Mandibular Symphysis of Large-Bodied Hominoids

RICHARD J. SHERWOOD,[1] LESLEA J. HLUSKO,[2] DANA L. DUREN,[1] VICTORIA C. EMCH,[3] AND ALAN WALKER[4]

Abstract   The hominoid mandibular symphysis has received a great deal of attention from anatomists, human biologists, and paleontologists. Much of this research has focused on functional interpretations of symphyseal shape variation. Here, we examine the two-dimensional cross-sectional shape of the adult mandibular symphysis for 45 humans, 42 chimpanzees, 37 gorillas, and 51 orangutans using eigenshape analysis, an outline-based morphometric approach. Our results demonstrate that a large proportion of the variation described by the first eigenshape correlates with proposed functional adaptations to counteract stresses at the mandibular midline during mastication. Subsequent eigenshapes describe subtle aspects of shape variation in the mandibular symphysis. The morphology associated with these eigenshapes does not conform with functional predictions, nor does it show a relationship with sexual dimorphism. However, eigenshapes provide for considerable taxonomic discrimination between the four taxa studied and may consequently prove useful in the analysis of fossil material. Comparison with elliptical Fourier analysis of the mandibular symphysis identifies eigenshape analysis as providing superior taxonomic discrimination. The results presented here demonstrate that the cross-sectional shape of the mandibular symphysis results from a complex interplay of functional and nonfunctional influences and for the first time identifies and quantifies the specific aspects of variation attributable to these factors.

The mammalian mandibular symphysis has received a great deal of attention from anatomists, human biologists, and paleontologists. This is due, in part, to interest in the complex biomechanical stresses placed on the mandible during mastication (Beecher 1979; Hylander 1984; Hylander et al. 1987; Hylander and Johnson 1994; Daegling and Hylander 1997, 2000; Vinyard and Ravosa 1998; Daegling 2001; Taylor 2002), the wide diversity of symphyseal forms present (Beecher 1977; McCrossin and Benefit 1993; Lieberman and Crompton 2000;

[1]Lifespan Health Research Center, Wright State University, Kettering, OH 45420.
[2]Department of Integrative Life Sciences, University of California, Berkeley, CA 94720.
[3]5366 Ash Road, Doylestown, PA 18901.
[4]Department of Anthropology, Pennsylvania State University, State College, PA 16802.

Nicolay and Sherwood 2000), the frequent preservation of mandibular specimens in the mammalian fossil record (White and Johanson 1982; Beecher 1983; Daegling and Grine 1991; Tobias 1991; Ward 1991; Wood 1991; Ravosa and Simons 1994; Brown 1997; Ravosa 1996, 2000; Takai et al. 2000), and, finally, an anthropocentric interest in the unique morphology of the human chin (Lam et al. 1996; Schwartz and Tattersall 2000; Dobson and Trinkaus 2002). Here, we study the two-dimensional symphyseal morphology of extant large-bodied hominoids in an attempt to identify factors that influence variation in mandibular shape.

Background

There is a extensive literature detailing the functional environment of the mandibular symphysis, which demonstrates an adaptive morphological response to the biomechanical loads experienced at various points in the masticatory cycle in primates (Beecher 1977, 1979, 1983; Hylander 1985; Daegling 1989, 2001; Daegling and Grine 1991; Brown 1997; Daegling and Hylander 1998, 2000; Vinyard and Ravosa 1998; Ravosa 1999, 2000; Daegling and Jungers 2000; Taylor 2002; Taylor and Groves 2003). For cercopithecoids these studies have demonstrated that variation in symphyseal cross-sectional shape correlates with the variation in the stresses experienced.

This correlation between form and function is not surprising, given that the mandibular symphysis is a focal point for the unique set of bending and shear forces to which the mandible is subjected during behaviors such as gape and mastication (Hylander 1975, 1979, 1981, 1985, 1986, 1992; Beecher 1977, 1979; Hiiemae 1978; Demes et al. 1984; Wolff 1984; Hylander and Crompton 1986; Hylander et al. 1987; Daegling 1989, 1993; Daegling and Grine 1991; Daegling and Hylander 1998; Daegling and Jungers 2000; Taylor 2002). During mouth opening, the bilateral contraction of the lateral pterygoid muscles produces medial transverse bending, resulting in "tensile stress along the labial aspect of the symphysis and compressive stress along its most lingual aspect" [Hylander 1985, p. 317; see also Hylander (1981)]. During mastication, stress patterns are more complicated, with dorsoventral shear and lateral transverse bending of the corpora showing the greatest magnitude. Lateral transverse bending, generally referred to as wishboning, presents symphyseal stress patterns opposite to that seen during opening, with compressive stress along the labial aspect of the symphysis and tensile stresses on the lingual aspect (Hylander 1979, 1984, 1985; Ravosa 1999; Daegling 2001). These two examples clearly demonstrate that stresses and strains imposed on the mandibular symphysis are varied and complex. In addition, in vivo strain analysis in macaques has demonstrated that maximum stresses are placed on the symphysis during wishboning (Hylander 1984, 1985). It is reasonable to assume that strong selective pressure would operate on the shape of the mandibular symphysis because bite forces exceeding the strength of a mandible during wishboning would be detrimental to the individual.

Daegling (2001) described three possible structural options for minimizing the regional stresses in the symphysis: (1) increase the relative size of the symphyseal section; (2) alter symphyseal shape, primarily by increasing the dimension in the dorsoventral axis; and (3) rotate the major axis of the mandibular symphysis. Although the first option would successfully strengthen the symphysis, Daegling argues that this is an excessive or inefficient use of bone tissue and therefore an unlikely adaptive solution. The remaining two options, either independently or in combination, would increase the second moment of area about the vertical axis, thus producing a stronger symphysis while minimizing material usage (Hylander 1984, 1985; Daegling 2001). Allometric analyses (Hylander 1985; Vinyard and Ravosa 1998) have demonstrated a consistent pattern of scaling in symphyseal dimensions in cercopithecoids, indicating that alteration of symphyseal shape, seen as the elaboration of the superior transverse torus, adequately counters stresses resulting from wishboning during mastication in this diverse group. Great apes, however, do not fit the cercopithecoid pattern, and Daegling (2001), noting that the "superior transverse torus is inconstant among" hominoids (p. 20), suggests that changes in the inclination of the symphysis may serve as the primary, or at least an additional, mechanism to counter wishboning stresses in this group.

A purely mechanical model may not be sufficient, however, to fully explain the observed morphological variation of the mandibular symphyseal cross-section. For example, Ward (1991), in discussing the morphology of *Paranthropus* mandibles, suggested that they are "overdesigned" relative to the forces placed on them [see Daegling and Hylander (1997) for a response to this suggestion]. In addition, differences that have been reported in the pattern of scaling of the mandibular symphysis of hominoids relative to cercopithecoids (Bouvier 1986; Ravosa 2000; Daegling 2001) argue against a strict biomechanical control of symphyseal shape. In general, symphysis width and length exhibit positive allometry relative to body mass in cercopithecines (Hylander 1985; Vinyard and Ravosa 1998; Daegling 2001). Hominoids diverge from this pattern by having relatively shallow superior tori and elongated symphyses in larger-bodied individuals (Daegling 2001). Furthermore platyrrhine symphyseal width scales isometrically with mandibular length (Bouvier 1986), whereas cercopithecines show positive allometry for the same measures.

Mandibular shape may also be constrained to some degree by phylogenetic inertia. In situations where selection is reduced or absent, evolutionary change in a trait may be minimized. Such traits would be expected to be similar among closely related taxa and therefore would be useful in systematic analyses. The utility of the mandibular symphysis in systematic inquiry has been suggested, or applied, by several researchers for a wide variety of hominoids (Kelley and Pilbeam 1986; Leakey et al. 1995; Daegling and Jungers 2000; Dunsworth and Walker 2002; Ward and Duren 2002; Taylor and Groves 2003; Kimbel et al. 2004).

In addition to biomechanical and phylogenetic constraints, other epigenetic influences may also play a role in determining symphyseal morphology. As with any complex phenotype, symphyseal shape results from the interplay of different genetic and nongenetic, as well as adaptive and nonadaptive, factors (Gould 1997, 2002). Gould and Lewontin (1979) used the term *epiphenomenal* to describe the nonadaptive forces and the architectural term *spandrel* to "designate the class of forms and spaces that arise as necessary byproducts of another decision in design, and not as adaptations for direct utility in themselves" (Gould 1997, p. 10,750). Gould (1997, 2002) later justified the retention of *spandrel*, originally used metaphorically, within biology, claiming "evolutionary biology needs such an explicit term for features arising as byproducts, rather than adaptation, whatever their subsequent exaptive utility" (Gould 1997, p. 10,750).

Considering the variety of influences on morphology, Lovejoy et al. (1999) proposed a classification system for mammalian postcranial traits derived from current knowledge of limb development. Their five categories help to classify traits that are functionally and phylogenetically relevant versus those that are less so. In this system Type 1 traits result from changes in the genetic patterning mechanism with a real or direct effect on fitness. These traits experience strong directional or stabilizing selection. Type 2 traits are pleiotropically related to Type 1 traits but do not directly interact with selection. Type 3 traits result from modifications of overall systemic factors, such as allometric effects related to body size. Type 4 traits result from the influence of the environment on systemic assembly mechanisms; that is, they do not result from changes in genetic patterning mechanisms but from habitual behaviors during development. These traits are particularly useful in the study of functional morphology but have little to no phyletic value. Finally, similar to Type 4 traits, Type 5 traits result from environmental stimuli but, because of greater variability in expression, are not indicative of a significant behavior and are uninformative to both phylogeny and behavior. All traits are considered to lie along a continuum ranging from traits whose expression and variance are defined by strong selective factors, to traits whose trajectories are largely defined by covariance and codependence with other traits (equivalent to Gould's spandrels), to traits whose variable expression is maintained through phylogenetic inertia (low trait variation) or subjected to stochastic processes (high trait variation).

Although the focus of many studies is to examine the direct response of bone to biomechanical stimuli, a variety of mechanisms for the covariance of phenotypes has been posited, including genetic covariance (pleiotropy), epigenetic effects, and functional and developmental constraints (Olson and Miller 1958; Cheverud et al. 1979; Cheverud and Buikstra 1981; McGrath et al. 1984; McCollum 1999; McCollum and Sharpe 2001). Aspects of dental morphology are commonly considered as influencing symphyseal morphology in large-bodied primates. For example, in considering the cause of the hominoid deviation from the cercopithecoid pattern, Daegling (2001) suggested that the symphysis in large-bodied hominoids "may reflect a structural requirement of accommodating

relatively large canine roots, especially in males of dimorphic species" (p. 20). Similarly, it has also been posited that the length of the canine root may influence mandibular corpus proportions (Wood 1978; Chamberlain and Wood 1985; Kimbel and White 1988). Vinter et al. (1996) demonstrated the influence of the dentition on mandibular variables, such as the angle between the corpus and ramus. If this relationship is further demonstrated, mandibular morphology may be interpreted as an epigenetic response to tooth root morphology, development, and function. More research on the genetic and developmental mechanisms determining mandibular symphyseal shape is needed to clarify these relationships.

Eigenshape Analysis

Variation in mandibular symphyseal shape has broad implications across all of primate biology. Given that we do not have a clear understanding of the interplay between genetic and nongenetic influences on symphyseal cross-section, further analyses that elucidate this relationship are critical. The study conducted here attempts to elucidate the influences of cross-sectional shape of the mandibular symphysis on variation.

The mandibular symphysis has a complex curvilinear shape and lacks clearly identifiable landmarks, making it a challenging anatomical region to study (Scott 1980). Consequently, linear metric analyses tend to oversimplify the shape. However, two broad approaches have been developed for characterizing more complicated anatomical shapes: landmark-based and outline-based analytical platforms. Landmark-based approaches (Bookstein et al. 1985; Bookstein 1991; Zelditch et al. 1995; MacLeod 2002a) identify a discrete set of points on the organism or structure and use these points as the basis for comparison. Landmarks are defined as "points whose comparisons are consistent with the rules of homology and that have reliable anatomical definitions" (Bookstein et al. 1985, p. 6). However, not all structures of interest present a sufficient number of such homologous points to be useful in a landmark-based analysis. The second approach, outline-based analysis, may be more appropriate in these cases (Scott 1980). Two common outline approaches are elliptical Fourier analysis (Ferson et al. 1985; Rohlf 1986; Daegling and Jungers 2000) and eigenshape analysis (Lohmann 1983; Lohmann and Schweitzer 1990; MacLeod and Rose 1993; MacLeod 1999; 2002a, 2002b).

The mandibular symphysis of primates provides a good candidate for an outline approach because it presents a continuously curved surface that lacks clearly definable landmarks. Following MacLeod and Rose (1993), we use a standard eigenshape analysis (see also Macleod 1999, 2002a).

An extensive comparison of eigenshape and Fourier analyses is beyond the scope of this paper and has been discussed thoroughly elsewhere (Lohmann 1983; MacLeod and Rose 1993; Macleod 1999). To summarize briefly, Macleod (2002a) advocates the use of eigenshape analyses because (1) ϕ^* functions (the

shape function used in eigenshape analyses) always remain single valued, (2) they represent any outline as a mathematical function, and (3) they possess the ability to "move freely between the ordinative-analytic and geometric-representational domains" (MacLeod 2002a, p. 30). MacLeod and Rose (1993) claim that the "shape summaries possess a number of desirable analytic properties, including mutual independence of the various shape indices (the eigenshapes) and support of direct graphic portrayal of individual modes of shape variation in the form of empirically-determined shape models" (p. 302). Lohmann (1983) adds that with eigenshape analysis, "unlike . . . Fourier shape analysis, the original shape can always be reconstructed precisely from its eigenshape representation" (p. 669). It must be noted, however, that Rohlf (1986) claims that "when *all* eigenvectors and *all* harmonics are retained both [eigenshape and Fourier] approaches represent orthogonal rotations of the same points" (p. 845). At the time of Rohlf's comment, the mid 1980s, the described benefit of Fourier analysis was a reduction in computer time and hence computational cost; this is clearly no longer the issue it once was. We believe, based on this discussion, that there is an a priori reason to consider that eigenshape analysis is a superior approach for describing and analyzing the shape of the mandibular symphysis. However, because a Fourier analysis of the mandibular symphysis has already been conducted (Daegling and Jungers 2000), we are able to test this assumption empirically by comparing that study with our own.

Our investigation of mandibular symphyseal cross-sectional shape first tests the hypothesis that all variation between and within taxa can be attributed to functional differences. Following the functional analysis of Daegling (2001), we predict that cross-sectional symphyseal variation will be either an increase in the dimensions along the dorsoventral axis or rotation of the major axis in response to the stresses experienced during mastication. Although this hypothesis is clearly overly simplistic, it does provide a foundation on which to define those regions of the mandibular symphysis that are in accord with functional predictions of dorsoventral expansion or rotation of the symphyseal major axis, and those that are not. We then test whether or not the variation that violates this assumption can be explained by sexual dimorphism and thereby may be indicative of an epigenetic influence of other dentognathic features, such as canine size.

Materials and Methods

Sample.   We examined mandibles of humans (*Homo sapiens*), chimpanzees (*Pan troglodytes*), gorillas (*Gorilla gorilla*), and orangutans (*Pongo pygmaeus*) from the Hamann-Todd collection, Cleveland Museum of Natural History, as well as a collection of orangutan (*P. pygmaeus*) mandibles from the National Museum of Natural History (Table 1). All specimens were judged to be adult on the basis of full eruption and occlusion of the permanent dentition. Using digital calipers, we took two linear metric measurements frequently used in descriptions of the

Table 1. Sample Size by Taxon and Sex

Genus	Male	Female
Homo	28	17
Pan	21	21
Gorilla	17	20
Pongo	26	25

mandibular symphysis (symphyseal width and length; Figure 1) for all specimens (all measurements were to the nearest 0.01 mm). Symphyseal width was defined as the maximum dimension of the symphysis in the sagittal plane taken parallel to the occlusal plane. Symphyseal length was defined as the maximum distance from the midline crest of the incisor alveolus and the most inferior point of the symphysis.

Symphyseal Outline. Midline symphyseal outlines were obtained by molding the symphysis with a quick-setting molding putty (Coltène President soft putty). A wooden stick was placed at the alveolar margin of the symphysis and directed lingually to rest on a second stick spanning the posterior margin of the tooth row. This was done in order to later align the specimen for eigenshape analysis. Molds were separated from the mandibles and sectioned to provide a midline outline of the symphysis.
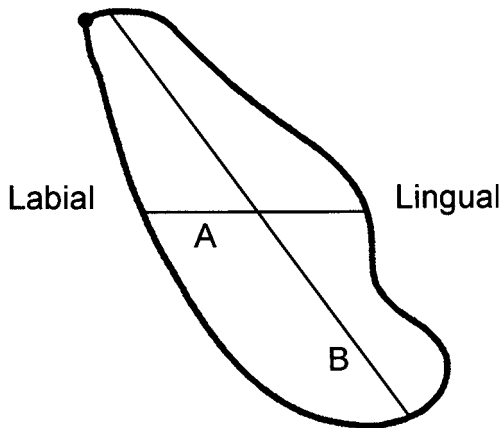

Figure 1. Mandibular symphyseal measures. Symphyseal width (A) is measured as the maximum dimension parallel to the occlusal plane. Symphyseal length (B) is measured as the maximum distance from the midline crest of the incisor alveolus to the most inferior point of the symphysis. The dot indicates the starting point for outline digitization used in the eigenshape analysis.

The perimeter of the symphyseal outline was digitized using an image analysis system, including a CCD camera (Panasonic WV-CD50) connected to an Image Technology PC Vision Plus frame grabber. Optimas software (Media Cybernetics) was used to digitize the images, starting at the infradentale and continuing around the symphysis, capturing first the labial and then the lingual surfaces (see Figure 1); teeth were excluded from the outline. The digitized outline was converted to 200 evenly spaced *x-y* coordinates by Optimas. This set of coordinates was then converted into 100 ϕ^* coordinates. As defined by Zahn and Roskies (1972), ϕ coordinates characterize a shape by noting the net angular deviation from a line at each step; ϕ^* coordinates differ from ϕ coordinates by describing the net angular deviation from a circle. Because ϕ and ϕ^* coordinates are angular measures, they provide a useful method for analyzing shape independent of the effects of scale. Once converted, the ϕ^* (or ϕ) coordinates are then subjected to a singular value decomposition (Lohmann 1983; Rohlf 1986; Macleod and Rose 1993; MacLeod 1999; 2002a). (Programs for coordinates conversion, singular value decomposition, and shape model construction were made available by Norman MacLeod and are currently available at http://www.nhm.ac.uk/hosted_sites/paleonet/ftp/ftp.html.) Following the procedure of MacLeod and Rose [1993; see also MacLeod (1999)], the ϕ^* functions were not standardized and the covariance matrix was used for the singular value decomposition.

To compare our results with the results of Daegling and Jungers (2000), we subjected the eigenshape scores to a discriminant function analysis to test the ability to distinguish between taxa and sexes. This was done using SPSS (version 11.0.1), with prior probabilities computed from group sizes, within-group covariance used, and independent variables entered together.

Results

African Apes. To illustrate the use of eigenshape analysis, we begin by restricting the comparison to the mandibular symphyses of the chimpanzee and gorilla. Figure 2 shows bivariate plots of the first four eigenshape values. Shape models generated from the analysis are displayed along the axes (Lohmann and Schweitzer 1990; Macleod and Rose 1993; MacLeod 1999, 2002a). These shape models provide a more meaningful description of features described by each component and how that shape varies along the axis. As noted, ϕ^* coordinates are calculated as the net deviation from a circle. This relationship is demonstrated by the first eigenshape scores (eigenshape 1; $\lambda = 81.06\%$) [following Macleod and Rose (1993), λ refers to the percentage of variation explained by the given eigenshape), as seen in Figure 2A; low values along the eigenshape 1 axis are represented by fairly circular shapes, whereas high values are much more elliptical. Note also that the depth of the genial fossa increases with higher values.

Variation along the subsequent eigenshape axes is subtle because of the strong similarity in form of the African ape symphysis. For all eigenshapes little

change is seen along the labial surface of the symphysis. Changes along eigenshape 2 ($\lambda = 6.31\%$) are primarily seen in the depth of the superior torus; low values are characterized by a deep torus, and high values are characterized by a relatively shallow torus. Minor changes are also seen in the depth of the inferior torus. Changes along the eigenshape 3 axis (Figure 2B; $\lambda = 2.78\%$) are primarily seen in superior aspects of the symphysis, particularly notable toward the alveolar margin. Low values are represented by a deep, somewhat curved profile from superior torus to alveolar margin. High values show the alveolar margin as less curved and thinner and as forming a true planum alveolare. The inferior torus and genial fossa show little change along this axis. Eigenshape 4 (Figure 2C; $\lambda = 1.40\%$), like eigenshape 3, primarily shows changes along the superior torus from deep to shallow with concomitant changes in the depth of the genial fossa.

Figure 3 illustrates the shape variation within the space defined by the first three eigenshapes. As noted by MacLeod and Rose (1993), it is important to recognize that these models represent mathematical abstractions of the shapes and, although a sizable proportion of the variation is explained by these three axes (90.15%), there remains residual variation that may contribute to an individual shape in interesting ways. Having described the shape changes seen along the axes, we can now examine the distribution of eigenshape values for individual specimens. Results show that gorillas tend to score lower on eigenshape 1 than chimpanzees. As noted, this component indicates relative circularity, or in other words, if length is held constant, eigenshape 1 essentially becomes an indicator of symphyseal width. Gorillas, therefore, are seen as having a relatively wider symphysis than chimpanzees; this is supported by a plot of symphyseal width to length (Figure 4) [see also Ravosa (2000) and Taylor (2002)].

Although eigenshape 1 may be interpreted as analogous to the width and length metrics described, the remaining eigenshapes do not have simple metric analogues. It is interesting to note, therefore, that eigenshape scores for the variables presented visually discriminate between the two taxa very well. The scores do not, however, discriminate between sexes within taxa, despite large levels of body size dimorphism in gorillas.

Eigenshape of Large-Bodied Hominoids.   The next step was to subject the entire sample to eigenshape analysis. Plots of the eigenshape functions are seen in Figure 5. As with the African ape example, shape models become progressively more circular with lower eigenshape 1 scores ($\lambda = 76.11\%$) and more elliptical with higher scores. Gorillas and chimpanzees retain the same relative position as before, namely, with gorillas showing slightly more circular outlines. Despite a size difference, orangutans cluster with chimpanzees in having more elliptical outlines. Humans show a wide range of eigenshape 1 scores, with values overlapping much of the ape distribution. This is not surprising because human and ape symphyses are both strongly elliptical, albeit in different ways.
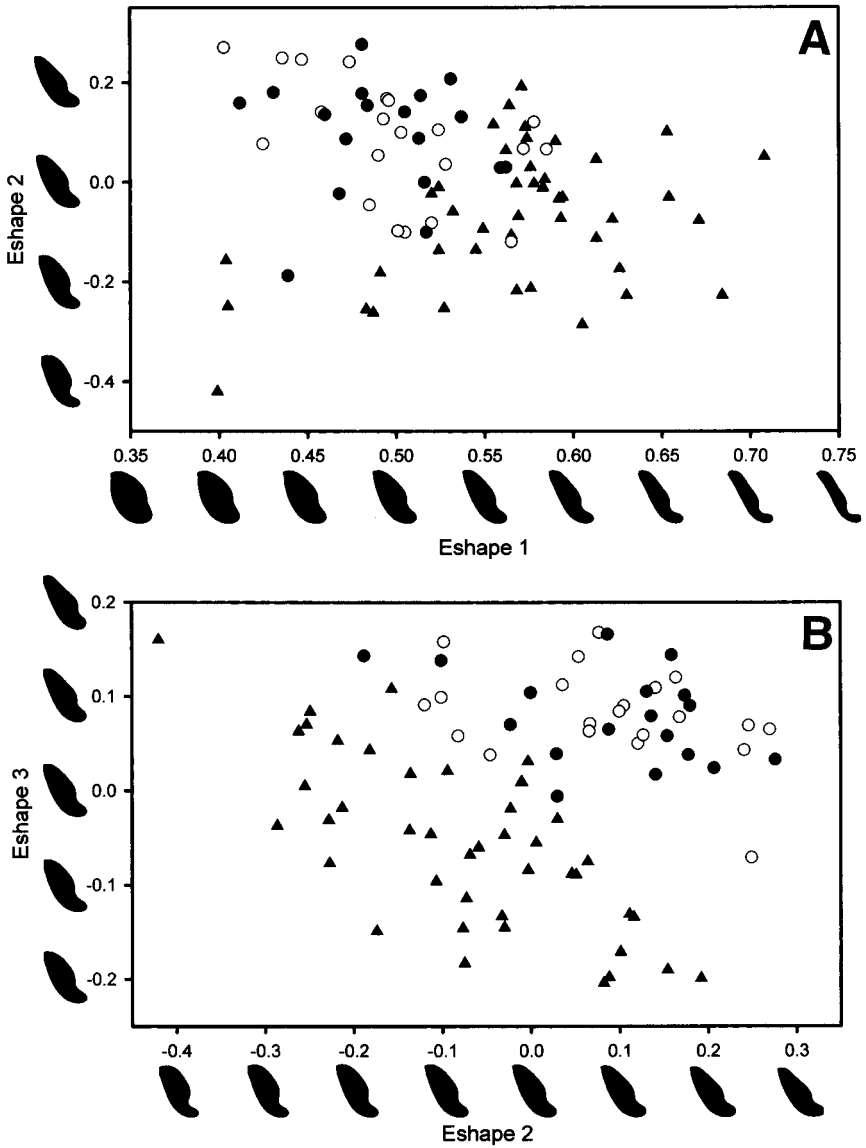
Figure 2. Scatterplots of the first four eigenshape functions for African apes. Axis values have been enhanced with shape models to better indicate the shape variation described by each eigenshape. Gray triangles, chimpanzee females; black triangles, chimpanzee males; light-gray circles, gorilla females; dark-gray circles, gorilla males.
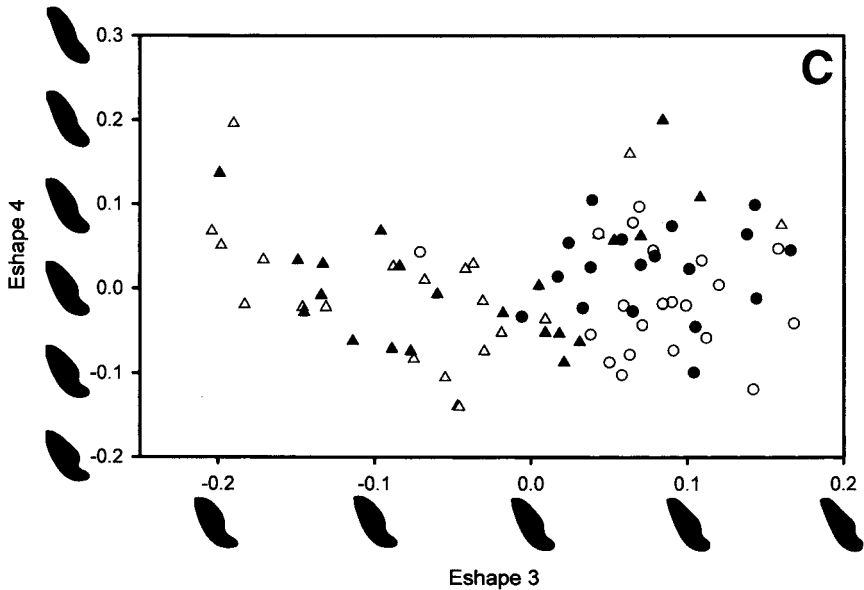
Figure 2. Continued

Variation along the eigenshape 2 axis ($\lambda = 8.38\%$) can simply be described as the "chin to no-chin" axis. In the chimpanzee and gorilla comparison little variation was seen in the labial surface of the symphysis for any of the eigenshapes. Shape models corresponding to low values along the eigenshape 2 axis show a very human morphology with an obvious chin. As values increase along the axis, shapes give way to a rather indeterminate shape and then an easily recognizable ape morphology identifiable by a pronounced simian shelf.

Predominant changes along the eigenshape 3 axis ($\lambda = 4.55\%$) are seen in the depth of the genial fossa, progressing from deep to shallow. As in the African ape example, change along the superior torus is predominantly seen as a reduction in thickness at the alveolar margin. There is also an obvious relationship between the depth of the genial fossa and the inferior torus. As the former loses depth, the latter gains it. Eigenshape 4 ($\lambda = 1.49\%$) primarily reflects changes along the lingual margin of the superior half of symphysis. The acquisition of a well-developed superior torus is seen as values progress from low to high.

Effects of Dimorphism. In order to investigate possible sex differences in symphyseal shape, we subjected sex-specific groups for each taxon to eigenshape analysis. Models for the average shape for each sex are seen in Figure 6. Note that there is little difference between the sexes, with the exception of the gorilla.
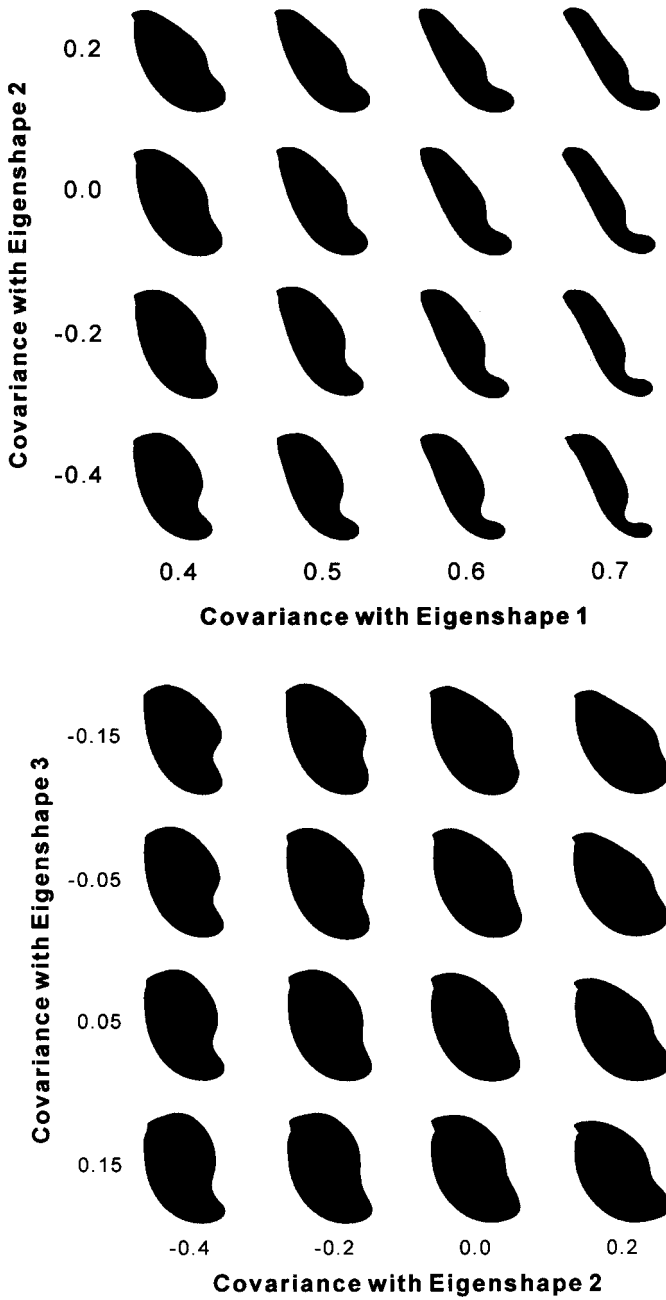
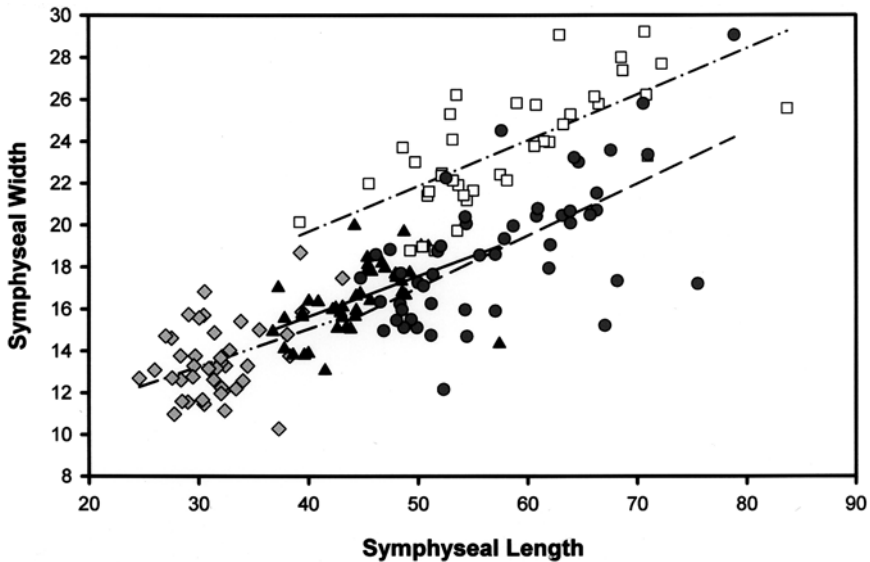**Figure 3.** Two-dimensional shape models for the mandibular symphysis of African apes.

Figure 4. Bivariate plot of symphyseal measures for all taxa. Lines are species-specific regression lines: human, dash/double-dotted line [SL = 0.18(SW) + 7.89; r = 0.38]; chimpanzee, solid line [SL = 0.19(SW) + 7.92; r = 0.50]; gorilla, dash/single-dotted line [SL = 0.22(SW) + 10.92; r = 0.71]; orangutan, dashed line [SL = 0.25(SW) + 4.57; r = 0.64]. Diamonds, humans; triangles, chimpanzees; squares, gorillas; circles, orangutans.

In this group females show a slightly more prominent superior torus than the males.

The ability to discriminate sexes was also tested both within individual taxa and for the data sets as a whole (Tables 2 and 3). Overall, discrimination of sexes is poor, with error rates averaging about 40%. The one exception is found in the gorilla, where the error rate was marginally better at 27%. A MANOVA test of within-species sex differences using eigenshape scores (Table 4) found no significant sex difference in shape for any taxon.

Systematic Classification. An analysis for systematic classification was also done using eigenshape scores. We found that the overall error rate is 16.6% when discriminating among all four taxa and 18.5% for just the great apes (Table 5). By using eigenshape scores with all four taxa, the discriminant analysis did not misclassify any chimpanzees as gorillas or vice versa. By restricting the discriminant analysis based on eigenshape scores to just the great apes, a single gorilla was misclassified as a chimpanzee (3% of the gorilla sample).
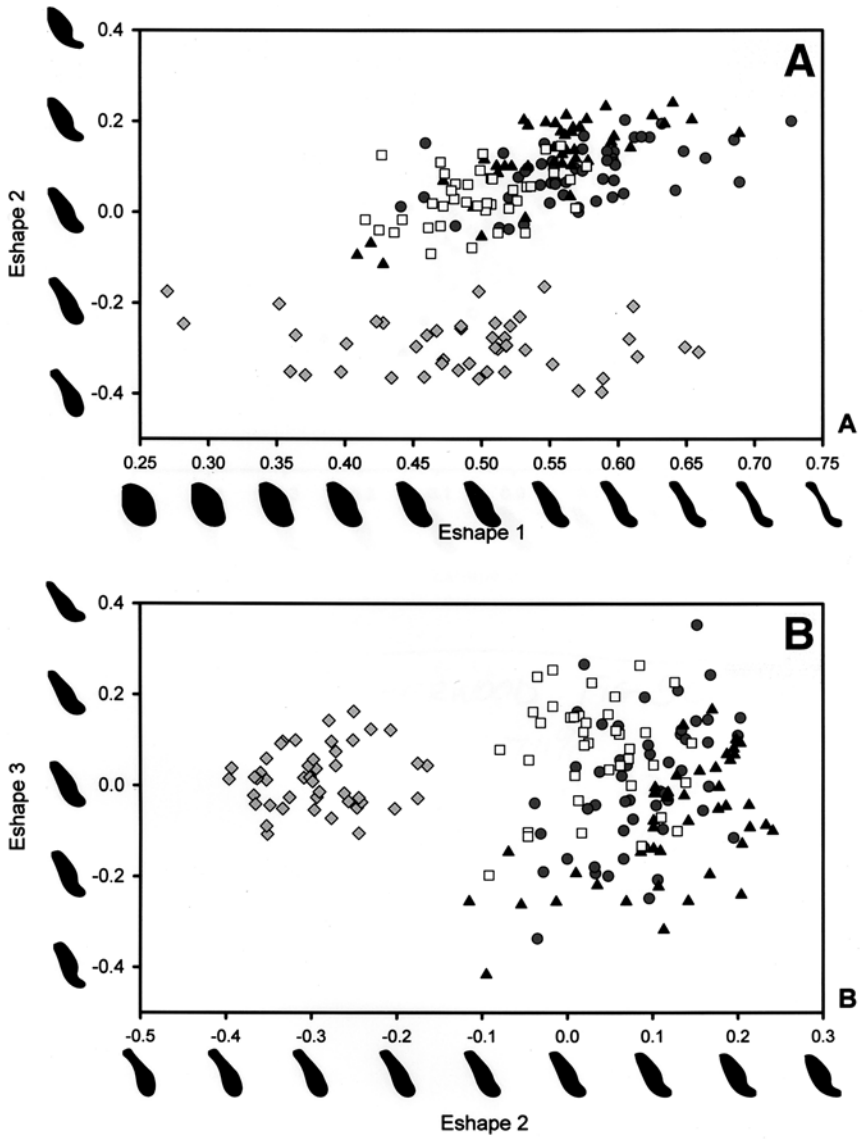
Figure 5. Scatterplots of the first four eigenshape functions for all taxa. Axis values have been enhanced with shape models to better indicate the shape variation described by each eigenshape. Circles, orangutans; triangles, chimpanzees; diamonds, humans; squares, gorillas.
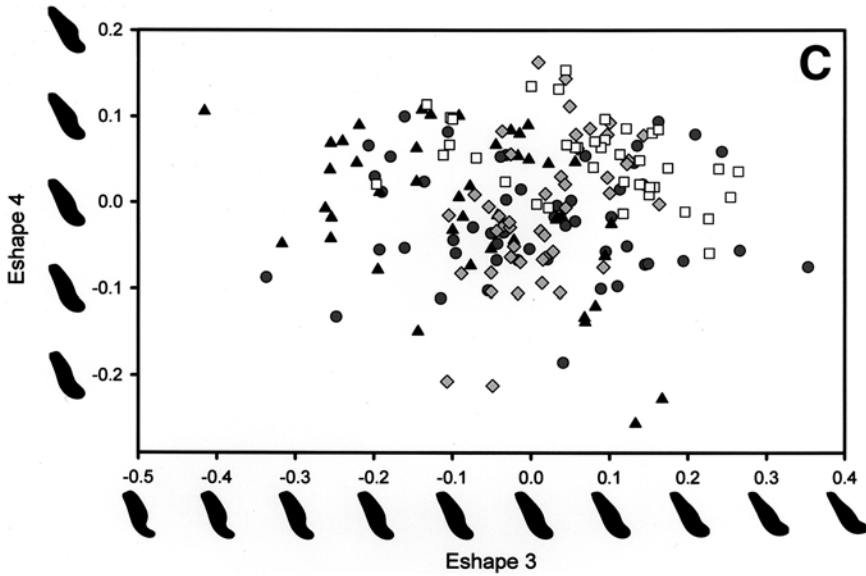
Figure 5.   Continued

Discussion

Our results show that eigenshape is well suited for the analysis of the two-dimensional cross-sectional shape of the mandibular symphysis. We were able to identify shape variation within and between taxa with a high level of specificity. The results from this refined approach identify those aspects of mandibular symphyseal shape that appear to conform to functional predictions and those aspects that do not. In addition, our results have implications for taxonomic discrimination and sexual dimorphism.

As noted, the first eigenshape largely describes deviation from a circle. In terms of the mandibular symphysis, this first eigenshape value essentially describes the variation of dorsoventral width of the symphysis relative to a constant length. Dorsoventral width has been identified as a possible structural option for minimizing the regional stresses in the symphysis during wishboning (Daegling 2001). The first eigenshape, which accounts for a significant proportion (76–80%) of the variation in symphyseal cross-sectional shape, is in accord with predictions from functional studies. Further analyses are needed to determine whether the dorsoventral width of the mandible results from environmental influences on a genetic patterning mechanism (Type 1 trait) or a systemic assembly mechanism for bone growth (Type 4 trait).

The second and third eigenshapes, in contrast to the first eigenshape, do not describe variation that can be attributed to Daegling's (2001) functional
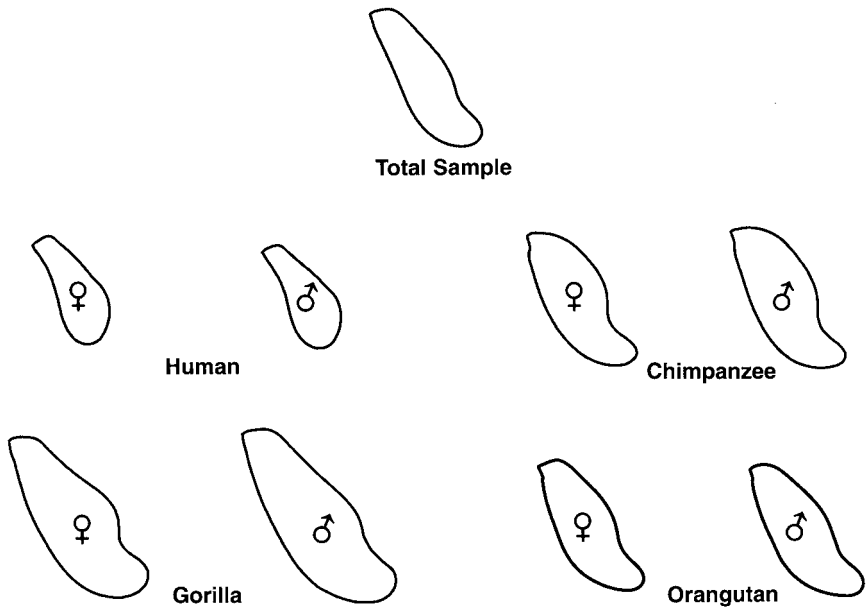
Figure 6.   Mean shape models for the total sample and for sex-specific samples of each taxon.

predictions. Because both eigenshapes 2 and 3 are, by definition, independent of eigenshape 1, they can be used to investigate morphology unrelated to biomechanical stresses (Lovejoy et al. 1999). As noted, several researchers have suggested that canine root growth and size influences mandibular dimensions (Wood 1978; Chamberlain and Wood 1985; Kimbel and White 1988; Daegling 2001). If symphyseal dimensions are in direct response to the size of the dentition, they would be classified as a Type 2 trait or as a spandrel in the parlance of Gould and Lewontin (1979). If this were true, one would expect a significant sex difference in taxa with highly dimorphic canines. Again, the inability of the first five

Table 2.   Results of Discriminant Function Analysis Using Eigenshape Scores (Eigenshapes 1–5)

Taxon	Actual Sex	Predicted Sex	
		Male	*Female*
All taxa (57.7% accuracy)	Male	61	31
	Female	43	40
Great apes only (65.4% accuracy)	Male	43	21
	Female	24	42

Table 3. Results of Species-Specific Discriminant Function Analysis Using Eigenshape Scores (Eigenshapes 1–5)

Species	Actual Sex	Predicted Sex	
		Male	*Female*
Humans (62.2% accuracy)	Male	24	4
	Female	13	4
Chimpanzee (61.9% accuracy)	Male	12	9
	Female	7	14
Gorilla (73.0% accuracy)	Male	14	3
	Female	7	13
Orangutan (60.8% accuracy)	Male	16	10
	Female	10	15

Table 4. Sexual Dimorphism in Symphyseal Shape by Species

Species	Wilks's Lambda	F Value	P
Homo	0.88	1.02	0.42
Pan	0.93	0.54	0.74
Gorilla	0.85	1.11	0.38
Pongo	0.84	1.71	0.15

Table 5. Results of Discriminant Function Analyses Using Eigenshape Values (Eigenshapes 1–5)

Original Group	Predicted Group Membership			
	Human	*Chimpanzee*	*Gorilla*	*Orangutan*
All taxa[a]				
Human	44	0	1	0
Chimpanzee	0	32	0	10
Gorilla	0	0	32	5
Orangutan	0	9	4	38
Great apes[b]				
Chimpanzee		36	0	6
Gorilla		1	30	6
Orangutan		8	3	40

a. 83.4% of original grouped cases correctly classified.
b. 81.5% of original grouped cases correctly classified.

eigenshapes to discriminate males and females consistently for any of the samples included in this analysis, along with the MANOVA results indicating no within-species sex differences, suggests that root size and morphology do not play a role in determining symphyseal morphology. Therefore we interpret the variation seen in eigenshapes 2 and 3 as not indicative of a Type 2 trait or spandrel. Lovejoy's Type 3 traits are primarily a result of allometric factors. Again, the inability to accurately discriminate the sexes in highly dimorphic species (gorilla and orangutan) indicates that overall allometric effects may not play a significant role in these eigenshapes.

Daegling and Jungers (2000) suggested that the primary utility of shape analysis of the mandibular symphysis may be for taxonomic identification of fossil specimens. The potential for such analyses is portrayed in Figure 5 by distributions of eigenshape scores for three taxa (chimpanzee, gorilla, and human). These distributions are well defined, virtually nonoverlapping, and show near perfect discrimination. This utility, however, may be called into question when examining the broad distribution of scores for orangutans.

In our analysis the variation in eigenshape scores for orangutans is roughly equivalent to that of the African apes combined. In her study of mandibular variation, Brown (1997) similarly found a higher level of variation in orangutan morphology and identified three possible reasons: (1) intersubspecies variation between Bornean (*P. pygmaeus pygmaeus*) and Sumatran (*P. p. abelli*) specimens; (2) lack of the anterior belly of the digastric muscle; or (3) presence of multiple male morphologies. More specifically, Brown (1997) found that Bornean orangutans possess "symphyseal sections that are generally larger, thicker, and more bulbous than those from Sumatra," whereas sections of Sumatran orangutans "are long and narrow with extensive inferior transverse tori" (Brown 1997, p. 166). Not all specimens used in the current analysis have a known subspecies designation; among specimens for which the subspecies is known, *P. p. pygmaeus* is the most common (*P. p. pygmaeus*, $n = 38$; *P. p. abelli*, $n = 9$; unknown, $n = 4$). In contrast to Brown's (1997) results, comparison of eigenshape scores between subspecies samples of known individuals reveals no clear differences. This may be due to our small sample of *P. p. abelli.* However, until a larger sample can be obtained, we conclude that subspecies variation alone cannot account for this large range of variation.

A second cause of variation within this genus may be the differing muscular anatomy of orangutans compared to other large-bodied hominoids. Unlike the African great apes and humans, orangutans lack an anterior belly of the digastric muscle extending from the hyoid and attaching to the digastric fossae on the inferior surface of the mandibular symphyseal region. The functions of the digastric muscles are to assist in retrusion and opening of the mandible (Hylander 1992). It is possible that the lack of a digastric muscle and the concomitant strains it produces may alter the morphology in the inferior torus of orangutans. Examination of other animals with similar morphology (e.g., *Alouatta*) is necessary before this variation can be fully understood.

A third consideration concerns hormonal differences in orangutan males. There is a growing body of evidence indicating that testosterone suppression in subordinate orangutan males may result in relatively small bodied individuals (Rodman 1988; Brown 1997). Although canine dimorphism has been shown not to affect the symphysis shape in normal males, the combination of a male canine morphology and reduced corpus dimensions in these individuals may result in a unique anatomy, and hence increased variation. This would have had virtually no effect on our study, given that none of the individuals included in these analyses were unusually small or unusually proportioned males.

The apparent discrepancy between the distributions of eigenshape scores between orangutans and the other taxa is not of minor concern and raises several interesting questions when considering applications to the fossil record. As noted, without orangutans, eigenshape scores almost perfectly discriminate between the three remaining taxa. If the analysis were to end there, one could assume, as did Daegling and Jungers (2000), that the mandibular symphysis would be an effective tool in systematic assignment of unknown specimens. The addition of the more variable orangutan results in error rates that may not be acceptable when attempting to assign fossil specimens.

Of course, this raises the question of what should be considered a "typical" primate distribution for symphyseal shape descriptors. We have made the implicit assumption that the orangutan distribution is atypical for hominoids and have sought additional explanations for the perceived pattern. Given the small number of taxa considered in this study, it is also possible that orangutans typify primates in terms of symphyseal variation and that chimpanzees, gorillas, and humans have relatively low levels of variation. The possibility that the African great apes and humans demonstrate a reduced level of mandibular symphyseal morphological diversity should be pursued through further analyses.

Comparison of Analytical Approaches.   Complex analyses of shape require a considerably more involved data-collection protocol than is frequently feasible. Therefore linear metric methods are often implemented. However, as noted previously, such approaches tend to oversimplify the morphology and therefore may result in insufficient resolution.

Ravosa (2000) suggested that linear metric data are often sufficient when trying to reconstruct habits of extinct species. Similarly, our results suggest that linear metrics may provide a good proxy measure for more complicated descriptions of the two-dimensional cross-section of the mandibular symphysis, depending on the research question. The first eigenshape in our analysis serves as an analogue of the relative dorsoventral width of the symphysis if length is held constant. Because this variation is in accord with the functional predictions of the mandibular symphysis, we suggest that this metric measurement may provide an ideal alternative to more complicated shape data when the primary question concerns adaptations to the stresses encountered during mastication.

However, we suggest that when the research question is concerned with shape differences, linear metrics can be problematic. Metric data are often framed as ratio data in an effort to control for size. Such ratios provide a unitless measure often referred to as "shape" (Bookstein 1991; MacLeod and Rose 1993). MacLeod and Rose (1993) discussed the problems with ratio data, including the similarity of ratio values from differing shapes. This is demonstrable in our data set by calculating a ratio of symphyseal width to symphyseal length. With this simple ratio, gorillas ($\bar{x} = 0.41 \pm 0.01$) and humans ($\bar{x} = 0.43 \pm 0.02$) would be indistinguishable, despite the obvious shape differences.

Scott (1980, p. 766) declared that "outlines are rich in information for the taxonomist." If this is true, the question is then, Which outline approach is best? MacLeod and Rose (1993) and Lohman (1983) expressed a preference for eigenshape analysis on theoretical grounds, whereas Rohlf (1986) considered Fourier and eigenshape analyses to be roughly equivalent. Comparison of eigenshape data with the Fourier approach of Daegling and Jungers (2000) shows many similarities. In both cases overall variation in gorilla symphyseal shape is somewhat less than that in chimpanzees, whereas orangutan variation is greater than both. The reduced gorilla variation and the extreme variation in orangutan symphyses is more pronounced in the Fourier analysis, but not to the extent that the interpretations presented here would change.

Discriminant function analyses based on both Fourier and eigenshape analyses demonstrate an ability to distinguish between taxa with minimal error. However, discrimination based on eigenshape scores shows an overall reduction in classification error, with virtual elimination of some types of misclassifications (as noted, gorillas and chimpanzees showed near perfect separation). In their Fourier discriminant function analysis, Daegling and Jungers (2000) reported an overall error rate of 22–33% in assigning specimens correctly to taxa when examining just the great apes. When a similar analysis is done with eigenshape scores, the overall error rate is 16.6% when discriminating among all four taxa and 18.5% for just the great apes (see Table 2). Although these error rates are only slightly lower than those in Daegling and Jungers's analysis, the type of error may hold some interest. In the Fourier analysis 10% of gorillas were incorrectly classified as chimpanzees and 15% of chimpanzees were incorrectly classified as gorillas. Eigenshape analysis showed no errors in assigning gorillas to chimpanzee or vice versa when all taxa were examined, and only one gorilla (3%) was incorrectly classified as a chimpanzee when the analysis was restricted to great apes. In both the eigenshape and Fourier analyses errors were made in classifying chimpanzee or gorilla as orangutan, and orangutan as either of those taxa. These errors are not surprising, given the large variation seen in the orangutan sample. In addition, in the eigenshape analysis one error was made in classifying a human (a 30-year-old white female) as a gorilla; no apes were misclassified as human. It is difficult to assess, however, whether the reduction in error seen in these eigenshape analyses is solely due to differences in methodology or whether it may be related to differences in the samples used.

Shape and Size.   Finally, we highlight a potential caveat to shape-based analyses that attempt to remove size (i.e., scale) from the analysis. Because ϕ^* coordinates are angular in nature, they do effectively remove size, in the strict mathematical sense, before analysis. However, size may still play a role in determination of the morphology of the symphysis because of allometry. Although we did not focus on allometric effects in this analysis, the major feature of symphyseal shape noted in this study clearly revolves around the shape of the superior transverse torus. The eigenshape axes shown in Figures 2 and 5 show that the superior torus clearly influences other aspects of shape, such as depth of the genial fossa and thickness of the inferior torus and alveolar margin. Given that the *size* of the superior torus is highly correlated with overall size of the mandible, it should not be surprising that *shape* of the superior torus (and related parts of the symphysis) is, in some way, also related to size differences between taxa (Daegling 2001).

   This criticism that shape and size are not independent is not novel (Gould 1966), but we raise it in order to argue that it should not be used to discount the value of shape analyses. There are clear cases where metrics will fall short of techniques, such as eigenshape analysis, in providing useful descriptions of morphology [see Scott (1980), MacLeod and Rose (1993), and Macleod (2002a)]. For example, it would be difficult to capture the subtle shape differences in the mandibular symphysis described in this study with a small set of scalar metrics.

Conclusion

   We used an outline approach, eigenshape analysis, to examine the two-dimensional cross-sectional shape of the mandibular symphysis of extant large-bodied hominoids. To some degree, variation along the first eigenshape mimics the variation seen in metric analyses by describing variation in relative width of the symphysis. This variation may be indicative of an adaptive response to the stresses of normal activities and accounts for 76–80% of the variation between these taxa. Subsequent eigenshapes identify subtle aspects of morphological variation in the superior transverse torus that do not appear to be functionally influenced and are not sexually dimorphic. Because there was no apparent effect of canine size on symphyseal morphology in sexually dimorphic species, contrary to previous suggestions that dimorphic canines may have an effect on mandibular morphology, additional factors that may contribute to these second, third, and fourth eigenshapes need to be considered.

   Using the first four eigenshapes, strong discrimination among the African ape and human symphyses suggests that eigenshape analyses may prove useful in systematic studies of fossil specimens. The large variation seen in orangutan symphyses, however, suggests that patterns of variation may differ in some taxa and that caution should be exercised.

It is clear that Scott's optimistic assertion that "outlines are rich in information" (Scott 1980, p. 766) is true for the mandibular symphysis of hominoids and that eigenshape analysis is an effective means to extract that information. Further application of this method to other taxa, such as the "anterior digastric-less" *Alouatta* or the strongly dimorphic *Papio*, will continue to refine the role of biomechanical, phylogenetic, and pleiotropic influences on mandibular symphyseal cross-sectional morphology.

Literature Cited

Beecher, R. M. 1977. Function and fusion at the mandibular symphysis. *Am. J. Phys. Anthropol.* 47:325–335.

Beecher, R. M. 1979. Functional significance of the mandibular symphysis. *J. Morphol.* 159:117–130.

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

Bookstein, F. L. 1991. *Morphometric Tools for Landmark Data: Geometry and Biology*. Cambridge, England: Cambridge University Press.

Bookstein, F. L., B. Chernoff, R. L. Elder et al. 1985. *Morphometrics in Evolutionary Biology*. Philadelphia: Academy of Natural Sciences.

Bouvier, M. 1986. Biomechanical scaling of mandibular dimensions in New World monkeys. *Int. J. Primatol.* 7:551–567.

Brown, B. 1997. Miocene hominoid mandibles: Functional and phylogenetic perspectives. In *Function, Phylogeny, and Fossils*. D. R. Begun, C. V. Ward, and M. D. Rose, eds. New York: Plenum Press, 153–172.

Chamberlain, A. T., and B. A. Wood. 1985. A reappraisal of variation in hominid mandibular corpus dimensions. *Am. J. Phys. Anthropol.* 66:399–406.

Cheverud, J. M., and J. E. Buikstra. 1981. Quantitative genetics of skeletal nonmetric traits in the rhesus macaques on Cayo Santiago. II. Phenotypic, genetic, and environmental correlations between traits. *Am. J. Phys. Anthropol.* 54:51–58.

Cheverud, J. M., J. E. Buikstra, and E. Twichell. 1979. Relationships between nonmetric skeletal traits and cranial size and shape. *Am. J. Phys. Anthropol.* 50:191–198.

Daegling, D. J. 1989. Biomechanics of cross-sectional size and shape in the hominoid mandibular corpus. *Am. J. Phys. Anthropol.* 80:91–106.

Daegling, D. J. 1993. Shape variation in the mandibular symphysis of apes: An application of a median axis method. *Am. J. Phys. Anthropol.* 91:505–516.

Daegling, D. J. 2001. Biomechanical scaling of the hominoid mandibular symphysis. *J. Morphol.* 250:12–23.

Daegling, D. J., and F. E. Grine. 1991. Compact bone distribution and biomechanics of early hominid mandibles. *Am. J. Phys. Anthropol.* 86:321–339.

Daegling, D. J., and W. L. Hylander. 1997. Occlusal forces and mandibular bone strain: Is the primate jaw "overdesigned"? *J. Hum. Evol.* 33:705–717.

Daegling, D. J., and W. L. Hylander. 1998. Biomechanics of torsion in the human mandible. *Am. J. Phys. Anthropol.* 105:73–87.

Daegling, D. J., and W. L. Hylander. 2000. Experimental observation, theoretical models, and biomechanical inference in the study of mandibular form. *Am. J. Phys. Anthropol.* 112:541–551.

Daegling, D. J., and W. L. Jungers. 2000. Elliptical Fourier analysis of symphyseal shape in great ape mandibles. *J. Hum. Evol.* 39:107–122.

Demes, B., H. Preuschoft, and J. E. A. Wolff. 1984. Stress-strength relationships in the mandibles of hominoids. In *Food Acquisition and Processing in Primates*, D. J. Chivers, B. A. Wood, and A. Bilsborough, eds. New York: Plenum Press, 369–390.

Dobson, S. D., and E. Trinkaus. 2002. Cross-sectional geometry and morphology of the mandibular symphysis in middle and late Pleistocene *Homo*. *J. Hum. Evol.* 43:67–87.

Dunsworth, H., and A. Walker. 2002. Early genus *Homo*. In *The Primate Fossil Record*, W. C. Hartwig, ed. Cambridge, England: Cambridge University Press, 419–435.

Ferson, S., F. J. Rohlf, and R. K. Koehn. 1985. Measuring shape variation of two-dimensional outlines. *Syst. Zool.* 34:59–68.

Gould, S. J. 1966. Allometry and size in ontogeny and phylogeny. *Biol. Rev. Camb. Philos. Soc.* 41:587–640.

Gould, S. J. 1997. The exaptive excellence of spandrels as a term and prototype. *Proc. Natl. Acad. Sci. USA* 94:10,750–10,755.

Gould, S. J. 2002. *The Structure of Evolutionary Theory*. Cambridge, England: Belknap Press.

Gould, S. J., and R. J. Lewontin. 1979. The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. *Proc. R. Soc. Lond.* 205:581–598.

Hiiemae, K. M. 1978. Mammalian mastication: A review of the activity of the jaw muscles and the movements they produce in chewing. In *Development, Function, and Evolution of Teeth*, P. M. Butler and K. A. Joysey, eds. London: Academic Press, 359–398.

Hylander, W. L. 1975. The human mandible: Lever or link? *Am. J. Phys. Anthropol.* 43:227–242.

Hylander, W. L. 1979. The functional significance of primate mandibular form. *J. Morphol.* 160:223–240.

Hylander, W. L. 1981. Patterns of stress and strain in the macaque mandible. In *Craniofacial Biology*, D. S. Carlson, ed. Craniofacial Growth Series, Monograph 10. Ann Arbor, MI: Center for Human Growth and Development, University of Michigan, 1–37.

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

Hylander, W. L. 1985. Mandibular function and biomechanical stress and scaling. *Am. Zool.* 25:315–330.

Hylander, W. L. 1986. In-vivo bone strain as an indicator of masticatory bite force in *Macaca fascicularis*. *Arch. Oral Biol.* 31:149–157.

Hylander, W. L. 1992. Functional anatomy. In *The Temporomandibular Joint: A Biological Basis for Clinical Practice*, B. G. Sarnat and B. G. Laskin, eds. Philadelphia: W. B. Saunders, 60–92.

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

Hylander, W. L., and K. R. Johnson. 1994. Jaw muscle function and wishboning of the mandible during mastication in macaques and baboons. *Am. J. Phys. Anthropol.* 94:523–547.

Hylander, W. L., K. R. Johnson, and A. W. Crompton. 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.

Kelley, J., and D. Pilbeam. 1986. The Dryopithecines: Taxonomy, comparative anatomy, and phylogeny of Miocene large hominoids. In *Comparative Primate Biology*, v. 1, *Systematics, Evolution, and Anatomy*, D. R. Swindler and J. Erwin, eds. New York: Alan R. Liss, 361–411.

Kimbel, W. H., Y. Rak, and D. C. Johanson. 2004. *The Skull of Australopithecus afarensis*. Oxford: Oxford University Press.

Kimbel, W. H., and T. D. White. 1988. Variation, sexual dimorphism, and the taxonomy of *Australopithecus*. In *Evolutionary History of the "Robust" Australopithecines*, F. E. Grine, ed. New York: Aldine de Gruyter, 175–191.

Lam, Y. M., O. M. Pearson, and C. M. Smith. 1996. Chin morphology and sexual dimorphism in the fossil hominid mandible sample from Klasies River Mouth. *Am. J. Phys. Anthropol.* 100:545–557.

Leakey, M. G., C. S. Feibel, I. McDougall et al. 1995. New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature* 376:565–571.

Lieberman, D. E., and A. W. Crompton. 2000. Why fuse the mandibular symphysis? A comparative analysis. *Am. J. Phys. Anthropol.* 112:517–540.

Lohmann, G. P. 1983. Eigenshape analysis of microfossils: A general morphometric procedure for describing changes in shape. *Math. Geol.* 15:659–672.

Lohmann, G. P., and P. N. Schweitzer. 1990. On eigenshape analysis. In *Proceedings of the Michigan Morphometrics Workshop*, F. J. Rohlf and F. L. Bookstein, eds. Ann Arbor, MI: University of Michigan Museum of Zoology, 145–166.

Lovejoy, C. O., M. J. Cohn, and T. D. White. 1999. Morphological analysis of the mammalian postcranium: A developmental perspective. *Proc. Natl. Acad. Sci. USA* 96:13,247–13,252.

Macleod, N. 1999. Generalizing and extending the eigenshape method of shape space visualization and analysis. *Paleobiology* 25:107–138.

Macleod, N. 2002a. Geometric morphometrics and geological shape-classification systems. *Earth Sci. Rev.* 59:27–47.

Macleod, N. 2002b. Phylogenetic signals in morphometric data. In *Morphology, Shape, and Phylogeny*, N. Macleod and P. L. Forey, eds. London: Taylor and Francis, 100–138.

Macleod, N., and K. D. Rose. 1993. Inferring locomotor behavior in Paleogene mammals via eigenshape analysis. *Am. J. Sci.* 293A:300–355.

McCollum, M. A. 1999. The robust australopithecine face: A morphogenetic perspective. *Science* 284:301–305.

McCollum, M. A., and P. T. Sharpe. 2001. Developmental genetics and early hominid craniodental evolution. *BioEssays* 23:481–493.

McCrossin, M. L., and B. R. Benefit. 1993. Recently recovered *Kenyapithecus* mandible and its implications for great ape and human origins. *Proc. Natl. Acad. Sci. USA* 90:1962–1966.

McGrath, J. W., J. M. Cheverud, and J. E. Buikstra. 1984. Genetic correlations between sides and heritability of asymmetry for nonmetric traits in rhesus macaques on Cayo Santiago. *Am. J. Phys. Anthropol.* 64:401–411.

Nicolay, C. W., and R. J. Sherwood. 2000. Eigenshape and biomechanical analysis of the phyllostomid mandibular symphysis. *Am. Zool.* 40:1148.

Olson, E., and R. Miller. 1958. *Morphological Integration*. Chicago: University of Chicago Press.

Ravosa, M. J. 1996. Mandibular form and function in North American and European Adapidae and Omomyidae. *J. Morphol.* 229:171–190.

Ravosa, M. J. 1999. Anthropoid origins and the modern symphysis. *Fol. Primatol.* 70:65–78.

Ravosa, M. J. 2000. Size and scaling in the mandible of living and extinct apes. *Fol. Primatol.* 71:305–322.

Ravosa, M. J., and E. L. Simons. 1994. Mandibular growth and function in *Archaeolemur. Am. J. Phys. Anthropol.* 95:63–76.

Rodman, P. S. 1988. Diversity and consistency in ecology and behavior. In *Orangutan Biology*, J. H. Schwartz, ed. New York: Oxford University Press, 31–51.

Rohlf, F. J. 1986. Relationships among eigenshape analysis, Fourier analysis, and analysis of coordinates. *Math. Geol.* 18:845–857.

Schwartz, J. H., and I. Tattersall. 2000. The human chin revisited: What is it and who has it? *J. Hum. Evol.* 38:367–409.

Scott, G. H. 1980. The value of outline processing in the biometry and systematics of fossils. *Palaeontology* 23:757–768.

Takai, M., F. Anaya, N. Shigehara et al. 2000. New fossil materials of the earliest new world monkey, *Branisella boliviana*, and the problem of platyrrhine origins. *Am. J. Phys. Anthropol.* 111:263–281.

Taylor, A. B. 2002. Masticatory form and function in the African apes. *Am. J. Phys. Anthropol.* 117:133–156.

Taylor, A. B., and C. P. Groves. 2003. Patterns of mandibular variation in *Pan* and *Gorilla* and implications for African ape taxonomy. *J. Hum. Evol.* 44:529–563.

Tobias, P. V. 1991. *Olduvai Gorge,* v. 4A and 4B, *Homo habilis: Skulls, Endocasts and Teeth.* Cambridge, England: Cambridge University Press.

Vinter, I., J. Krmpotic-Nemanic, D. Ivankovic et al. 1996. The influence of the dentition on the shape of the mandible. *Colleg. Antropol.* 20:555–560.

Vinyard, C. J., and M. J. Ravosa. 1998. Ontogeny, function, and scaling of the mandibular symphysis in papionin primates. *J. Morphol.* 235:157–175.

Ward, S. C. 1991. Taxonomy, paleobiology, and adaptations of the "robust" australopithecines. *J. Hum. Evol.* 21:469–483.

Ward, S. C., and D. L. Duren. 2002. Middle and late Miocene African hominoids. In *The Primate Fossil Record*, W. C. Hartwig, ed. Cambridge, England: Cambridge University Press, 385–397.

White, T. D., and D. C. Johanson. 1982. Pliocene hominid mandibles from the Hadar formation, Ethiopia: 1974–1977 collections. *Am. J. Phys. Anthropol.* 57:501–544.

Wolff, J. E. A. 1984. A theoretical approach to solve the chin problem. In *Food Acquisition Processing in Primates*, D. J. Chivers, B. A. Wood, and A. Bilsborough, eds. New York: Plenum Press, 391–405.

Wood, B. A. 1978. Allometry and hominid studies. In *Geological Background to Fossil Man*, W. W. Bishop, ed. Edinburgh: Scottish Academic Press, 125–128.

Wood, B. 1991. *Koobi Fora Research Project*, v. 4, *Hominid Cranial Remains.* Oxford: Clarendon Press.

Zahn, C. T., and R. Z. Roskies. 1972. Fourier descriptors for plane closed curves. *IEEE Trans. Comp.* C21:269–281.

Zelditch, M. L., W. L. Fink, and D. L. Swiderski. 1995. Morphometrics, homology, and phylogenetics: Quantified characters as synapomorphies. *Syst. Biol.* 44:179–189.