1.86
Exp. B	Apple skin	52	388	597	(145)	37	34	216	270	(37)	17	1.80
Exp. C	Apple skin	26	558	837	(172)	31	30	384	837	(172)	45	1.45
Mean[1]	Apple skin		495		(128)	26		295		(78)	24	1.69
	Chow		855		(184)	22		364		(86)	24	2.29
Macaque 4												
Exp. A												
Ros. 1	Apple skin	19	373	529	(119)	32	17	300	363	(40)	13	1.24
Ros. 2	Apple skin	19	224	301	(64)	29	17	177	205	(18)	10	1.27
Exp. B	Apple skin	29	558	770	(114)	20	26	345	504	(72)	21	1.62
Exp. C	Apple skin	54	234	419	(83)	35	43	132	310	(63)	48	1.77
Exp. D	Apple skin	29	739	934	(110)	15	32	384	721	(155)	40	1.92
Exp. E	Chow	20	776	1106	(145)	19	20	716	928	(122)	17	1.08
Mean[1]	Apple skin		426		(98)	26		268		(70)	26	1.56
	Chow		776		(145)	19		716		(122)	17	1.08
Macaque 5												
Exp. A	Apple skin	28	394	752	(140)	36	25	182	284	(46)	25	2.16
	Chow	30	433	768	(175)	40	32	324	532	(74)	23	1.34
Exp. B	Apple skin	50	474	708	(102)	22	23	257	457	(88)	34	1.84
	Popcorn kernel	50	705	1117	(198)	28	37	633	1119	(188)	30	1.11
Mean[1]	Apple skin		434		(121)	29		220		(67)	30	2.00
	Hard/tough foods[2]		569		(187)	34		479		(131)	26	1.23
Grand Mean[3]	Apple skin		509		(108)	23		304		(77)	26	1.74
	Hard/tough foods[2]		724		(169)	24		501		(114)	23	1.55

[1] Subject means are based on the mean values for each food type (i.e., apple skin or hard/tough foods).
[2] Hard/tough foods include chow and popcorn kernels.
[3] Grand means for each food type are based on the mean values of each subject.
N, SD and CV indicate number of power strokes, standard deviation and coefficient of variation, respectively.
Abbreviations: Exp., Experiment; Ros. 1 and Ros. 2 indicate rosettes 1 and 2, respectively.
The letters A, B, C, D, and E refer to separate experiments.

will present strain data recorded during both the chewing of apple skin and the chewing of comparatively hard or tough foods (Hylander and Johnson, 1997). For reasons to be discussed later, however, we intend to focus most of our attention on data recorded during the chewing of hard or tough foods.

Strain magnitude and W/B strain ratios

The largest mandibular strains in all three species are associated with the chewing of hard or tough food items (Tables 1, 2, and 3). Furthermore, with the exception of the one experiment where the rosette was posi-

TABLE 2. *Descriptive statistics of working- and balancing-side mandibular corpus shear strain magnitudes and W/B shear strain ratios for galagos during mastication*

Subject/food	Working-side shear					Balancing-side shear					W/B shear ratio
	N	Mean	Largest	SD	CV	N	Mean	Largest	SD	CV	
Galago 3											
Chow	18	1459	2653	(755)	52	19	330	746	(171)	52	4.42
Galago 5											
Apple[1]	36	325	607	(138)	42	23	62	172	(41)	66	5.24
Galago 6											
Gelatin candy 1	13	1171	1575	(227)	19	10	85	100	(14)	16	13.78
Gelatin candy 2	13	839	1082	(231)	28	23	72	110	(18)	25	11.65
Dried prune	29	565	1254	(321)	57	11	66	123	(35)	53	8.56
Mean[2]											
Hard/tough foods[3]		858		(260)	35		74		(22)	32	11.33
Galago 7											
Gelatin candy 1	50	1163	1563	(213)	18	35	227	370	(51)	22	5.12
Gelatin candy 2	19	1385	2161	(335)	24	21	259	390	(68)	26	5.35
Mean[3]											
Hard/tough foods[3]		1274		(274)	21		243		(60)	24	5.24
Grand mean[4]											
Hard/tough foods[3]		1197		(430)	36		216		(84)	36	7.00

[1] This subject chewed apple pulp but not apple skin.
[2] Subject means are based on the mean values for each food type (i.e., apple skin or hard/tough foods).
[3] Hard/tough foods include gelatin candy, dried prune and chow.
[4] Grand means for each food type are based on the mean values of each subject.
N, SD and CV indicate number of power strokes, standard deviation and coefficient of variation, respectively.
Gelatin candy 1 and 2 refer to different chewing sequences associated with this food.

TABLE 3. *Descriptive statistics of working- and balancing-side mandibular corpus shear strain magnitudes and W/B shear strain ratios for owl monkeys during mastication*

Subject/food	Working-side shear					Balancing-side shear					W/B ratio shear
	N	Mean	Largest	SD	CV	N	Mean	Largest	SD	CV	
Owl Monkey 1											
Apple skin	22	961	1372	(269)	28	14	889	1343	(288)	32	1.08
Gelatin candy 1	30	1263	1629	(208)	16	15	894	1248	(289)	32	1.41
Gelatin candy 2	20	1289	1570	(205)	16	19	905	1338	(230)	25	1.42
Dried prune	36	1333	2333	(361)	27	26	1236	2197	(409)	33	1.08
Mean[1]											
Apple skin		961		(269)	28		889		(288)	32	1.08
Hard/tough foods[2]		1295		(258)	20		1012		(309)	30	1.31
Owl Monkey 2											
Apple skin	26	504	824	(152)	30	39	377	661	(110)	29	1.34
Gelatin candy	50	938	1229	(127)	14	50	711	935	(89)	13	1.32
Dried prune	29	793	1105	(187)	24	23	727	956	(107)	15	1.09
Dried apricot	43	747	1085	(161)	22	37	543	852	(178)	33	1.38
Mean[1]											
Apple skin		504		(152)	30		377		(110)	29	1.34
Hard/tough foods[2]		826		(158)	20		660		(125)	20	1.26
Grand mean[3]											
Apple skin		733		(211)	29		633		(199)	31	1.21
Hard/tough foods[2]		1061		(208)	20		836		(217)	25	1.28

[1] Subject means are based on the mean values for each food type (i.e., apple skin or hard/tough foods).
[2] Hard/tough foods include gelatin candy, dried prune and dried apricot.
[3] Grand means for each food type are based on the mean values of each subject.
N, SD and CV indicate number of power strokes, standard deviation and coefficient of variation, respectively.
Gelatin candy 1 and 2 refer to different chewing sequences associated with this food.

tioned very near the lower border of the mandible (macaque 2, exp. C), the largest average maximum shear strains (γmax) occur along the working side. In addition, the average W/B γmax ratios for the two anthropoid species tend to be much smaller than the W/B ratios for galagos. This is primarily because the average balancing-side strains in owl monkeys and macaques (836 $\mu\epsilon$ and 501 $\mu\epsilon$, respectively) are very much larger than those of galagos (216 $\mu\epsilon$). Species differences in both the absolute strains and in the
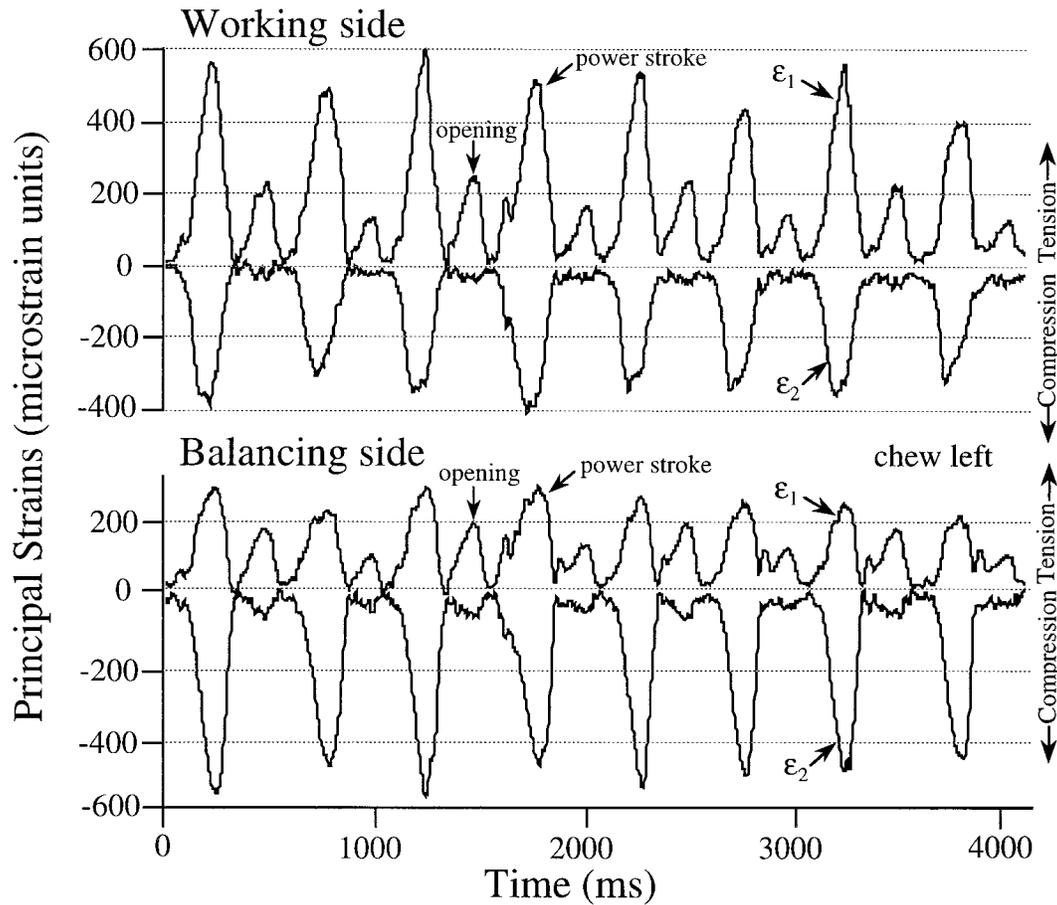
Fig. 2.   Plot indicating the simultaneous principal strains recorded from the working- and balancing-
sides of the mandibular corpus in a large adult male macaque (macaque 4) during the chewing of monkey
chow on the left side. This is the only experiment where simultaneous working- and balancing-side strains
were recorded. See text for discussion.

W/B ratios can be readily seen in Tables 1, 2, and 3. For example, the grand mean W/B ratios for owl monkeys and macaques during the chewing of hard or tough foods are about 1.3 and 1.6, respectively. In contrast, the grand mean ratio for galagos during the chewing of hard or tough foods is 7.0.

The differences in the magnitude of strains between working and balancing sides in the two anthropoids and the greater galagos can also be seen in Figures 2, 3, and 4. As seen in Figures 2 and 3, the magnitude of the working-side principal strains (ϵ_1 and ϵ_2) appear to be somewhat similar to balancing-side principal strains for both macaques and owl monkeys. Note that Figure 2 actually demon-

strates *simultaneous* working- and balancing-side mid-corpus principal strains in a large male macaque during the chewing of monkey chow (macaque 4, exp. E). As noted earlier, this is the only experiment where simultaneous strains from both left and right sides of the mandible were recorded. Furthermore, none of the data in Table 1 consist of simultaneous strains. Figure 3 is based on owl monkey mandibular strains recorded from a single rosette, and therefore the working- and balancing-side mid-corpus strains are *sequential*, rather than simultaneous. In this figure the subject (owl monkey 2) first chewed a hard dried prune on the left side and then switched and chewed on the
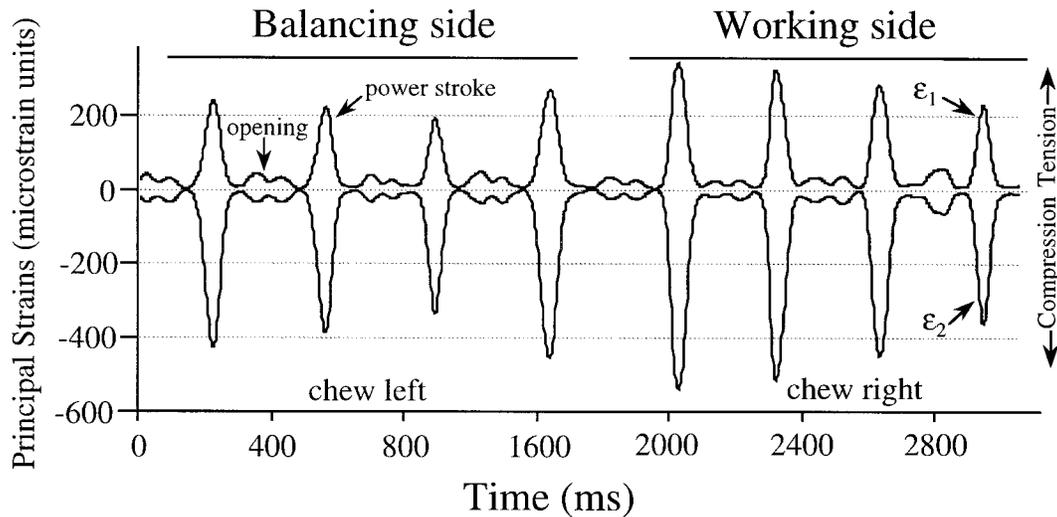
Fig. 3. Plot indicating the sequential principal strains recorded from the working- and balancing-sides of the mandibular corpus in an adult female owl monkey (owl monkey 2) during the chewing of hard prune. The first four power strokes indicate balancing-side strains (chew left) whereas the last four power strokes indicate working-side strains (chew right). See text for discussion.

right side. The first four power strokes in this figure are balancing-side corpus strains because the rosette is located along the right mandibular corpus. The last four power strokes are working-side corpus strains.

In contrast to the anthropoid pattern of slightly smaller balancing-side shear strains relative to working-side strains, Figure 4 indicates that in galagos (galago 7), the magnitude of principal strains along the balancing side mid-corpus area (the four power strokes in Fig. 4B) are very much smaller than those along the working side (the four power strokes in Fig. 4A). This figure also demonstrates simultaneous principal strains recorded from a rosette positioned along the dorsal interorbital region. As this particular rosette is located exactly in the midsagittal plane, there are no working- or balancing-side interorbital strains. Instead, there are simply interorbital strains during chewing on the left and interorbital strains during chewing on the right.

Although the interorbital strains are small, more important for our purposes here is that the relative size of these interorbital strains is presumably indicative of how forceful the subject chewed, i.e., the larger the level of masticatory force, the larger the

level of interorbital strain. Note that the interorbital strains are larger in Figure 4B than in Figure 4A. This was generally the case for all of the recorded chewing sequences for this subject. Thus, this subject (galago 7) apparently chewed more forcefully when the balancing-side mandibular strains were being recorded. This suggests that if this subject had chewed on left and right sides with a near equal intensity of masticatory force, the W/B γmax ratio would have been even larger than the 5.2 value listed in Table 2.

Finally, although not necessarily germane to the hypotheses tested in this study, Figures 2 and 3 also demonstrate that there are easily detectable and frequently significant levels of mandibular mid-corpus strains in anthropoids during jaw opening. This is particularly the case for the large male macaque (Fig. 2). In contrast, galagos mandibular strains during jaw opening are usually quite small and ordinarily undetectable.

DISCUSSION

As in our most recent studies, we have presented strain data recorded during both the chewing of apple skin and the chewing of hard or tough foods (Hylander and Johnson,
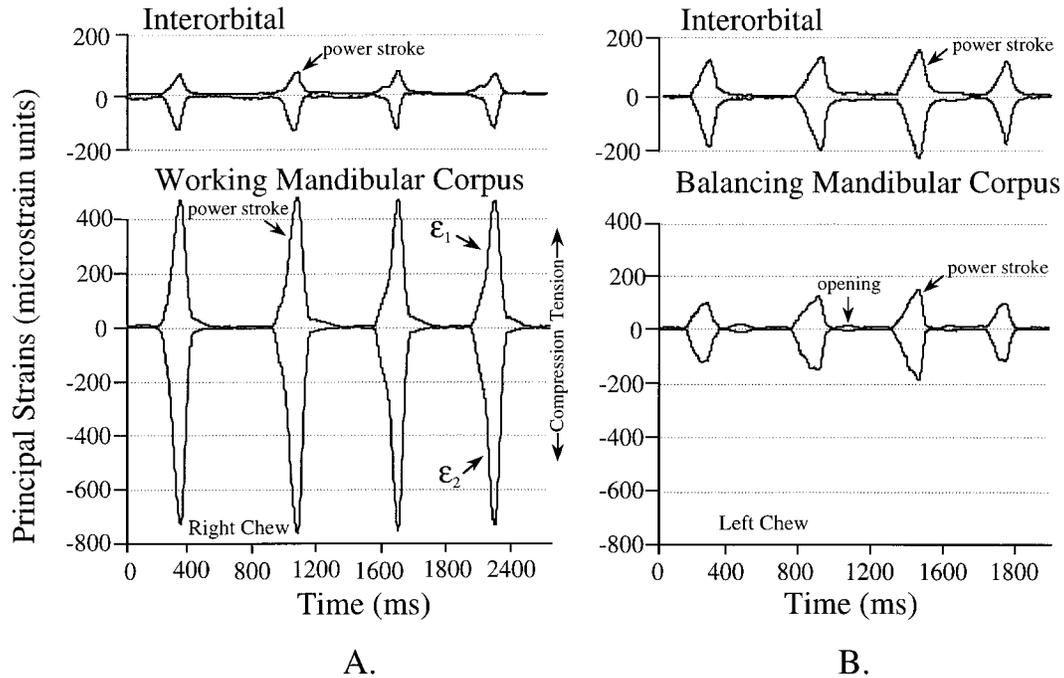
Fig. 4. Plot indicating sequential and simultaneous principal strains recorded from the interorbital region and the right side of the mandibular corpus in an adult male thick-tailed galago (galago 7) during the chewing of hard prune. **A**: Working-side mandibular strains (chew right). **B**: Balancing-side mandibular strains (chew left). Note that the interorbital strains are much larger during chewing on the left than chewing on the right, indicating that for these chewing cycles the most forceful chews are associated with chewing on the left. In spite of this outcome, the balancing-side strains for chewing on the left are still much smaller than the working-side strains during chewing on the right. See text for discussion.

1997). The data recorded during the chewing of apple skin facilitate the direct comparison of mandibular corpus strains with strains recorded from other regions of the face during the chewing of apple skin (e.g., Hylander et al., 1991). Furthermore, these data also facilitate the interspecific comparison of mandibular corpus strains as presumably the mechanical properties of apple skin are virtually identical and therefore the chewing of apple skin requires similar levels of masticatory force prior to swallowing. For this study, however, we intend to focus our attention largely on data recorded during the chewing of hard or tough foods for the following reasons.

First, as already noted, none of the galagos chewed apple skin. Second, data associated with the chewing of hard or tough foods are important because structural adaptations to counter masticatory stress are presumably in response to the more forceful masticatory loading regimes. Third, and

most importantly, earlier work has established that W/B masseter muscle force ratios are frequently influenced by overall masticatory force levels (Hylander et al., 1992; Hylander and Johnson, 1997). In most macaques the lowest W/B masseter force ratios (which begin to approach 1.0) are associated with the more forceful power strokes. Thus, as the magnitude of masticatory force levels frequently influence W/B ratios for jaw-adductor muscle force, in a comparative study such as this all subjects should be required to chew in a relatively forceful manner so as to insure maximum recruitment levels of balancing-side jaw-adductor muscle force.

A test of the allometric constraint- and symphyseal fusion-muscle recruitment hypotheses

The data presented in Tables 1, 2, and 3 clearly refute the allometric constraint-muscle recruitment hypothesis and strongly

support the symphyseal fusion-muscle recruitment hypothesis in that compared to galagos, 1) the average amount of balancing-side strain is much larger in both macaques and owl monkeys, and 2) the W/B strain ratios for owl monkeys and macaques are very similar to one another, i.e., about 1.3 and 1.6, respectively, whereas the W/B strain ratio for thick-tailed galagos is much larger, i.e., 7.0. Furthermore, the W/B strain ratios for macaques and galagos during mastication are very similar to those during isometric transducer biting (1.8 and 7.1, respectively) (Hylander, 1979a).

Allometry, muscle recruitment, and mandibular strain

The observations that the smallest and largest primates in this sample (owl monkeys and macaques, respectively) have W/B strain ratio values more similar to one another, and the intermediate-sized galago species has W/B strain ratios considerably larger indicates that allometric constraints, as outlined in the Introduction, are of negligible importance within this particular group of primates. Moreover, even when considering the W/B strain ratios for only the two anthropoids, there is no evidence to support the allometric constraint hypothesis because this hypothesis predicts that the W/B strain ratios should be smallest in macaques. Instead, the data indicate that the smallest overall ratios are found in the owl monkeys (hard/tough foods: about 1.6 and 1.3 for macaques and owl monkeys; apple skin: about 1.7 and 1.2 for macaques and owl monkeys).

A comparison of interspecific mandibular strains during the chewing of certain foods, however, reveals possible allometric effects. Presumably the dried gelatin candies eaten by two of the galagos (galagos 6 and 7) and the two owl monkeys have very similar mechanical properties. If so, as the mechanical properties of food items largely determine how forceful an animal must chew or bite so as to break this item down, presumably the level of bite force distributed along premolar and molar shearing crests and crushing and grinding surfaces in these two species are more or less the same during the chewing of this food. As the owl monkey mandible is about the same size as (or

perhaps slightly smaller than) the galago mandible and the gelatin candy eaten by these two species is the same size and shape, it is not surprising that the average working-side mandibular strains for this food are similar (owl monkeys, 1107 µε; galagos, 1140 µε). There is, however, about five times more strain along the balancing-side corpus in owl monkeys than in galagos (805 µε and 161 µε, respectively). Rather than being linked to allometric constraints, these large differences in balancing-side strains are likely functionally linked to differences in balancing-side jaw-adductor muscle force and symphyseal morphology.

Although the hard and/or tough foods eaten by macaques (popcorn kernels and monkey chow) differ in their mechanical properties from those eaten by owl monkeys (gelatin candy and dried prunes and apricots), presumably the mechanical properties of the apple skin that was eaten by these two species are very similar. The average working-side mandibular strains during apple-skin chewing in macaques (509 µε) are smaller than those recorded from owl monkeys (733 µε). On average during the chewing of apple skin the working-side (and balancing-side) mandibular strains in macaques are about 69% (and 48%) of the corresponding values recorded from owl monkeys. Presumably these differences in mean values suggest that the owl monkey mandible is strained and stressed significantly more than the macaque mandible during the chewing of apple skin, although there is considerable overlap in strain values between these two species. Furthermore, these differences are probably partially due to masticatory forces of similar magnitude acting on mandibles that are very dissimilar in size. It is also possible, however, that these strain differences are also influenced by the relative size of the ingested food items. As we did not adjust or scale the relative size of the pieces of apple skin offered to the various subjects, we are unable to partition what portion of the differences in strain are due to mandibular size differences, and what portion is due to initial food size differences.

Finally, there is at least one additional allometric factor that influences balancing-side jaw-adductor recruitment patterns. Compared to small free-ranging mamma-

lian herbivores, large free-ranging herbivores tend to eat a greater proportion of foods composed of hard and/or tough difficult-to-chew materials (Bell, 1971; Rensberger, 1973). A literature survey extends this finding to extant primates (Kay, 1973; Kay and Hylander, 1978; Beecher, 1983; Ravosa, 1991, 1996). As demonstrated experimentally in macaques, a dietary shift to harder and/or tougher foods is likely associated with not only an absolute increase in total masticatory force, but a disproportionate increase in the recruitment of balancing-side jaw-adductor muscle force relative to working-side jaw muscle force (Hylander, 1979a; Hylander et al., 1992). Thus, although allometric constraints may indeed influence balancing-side muscle recruitment patterns, this may have more to do with the mechanical properties of selected food items, and less so with the constraints on jaw-muscle force production associated with increasing body size. This food selection factor, as argued elsewhere, may be importantly related to why symphyseal fusion is associated with large body size in some mammalian lineages (Scapino, 1981; Ravosa and Hylander, 1994).

Increased vertical and transverse muscle force and symphyseal fusion

If symphyseal fusion in primates is indeed functionally linked to an increase in balancing-side jaw-adductor muscle force, is this linkage confined mainly to the vertical component of jaw-adductor muscle force, is it confined mainly to the transverse component of this muscle force, or are both force components of near equal importance? Although we are unable to answer these interrelated questions at this time, there are important implications associated with these questions as these two force components tend to load the symphysis in two very different ways.

An increase in vertically directed jaw-adductor muscle force causes an increase in vertically directed bite force, i.e., an increase in crushing or vertical shear along the teeth. Furthermore, as vertical force from the balancing-side muscles is transferred to the working side, this causes an increase in dorsoventral shear stress throughout the symphysis, as well as increased bending of

the symphysis due to twisting of the balancing-side mandibular corpus about its long axis (Hylander, 1984, 1985). Thus, perhaps symphyseal fusion in primates is an adaptive response to counter some combination of dorsoventral shear and bending of the symphysis (cf. Hylander, 1975, 1979a, 1979b; Beecher, 1977, 1983; Ravosa, 1991, 1996; Ravosa and Hylander, 1994; and Ravosa and Simons, 1994), and if so, fusion is functionally linked to increasing the amount of vertically directed bite force, i.e., increased crushing and vertical shearing along the postcanine dentition.

In contrast to the consequences of an increase in vertically directed jaw-adductor muscle force, an increase in transversely directed muscle force causes an increase in the transverse component to the bite force, i.e., an increase in grinding or transverse shear along the teeth. Moreover, as increased transversely directed muscle force is also transferred across the symphysis from the balancing- to the working-side corpus, this causes an increase in lateral transverse bending or wishboning of the symphysis (Hylander and Johnson, 1994). Thus, perhaps symphyseal fusion in primates is an adaptive response to counter wishboning of the symphysis (Ravosa and Hylander, 1994), and if so, fusion is functionally linked to increasing the amount of transversely directed bite force, i.e., increased grinding or vertical shearing along the postcanine dentition.

Unfortunately our strain data are unable to resolve the issue regarding the relative importance of these force components on symphyseal fusion. Although symphyseal strains in macaques have been partially characterized, indicating that the macaque mandibular symphysis experiences varying degrees of dorsoventral shear, bending due to twisting of the mandibular corpora about their long axes, and wishboning (Hylander, 1984, 1985), we have no symphyseal strain data for galagos or owl monkeys. Despite this lack of data, however, we can reasonably assume that increased balancing-side jaw-adductor activity in these two species contributes to increased vertical bite force magnitudes (cf. Hylander, 1977), and therefore this increased activity causes varying

amounts of dorsoventral shear along their symphyses. In addition, due to the geometry of jaw-adductor muscles in galagos and owl monkeys, it is also likely that their symphyses are bent due to twisting of the mandibular corpora about their long axes (cf. Hylander, 1979a). What we do not know, however, is whether the mandibular symphysis of owl monkeys and galagos experiences wishboning.

As noted earlier, although we originally calculated descriptive statistics for strain directions, these data are not reported here. This is because doing so would have lengthed this manuscript considerably while duplicating much of what has already been published (Hylander, 1979a; Hylander et al., 1987). Furthermore, and more importantly, these data are unable to help resolve the issue regarding symphyseal loading patterns in galagos and owl monkeys. This is because due to the small size of the galago and owl monkey mandibles and the relatively large size of the strain gage rosettes, we were forced to record strain from a very restricted area of the corpus in these subjects. This in turn meant that we were unable to test various hypotheses regarding loading patterns of the corpus by examining changes in strain directions relative to alterations in rosette position. Although our limited directional data on owl monkeys and galagos are consistent with the hypotheses that their working-side corpora are directly sheared and twisted about their long axes whereas their balancing-side corpora are directly sheared, twisted about their long axes, and bent in the parasagittal plane, it is unclear as to whether or not the owl monkey and galago mandible experiences wishboning.

We intend to pursue the issue of symphyseal loading indirectly by doing a detailed EMG analysis of the superficial and deep portions of the masseter muscle during the chewing of hard and/or tough foods in baboons, macaques, thick-tailed galagos and owl monkeys (Hylander, Ravosa, Ross, Wall, and Johnson, n.d.). This analysis will enable us to determine the recruitment patterns of one portion of the jaw-adductor muscle mass that has a predominantly vertical orientation, the superficial masseter, and one with a relatively larger and arguably predominant transverse orientation, the deep masseter. These data should give us additional insights as to whether there are important and major differences in recruitment patterns in these muscles, and therefore in symphyseal loading patterns, within these primates. We are particularly interested in the relative magnitude of working- and balancing-side jaw-adductor muscles, i.e., W/B ratios of superficial and deep masseter EMG activity, as well as differential timing patterns of the various parts of the deep and superficial masseter. Most notably, during the power stroke of mastication, do only anthropoids have relatively small W/B ratios for the superficial and/or deep masseters, and do owl monkeys, but not galagos, exhibit the late activity of the balancing-side deep masseter which has been shown to contribute to wishboning stresses in the symphysis of macaques and baboons (Hylander and Johnson, 1994)?

Finally, although symphyseal fusion has evolved independently in many mammalian lineages, we have intentionally focused our attention on the evolution of symphyseal fusion in primates. This is primarily for the obvious reason that our data are drawn exclusively from various species of primates. There is, however, at least one notable problem with the hypothesis linking symphyseal fusion or strengthening and increased balancing-side muscle force. EMG data recorded from the jaw adductors of the North American opossum (*Didelphis marsupialis*) suggest that during mastication, the overall balancing-side muscle force is perhaps as large as the working-side muscle force (Crompton, 1985, 1995; and Crompton and Hylander, 1986). The reason such a finding is a problem for this hypothesis is simply because opossums have a mobile unfused symphysis, rather than a rigid fully fused symphysis.

Similar to our EMG study of primate jaw muscles, a quantitative analysis of peak EMG activity of the superficial and deep masseter in adult opossums is currently in progress (Hylander, Johnson, and Crompton, n.d.). If this analysis confirms that jaw-muscle recruitment patterns in opossums are more similar to anthropoid pri-

mates than they are to greater galagos, this will indicate that symphyseal strengthening (fusion) and increased balancing-side muscle force are not functionally linked in all mammalian lineages.

CONCLUSIONS

This study tested two competing hypotheses about recruitment patterns of balancing-side jaw-adductor muscles in primates during mastication. One hypothesis suggests that increased balancing-side jaw-adductor force is functionally linked to the evolution of symphyseal strengthening or fusion, whereas the other claims that this force increase is due to allometric constraints associated with the evolution of increasing body size. The mandibular bone strain data recorded from long-tailed macaques, thick-tailed galagos, and owl monkeys, clearly refute the allometric constraint-muscle recruitment hypothesis and strongly support the symphyseal fusion-muscle recruitment hypothesis. The data indicate that anthropoids both larger and smaller than thick-tailed galagos have balancing-side muscle force recruitment patterns that are quite similar to one another, and both are quite unlike the pattern found in galagos.

Currently it is unclear as to whether symphyseal fusion in primates is functionally linked to an increase in vertically directed or transversely directed muscle and bite forces. If it is linked to increased vertically directed forces, then presumably symphyseal fusion is an adaptive response to counter some combination of dorsoventral shear and bending of the symphysis due to twisting of the mandibular corpora about their long axes. If it is linked to transversely directed forces, than presumably symphyseal fusion is an adaptive response to counter lateral transverse bending or wishboning.

ACKNOWLEDGMENTS

LITERATURE CITED

Beecher RM (1977) Function and fusion at the mandibular symphysis. Am. J. Phys. Anthropol. *47*:325–336.

Beecher RM (1979) Functional significance of the mandibular symphysis. J. Morphol. *159*:117–130.

Beecher RM (1983) Evolution of the mandibular symphysis in Notharctinae (Adapidae, Primates). Int. J. Primatol. *4*:99–112.

Bell RHV (1971) A grazing ecosystem in the Serengeti. Scientific Am. *225*:86–93.

Connolly R, and Quimby FW (1978) Acepromazine-ketamine anesthesia in the rhesus monkey (*Macaca mulatta*). Lab. Anim. Sci. *28*:72–74.

Crompton AW (1985) Origin of the mammalian temporomandibular joint. In DS Carlson, JA McNamara, and KA Ribbons (eds.): Developmental Aspects of Temporomandibular Joint Disorders. Monograph #16, Craniofacial Growth Series, Center for Human Growth and Development, University of Michigan, Ann Arbor, Michigan, pp. 1-18.

Crompton AW (1995) Masticatory function in nonmammalian cynodonts and early mammals. In JJ Thomason (ed.): Functional Morphology in Vertebrate Paleontology, Cambridge: Cambridge University Press, pp. 55-75.

Crompton AW, and Hylander WL (1986) Changes in mandibular function following the acquisition of a dentary-squamosal jaw articulation. In N Hotten III, PD Maclean, JJ Roth and EC Roth (eds.): The Ecology and Biology of Mammal-like Reptiles, Washington D.C.: Smithsonian Press, pp. 263-282.

Hylander WL (1975) Incisor size and diet in anthropoids with special reference to cercopithecidae. Science *189*:1095–1098.

Hylander WL (1977) In vivo bone strain in the mandible of *Galago crassicaudatus*. Am. J. Phys. Anthropol. *46*:309–326.

Hylander WL (1979a) Mandibular function in *Galago crassicaudatus* and *Macaca fascicularis*: An in vivo approach to stress analysis of the mandible. J. Morphol. *159*:253–296.

Hylander WL (1979b) The functional significance of primate mandibular form. J. Morphol. *160*:223–240.

Hylander WL (1984) Stress and strain in the mandibular symphysis of primates: A test of competing hypotheses. Am. J. Phys. Anthropol. *64*:1–46.

Hylander WL (1985) Mandibular function and biomechanical stress and scaling. Am. Zool. *25*:315–330.

Hylander WL (1986) In vivo bone strain as an indicator of masticatory bite force in *Macaca fascicularis*. Arch. Oral Biol. *31*:149–157.

Hylander WL, and Crompton AW (1986) Jaw movements and patterns of mandibular bone strain during mastication in the monkey *Macaca fascicularis*. Arch. Oral Biol. *31*:841–848.

Hylander WL, and Johnson KR (1989) The relationship between masseter force and masseter electromyogram during mastication in the monkey *Macaca fascicularis*. Arch. Oral Biol. *34*:713–722.

Hylander WL, and Johnson KR (1993) Modelling relative masseter force from surface electromyograms during mastication in non-human primates. Arch Oral Biol. *38*:233–240.

Hylander WL, and Johnson KR (1994) Jaw muscle function and wishboning of the mandible during mas-

tication in macaques and baboons. Am. J. Phys. Anthropol. *94:*523–547.

Hylander WL, and Johnson KR (1997) In vivo bone strain patterns in the zygomatic arch of macaques and the significance of these patterns for functional interpretations of craniofacial form. Am. J. Phys. Anthropol. *102:*203–232.

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

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

Hylander WL, Johnson KR, and Crompton AW (1998) Masseter force in the North American opossum: Testing the symphyseal fusion-muscle recruitment hypothesis. Arch. Oral Biol. (in review).

Hylander WL, Picq PG, and Johnson KR (1991) Masticatory-stress hypotheses and the supraorbital region of primates. Am. J. Phys. Anthropol. *86:*1–36.

Hylander WL, Ravosa MJ, Ross CF, Wall CE, and Johnson KR (1997) The relationship between symphyseal fusion and jaw-adductor muscle force in primates: An EMG study. Am. J. Phys. Anthropol. (in review).

Kay RF (1973) Mastication, molar tooth structure and diet in primates. Ph.D. Thesis, Yale University.

Kay RF, and Hylander WL (1978) The dental structure of mammalian folivores with special reference to primates and phalangeroidea (Marsupialia). In G Montgomery (ed.): The Ecology of Arboreal Folivores. Washington, D.C.: Smithsonian Institution Press, pp. 173–191.

Ravosa MJ (1991) Structural allometry of the prosimian mandibular corpus and symphysis. J. Hum. Evol. *20:*3–20.

Ravosa MJ (1996) Mandibular form and function in North American and European Adapidae and Omomyidae. J. Morphol. *229:*171–196.

Ravosa MJ, and Hylander WL (1993) Functional analysis of the galago circumorbital region. Am. J. Phys. Anthropol. *90:*Suppl. *16:*168.

Ravosa MJ, and Hylander WL (1994) Function and fusion of the mandibular symphysis in primates: stiffness or strength? In JG Fleagle and RF Kay (eds.): Anthropoid Origins. New York: Plenum, pp. 447–468.

Ravosa MJ, and Simons EL (1994) Mandibular growth and function in *Archeolemur.* Am. J. Phys. Anthropol. *95:*63–76.

Rensberger JM (1973) *Sanctimus* (Mammalia, Rodentia) and the phyletic relationships of the large arikareean geomyoids. J. Paleontol. *47:*835–853.

Ross CF (1993) The Functions of the Postorbital Septum and Anthropoid Origins. Ph.D. Thesis, Duke University.

Ross CF, and Hylander WL (1996) In vivo and in vitro bone strain in the owl monkey circumorbital region and the function of the postorbital septum. Am. J. Phys. Anthropol. *101:*183–215.

Scapino RP (1981) Morphological investigations into functions of the jaw symphysis in carnivorans. J. Morphol. *167:*339–375.