

Chapter 2

A Nonprimate Model for the Fused Symphysis: In Vivo Studies in the Pig

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Contents

2.1 Summary	19
2.2 Introduction	20
2.3 Material and Methods	23
2.3.1 In Vivo Experiments	23
2.3.2 Skeletal Investigation	26
2.4 Results	26
2.4.1 Mastication	26
2.4.2 Fusion of the Mandibular Symphysis	30
2.5 Discussion	31
2.5.1 Mastication	31
2.5.2 Symphyseal Strain, Fusion, and Morphology	33
2.6 Conclusions	35
References	36

2.1 Summary

As in anthropoid primates, the mandibular symphysis in suoid artiodactyls is fused. Pigs (*Sus scrofa*) share the features that are thought to have influenced fusion in primates, including large size, tough diet, isognathly, and recruitment of balancing-side muscles to produce a transverse power stroke. The symphysis is elongated rostro-caudally, stiffening it against transverse bending. In a sample of 17 young swine, we placed rosette and single-element strain gages at various rostro-caudal locations along the symphysis, mostly on the labial surface. Two pigs had ultrasound crystals implanted in the lower borders of the mandibular rami. Mandibular deformation was measured during awake chewing. Only in two pigs could a pattern of strain consistent with lateral transverse bending be identified during the power stroke. Instead, the predominant closing/power stroke strain pattern consisted of

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compression on the lingual surface of the symphysis, while the labial surface was tensed. No rostro-caudal gradient of strain could be detected. This pattern of deformation suggests a tendency to rotate the mandibular bodies with eversion of the lower border. Symphyseal deformation also accompanied opening, with a somewhat similar pattern but diminished magnitude. Overall, strain levels at the symphysis were high compared to other tooth-bearing bones, but decreased in older animals with more completely fused sutures. A survey of 115 dried skulls revealed that fusion begins at the age of 2 months, which coincides with natural weaning. Fusion commences on the compressed lingual surface.

2.2 Introduction

Although pigs and peccaries (families Suidae and Tayassuidae, Suoidea, Cetartiodactyla) are only very distantly related to anthropoid primates, convergences with respect to the masticatory system have been noted by many authors (Ström et al., 1986; Bermejo et al., 1993; Herring, 1998). Similarities between anthropoids and the suoids include the general (but not the detailed) anatomy of the adductor muscles of the mandible, the morphology and movements of the temporomandibular joint, and the bunodont dentition. To a considerable extent, these similarities correspond to generalized, often tough, diets for which both groups of species have adopted comparable strategies for food reduction, consisting of strong vertical closing movements coupled with short but powerful transverse power strokes. Another notable similarity between suoids and anthropoids is the early fusing mandibular symphysis.

As the primitive mammalian state is an unfused symphysis, it is the repeated fusion that has taken place in different lineages that needs explanation. The advantage of fusion is presumed to be biomechanical and to involve stiffening and/or strengthening the joint for repetitive loading during feeding. A number of factors have been considered correlated with symphyseal fusion in primates and other taxa, including large body size, robust construction of the mandible, tough diet, isognathly, extensive recruitment of balancing-side muscles during mastication, transversely oriented occlusal plane, transversely oriented zygomaticomandibularis (ZM, also called deep masseter), and a pattern of balancing-side contraction in which the ZM is strongly active when the superficial masseter and medial pterygoid activity are diminished (Scapino, 1981; Ravosa and Hylander, 1994; Lieberman and Crompton, 2000; Hogue and Ravosa, 2001). Pigs are well developed in all of these characteristics (Herring and Scapino, 1973; Herring, 1976; Herring et al., 2001; Rafferty et al., 2003). Incisor usage, although possibly involved (Greaves, 1988), is not a reliable predictor of symphyseal fusion. Pigs, like many other fused-symphysis taxa (Ravosa and Hylander, 1994), assign difficult ingestion tasks to the premolars rather than the incisors (Herring and Scapino, 1973). Thus in many ways, pigs seem to be a typical example for the fused symphysis. However, the possession of these characteristics does not explain how the fused pig symphysis functions.

The pig symphysis is more horizontally oriented than that of most anthropoids, particularly humans. Pig lower incisors are extremely procumbent, and the long axis of the symphysis lies close to the occlusal plane, especially as viewed on the lingual surface. This orientation should very effectively stiffen the symphysis against bending in the transverse plane. Zhang has calculated that stresses and strains should be similar in the human and pig symphyses; but if the pig symphysis were oriented vertically as in humans, the greater muscle forces and moment arms of the pig jaw would increase stress and strain to injurious levels (Zhang, 2001). At the same time, the horizontally elongated pig symphysis converts the expectations of transverse bending from a difference in polarity between the labial and the lingual surfaces to a comparison of rostral-caudal position.

The literature about loading of a fused symphysis has changed over time. When DuBrul and Sicher first speculated about symphyseal stresses, their emphasis was on jaw protrusion and the action of the lateral pterygoid muscles in producing what they called wishboning, but is more accurately described as medial transverse bending (DuBrul and Sicher, 1954). This is an activity that should accompany jaw opening, rather than the power stroke of mastication (Fig. 2.1). That the primate symphysis does bend medially during jaw opening has been well documented by Hylander's strain gage studies of macaques (Hylander, 1984; Hylander and Johnson, 1994) and by repeated demonstrations in human subjects that the dental arches are closer together when the jaws are opened (e.g., Chen et al., 2000). Although there are no previous data for pig, a dynamic model of pig mastication based on direct measurements of the mandible and jaw muscles plus electromyographic data from the literature predicted that medial transverse bending during opening would reach a peak torque approximately 60% of maximum and would include a minor twisting component due to asymmetrical activation of the lateral pterygoid muscles (Zhang, 2001). However, because the opening strains on the macaque symphysis are relatively low compared to the strains observed during the power stroke (Hylander, 1985), they have received little attention in recent papers. Instead, attention has been focused on power stroke strains.

Of the multiple deformation patterns theoretically possible during the power stroke (Beecher, 1977; Beecher, 1979; Scapino, 1981; Hylander, 1984), emphasis has been placed on dorso-ventral shear and lateral transverse bending (Fig. 2.1). Dorso-ventral shear is thought to be most important early in the power stroke when the working-side teeth engage the bolus while the balancing side continues to be closed by adductor muscle contraction; dorso-ventral forces have been associated with partial symphyseal fusion in some prosimians (Beecher, 1977). In Zhang's simulation of mastication, dorso-ventral shear was the largest predicted force in the pig symphysis (Zhang, 2001).

Lateral transverse bending takes place primarily at the end of the power stroke when the lateral pull of the balancing-side ZM opposes the laterally directed working-side occlusal load. Zhang's dynamic simulation predicted that lateral transverse bending during the power stroke would produce torques at least 40% larger than those from medial transverse bending during opening (Zhang, 2001). Furthermore, Zhang found that lateral transverse bending could arise not only from

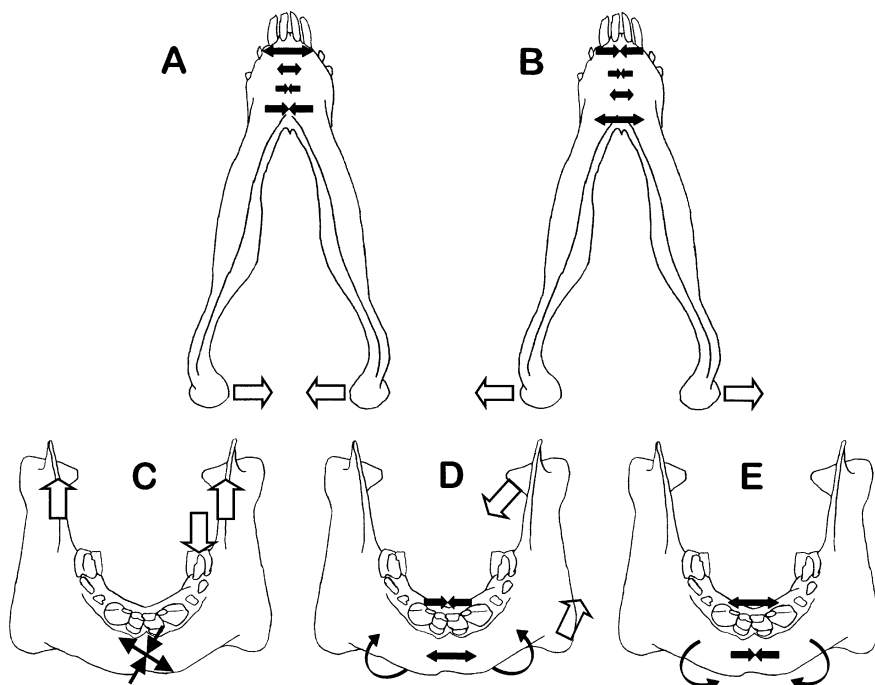


Fig. 2.1 Theoretical patterns of deformation of the pig symphysis. **A** and **B** are ventral views of the mandible and show the labial surface of the symphysis. **C–E** are anterior views and show the labial surface below and the lingual surface above the procumbent incisors. The open arrows indicate load directions. The solid double-headed arrows indicate tensile strain, while the opposed solid arrows indicate compressive strain. The thin curved arrows indicate rotation of the mandibular rami around their long axes. **A.** Medial transverse bending, such as might be caused by the medial component of lateral pterygoid muscle pull on the condyles. Both labial and lingual surfaces of the symphysis are expected to show a pattern of relative tension rostrally and relative compression caudally. **B.** Lateral transverse bending, such as might be caused by lateral pull of the ZM on the balancing side resisted by the occlusion on the working side. Both surfaces of the symphysis are expected to show a pattern of relative compression rostrally and relative tension caudally. **C.** Dorso-ventral shear, such as might be caused by a unilateral occlusal load with bilateral muscle force. Both surfaces of the symphysis are expected to show a 45° strain pattern. **D.** Rotation of mandibular rami with eversion of the ventral borders. Loads that could produce eversion include the ventral component of lateral pterygoid pull and the dorsal pull of the masseter. The symphysis is expected to be compressed lingually and tensed labially by bending in the coronal plane. **E.** Rotation of the mandibular rami with inversion of the ventral borders. The symphysis is expected to show lingual tension and labial compression

ZM contraction and molar occlusion but also from the tendency of the working-side superficial masseter to evert the mandible and from jaw joint reaction forces (Fig. 2.1). Authors who have analyzed other artiodactyls and carnivorans have also emphasized the significance of multiple transverse forces in determining symphyseal morphology (Scapino, 1981; Lieberman and Crompton, 2000; Hogue and Ravosa, 2001).

The main goal of this contribution was to ascertain whether the general conclusions about strain in the fused symphysis are valid for pigs, specifically (1) medial transverse bending occurs during opening, but is relatively small; (2) dorso-ventral shear occurs at the beginning of the power stroke; and (3) the largest strains are those of lateral transverse bending occurring at the end of the power stroke. Because of the horizontal orientation of the pig symphysis, transverse bending was expected to cause rostro-caudal differences in strain (Fig. 2.1). In particular, medial transverse bending should cause tensile strain rostrally and compressive strain caudally on both lingual and labial surfaces of the symphysis. Lateral transverse bending should cause the opposite pattern, rostral compression, and caudal tension. Dorso-ventral shear should present as a 45° orientation of strain. Figure 2.1 also depicts a third possible type of deformation caused by the rotation of each mandibular body about its own long axis, resulting in either eversion or inversion of the ventral border and bending of the symphysis in a coronal plane (terminology from Beecher, 1977). During the experiments we became aware that at least some of the animals showed incomplete surface fusion of the symphysis. Thus, a secondary goal was to establish the pattern and progress of fusion using a sample of age-known pig skulls.

2.3 Material and Methods

2.3.1 *In Vivo Experiments*

In vivo data on symphyseal deformation were gathered from a total of 17 young swine of various breeds and both sexes (Table 2.1). All animal procedures were reviewed and approved by the University of Washington Institutional Animal Care and Use Committee. The instrumentation varied (Fig. 2.2) and included (1) single-element strain gages (EP-08-125BT-120, Vishay Micro-Measurements, Raleigh NC) glued (cyanoacrylate) to bone in a transverse orientation across the midline; (2) stacked rosette strain gages (SK-06-030WR-120, Vishay Micro-Measurements) glued to bone either in the midline or on one side of the symphysis; and (3) pairs of 2-mm piezoelectric crystals with attachment pegs (2P-34C-40-NS, Sonometrics, London, Ont.) for digital sonomicrometry. The pegs were placed into small holes drilled in the lower borders of the left and right mandibular rami below the cheek tooth row after minor reflection of the inserting fibers of the digastric muscle. The sonomicrometry system has a theoretical resolution of 15 μm .

Before the recording session, each pig was acclimated to the laboratory environment. On the day of the recording, the animal was anesthetized by mask with isoflurane for surgical placement of transducers. The labial aspect of the symphysis and/or mandible was exposed from an extra-oral approach, whereas the lingual aspect employed an intra-oral incision through the gingival tissue. Preparation of the strain gages and bone followed standard methods (Rafferty et al., 2000). Gage orientation was measured with a protractor, and crystal locations were documented before closure of the periosteal and skin incisions. Lead wires were exited through the

Table 2.1 Subjects and instrumentation

ID, breed,* sex	Age (months)	Symphysis	Sonomicrometry	Single-element gage**	Rosette gage**
Pigs with intact mandible					
347 mini M	6	Mostly fused			Labial left 3 mm, 69%
356 mini F	3	Mostly fused	33.6 mm apart transversely 29 mm posterior to symphysis		
362 mini F	5	Fused	25.0 mm apart transversely 21 mm posterior to symphysis		Labial 63% Labial 79%
368 mini F	3	Partly fused		Labial 40% Labial 68%	
387 mini M	5	Fused			Labial right 11 mm, 86%
102 micro F***	2	Open, tight		Lingual 41%	
103 micro F	2	Open, tight		Lingual 28%	Lingual left 5 mm, 32%
Pigs with stabilized right mandibular osteotomy					
341 farm F	2	Open			Labial 56%
342 farm F	2.5	Open			Labial 54%
343 mini M	3	Partly fused			Labial 74%
345 mini F	2	Open			Labial 59%
346 mini F	2	Open			Labial 60%
353 mini F	3	Open			Labial 62%
354 mini F	2.5	Open, tight		Labial 82%	
357 farm F	3	Partly fused			Labial 51%
358 farm M	2	Mostly open		Labial 60%	
359 farm F	1.5	Mostly open			Labial 40%

*Farm pigs were of unknown breed. Minipigs were Hanford or Sinclair breeds, both relatively long-snouted. Micropigs were Yucatans, which have short upper jaws and no incisor occlusion.

**The labial surface is inferior, the lingual superior. Most gages were in the midline; the exceptions are noted by indication of the side and the distance from the midline to the center of the gage. The percentage indicates the relative position on the symphysis from rostral (anterior) to caudal (posterior), with 0% indicating the rostral edge and 100% the caudal edge (see Fig. 2.2B).

***This pig had previous surgery to reduce the size of the tongue.

incisions and connected respectively to strain gage conditioner/amplifiers (Vishay 2120A) and the sonomicrometry transceiver (Sonometrics). All animals had additional instrumentation or procedures on other parts of the skull. Most of these procedures were unlikely to affect the symphysis, with two exceptions. First, as indicated in Table 2.1, ten of the pigs also had an osteotomy performed at the junction of the right mandibular ramus and body, necessitating a partial reflection of the masseter muscle. The osteotomy was stabilized using a metal appliance screwed into the bone. The results are included here to improve the sample size, but treated cautiously because the procedure may have altered the mechanics of the symphysis

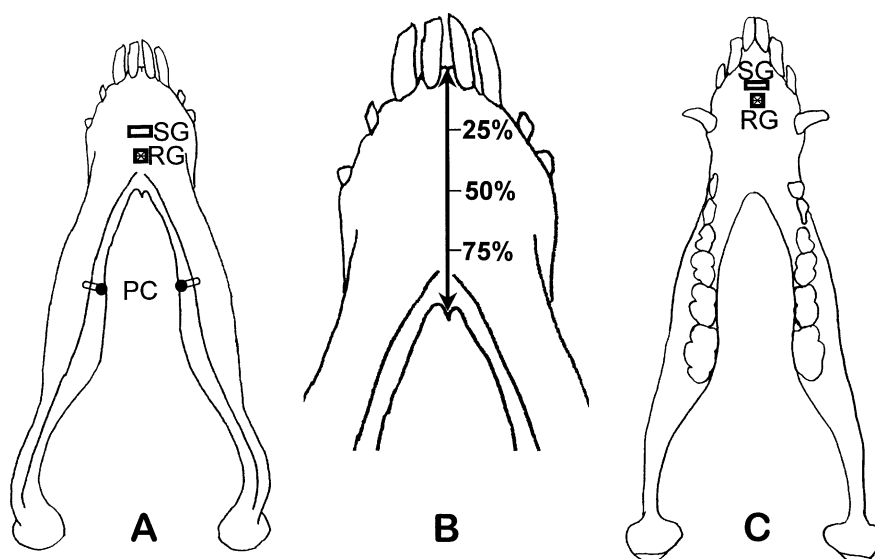


Fig. 2.2 Pig mandibles, showing methodology used. **A.** Ventral aspect, showing a single-element gage (SG) on the labial surface of the symphysis at about the 50% position and a rosette gage (RG) at about 70%. Two piezoelectric crystals (PC) for sonomicrometry are shown as dots on stems; the stems were implanted into the ventro-medial edges of the mandibular rami, leaving the crystals exposed. **B.** Enlargement of the symphysis in **A**, showing the method for determining the rostro-caudal position of gages. **C.** Dorsal (occlusal) view (from an older pig) showing a single-element gage on the lingual surface of the symphysis at about the 25% position and a rosette gage at about 35%

and did cause the animals to favor the left side during chewing. Second, one pig had had previous surgery to reduce the size of the tongue (Table 2.1). Food handling was somewhat unusual in this animal, which may have influenced symphyseal mechanics during the opening stroke of mastication, when the bolus is manipulated. Fine-wire electromyography (EMG) electrodes were placed through the skin into the bilateral masseter muscles and often additional muscles via hypodermic needles. These were connected to high-impedance probes (Grass 7HIP5G, East Warwick, RI) and preamplifiers (7P3, bandpass 100–5000 Hz). Analog strain and EMG signals were digitized at 500 Hz and recorded to computer (AcqKnowledge, BioPac Systems, Santa Barbara, CA), and digital sonomicrometry signals were recorded to a separate computer running Sonometrics software. To correlate the two computer records, one analog signal was recorded on the Sonometrics computer and one sonomicrometry signal was converted to analog and recorded on the AcqKnowledge computer. Local anesthetic (lidocaine) was applied to the incisions. Analgesics (ketorolac tromethamine and/or buprenorphine hydrochloride) were administered intramuscularly, and the pig was then permitted to recover from anesthesia and to eat freely. The standard diet of pig chow pellets was used. After about 15 min of chewing was recorded, the pig was re-anesthetized and euthanized. The head was removed, skinned, and the instrumentation was checked for damage and location.

The EMG recordings were used to identify the side of chewing. Pigs typically alternate the side of chewing with each stroke. Although occlusion is usually bilateral in pigs, the directionality is strongly unilateral. The side of the power stroke can be identified by late activity in the working-side masseter/medial pterygoid and balancing side temporalis/ZM. This activity pattern moves the lower incisors from the working-side past the midline to the balancing-side (Herring, 1976). Strain recordings were analyzed quantitatively. After exporting the analog signals to Excel, baseline strain was subtracted and voltages converted to microstrain. Data from the three elements of the rosette gages were used to compute the magnitude and orientation of the principal strains (Tech Note 515, Measurements Group). Peaks were identified as relative maxima of shear strain (maximum principal strain minus minimum principal strain) and were classified as “opening,” “early closing,” or “late closing” by their timing relative to the EMG of the masseter and other muscles. Sonometric deformation data were converted to strain by dividing the distance between pairs of crystals. Although right and left masticatory cycles (whenever they could be identified) were analyzed separately, there were no consistent differences in symphyseal strain, so data from both chewing sides were averaged.

2.3.2 Skeletal Investigation

In a sample of 115 mandibles of pigs of known age, not including any of the animals used in the present study, fusion of the symphysis was assessed by examining its outer surface under magnification. Of these mandibles, 2 were from Yucatan micropigs, 10 were from domestic farm pigs, and the remainder were from Hanford/Sinclair minipigs. To be classified as unfused, a suture had to be visible along the entire midline junction. To be classified as fused, the suture had to be visibly co-ossified everywhere, but between the incisor alveoli. All other conditions were classified as “partially fused,” and the locations of the unfused portions were noted.

2.4 Results

2.4.1 Mastication

Most subjects showed at least two distinct strain peaks during chewing, one corresponding to the opening stroke and the other, usually larger, corresponding to the closing/power stroke (i.e., concurrent with masseter EMG). The exceptions were #347 (Fig. 2.3B), which lacked measurable opening strain, and #357 and #362, which had opening strains for about half of their chewing cycles. Closing peaks were seen in all animals and were often bi- or even trimodal. However, the complex closing waveforms were variable, and in most cases it was not possible to classify

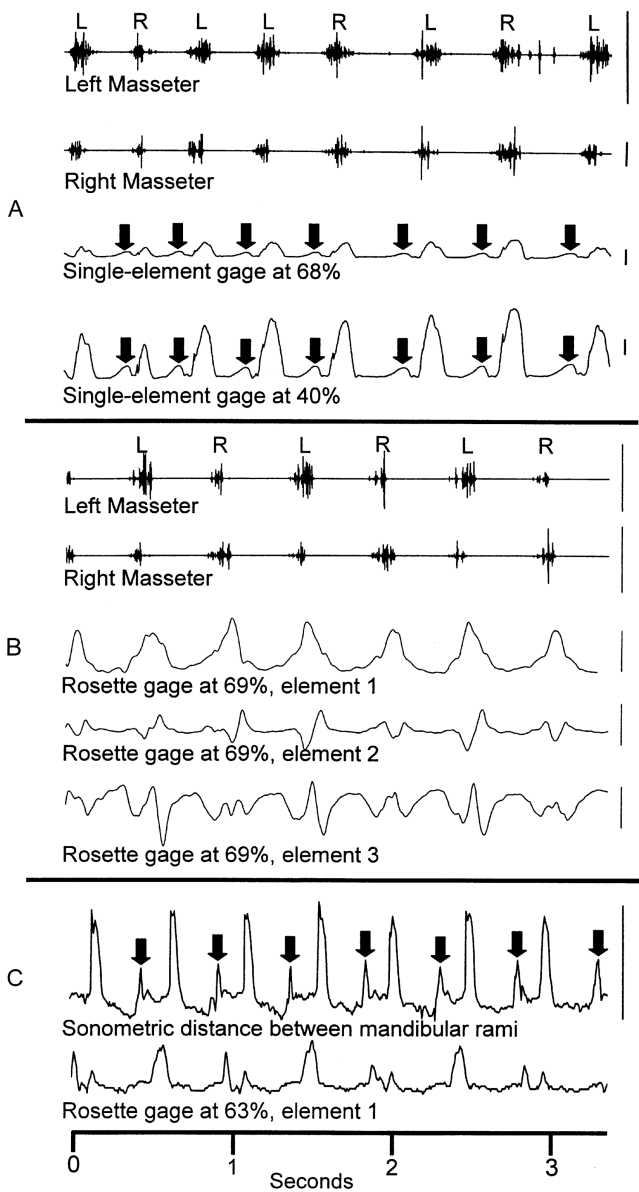


Fig. 2.3 Examples of raw recordings of mastication. Scale is indicated by the vertical bars to the right of each trace. For muscles the scale bar is 1 V, for the strain channels in **A** and **B** the bar is 1000 $\mu\epsilon$, and for the sonometric trace in **C** the bar is 1 mm. The strain channel in **C** is uncalibrated. The working side is designated as left (L) or right (R) based on muscle pattern; this information is not available for **C**. **A**. #368, single-element gages at 40% and 60%. Both gages show an opening peak (arrows) and a larger, relatively simple closing peak. Strains were always tensile and always higher in the more rostral location. **B**. #347, one rosette gage 3 mm off midline at the 69% position. Element 2 was roughly aligned with the rostro-caudal axis

Table 2.2 Mandibular distortion in the transverse direction during chewing: single-element gages and sonomicrometry

Subject (<i>n</i>)	Location	Opening	Closing
Labial single-element gage on symphysis, in rostro-caudal order			
368 (22)	40%	+835 ± 140 με	+2937 ± 726 με
368 (22)	60%	+271 ± 40 με	+609 ± 291 με
358* (6)	60%	+336 ± 80 με	+1575 ± 202 με
354* (6)	82%	+82 ± 66 με	+324 ± 22 με
Lingual single-element gage on symphysis, in rostro-caudal order			
103 (4)	28%	+204 ± 28 με	−160 ± 26 με
102** (6)	41%	−579 ± 55 με	−883 ± 213 με
Sonomicrometry crystals			
356 (21)	Ventral rami of mandible	+0.35 ± 0.11 mm (1.1%)	+0.39 ± 0.07 mm (1.2%)
362 (25)	Ventral rami of mandible	+0.31 ± 0.06 mm (1.2%)	+0.64 ± 0.08 mm (2.6%)

n = Number of chewing cycles analyzed, right and left combined
μ*ε* = microstrain
*Mandibular osteotomy
**Tongue reduction

them as either early or late closing. Examples of recordings from each type of instrumentation are shown in Fig. 2.3, and strains are summarized in Tables 2.2 and 2.3.

2.4.1.1 Opening Strains

Linear measures of transverse deformation during opening were almost universally tensile (Table 2.2). The distance between mandibular rami increased by about 1%. At the symphysis, all single-element gages on the labial surface were in tension, as was one of the two lingual surface gages (#103). The compressive value from the other lingual gage (Table 2.2) is suspect, because it was from the animal with a reduced tongue and abnormal food handling (#102).

The rosette results (Table 2.3) support the finding of transverse tension on both surfaces of the symphysis during opening in that the maximum principal strain was oriented transversely or between 45° and 90° in all pigs. The magnitude of tensile strain was usually very much greater than that of compressive strain (the exception, #387, had the most laterally displaced gage of the sample).

Because of adequate sample size, the rosette results were also used to compare intact and osteotomized groups. No significant differences were found. The magnitude of shear strain during opening in pigs with intact mandibles was 112 ± 135 μ*ε*



Fig. 2.3 (continued) (8° off sagittal). This animal was the oldest of the sample; the symphysis showed negligible opening strains and a complex, usually triphasic closing pattern that depended in part on chewing side. C. #362, piezoelectric sonomicrometry crystals 21 mm posterior to the symphysis. The rami separate about 0.3 mm during opening (*arrows*), return to rest, and then separate again, more extensively, during closing

Table 2.3 Magnitude ($\mu\epsilon \pm$ s.d.) and orientation of principal strains during mastication: rosette gages on the symphysis

Subject (<i>n</i>)	Location	Opening		Closing			
		Tension	Compression	Orientation*	Tension	Compression	Orientation*
Lingual gage, intact mandible							
103 (4/15)	32%, Lft 5 mm	29 ± 4	-17 ± 5	98° ± 8 T	72 ± 27	-168 ± 55	-3° ± 13 S
Labial gages, intact mandible							
362 (4/17)	63%	73 ± 13	-39 ± 8	94° ± 2 T	early 146 ± 32 late 92 ± 19	early -13 ± 15 late -129 ± 24	early 94° ± 19 T late -7° ± 7 S
362 (4/17)	79%	55 ± 4	-28 ± 3	93° ± 2 T	early 219 ± 49 late 138 ± 29	early -17 ± 32 late -173 ± 32	early 92° ± 23 T late -22° ± 28 45/S
347 (0/24)	69%, Lft 3 mm	Negligible strain levels		68° ± 6 T/45	106 ± 31	-97 ± 37	36° ± 20 45
387 (17/17)	86%, Rt 11 mm	137 ± 62	-169 ± 38		early 125 ± 24 late 133 ± 46	early -134 ± 66 late -218 ± 62	early -46° ± 14 45 late -27° ± 8 45/S
Labial gages, osteotomized mandible							
359 (18/18)	40%	701 ± 157	-41 ± 19	72° ± 1 T/45	765 ± 364	-128 ± 50	66° ± 3 T/45
357 (8/17)	51%	80 ± 14	-14 ± 10	93° ± 4 T	180 ± 47	-80 ± 23	55° ± 15 45
342 (28/41)	54%	86 ± 20	-52 ± 16	-36° ± 24 45	210 ± 41	-231 ± 42	76° ± 3 T
341 (20/21)	56%	157 ± 43	-72 ± 24	112° ± 2 T/45	437 ± 94	-163 ± 65	-55° ± 3 45
345 (11/11)	59%	232 ± 71	-17 ± 15	108° ± 6 T/45	400 ± 117	-192 ± 75	70° ± 4 T/45
346 (20/20)	60%	70 ± 18	-28 ± 14	107° ± 38 T/45	310 ± 45	-294 ± 50	72° ± 1 T/45
353 (37/37)	62%	117 ± 46	-77 ± 37	86° ± 34 T	352 ± 116	-293 ± 80	75° ± 25 T
343 (11/9)	74%	102 ± 7	-21 ± 3	75° ± 4 T	501 ± 81	-168 ± 21	59° ± 3 45

n = Number of chewing cycles analyzed, right and left combined. The first value is for opening and the second for closing.
*Orientation of tensile strain, with 90° being transverse and 0°/180° being rostro-caudal. Positive values are assigned to tensile vectors oriented from caudal left to rostral right, and negative values to those oriented from caudal right to rostral left. For simplification, these orientations were categorized as “T” (transverse) if they were within 15° of 90°, “45°” if within 15° of \pm 45°, and “S” (sagittal) if within 15° of 0°/180°. If the value fell between two of these categories, both are given.

($n = 4$ subjects), as compared to $233 \pm 214 \mu\epsilon$ ($n = 8$) for those with stabilized osteotomies.

Rostro-caudal position was not correlated with strain levels; but on the more thoroughly sampled labial side of the symphysis, the gages located at 40% (#368, Table 2.2 and Fig. 2.3A, and #359, Table 2.3) gave higher tensile strains than those located more caudally.

2.4.1.2 Closing Strains

Deformations for closing were typically much larger in magnitude than those for opening, but surprisingly similar to opening in pattern (Tables 2.2 and 2.3). The major pattern difference is that during closing, both pigs with lingual gages showed strong compression in the transverse direction. On the labial side, symphyseal strains remained predominantly tensile and between 45° and 90° for at least one phase of closing for every pig. As in opening, strain levels were not correlated with rostro-caudal position. However, compared to opening tensile orientations, closing tensile orientations were more often 45° and less often transverse (Table 2.3). There were only two subjects with distinct early and late closing peaks (#362 and #387, Table 2.3), and these suggested that tensile strain was initially transverse or 45° and then became more sagittal. As measured by sonomicrometry, the distance between the mandibular rami increased; at least in #362, the magnitude of this closing deformation was double that of opening (Fig. 2.3C).

A comparison between intact pigs and those with mandibular osteotomies using rosette data for closing strains showed that overall strain levels were higher in the osteotomized group (shear strain averaged $265 \pm 63 \mu\epsilon$ for four intact mandibles and $588 \pm 182 \mu\epsilon$ for eight osteotomized mandibles, $p < 0.01$). However, the osteotomized pigs were also generally younger than the intact group and open symphyses were more common (Table 2.1); for both groups combined, strain levels were found to be inversely correlated with age ($r = -0.81$, $p < 0.01$).

2.4.2 Fusion of the Mandibular Symphysis

Table 2.4 shows the results of the survey of symphyseal fusion in mandibles of known age. In very young animals (less than 1 month), the open suture was wider at the caudal margin than elsewhere. Fusion was not seen in animals less than 2 months old. By the age of 2 months, many symphyses had begun fusing, and all symphyses from pigs older than 2 months were at least partially fused. The first completely fused symphyses were also seen in the third month of life, but the time of complete fusion was variable, with partial fusion still seen in one 6-month-old pig. Of the 33 partially fused symphyses, all showed fusion on the rostral part of the lingual surface. A visible suture was most common on the labial surface, either rostral or caudal ($n = 13$), the caudal edge ($n = 11$), and the caudal part of the lingual surface ($n = 7$). Two symphyses had visible suture segments in more than one region.

Table 2.4 Condition of the symphyseal suture in 115 pig mandibles as a function of age

Age	Unfused	Partially fused	Fused
Less than 2 months	11	0	0
2 months	8	5	0
2.25–3 months	0	10	8
3.25–4 months	0	12	13
4.25–5 months	0	5	19
5.25–6 months	0	1	9
Over 6 months	0	0	14

2.5 Discussion

2.5.1 Mastication

2.5.1.1 Opening

Opening deformation of the mandible has always been assumed to be dominated by the contraction of the lateral pterygoid muscles (DuBrul and Sicher, 1954). The expected strain pattern was medial transverse bending, manifested as rostral tension decreasing or changing to compression caudally (Fig. 2.1A), with some minor twisting resulting from asymmetrical contraction (Zhang, 2001). The results were only partially consistent with these expectations. Transverse tension was found in most subjects, but indications of a rostro-caudal gradient were weak. Both animals with gages in multiple locations, #368 (Table 2.2) and #362 (Table 2.3), showed greater tension in the more rostral gage. However, there was no caudal compression.

The fact that the predictions of medial transverse bending were not completely fulfilled indicates that some corrections to this model are necessary. First, the assumption of a strong rostro-caudal gradient is predicated on the center of bending being located in or near the symphysis. However, given the fact that the center of mass of the pig mandible is at the back of the tooth row (Zhang et al., 2001), it is likely that the center of bending is well caudal to the entire symphysis. This would explain the absence of a strong rostro-caudal gradient. A second consideration is that the lateral pterygoid muscles, which attach well above the center of mass, should produce not only medial transverse bending but also eversion of the rami (Fig. 2.1D). Eversion would be expected to produce transverse tension on the inferior labial surface with no particular gradient, as was observed. Eversion should also produce compression on the superior lingual surface, for which our data were equivocal, with one pig (#102) showing compression and one (#103) tension. One feature that was consistent with eversion but not with medial transverse bending was the finding of increasing distance between the mandibular rami, as measured by sonomicrometry. This increase in dimension is the reverse of the narrowing documented in the human mandible during opening (Chen et al., 2000). Unfortunately, our finding was based on only two animals, one of which had no strain gage information. It is also possible that the contraction of the overlying digastric muscles

disturbed the position of the sonomicrography crystals during opening and that the finding of widening was spurious.

Somewhat surprisingly, given that the osteotomy separated a fragment with the attachment of the right lateral pterygoid from the rest of the mandible, the results from the osteotomized pigs were indistinguishable from those of the intact pigs (Tables 2.2 and 2.3). This suggests: (1) the fixation of the osteotomy was rigid and transmitted strains efficiently, and/or (2) forces from just one side are sufficient to produce characteristic symphyseal strain patterns, and/or (3) additional muscles, such as the digastric, mylohyoid, and geniohyoid, are at least as important as the lateral pterygoid in producing symphyseal strain.

In short, the symphysis is almost always tensed transversely on its labial surface during opening. However, neither can we distinguish between medial transverse bending and eversion as the primary cause of the tension nor can we eliminate a role for muscles other than the lateral pterygoid.

2.5.1.2 Closing

Closing is a more complicated situation than opening in that (1) muscle activity is always asymmetrical; and (2) in addition to the muscle forces acting on the mandible, there are reaction forces at the teeth and at the jaw joints. In pigs, molar occlusal forces and jaw joint reactions are usually similar on the working and balancing sides, but incisor occlusal forces are highly asymmetrical because they depend on the direction of jaw movement (Rafferty et al., 2003).

We had expected to see two distinct phases of closing. Early in the movement, as the teeth engaged the bolus, we expected dorso-ventral shear, manifested as 45° strains on the symphysis. Toward the end of the movement, as the jaw moved toward the balancing side, we expected lateral transverse bending, manifested as rostral compression and caudal tension. However, the comparison between early and late closing proved to be impossible, except in two pigs. These two subjects did seem to fit the model in that tensile strain was more sagittal for late closing, as expected for rostral areas during lateral transverse bending (Fig. 2.1B). However, a true sagittal orientation (7°) was only seen in the more rostral gage of #362 (Table 2.3).

In the remaining 15 pigs, although the time course of symphyseal strain was often complex, the phases of closing were so blended that we could not discern separate phases. Because the averages reported in Tables 2.2 and 2.3 are for the peak strains, they would represent either overlapping occlusal and grinding phases or the larger of the two. Because of the preponderance of tensile strain orientations near 45° (Table 2.3), dorso-ventral shear may be the largest force imposed on the symphysis, as was suggested by Zhang's kinetic model (Zhang, 2001). However, the frequency of 45° tension could have other origins as well, including torque from incisor or molar occlusal loads. In this context, it is interesting to note that #103, one of the few pigs that never showed the 45° orientation, was a Yucatan, a breed lacking incisor occlusion.

The most surprising aspect of the closing results is that except for the late closing of #362 and #387, the observed pattern is clearly not lateral transverse bending as depicted in Fig. 2.1B. Transverse strains in the symphysis were everywhere tensile

on the labial side, and there was no pattern of increasing tension caudally in the sample as a whole. The two pigs with dual gages showed opposite patterns. Pig #362 did show higher caudal strain levels, a reversal of its opening pattern (Table 2.3). However, #368 had much lower transverse tension in the caudal than in the rostral gage, the same pattern it had for opening (Table 2.2). Admittedly, our failure to find a consistent rostro-caudal gradient could be due to the non-uniformity of the sample, with only two animals multiply instrumented. Nevertheless, the deformations observed are all consistent with an alternate explanation, that of eversion (Fig. 2.1D). Eversion accounts for the widening of the mandibular rami and explains the compression on the lingual surface of the symphysis as well as the tension on all locations along the labial surface. Eversion is also consistent with the torsional strains observed bilaterally on the mandibular corpus of chewing pigs (Herring et al., 2001). Asymmetrical eversion of the rami could also have had a role in producing the modal orientation of 45° seen on the labial surface. Asymmetrical eversion during closing could arise from masseter contraction. Late in the closing movement, the working-side masseter is highly active even though the balancing-side activity has ceased (Herring and Scapino, 1973). In addition, the morphology of the jaw joint may be important (Zhang, 2001). Because the articular surface slopes from dorso-lateral to ventro-medial (Herring et al., 2002), the vertical reaction loads on the condyles would tend to push them medially, thus causing eversion (Fig. 2.1D).

The comparison of pigs with intact mandibles and those with stabilized osteotomies is also helpful in considering the origin of the apparent eversion during closing. The overall level of strain was higher in the osteotomy sample, at least for the more thorough rosette data. This finding may be due to the younger average age of the osteotomy pigs (Table 2.1) and their less fused symphyseal sutures, as discussed further below. The general 45° /transverse orientation of peak tensile strain was the same in both groups. From previous work on the osteotomy sample, we know that during closing (as opposed to opening) the osteotomy site was compliant rather than stiff (Sun et al., 2006), that the animals were chewing primarily on the opposite side (Rafferty et al., 2006), and that the jaw joint loads on the osteotomy side were decreased and no longer vertically oriented, while those on the opposite side were normal in magnitude and orientation (Rafferty et al., 2006). By elimination, then, the most likely hypothesis to explain mandibular eversion is contraction of the working-side masseter, perhaps coupled with working-side incisor contact.

Summarizing, strain patterns in the pig symphysis suggest that dorso-ventral shear or twisting, possibly involving incisor contact, are important during closing. Transverse strains do occur, but they appear to arise primarily from eversion of the mandibular rami, not from lateral transverse bending.

2.5.2 Symphyseal Strain, Fusion, and Morphology

The range of shear strain (approximately 200–900 $\mu\epsilon$, calculated from Table 2.3) is similar to or higher than the strain magnitudes reported for fused primate symphyses

(Hylander, 1984; Hylander, 1985). Indeed, the maximal values fall at the high end of our previous recordings from other areas of the pig skull. Symphyseal strain was in general greater than strain on the tooth-bearing mandibular body, maxillary and premaxillary, and comparable to strain on the mandibular condyle and squamosal bone (Herring et al., 2001; Rafferty et al., 2003; Rafferty et al., 2006). However, the higher values (400–900 $\mu\epsilon$) belong to younger pigs with unfused symphyses, and the lowest values (200–350 $\mu\epsilon$) belong to the older pigs with fused symphyses (#347, #362, #387). These latter values are quite similar to strains on the other tooth-bearing parts of the skull. There is a strong implication that fusion decreases symphyseal strain, a conclusion that also arose from our previous study of the sagittal suture (Sun et al., 2004). It is difficult to compare the rosette strain magnitudes to our previous studies on sutures, which used single-element gages, because single-element gages typically report higher strains from similar locations, probably because they are less stiff. The single-element data on the symphysis are skimpy, but the top values of 1600–3000 $\mu\epsilon$ (Table 2.2) are as high as any we have recorded from open cranial sutures (Rafferty and Herring, 1999; Herring et al., 2001; Rafferty et al., 2003; Sun et al., 2004). In short, as hypothesized by Zhang (2001), the pig symphysis appears to be a very highly stressed region of the skull, and fusion serves to decrease strain to a level more comparable to that of the neighboring tooth-bearing bones.

The two animals that showed indications of lateral transverse bending during the power stroke were both older pigs with fused symphyses, suggesting an association. We therefore carefully examined the recordings from the third older pig, #347 (Table 2.1), for which separate early and late closing peaks could not be calculated. The closing strains from this animal were, in fact, complex (Fig. 2.3B). Our inability to identify separate peaks was due to a trimodal strain pattern plus side differences. It is quite possible that lateral transverse bending was one element of this blend. If so, then fusion of the symphysis may be a prerequisite for the detection of strain patterns characteristic of the different phases of closing. In younger animals with unfused symphyses, the large strains associated with separation of the suture may overwhelm pattern details.

Although the pig symphysis shows high strain levels and the pig oral apparatus has all of the features of muscle anatomy and contraction pattern that should promote transverse bending, this pattern of deformation was not dominant even in older individuals. Instead, most of the strains observed were more compatible with a rotation that everts the lower border of the mandible. In retrospect, symphyseal morphology itself may account for this. The rostro-caudally elongated symphysis is stiffened against transverse bending, but its comparatively small dorso-ventral dimension leaves it vulnerable to rotation and dorso-ventral shear. Thus the fact that we seldom observed transverse bending does not mean that it does not occur, just that the pig symphysis is fortified against this type of loading. Because much of the mechanical environment of the pig symphysis is related to its horizontal orientation, which helps it resist deformation in the transverse plane, it is interesting to note that symphyseal orientation can become more vertical under certain dietary or occlusal modifications (Ferrari and Herring, 1995; Ciochon et al., 1997). In Yucatan swine,

which characteristically lack incisor occlusion, the symphysis is more vertical than in normally configured pigs.

The timing of fusion of the pig symphysis may not be coincidental. Under natural conditions, piglets are not weaned before 2 months of age (Pond and Houpt, 1978), the age at which symphyseal fusion begins (Table 2.4). Masticatory strains could conceivably have a role in inducing fusion. The first region of the symphysis to fuse, the rostral part of the lingual surface, is the only sampled part of the symphysis that is often under compressive loading. The labial surface shows no rostro-caudal order of fusion, which corresponds to the lack of any rostro-caudal gradient in strain. We have no data from the late-fusing caudal edge, but this is a complex area with many muscle attachments and large nutrient foramina, and is likely to be under a unique strain regime.

2.6 Conclusions

The pig symphysis undergoes two major peaks of deformation in each chewing cycle, a smaller one coinciding with opening and a larger one coinciding with contraction of the jaw closing musculature. Separate phases for early and late power stroke were a rarity, seen only in the oldest animals of the sample. Opening and closing deformations were more similar in pattern than was expected. Both opening and closing featured tensile strain on the labial surface of the symphysis and separation of the mandibular rami. Neither opening nor closing peaks showed rostro-caudal gradations in strain. However, tensile strain was more often transverse during opening and 45° during closing. Further, during closing the lingual surface showed transverse compression, whereas this surface was inconsistent during opening. We consider the opening pattern as consistent with a mild degree of medial transverse bending plus some eversion of the mandibular rami, possibly caused by the lateral pterygoid muscles. The closing pattern indicates dorso-ventral shear and strong eversion of the ramus, for which working-side masseter muscle contraction seems the most likely cause. Lateral transverse bending was rarely observed.

These patterns of deformation differ somewhat from those of anthropoid primates (Hylander, 1984; Hylander and Johnson, 1994), particularly in the absence of unequivocal transverse bending in either direction. Anatomical differences between suoids and anthropoids may account for the difference. The relative absence of transverse bending in pigs may reflect stiffening from the rostro-caudal elongation of the symphysis rather than the absence of load. In addition, the suoid symphysis is distant from the mandible's center of mass (Zhang et al., 2001), which would tend to obscure the rostro-caudal gradients for which we were looking. Finally, the occlusion of the procumbent incisors and the curvature of the symphyseal surfaces are clearly different in pigs from anthropoid primates, but as yet we do not know how these factors influence strain.

The status of the symphyseal junction was an important determinant of strain. In addition to the fact that lateral transverse bending was only discernible in pigs with

fused symphyses, magnitudes of strain were higher in young pigs with unfused symphyses and decreased to more typical bone levels when fusion began. Nevertheless, it is clear that even the youngest pigs did not show the degree of movement seen in prosimians and artiodactyls with permanently unfused symphyses (Beecher, 1977; Lieberman and Crompton, 2000), and that the unfused pig symphysis is functionally more similar to a cranial suture (Sun et al., 2004) than to a mobile joint. The first part of the symphysis to fuse, the rostral section on the lingual surface, is the most compressed section. The onset of fusion at 2 months of age corresponds with weaning and suggests that masticatory forces have played an evolutionary or developmental role in fusing the symphysis.

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