Bite Force Production Capability and Efficiency in Neandertals and Modern Humans

Carol F. O'Connor,[1] Robert G. Franciscus,[2,3]* and Nathan E. Holton[2]

[1]*Department of Research and Development, Renton Technical College, Renton, Washington 98056*
[2]*Department of Anthropology, University of Iowa, Iowa City, Iowa 52242*
[3]*Neuroscience Graduate Program, University of Iowa, Iowa City, Iowa 52242*

ABSTRACT Although there is consensus that Neandertal craniofacial morphology is unique in the genus *Homo*, debate continues regarding the precise anatomical basis for this uniqueness and the evolutionary mechanism that produced it. In recent years, biomechanical explanations have received the most attention. Some proponents of the "anterior dental loading hypothesis" (ADLH) maintain that Neandertal facial anatomy was an adaptive response to high-magnitude forces resulting from both masticatory and paramasticatory activity. However, while many have argued that Neandertal facial structure was well-adapted to dissipate heavy occlusal loads, few have considered, much less demonstrated, the ability of the Neandertal masticatory system to generate these presumably heavy loads. In fact, the Neandertal masticatory configuration has often been simultaneously interpreted as being disadvantageous for producing large bite forces. With rare exception, analyses that attempted to resolve this conflict were qualitative rather than quantitative. Using a three-dimensional digitizer, we recorded a sequence of points on the cranium and associated mandible of the Amud 1, La Chapelle-aux-Saints, and La Ferrassie 1 Neandertals, and a sample of early and recent modern humans (n = 29), including a subsample with heavy dental wear and documented paramasticatory behavior. From these points, we calculated measures of force-production capability (i.e., magnitudes of muscle force, bite force, and condylar reaction force), measures of force production efficiency (i.e., ratios of force magnitudes and muscle mechanical advantages), and a measure of overall size (i.e., the geometric mean of all linear craniofacial measurements taken). In contrast to the expectations set forth by the ADLH, the primary dichotomy in force-production capability was not between Neandertal and modern specimens, but rather between large (robust) and small (gracile) specimens overall. Our results further suggest that the masticatory system in the genus *Homo* scales such that a certain level of force-production efficiency is maintained across a considerable range of size and robusticity. Natural selection was probably not acting on Neandertal facial architecture in terms of peak bite force dissipation, but rather on large tooth size to better resist wear and abrasion from submaximal (but more frequent) biting and grinding forces. We conclude that masticatory biomechanical adaptation does not underlie variation in the facial skeleton of later Pleistocene *Homo* in general, and that continued exploration of alternative explanations for Neandertal facial architecture (e.g., climatic, respiratory, developmental, and/or stochastic mechanisms) seems warranted. Am J Phys Anthropol 127:129–151, 2005. © 2004 Wiley-Liss, Inc.

Facial features exhibited by Neandertals have long been considered unique within the genus *Homo*. These include: elongated vertical facial dimensions; midsagittal upper facial projection; broad squared anterior palates; relatively wide and square-shaped piriform apertures; broad, projecting nasal bridges; depressed internal nasal floors; swept-back zygomatic arches; inflated infraorbital areas; and long mandibles with high coronoid and/or low condylar processes, retromolar spaces, and relatively large anterior dentition (Smith, 1983; Stringer et. al, 1984; Trinkaus, 1987; Smith and Paquette, 1989; Franciscus, 1999, 2003; Rak and Hylander, 2003). While individually these features may not be apomorphies in the strict sense (Franciscus, 1995, 1999, 2003; Franciscus and Trinkaus, 1995; Yaroch, 1996), the pattern they produce collectively in the Neandertal face is universally considered unique.

No consensus exists, however, regarding the potential adaptive bases for this uniqueness and the

evolutionary mechanisms that produced it, although workers have developed and/or tested various hypotheses. These include: cold adaptation (Coon, 1962), possibly in balance with random genetic drift (Howell, 1951, 1952; Hublin, 1990, 1998, 2000) and altered growth patterns (Brothwell, 1975; Smith, 1991; Ponce de León and Zollikofer, 2001); respiratory moisture retention in cold and/or arid climates (Sergi, 1962; Franciscus and Trinkaus, 1988); and masticatory biomechanics (Heim, 1976; Smith, 1983; Rak, 1986; Demes, 1987; Trinkaus, 1987; Smith and Paquette, 1989; Antón, 1990, 1994a; Couture, 1993; Spencer and Demes, 1993). In recent years, the last has received by far the most attention in the paleoanthropological literature.

Large, heavily worn anterior dentition, differential dental wear patterns, and degenerative remodeling of the temporomandibular joint have been cited as evidence for excessive or unusual paramasticatory activity in Neandertals (Stewart, 1959; Coon, 1962; Brace, 1962, 1963; Brace et al., 1981; Smith, 1983; Trinkaus, 1983; Smith and Paquette, 1989). According to the "anterior dental loading" or "teeth-as-tools hypothesis" (ADLH), Neandertal facial anatomy was an adaptive response to the heavy anterior dental loads that resulted from such activity. Characteristic features, particularly midfacial prognathism and elongated vertical dimensions (Smith, 1983; Rak, 1986), and changes in the infraorbital areas (Smith, 1983; Rak, 1986; Demes, 1987), are interpreted as adaptations for effectively dissipating these loads. Further, the "corollary" of this hypothesis is used by some to explain the emergence of modern craniofacial form: technological improvements in the later Pleistocene (e.g., cooking, blade technology, composite tools) reduced the frequency and extent of dental loading, thereby relaxing the need for large teeth and large faces (Brace, 1963, 1995; Smith, 1983, 1985; Wolpoff, 1996).

A critical assumption made by supporters of the ADLH is that the forces Neandertals generated during paramastication were unusually heavy: "massive anterior dental loads" (Smith, 1983); "heavy occlusal loads" (Rak, 1986); "presumably high forces" (Demes, 1987); and "extensive, vertical-occlusally derived forces" (Smith and Paquette, 1989). Although this assumption appears sound, given the dental evidence, it has not been convincingly demonstrated. Before the argument that Neandertal facial structure was well-adapted to dissipate heavy occlusal loads can be made, the ability of their masticatory system to generate these presumably heavy loads must be established.

Paradoxically, the masticatory configuration in Neandertals has been simultaneously perceived as *disadvantageous* for producing large bite forces (Smith, 1983; Rak, 1986; Trinkaus, 1987). Trinkaus (1987) pointed to their relatively posteriorly positioned zygomatico-ramal region (and associated musculature) and relatively anteriorly positioned dentition as evidence of their reduced ability to pro-

duce heavy occlusal loads, perhaps even in relation to their ancestors. Even proponents of the ADLH recognize that this typical combination of prognathism and posteriorly positioned musculature would compromise bite force potential in Neandertals (Smith, 1983; Rak, 1986; Smith and Paquette, 1989). As noted by Spencer and Demes (1993), it is somewhat contradictory that Neandertal faces would become more adept at dissipating high occlusal loads and simultaneously less adept at generating them. With rare exceptions (Antón, 1990, 1994a; Couture, 1993; Spencer and Demes, 1993), analyses that attempted to resolve this conflict were largely qualitative rather than quantitative.

At issue are both the amount of bite force Neandertals could generate (i.e., their force production capability) and the relative ease with which they did so (i.e., their force production efficiency). Because it requires estimates of muscle force magnitudes, the former is more difficult to quantify than the latter; only Antón (1990, 1994a) attempted to do so for Neandertals. She found that despite much larger muscle force estimates, bite force estimates were absolutely smaller in Amud 1 than in recent humans. She further found that even moderate levels of occlusal loading produced substantial condylar reaction forces in the Neandertal. Antón (1990, 1994a) concluded that Neandertals were both less capable of and less efficient at producing incisal bite force than recent humans. She rejected the ADLH, attributing their anterior dental attrition to repetitive rather than high-magnitude loading.

Couture (1993), studying maxillary projection in Neandertals, examined the impact of anatomical changes in the Neandertal face, relative to pre-Neandertals and recent humans (Eskimos and Aboriginal Australians) with regard to mastication and paramastication. Examining mechanical advantage as a ratio of the moment arm of the masseter and the moment arm of bite force, it was determined that the samples exhibited similar masseter moment arm lengths. Bite force moment arm lengths in the Neandertal sample were distinct from the modern samples due to the increased distance between the temporomandibular joint (TMJ) and bite point (both molar and incisal). Given these differences, Couture (1993) found that the Neandertal sample still maintained masticatory efficiency similar to her modern human samples in cases of mastication and paramastication. As a result of these similarities, coupled with the distinct facial morphology of Neandertals, Couture (1993) concluded that the Neandertal face is difficult to explain in terms of masticatory function.

Spencer and Demes (1993) formulated several expectations for increased anterior tooth use, based on the biomechanical model of Greaves (1978). Using estimates of bite and muscle position, they compared the bite force production efficiency of closely related populations, one known (or assumed, in the case of the Neandertals) to be specialized for ante-

rior tooth use and the other not specialized. That is, rather than comparing Neandertals directly to modern humans, they made separate pairwise comparisons of Neandertals with Middle Pleistocene specimens from Europe and Africa, and of Inuits with Native Americans. The authors found a number of similarities in the adaptations exhibited by the specialized populations (i.e., Neandertals and Inuits) compared to their nonspecialized counterparts (i.e., Middle Pleistocene specimens and Native Americans). They attributed these similarities to heightened use of the anterior dentition. Spencer and Demes (1993) concluded that Neandertals were well-designed for incisal use compared with Middle Pleistocene specimens, and did not reject the ADLH. If a comparison of the Neandertals with the Inuits and the Native Americans is made, however, their results (like those of Antón, 1990, 1994a) suggest that Neandertals were less efficient producers of incisal bite force than both specialized and nonspecialized recent humans.

Although the above quantitative studies contributed greatly to our understanding of Neandertal masticatory biomechanics, all have certain shortcomings that we argue warrant further examination of this problem. We believe the primary weakness in Antón (1990, 1994a) is her extremely small sample: she used only one Neandertal and one unspecified recent human in her analysis. Second to this are several assumptions and simplifications that Antón (1990, 1994a) made in her biomechanical analysis that may have biased her results (see Discussion for details). Since most Pleistocene crania lack an associated mandible, Spencer and Demes (1993) considered only cranial morphology in their study. Although this approach increased the available specimens and arguably allowed for a more suitable comparative framework, it did not provide a complete representation of the masticatory system. Muscle moment arms could not be estimated, since they depend on both origin and insertion; instead, the authors used the anteroposterior position of the origin to approximate muscle leverage. Further, they measured only a single point on the cranium to assess muscle position. Finally, because they did not estimate muscle-force magnitudes, their results pertain only to the question of how efficient Neandertals were at producing bite force, but not to how large those forces may have been. Similarly, Couture (1993) did not consider force-magnitude production, evaluating only mechanical advantage. Moreover, she quantified the mechanical advantage of masseter only, leaving out consideration of the temporalis and medial pterygoid muscles.

The goal of this study was to test the ADLH by incorporating the strengths of previous studies while addressing some of their weaknesses. Since high-magnitude loads are clearly implicated in the ADLH, we considered it important to assess both force-production capability and force-production efficiency. We believe that an analysis based on the entire masticatory system, rather than isolated elements, is likely to produce the most accurate assessment of these parameters.

Although an assessment of the adaptive basis of Neandertal craniofacial anatomy is enhanced by comparing Neandertals to their Middle Pleistocene predecessors, much can also be gained by a direct comparison of Neandertal bite force to that of modern humans. Actual values of bite force have been obtained for living humans, and the relationships between bite force, chewing muscle mass, and craniofacial variation have been studied extensively in a clinical context (e.g., Hannam and Wood, 1989; Waltimo et al., 1994; Raadsheer et al., 1999; Tuxen et al., 1999). Therefore, using modern humans as a comparison to Neandertals provides the opportunity to compare Neandertal estimates to real values obtained for a species of the genus *Homo* in addition to estimates derived from other fossil taxa.

Moreover, in addition to providing a direct comparison with other published results (e.g., Antón, 1994a), our comparison of modern humans to Neandertals also affords the opportunity to assess variations in bite force over a wide range of craniofacial size and robusticity variation and documented rather than inferred levels of paramasticatory behavior.

The following specific questions guided our study:

1. Force-production capability: Were Neandertals capable of generating significantly larger anterior dental loads compared with early modern and recent modern humans?
2. Force-production efficiency: Were Neandertals significantly more (or less) efficient at generating anterior dental loads compared with early modern and recent modern humans?

To gain a more complete understanding of Neandertal masticatory biomechanics in general, and the ADLH in particular, we also asked:

3. Differential condylar loading patterns: Were there significant differences in the condylar loading patterns of Neandertals during anterior biting compared with early modern and recent modern humans?
4. Craniofacial size and robusticity: How do force-production capability and force-production efficiency vary as a function of overall craniofacial size and robusticity across all specimens?

MATERIALS

The Neandertal specimens chosen for this study (Amud 1, La Ferrassie 1, and La Chapelle-aux-Saints) date to the earlier part of the Last Glaciation (i.e., between 70–40 kya; Grün and Stringer, 1991), and were selected based on their retention of reasonably complete and associated crania and mandibulae, as well as their prominence in previous studies of masticatory and facial biomechanics of

Neandertals (Heim, 1976; Rak, 1986; Trinkaus, 1987; Couture, 1993; Spencer and Demes, 1993; Antón, 1994a). We used the McGregor restoration to digitize the points on La Chapelle-aux-Saints. The precise locations for the digitized points on the reconstruction were guided by the use of a more recent and unrestored high-resolution cast (by M. Chech).

Our modern human sample is geographically, morphologically, and temporally diverse. Skhul 5 is the best-preserved specimen of the robust "early anatomically modern" sample from the Levantine site of Skhul (120–90 kya; Stringer et al., 1989; Mercier et al., 1993). It is widely considered to be the most modern of the Skhul sample in overall cranial shape, and despite substantial restoration of its midfacial region, it remains the best-preserved specimen from the site (Stringer, 1996), and indeed one of the best referents for early moderns in general (Lahr, 1996). It also provides the only possible comparison of the earliest modern humans to Neandertals currently available in terms of biomechanical properties estimated from directly associated, sufficiently intact crania and mandibulae. The inclusion of the relatively robust Levantine Ohalo 2 specimen (20 kya, Nadel et al., 1995) and the gracile South African Fish Hoek specimen (ca. 13 kya; R.G. Klein, personal communication) are included here primarily to augment Skhul 5 by extending the range of well-preserved Pleistocene modern specimens against which the Neandertals can be compared in terms of overall size and robusticity. Detailed observations from previous study of the original Pleistocene fossil specimens by one of us (R.G.F.), and comparison of standard measurements on our casts to published values on originals, were employed to validate the accuracy of all casts.

Our primary comparative sample consists of 20 adult (males = 10; females = 10) central California (Ohlone) Amerindians from the Ryan Mound (Ala-329), which dates from 500 AD to just before European contact (Coberly, 1973). The aggregate sample is characterized by extreme dental wear, among the most severe for any modern population yet described (Jurmain, 1990). Moreover, heavy wear is evident even in the deciduous dentitions of very young children.

The marked dental wear characterizing specimens from this and other contemporaneous central Californian sites probably occurred in large part due to the introduction of a large amount of grit in their diet by the processing of acorn, a process that included leaching and grinding (Moratto, 1984). In addition, the heavy wear on their anterior teeth was likely further promoted by paramasticatory behavior associated with such activities as processing fibers for baskets and cordage for twine (Molnar, 1972; Schulz, 1977; Larsen, 1985). In order to increase the geographic range and overall size range of our recent comparative sample, we also included 2 unprovenienced Australian Aboriginals (1 male, 1 female) with moderate dental wear, and 4 unprove-

nienced male specimens from the Indian subcontinent with moderate to light dental wear (Stanford University Teaching Collection). Comparisons of individual Neandertal and Pleistocene modern specimens therefore were made to our recent combined sample (n = 26), as well as to three recent subsamples: all recent females (n = 11; 10 Ohlone and 1 Australian Aboriginal); robust recent males I (n = 11; 10 Ohlone and 1 Australian Aboriginal); and gracile recent males II (n = 4; Indian subcontinent).

METHODS

Data collection

A sequence of 37 points was marked on each cranium and associated mandible, and was subsequently recorded using a three-dimensional digitizer (Faroarm, Faro Technologies, Inc.). These points (detailed below) included bite locations, reference points to establish the Frankfurt horizontal and occlusal planes, and specific locations that demarcated the extent of muscle attachment and muscle cross-sectional areas. Both sides of La Chapelle-aux-Saints, Skhul 5, Ohalo 2, and the recent modern specimens were measured, and the results averaged for each individual. Only the left sides of Amud 1, La Ferrassie 1, and Fish Hoek were considered intact enough to yield reliable measurements. The infratemporal fossa of Amud 1 is sufficiently damaged that it was necessary to substitute average values for this region, derived from digitizing recent casts of the La Chapelle and Grotte Guatarri 1 Neandertals. Also, given the damage to the pterygoid plates of Amud 1, it was necessary to estimate the origin point for the medial pterygoid based on the locational information from peripheral features, using the remainder of the Neandertal sample as a referent.

Estimation of model inputs

Muscle force vectors. The muscles modeled in this analysis were restricted to those that elevate the jaw and that are active during the power (i.e., crushing) stroke of the chewing cycle: the masseter, medial pterygoid, and temporalis. Muscles that act mainly to stabilize or depress the mandible, such as the lateral pterygoid and digastric (Pruim et al., 1980; Osborn and Baragar, 1985), were not included.

Macroscopically, the masseter, medial pterygoid, and temporalis are pennate in fiber arrangement and consist of one or more functional units (i.e., portions that contract independently and/or have different lines-of-action). Microscopically, they are composed mostly of slow-twitch fibers, although the precise composition and distribution of fibers vary with each muscle (Antón, 1994b). These factors (pennation, number of functional units, and fiber type) and others such as muscle length during contraction, velocity of contraction, and type of contraction all strongly influence muscle force production (Pitman and Peterson, 1989). Because few of these

factors are reflected in skeletal anatomy, muscle-force prediction in extinct hominids is problematic. By making several assumptions and simplifications, however, reasonable estimates of muscle force vectors can be derived from bony morphology. The assumptions and simplifications we made in the present analysis are detailed below.

First, we assumed that each muscle consisted of a single functional unit that could be replaced with a concentrated force vector. We estimated the direction, point of application, and magnitude of each muscle force vector from cranial and mandibular measurements (Fig. 1).

Direction was determined using the "straight-line approach:" the centroid of the insertion area on the mandible was joined to the centroid of the origin area on the cranium (Hiiemae, 1971; Jensen and Davy, 1975; Pruim et al., 1980; Osborn and Baragar, 1985, 1992; Baragar and Osborn, 1987; Koolstra et al., 1988; Koolstra and van Eijden, 1995; Trainor et al., 1995; Osborn, 1996). The point of application of each muscle force vector was taken as the centroid of its insertion area (Fig. 1a).

Given the minimal displacement of the mandible during the power stroke of mastication, we next assumed isometric muscle contractions at optimal muscle length. The maximum force a muscle can generate during an isometric contraction is equal to its physiological cross-sectional area (PCSA) multiplied by the intrinsic strength of skeletal muscle (σ_M; Weijs and Hillen, 1985b; Koolstra et al., 1988). PCSA is defined as the total cross-sectional area of all muscle fibers at a specified muscle length, most appropriately the length of contraction. In order to estimate muscle-force magnitudes, therefore, we had to first estimate muscle PCSA. We assumed that the following measurements of "raw PCSA" taken on dry skulls provided reasonable proxies of "actual PCSA" (modified from Antón, 1990, 1994a,b):

1. Masseter: The product of masseteric "length" and "width;" "length" was defined as the length of the muscle origin on the zygomatic arch; "width" was defined as the mediolateral distance, projected onto the Frankfurt horizontal plane, between the lateral edge of the zygomatic arch and the centroid of the muscle insertion area on the mandibular ramus.
2. Medial pterygoid: The area of the triangle formed by the following three points on the interior aspect of the mandible: the gonion, the anteroinferior point of muscle insertion, and the superoposterior point of insertion on the ramus.
3. Temporalis: The area enclosed by the temporal fossa, projected onto the Frankfurt horizontal plane (Fig. 1b).

Although representative of muscle size, the raw PCSAs were likely to either overestimate or underestimate the actual PCSAs. To determine the amount of correction necessary for each muscle, we
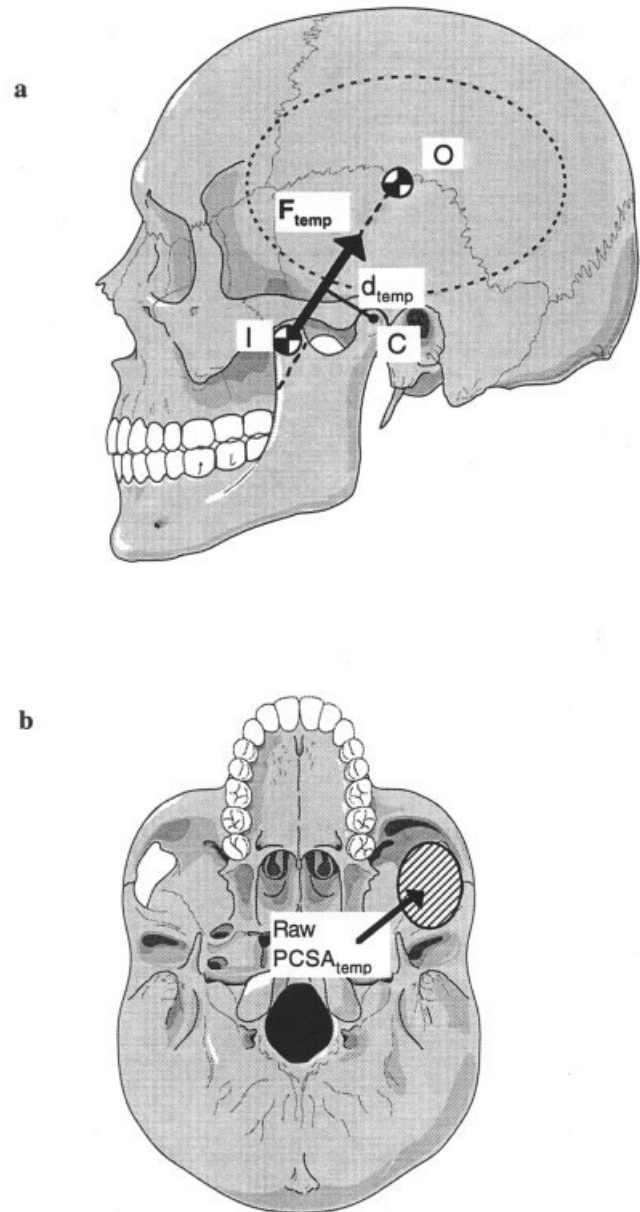

Fig. 1. Estimation of muscle force vectors (shown for temporalis). **a:** To determine direction of muscle force vector associated with temporalis (F_{temp}), centroid of insertion area on mandible (I) was connected to centroid of origin area on cranium (O); point of application was taken as centroid of insertion area on mandible (I); given direction and point of application of force vector, lever arm with respect to condyle (C) was determined (d_{temp}). **b:** To determine magnitude of muscle force vector associated with temporalis, area enclosed by temporal fossa was first measured (Raw $PCSA_{temp}$); this value was then scaled using correction factor for temporalis (CF_{TEMP}) and multiplied by intrinsic strength of skeletal muscle (σ_M).

compared the mean raw PCSAs calculated for the recent combined sample (n = 26) with published mean values of actual masticatory muscle PCSAs. Although the precise relationship between the bone proxies and actual PCSA is unclear (see Discussion), significant linear correlations were found between other facial dimensions and muscle cross-sectional

Muscle	Raw PCSA (cm^2)[1]	Actual PCSA (cm^2)[2]	CF[1]
Masseter	8.98	9.10	0.99
M. pterygoid	1.72	6.60	0.26
Temporalis	7.01	10.90	0.64

[1] Average of all recent modern specimen (n = 26).
[2] Taken from Weijs and Hillen (1985a, 1986).

area (Weijs and Hillen, 1986; Hannam and Wood, 1989). Thus, assuming a linear relationship between the raw and the actual muscle PCSA, we generated a set of correction factors ($CF_{MASS, i}$, $CF_{MPT, i}$, $CF_{TEMP, i}$) for the i-th specimen (i = 1, 2, ..., 26) according to:

$$CF_{MASS, i} = \frac{raw\ PCSA_{MASS, i}}{actual\ PCSA_{MASS}}$$

$$CF_{MPT, i} = \frac{raw\ PCSA_{MPT, i}}{actual\ PCSA_{MPT}}$$

$$CF_{TEMP, i} = \frac{raw\ PCSA_{TEMP, i}}{actual\ PCSA_{TEMP}}$$

where the "actual PCSAs" were taken from computed tomography studies of the human jaw muscles (Weijs and Hillen, 1985a, 1986). The 26 correction factors computed for each muscle were averaged to obtain the correction factors shown in Table 1. The raw PCSAs for both Pleistocene and recent modern specimens were then divided by the average correction factor for each muscle to obtain reasonable estimates of the actual muscle PCSAs. Implicit in this step is our assumption that the same set of correction factors applies to Neandertals as to Pleistocene and recent modern human samples. We base this on the more general assumption of structural similarity between Neandertal and modern human masticatory muscles (e.g., Rak, 1986; Demes, 1987; Antón, 1990, 1994a; Spencer and Demes, 1993), a hypothesis that to date has not been rejected (Antón, 1996a).

The final step in estimating muscle-force magnitudes was to multiply the corrected values of PCSA by the intrinsic strength of skeletal muscle, σ_M. Although experimentally determined values of σ_M range from as low as 9 N/cm^2 (Maughan et al., 1983) to as high as 140 N/cm^2 (Pruim et al., 1980), the majority of researchers found σ_M to be between 30–40 N/cm^2 for a variety of vertebrate skeletal muscle (Haxton, 1944; Hettinger, 1961; Weis-Fogh and Alexander, 1977; Nygaard et al., 1983; Weijs and Hillen, 1985b; van Spronsen et al., 1989). Following the recommendation of Zajac (1989), a value of 35 N/cm^2 was chosen for this analysis.

Bite force direction and lever arms. The bite force was assumed to act at the center of the biting tooth (M_1 for molar biting and I_2 for incisal biting), and its direction was taken perpendicular to the occlusal plane. Although some studies showed that
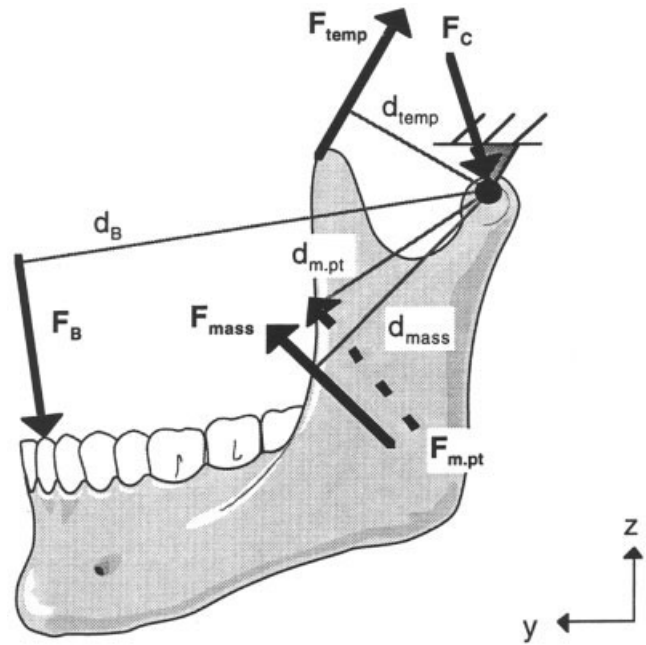

Fig. 2. Bilateral biting analysis in sagittal projection. Estimated muscle force vectors (F_{mass}, $F_{m.pt}$, F_{temp}) and lever arms (d_B, d_{mass}, $d_{m.pt}$, d_{temp}) were used to calculate magnitude of maximum bite force vector (F_B) and condylar reaction force vector (F_C) in sagittal plane.

maximum bite force does not necessarily occur perpendicular to the occlusal plane, especially in the incisal region (Hylander, 1978; Baragar and Osborn, 1987; Koolstra et al., 1988), this assumption was made to render the system statically determinate (see below). Once their direction and point of application were established, the lever arms of the bite force and the muscle forces relative to the condyle were calculated by taking the perpendicular distance between the line of action of a given force and the condylar axis (Figs. 1a, 2).

Biomechanical model description

The mandible was modeled as a three-dimensional rigid body rotating about an axis passing through the condyles. The following orthogonal coordinate system was used: the origin was fixed in the midsagittal plane along the line connecting the centers of the left and right condyles; the positive x-axis was directed along the same line to the right; the positive y-axis was directed anteriorly parallel to the Frankfurt horizontal; and the positive z-axis was directed superiorly, perpendicular to the Frankfurt horizontal. External forces acting on the mandible were assumed to consist only of bite force, muscle forces, and condylar reaction forces; given its relatively small mass, the force due to body weight of the mandible was neglected. As previously mentioned, the mandible was assumed to be in static equilibrium.

With muscle force vectors defined from the bony morphology as described above, *and without making*

any assumptions about bite force direction, the model contained nine unknowns: the three components of the bite force, the left condylar reaction force, and the right condylar reaction force. There are, however, only six equations of static equilibrium which these force components must satisfy. Systems in which the unknown forces outnumber the equations of equilibrium, such as this one, are statically indeterminate. Given the complexity of joint systems, muscle recruitment patterns, and articular contact regions, static indeterminacy is commonly encountered in biomechanical analyses. Several different approaches were developed to overcome this problem. In the "optimization" method, objective or constraint functions are formulated and optimized, thereby increasing the number of equations to the number of unknowns (Osborn and Baragar, 1985; Koolstra et al., 1988; Trainor et al., 1995). In the "reduction" method, reasonable assumptions and simplifications are made to reduce the number of unknowns to the number of equations (Throckmorton et al., 1980; Throckmorton, 1985; Throckmorton and Throckmorton, 1985). The latter approach was taken in this analysis.

To render the system statically determinate, we further assumed bilateral symmetry (i.e., both the morphology of the left and right halves of the mandible as well as the muscle forces acting on each half were symmetrical with respect to the midsagittal plane) and, as stated above, that bite force acted perpendicular to the occlusal plane.

Under these two assumptions, the three-dimensional analysis was essentially reduced to a two-dimensional one operating in the sagittal plane (Fig. 2). That is, the number of useful equations was reduced from six to three, and the number of variables reduced from nine to the following three:[1] magnitude of total bite force, anteroposterior component of resulting total condylar reaction force, and superoinferior component of resulting total condylar reaction force. "Total" simply refers to the sum of the left and right sides (since these are now collapsed into one plane), or for those specimens with damaged right sides, to twice the value calculated for the left side.

Force production capability

A bilateral symmetric biting analysis in a sagittal projection was done, using the model described above. This yielded the maximum bite force a specimen was capable of generating and the associated condylar reaction force under optimal muscular conditions (i.e., all muscles undergoing maximal isometric contractions simultaneously). We character-

ized the force production capability of the masticatory system by: the magnitude of total bite force (F_b); the magnitude of total condylar reaction force (F_c); and the total sum of muscle-force magnitudes (F_m).[2]

Force production efficiency

Generally speaking, the efficiency of a system can be expressed as the ratio of a designated output to the required input. Taking F_m as a measure of energy expended in producing F_b and the associated F_c, we defined force-production efficiency of the masticatory system as the "outputs" F_b and F_c scaled by the required "input" F_m. The expectation is that an efficient system maximizes bite force and minimizes condylar reaction force for a given muscle force, and should therefore have a relatively high bite to muscle force ratio (F_b/F_m), but a low condylar reaction to muscle force ratio (F_c/F_m). Although dimensionless, these ratios are a function of both muscle size and relative position. More importantly, they reflect the performance of the entire masticatory system, i.e., how they function together, rather than the performance of individual components.

To compare our results with those of Spencer and Demes (1993), we also assessed force-production efficiency by mechanical advantage, defined as the muscle force lever arm divided by the bite force lever arm (Throckmorton et al., 1980). A relatively large mechanical advantage value indicates that a muscle is well-positioned for producing a given bite force. Unlike force ratios, mechanical advantage does not account for muscle size, and measures the performance of each muscle separately.

Differential loading of the condyles

Bilateral symmetric biting requires that the condyles are loaded equally. During nonsymmetric biting, the reaction force will not be distributed evenly, however, and the extent of differential loading depends primarily on the mediolateral dimensions of the mandible. To explore condylar loading patterns and their implications for the ADLH, we performed a unilateral biting analysis in a frontal projection. By applying the principle of superposition to the results from symmetric biting analysis, we calculated the magnitude of the working-, or chewing-, side condylar reaction force ($F_{c,WORK}$), and the magnitude of the balancing-side condylar reaction force ($F_{c,BAL}$). The ratio of the working-side to the balancing-side condylar reaction force ($F_{c,WORK}/F_{c,BAL}$) was used to further illustrate the extent of differential loading (Fig. 3; see Appendix for details).

---

[1]The mediolateral component of the condylar reaction force remains indeterminate under the assumption of bilateral symmetry. Although from a mathematical viewpoint it can assume any value and still satisfy the equations of equilibrium, from a physiological viewpoint it most likely assumes one close to the minimum solution (i.e., zero).

[2]Since it is used to characterize the required input or physiological "cost" to the masticatory system, F_m is defined as the sum of the magnitudes of the masseter, medial pterygoid, and temporalis, rather than as the magnitude of their vector sum. This is a more appropriate characterization of the energy required to produce bite force, since it measures both useful and nonuseful muscle force; the latter measures only the useful muscle force generated.
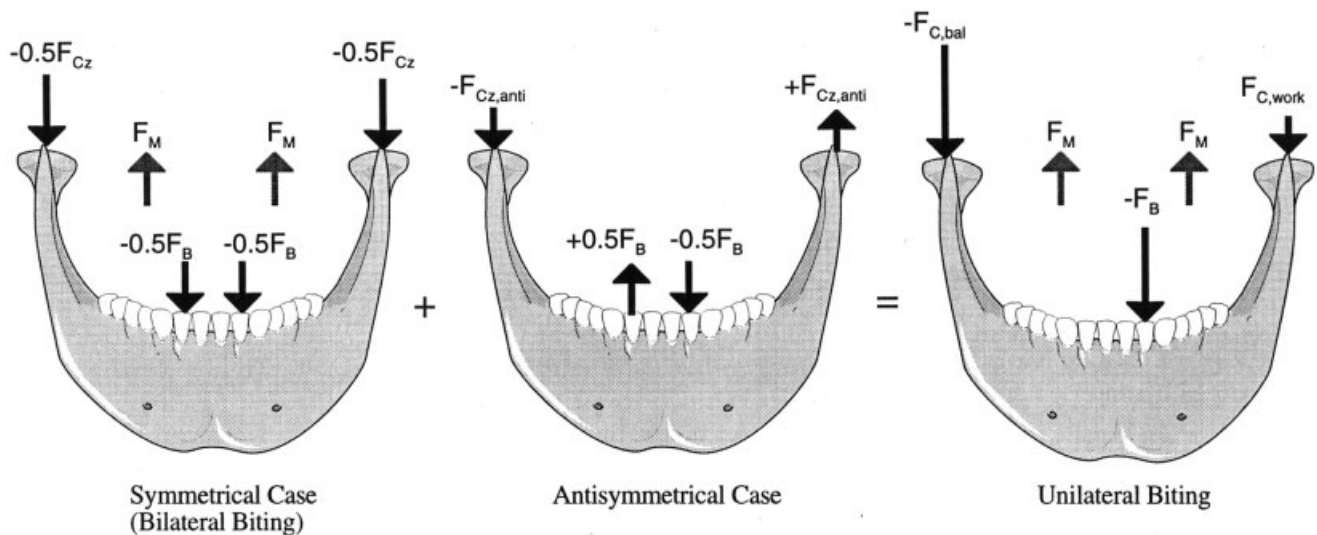
Fig. 3. Unilateral biting analysis in frontal projection, using principle of superposition. Results from symmetric case (i.e., bilateral biting) were added to results from antisymmetric case in which no muscle forces were acting; this yielded nonsymmetric case (i.e., unilateral biting) shown at right. For details, refer to Appendix.

Both the bilateral symmetric and unilateral nonsymmetric analyses were performed for incisal (I_2) biting to address the questions posed in the introduction. We also analyzed molar (M_1) biting to determine if any individual exhibited significant differences between anterior and posterior biting. All calculations, including the estimation of model inputs, were done using a custom-written FORTRAN program by the first author.

Model validation

Ideally, the theoretical value of each model variable should be compared with an experimentally measured value to verify its accuracy. While bite force can be measured directly with a force transducer, for technical and ethical reasons, muscle force and condylar reaction force can only be measured indirectly. We were therefore limited to comparing our calculated bite-force magnitudes (Fb) with published clinical values, since no such comparative data exist for Fc and Fm.

To further test the performance of our model across a considerable size and shape range, we digitized two adult *Pongo pygmaeus* specimens (one female cast and one male cast with no apparent dental or cranial pathologies). We compared our calculated bite-force magnitudes with an experimentally obtained maximum bite-force estimate for this species (Lucas et al., 1994).

Size and robusticity

The estimates of muscle physiological cross-sectional area and muscle force magnitudes provided obvious measures of individual masticatory size. Also of interest, however, were the degree and manner in which these masticatory variables and their derivatives correlated with bony measures of craniomandibular size across all specimens. Therefore, the logged geometric mean of the linear distances from the porion to all 37 digitized points was used as a measurement of overall size.

It is clear that size and robusticity can be very different parameters in skeletal morphometrics; this is especially evident in the long bones of the postcranial skeleton. Cranial robusticity, in contrast, is often equated with overall size implicitly and more explicitly as the size and development of various superstructures such as tori, ridges, and tubercles. Moreover, Lahr and Wright (1996) showed that the development of such discrete robusticity variables is highly positively correlated with overall cranial size in *Homo sapiens*. Cortical thickness in some parts of the skull, especially in the mandibular corpus, may well constitute a more explicit measure of robusticity in some cases. However, with this caveat in mind, we will refer to the geometric mean described here as a measure of each individual's overall size and general robusticity.

Statistical comparisons

Each of the six Pleistocene specimens was evaluated individually against the combined recent sample and the three recent subsamples for each masticatory variable (i.e., muscle PCSAs, lever arms, force magnitudes, and force ratios), using a modification of the standard two-tailed t-test given by Sokal and Rohlf (1981, p. 230). This test is designed for the comparison of a single observation with the mean of a sample:

$$t_s = \frac{Y_1 - \bar{Y}_2}{s_2 \sqrt{\dfrac{n_2 + 1}{n_2}}}$$

where Y_1 = Pleistocene specimen value; Y_2 = recent sample mean; s_2 = the recent sample standard de-

TABLE 2. Comparison of results with in vivo measurements: maximum molar and incisal bite force (Newtons)

Author(s)	n	Mean maximum molar Fb	Mean maximum incisal Fb
Homo sapiens			
Sinn et al., 1996	26	365	122
Dean et al., 1992	57	478	150
Tate et al., 1994	58	503	
Paphangkorakit and Osborn, 1997b	10		233
Kikuchi et al., 1997	4	585	265
van Spronsen et al., 1989	12	652	359
Braun et al., 1995	142	738	
Gay et al., 1994	10		39–392[1]
Waltimo et al., 1994	7	911	569
Pruim et al., 1980	7	965	
Waugh, 1937	105	1,235	
Present study	26	815	595
Pongo pygmaeus			
Lucas et al., 1994	3	≥2,000[2]	
Present study	2	1,650	

[1] Authors reported only a range of maximum incisal bite force.
[2] Estimate based on force required to fracture seeds broken in one bite.

viation; n_2 = the recent sample size; and the degrees of freedom for small sample size (<30) = $n_2 - 1$. With the small recent sample sizes used here, the power to detect a true difference $(1 - \beta)$ between each individual specimen and the comparative sample is low; however, rejection of the null hypothesis of equality should be viewed as a robust result. In this sense, the model provides a conservative measure of the biomechanical differences between the Pleistocene specimens and recent humans.

RESULTS

Model validation

We reconstructed several important masticatory variables (muscle force vectors, bite force direction, and lever arms) from the bony morphology. To evaluate the validity of our approach, the incisal and molar bite forces calculated for the recent combined sample were compared with experimental bite forces measured in vivo (Table 2). While our mean molar bite force value fell within the range of values reported in the literature, our mean incisal bite force did not. This is due primarily to our assumption of optimal muscular conditions for both bite positions; although electromyography (EMG) showed that activity is at or near peak in the masseter, temporalis, and medial pterygoid during maximum molar biting (Pruim et al., 1980), it is reduced from peak in all three muscles during incisal clenching (Møller, 1966; Vitti and Basmajian, 1977; Blanksma and van Eijden, 1990). Our bite force estimates should therefore be viewed as the *upper limit* of what each individual was actually capable of producing. Moreover, the presence of mechanoreceptors in the periodontal ligaments and the pulp cavity that serve to protect the dentition from damaging bite force levels is well-established (e.g., Hannam, 1969; Paphangkorakit

and Osborn, 1997a, 1998). Therefore, it is reasonable to expect our modeled bite force values to exceed actual recorded force values. Furthermore, with the exception of those reported by Waugh (1937), the bite-force values were produced by subjects who were unlikely to have engaged in excessive masticatory and/or paramasticatory behavior. In contrast, our recent human sample consisted primarily of individuals who undoubtedly engaged in both such behaviors. Given their well-developed masticatory systems, it is reasonable to expect the bite-force estimates of our sample to be higher than reported experimental values. This expectation is reinforced by the bite forces measured in Alaskan Eskimos (Waugh, 1937), a population for whom frequent, heavy use of the masticatory system is well-documented (Hylander, 1977). This intense use of their teeth and jaws is reflected in the rather large value for molar bite force shown in Table 2.

Also shown in Table 2 is the average bite force calculated for orangutans compared with an estimate derived in seed-cracking experiments. Lucas et al. (1994) measured the amount of force necessary to break seeds that they had observed orangutans breaking in a single bite; they took this as the lower limit on maximum bite force in orangutans. Although our model was designed specifically for the hominid masticatory system, when applied to a pongid it yielded a bite-force estimate that is only 18% lower than the experimental value. We take the model's predictive power within extant hominioids as further evidence for its predictive power, including fossil *Homo*. Despite our confidence in our approach, we nonetheless prefer to interpret our results in a relative rather than an absolute sense, and advise the reader to do so as well. Since each specimen was subject to the same assumptions and simplifications, the differences in values of muscle, bite, and condylar reaction force between specimens are of greater interest and meaning than the actual values themselves.

In total, 24 statistical comparisons were made for each masticatory variable (six Pleistocene specimens, and four comparative recent modern samples); for clarity, we limit our discussion to comparisons between each Pleistocene specimen and the recent combined sample (n = 26; hereafter referred to as "recent humans"). The molar biting analyses yielded results very similar to those of the incisal biting analyses. Therefore, we will not discuss posterior biting except to say that we observed no substantial deviations from the anterior biting patterns.

Estimated model inputs

Muscle-force magnitudes. With the exception of the masseter in Ohalo 2 and all three muscles in Fish Hoek, the muscle-force magnitudes of the Pleistocene specimens were larger than those of the recent humans (Table 3). This trend toward larger muscles was most pronounced in the medial ptery-

TABLE 3. Masticatory muscle force magnitudes (Newtons) compared with recent samples[1]

Masseter	Mean	s.d.	Min.	Max.	Amud 1 413	La Chapelle 458	La Ferrassie 1 382	Skhul 5 363	Ohalo 2 313	Fish Hoek 207
Females	325	36	256	370	>*	>**	>	>	<	<**
Males I	340	45	280	408	>	>*	>	>	<	<
Males II	241	40	186	282	>*	>*	>	>	>	<
Combined	319	52	186	408	>	>*	>	>	<	<
M. pterygoid	Mean	s.d.	Min.	Max.	Amud 1 444	La Chapelle 440	La Ferrassie 1 368	Skhul 5 504	Ohalo 2 431	Fish Hoek 226
Females	185	34	131	236	>***	>***	>***	>***	>***	>
Males I	286	70	193	399	>	>	>	>*	>	<
Males II	206	33	164	245	>**	>**	>*	>**	>**	>
Combined	231	70	131	399	>**	>**	>	>***	>**	<
Temporalis	Mean	s.d.	Min.	Max.	Amud 1 436	La Chapelle 452	La Ferrassie 1 509	Skhul 5 436	Ohalo 2 448	Fish Hoek 318
Females	360	34	318	434	>	>*	>**	>	>*	<
Males I	424	53	374	520	>	>	>	>	>	<
Males II	325	67	228	375	>	>	>	>	>	<
Combined	382	60	228	520	>	>	>*	>	>	<

[1] Recent human sample sizes for Tables 3–8 are: females, n = 11; males I, n = 11; males II, n = 4; and combined, n = 26; s.d., standard deviation; Max., maximum; Min., minimum.
* Significant at $P < 0.05$ without Bonferroni correction.
** Significant at $P < 0.01$.
*** Significant at $P < 0.001$ (with and without Bonferroni correction), based on modified t-test found in Sokal and Rohlf (1981).

TABLE 4. Lever arms (cm) of muscle forces and incisal bite force compared with recent samples[1]

Masseter	Mean	s.d.	Min.	Max.	Amud 1 3.76	La Chapelle 3.49	La Ferrassie 1 3.60	Skhul 5 3.63	Ohalo 2 4.08	Fish Hoek 3.26
Females	3.28	0.17	3.01	3.50	>*	>	>	>	>**	<
Males I	3.38	0.26	2.92	3.76	>	>	>	>	>*	<
Males II	3.38	0.21	3.07	3.51	>	>	>	>	>	<
Combined	3.34	0.21	2.92	3.76	>	>	>	>	>**	<
M. pterygoid	Mean	s.d.	Min.	Max.	Amud 1 3.82	La Chapelle 3.44	La Ferrassie 1 3.85	Skhul 5 3.46	Ohalo 2 3.38	Fish Hoek 3.15
Females	2.82	0.22	2.59	3.30	>**	>*	>**	>*	>	>
Males I	2.71	0.48	1.72	3.48	>	>	>*	>	>	>
Males II	3.34	0.23	3.14	3.68	>	>	>	>	>	<
Combined	2.86	0.41	1.72	3.68	>*	>	>*	>	>	>
Temporalis	Mean	s.d.	Min.	Max.	Amud 1 2.72	La Chapelle 2.21	La Ferrassie 1 2.99	Skhul 5 2.16	Ohalo 2 2.32	Fish Hoek 2.11
Females	2.21	0.20	1.85	2.54	>*	>	>**	>	>	<
Males I	2.16	0.24	1.76	2.54	>*	>	>**	>	>	<
Males II	2.01	0.24	1.73	2.21	>	>	>*	>	>	>
Combined	2.15	0.22	1.73	2.54	>*	>	>***	>	>	<
Bite force (I_2)	Mean	s.d.	Min.	Max.	Amud 1 10.50	La Chapelle 10.37	La Ferrassie 1 11.2	Skhul 5 9.11	Ohalo 2 8.78	Fish Hoek 7.92
Females	8.17	0.49	7.15	8.75	>**	>**	>***	>	>	<
Males I	8.10	0.55	7.28	9.10	>**	>**	>***	>	>	<
Males II	7.57	0.33	7.18	7.85	>**	>**	>**	>*	>*	>
Combined	8.05	0.53	7.15	9.10	>***	>***	>***	>	>	<

[1] Sample sizes and significance levels as in Table 3. Abbreviations as in Table 3.

goid: excepting Fish Hoek, the Pleistocene specimens had medial pterygoids roughly twice as powerful as those of recent humans. However, only the following differences were statistically significant: Amud 1, La Chapelle-aux-Saints, and Ohalo 2 all had significantly larger medial pterygoid force magnitude ($P < 0.01$), as did Skhul 5 ($P < 0.001$); La Chapelle-aux-Saints had significantly larger masseter force magnitude ($P < 0.05$); and La Ferrassie 1 had significantly larger temporalis force magnitude ($P < 0.05$).

Lever arms. Excluding Fish Hoek, which had only a longer medial pterygoid lever arm, all muscle force lever arms and incisal bite force lever arms were longer in the Pleistocene specimens than in the recent humans (Table 4). The differences in muscle force lever arm lengths were greatest for the medial

TABLE 5. Force production capability: force magnitudes (Newtons) compared with recent samples (left/right side summed)[1]

Fm	Mean	s.d.	Min.	Max.	Amud 1 2587	La Chapelle 2700	La Ferrassie 1 2516	Skhul 5 2606	Ohalo 2 2382	Fish Hoek 1500
Females	1,742	162	1,467	2,024	>***	>***	>***	>***	>***	<**
Males I	2,098	252	1,714	2,528	>	>*	>	>	>	<*
Males II	1,545	154	1,319	1,652	>**	>**	>*	>**	>**	<
Combined	1,862	293	1,319	2,528	>*	>**	>*	>*	>	<
Fb	**Mean**	**s.d.**	**Min.**	**Max.**	**Amud 1 790**	**La Chapelle 752**	**La Ferrassie 1 723**	**Skhul 5 826**	**Ohalo 2 791**	**Fish Hoek 481**
Females	552	68	440	678	>**	>*	>*	>**	>**	<
Males I	662	84	543	780	>	>	>	>	>	<
Males II	533	81	439	632	>	>	>	>*	>	<
Combined	595	94	439	780	>	>	>	>*	>	<
Fc	**Mean**	**s.d.**	**Min.**	**1,053**	**Amud 1 1385**	**La Chapelle 1479**	**La Ferrassie 1 1463**	**Skhul 5 1353**	**Ohalo 2 1039**	**Fish Hoek 692**
Females	945	89	756	1,053	>***	>***	>***	>**	>	<*
Males I	1,139	138	916	1,380	>	>*	>*	>	>	<*
Males II	738	89	645	857	>**	>**	>**	>**	>	<
Combined	995	180	645	1,380	>*	>*	>*	>	>	<

[1] Sample sizes and significance levels as in Table 3. Abbreviations as in Table 3.

TABLE 6. Force production efficiency: force ratios (%) in fossils compared with recent samples[1]

Fb/Fm × 100%	Mean	s.d.	Min.	Max.	Amud 1 30.5	La Chapelle 27.9	La Ferrassie 1 28.7	Skhul 5 31.7	Ohalo 2 33.2	Fish Hoek 32.1
Females	31.6	2.0	29.3	34.7	<	<	<	>	>	>
Males I	31.6	1.9	28.9	34.6	<	<	<	>	>	>
Males II	34.5	3.0	31.2	38.3	<	<	<	<	<	<
Combined	32.0	2.3	28.9	38.3	<	<	<	>	<	>
Fc/Fm × 100%	**Mean**	**s.d.**	**Min.**	**Max.**	**Amud 1 53.5**	**La Chapelle 54.8**	**La Ferrassie 1 58.1**	**Skhul 5 51.9**	**Ohalo 2 43.6**	**Fish Hoek 46.1**
Females	54.3	2.8	50.5	58.5	<	>	>	<	<**	<*
Males I	54.4	3.1	48.8	59.0	<	>	>	<	<**	<*
Males II	47.8	4.0	43.0	52.5	>	>	>	>	<	<
Combined	53.3	3.8	43.0	59.0	>	>	>	<	<*	<

[1] Sample sizes and significance levels as in Table 3. Abbreviations as in Table 3.

pterygoid, although significant only for Amud 1 and La Ferrassie 1 ($P < 0.05$). Other significant differences included Ohalo 2's longer masseter lever arm ($P < 0.01$), and the longer temporalis lever arm of Amud 1 ($P < 0.05$) and La Ferrassie 1 ($P < 0.001$). Overall, the differences in *incisal bite* force lever arm lengths relative to recent humans were more pronounced, especially for the Neandertals ($P < 0.001$ for all three). No other differences were statistically significant.

Force production capability

The magnitudes of total muscle force (Fm), total bite force (Fb), and total condylar reaction force (Fc) for bilateral incisal biting were substantially larger compared to the recent humans with the exception of Fish Hoek, which had uniformly smaller values (Table 5). However, while Amud 1, La Ferrassie 1, Skhul 5 ($P < 0.05$), and La Chapelle-aux-Saints ($P < 0.01$) all had significantly higher muscle-force magnitudes than the recent humans, only Skhul 5 was capable of generating a significantly higher bite force ($P < 0.05$). Further, only the Neandertals had

significantly larger condylar reaction forces ($P < 0.05$).

Force-production efficiency

Force ratios. Despite substantial differences in force magnitudes between the Pleistocene specimens and recent humans, only minor differences in force ratios were observed (Table 6). Collectively, the Neandertal sample exhibited a pattern of lower bite to muscle force ratios (Fb/Fm) and higher condylar reaction to muscle force ratios (Fc/Fm). They therefore appeared to be slightly less efficient at producing incisal bite force than the recent humans. Compared to Neandertals, Ohalo 2 and Fish Hoek had slightly higher bite to muscle force ratios (Fb/Fm) and lower condylar reaction to muscle force ratios (Fc/Fm) than the recent humans. This indicates that for an equal amount of muscle force, Ohalo 2 and Fish Hoek were able to generate slightly higher bite forces and slightly lower condylar reaction forces than recent humans, making them somewhat more efficient incisal biters overall. Finally, Skhul 5 exhibited a mixed pattern: both a lower bite to muscle

TABLE 7. Force production efficiency: muscle mechanical advantage (MA) compared with recent samples[1]

MA_{MASS}	Mean	s.d.	Min.	Max.	Amud 1 0.358	La Chapelle 0.336	La Ferrassie 1 0.321	Skhul 5 0.398	Ohalo 2 0.465	Fish Hoek 0.411
Females	0.403	0.024	0.359	0.425	<	<*	<**	<	>*	>
Males I	0.418	0.025	0.378	0.470	<*	<*	<**	<	>	<
Males II	0.447	0.029	0.414	0.484	<	<*	<*	<	>	<
Combined	0.416	0.028	0.359	0.484	<	<**	<**	<	>	<

MA_{MPT}	Mean	s.d.	Min.	Max.	Amud 1 0.364	La Chapelle 0.332	La Ferrassie 1 0.344	Skhul 5 0.380	Ohalo 2 0.384	Fish Hoek 0.398
Females	0.347	0.036	0.305	0.412	>	<	<	>	>	>
Males I	0.335	0.054	0.219	0.416	>	>	>	>	>	>
Males II	0.442	0.026	0.415	0.469	<	<*	<*	<	<	<
Combined	0.356	0.056	0.219	0.469	>	<	<	>	>	>

MA_{TEMP}	Mean	s.d.	Min.	Max.	Amud 1 0.259	La Chapelle 0.213	La Ferrassie 1 0.267	Skhul 5 0.237	Ohalo 2 0.264	Fish Hoek 0.267
Females	0.271	0.025	0.241	0.310	<	<	<	<	<	<
Males I	0.266	0.022	0.224	0.289	<	<*	>	<	<	<
Males II	0.266	0.037	0.220	0.307	<	<	>	<	<	<
Combined	0.268	0.024	0.220	0.310	<	<*	<	<	<	<

[1] Sample sizes and significance levels as in Table 3. Abbreviations as in Table 3.

force ratio (Fb/Fm), like the Neandertals, and a lower condylar reaction to muscle force ratio (Fc/Fm), like Ohalo 2 and Fish Hoek. We should emphasize that all differences with recent humans were minor, and only one reached statistical significance (Fc/Fm for Ohalo 2; $P < 0.05$).

Mechanical advantage. As with the force ratios, few differences in muscle mechanical advantages were statistically significant. Although lever arms in the Pleistocene specimens were generally longer than in the recent humans, in several instances the incisal bite force lever arm was disproportionately longer than a given muscle force lever arm. The mechanical advantage of such a muscle was therefore found to be smaller than that of the same muscle in recent humans (Table 7). This was the case for the masseter in Amud 1, La Chapelle-aux-Saints ($P < 0.01$), La Ferrassie 1 ($P < 0.01$), and Skhul 5; for the medial pterygoid in La Chapelle-aux-Saints and La Ferrassie 1; and for the temporalis in all Pleistocene specimens, although significant only for La Chapelle-aux-Saints ($P < 0.05$). The smaller values of mechanical advantage indicate that these muscles were less well-positioned for efficient incisal bite force production than in the recent humans. The larger values of mechanical advantage in the remaining cases (masseter in Ohalo 2 and Fish Hoek, and medial pterygoid in all specimens except La Chapelle-aux-Saints and La Ferrassie 1) indicate that these muscles were better-positioned than in the recent humans (not significant).

We can conclude that those individuals with uniformly smaller mechanical advantages, such as La Chapelle-aux-Saints and La Ferrassie 1, were less efficient producers of incisal bite force. The mechanical advantages of the remaining Pleistocene specimens are neither uniformly smaller nor uniformly larger. Therefore, we cannot make any definitive conclusions concerning their efficiency based solely on mechanical advantage.

Differential loading of the condyles

For unilateral incisal biting, the magnitudes of the working-side condylar reaction force ($Fc_{,WORK}$) and the balancing-side condylar reaction force ($Fc_{,BAL}$) were consistently larger in the Pleistocene specimens (again with the exception of Fish Hoek) than in the recent humans (Table 8). The differences were most pronounced in the Neandertals and Skhul 5: Amud 1, La Chapelle-aux-Saints, and La Ferrassie 1 had significantly larger working-side condylar reaction forces ($P < 0.05$), while Amud 1, La Chapelle-aux-Saints, and Skhul 5 had significantly larger balancing-side condylar reaction force ($P < 0.05$). In all specimens, both Pleistocene and recent, the balancing-side condylar reaction force was greater than the working-side condylar reaction force.

None of the differences in the ratio of working-side to balancing-side condylar reaction force ($Fc_{,WORK}/Fc_{,BAL}$) were statistically significant. The Neandertals and Fish Hoek did have slightly higher ratios than the recent humans (i.e., closer to unity), indicating that they were able to more evenly distribute the joint reaction force between the two condyles during nonsymmetric incisal biting. In contrast, the balancing-side condyle of Skhul 5 and Ohalo 2 sustained a larger portion of the total reaction force, as evidenced by their lower $Fc_{,WORK}/Fc_{,BAL}$ ratio.

Relationship of masticatory variables to overall size and robusticity

The distribution of overall size measured by the geometric mean for all specimens is shown in Figure 4. Not surprisingly, the Neandertals were among the largest, although the geometric mean of two

TABLE 8. Differential loading patterns of condyles in fossils compared with four recent samples[1]

$FC_{,WORK}$	Mean	s.d.	Min.	Max.	Amud 1 634	La Chapelle 663	La Ferrassie 1 621	Skhul 5 586	Ohalo 2 454	Fish Hoek 307
Females	420	39	345	460	>***	>***	>***	>**	>	<*
Males I	509	62	399	620	>	>*	>	>	<	<*
Males II	322	46	281	385	>**	>**	>**	>*	>	<
Combined	443	83	281	620	>*	>*	>*	>	>	<
$FC_{,BAL}$	Mean	s.d.	Min.	Max.	Amud 1 742	La Chapelle 782	La Ferrassie 1 732	Skhul 5 744	Ohalo 2 581	Fish Hoek 376
Females	516	51	411	593	>**	>***	>**	>**	>	<*
Males I	617	74	491	734	>	>	>	>	<	<*
Males II	412	40	364	462	>**	>**	>**	>**	>*	<
Combined	543	94	364	734	>*	>*	>	>**	>	<
$FC_{,WORK}/$ $FC_{,BAL}$ $\times 100\%$	Mean	s.d.	Min.	Max.	Amud 1 85.4	La Chapelle 84.8	La Ferrassie 1 84.8	Skhul 5 78.8	Ohalo 2 78.1	Fish Hoek 81.6
Females	81.3	2.6	75.8	84.7	>	>	>	<	<	>
Males I	82.6	2.3	79.8	87.6	>	>	>	<	<	<
Males II	78.0	4.2	73.0	83.3	>	>	>	>	>	<
Combined	81.3	3.1	73.0	87.6	>	>	>	<	<	>

[1] Sample sizes and significance levels as in Table 3. Abbreviations as in Table 3.
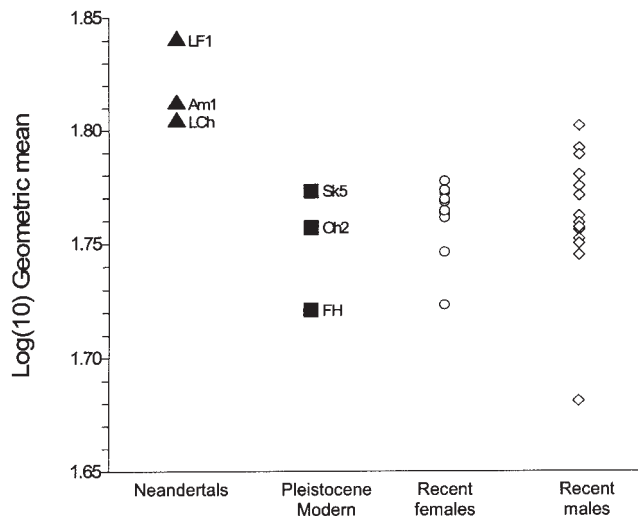
Fig. 4. Distribution of overall cranio-mandibular size as measured by geometric mean for all Pleistocene and recent human specimens. Geometric mean was calculated for each individual, using linear distances from porion to all 37 digitized points. Fossil hominid abbreviations as in Figure 5.

TABLE 9. Correlations between masticatory variables and geometric mean[1]

	r_s
Muscle-force magnitudes	
Masseter	0.815**
M. pterygoid	0.385*
Temporalis	0.656**
Lever arms	
Masseter	0.398*
M. pterygoid	0.244
Temporalis	0.503**
Bite force (I_2)	0.575**
Force-production capability	
Fm	0.702**
Fb	0.672**
Fc	0.725**
Force-production efficiency	
Fb/Fm	−0.164
Fc/Fm	0.235
MA_{MASS}	−0.318
MA_{MPT}	−0.191
MA_{TEMP}	0.039
Differential loading	
$Fc_{,WORK}$	0.688**
$Fc_{,BAL}$	0.717**
$Fc_{,WORK}/Fc_{,BAL}$	0.219

[1] Calculated from total sample (fossils and recent humans combined, n = 32), using Spearman's rank correlation.
* Significant at $P < 0.05$.
** Significant at $P < 0.01$.

recent specimens (one Ohlone male and the Australian Aboriginal male) approached that of La Chapelle-aux-Saints. As the largest specimen, La Ferrassie 1 was 44% larger in raw (i.e., unlogged) metric units than the smallest recent human (an Indian subcontinent male) and 31% larger than the smallest Pleistocene specimen (Fish Hoek). The early modern Skhul 5 specimen was approximately 10% smaller than the Neandertals and was virtually identical to the mean of the Recent Male I sample. The Ohlone females were comparatively quite large: Ohlone males averaged only 2% larger than the females, and Ohalo 2, considered to be a relatively large, robust male by Nadel and Hershkovitz (1991), was actually smaller than most Ohlone females. The

diminutive Fish Hoek specimen was smaller than all but one of the recent modern specimens (a very small and gracile Indian subcontinent male).

Correlations between each masticatory variable and overall size across our total sample (Pleistocene and recent hominids combined) are shown in Table 9. All force magnitudes were significantly correlated with overall size, as were muscle force magnitudes and all force lever arms except that of the medial pterygoid. In contrast, all force ratios and muscle mechanical advantages were statistically uncorre-

lated with overall size. In other words, force-production *capability* of the masticatory system scaled with increasing cranio-mandibular size, but force-production *efficiency* was maintained throughout the size range (Figs. 5, 6).

While measures of efficiency were statistically uncorrelated with overall size and robusticity across our sample, the signs of the correlations (i.e., regression slopes) in most cases suggest that efficiency and size/robusticity were inversely related (Fig. 6). That is, larger, more robust individuals appeared to be slightly less efficient than smaller, gracile hominids. Larger samples sizes might well result in statistical significance for this patterning; however, the relatively tighter coupling of force magnitudes with size/robusticity compared with efficiency measures is unlikely to change.

DISCUSSION

Model validity

In our model, we assumed that all three jaw elevators were maximally active during both bilateral and unilateral isometric incisal biting, that there were no regional differences of activation within each muscle, and that there was no antagonistic muscle activity. Electromyographic studies of the masticatory muscles show that this is generally not the case. During incisal clenching, activity in the masseter, medial pterygoid, and especially temporalis is reduced from peak (Møller, 1966; Vitti and Basmajian, 1977; Blanksma and van Eijden, 1990; Spencer, 1998); the lateral pterygoid is active (Hylander, 1992); and at least two functional portions are distinguishable in the temporalis and masseter (Blanksma and van Eijden, 1990). Furthermore, Hylander and Johnson (1985) and Ross and Hylander (2000) showed that differential muscle activity during incision occurs, with the superficial masseter exhibiting relatively higher activity than that found in the anterior temporalis. In addition, during unilateral biting, working-side muscle activity is typically greater than balancing-side (van Eijden et al., 1993). In the context of the present study, however, little would have been gained by reducing muscle forces to coincide with EMG patterns, since: the relationship between EMG activity and muscle force is tenuous; only substantial differences in muscle activation between the Pleistocene and recent comparative specimens might have changed our results, and there is no way to determine what such differences might be; and our goal was to estimate the upper bounds of potential bite force.

We also assumed that the muscle force vectors could be adequately estimated from cranial and mandibular measurements. The "straight-line" approach used here to determine muscle force direction and point of application from bony attachment areas is frequently used in biomechanical analyses (for masticatory biomechanics, see Pruim et al., 1980; Osborn and Baragar, 1985, 1992; Koolstra et
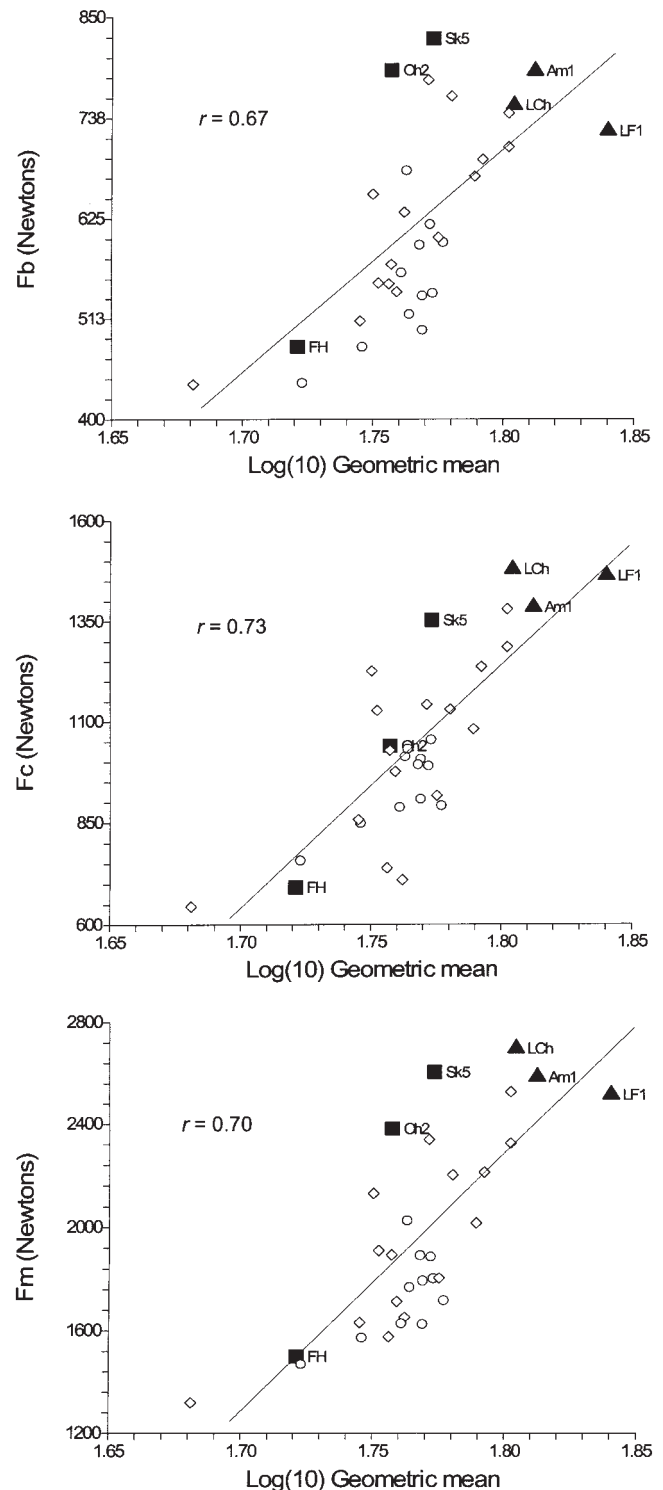

Fig. 5. Force magnitudes vs. overall size (geometric mean) for bilateral incisal biting. Magnitudes of bite force (Fb), condylar reaction force (Fc), and resultant muscle force (Fm) are plotted vs. geometric mean for each Pleistocene and recent modern specimen. Regression lines were obtained using least-squares. All force magnitudes were highly significantly correlated with overall size (*P* < 0.0001). Solid triangles, Neandertals; solid squares, Pleistocene modern; open circles, recent females; open diamonds, recent males. Sk5, Skhul 5; Oh2, Ohalo 2; FH, Fish Hoek; Am1, Amud 1; LCh, La Chapelle; LF1, La Ferassie 1.
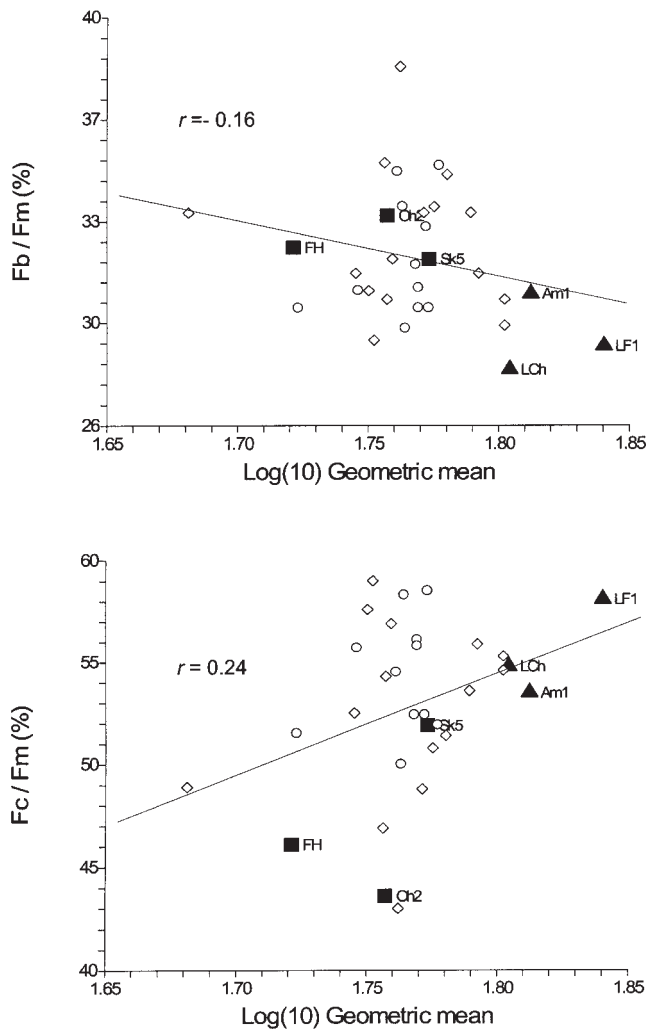
Fig. 6. Force ratios vs. overall size (geometric mean) for bilateral incisal biting. Ratio of bite-force magnitude to resultant muscle-force magnitude (Fb/Fm), and condylar reaction force magnitude to resultant muscle force magnitude (Fc/Fm), are plotted vs. geometric mean for each Pleistocene and recent modern specimen. Regression lines were obtained using least-squares. Neither force magnitude ratio was significantly correlated with overall size ($P = 0.3379$ and 0.2049, respectively), although weak trends toward inefficiency in larger specimen are indicated. Note that an efficient system maximizes bite force (i.e., high Fb/Fm) and minimizes condylar reaction force (i.e., low Fc/Fm). Symbol designations as in Figure 5. Fossil hominid abbreviations as in Figure 5.

al., 1988; Koolstra and van Eijden, 1995; Trainor et al., 1995; Osborn, 1996; for lower extremity biomechanics, see Brand et al., 1982; Herzog and Read, 1993; Glitsch and Baumann, 1997; for lumbar spine biomechanics, see McGill and Norman, 1986). Although functional units and other complexities are ignored by this approach, it provides a reliable first-order approximation of muscle-force direction and application point. Predicting muscle-force magnitude from bony morphology has proven more difficult (and controversial). Although the linear correlation between muscle-force magnitude and muscle PCSA during isometric contraction is well-estab-

lished (Weijs and Hillen, 1985b; Koolstra et al., 1988), the relationship between muscle PCSA and bony morphology is not. It is generally accepted that large, robust muscle scars reflect large muscles, but the precise nature of this relationship is not well-understood. This is especially true for multipennate muscles.

Antón (1994b, 1996b) investigated the extent to which bone proxies can predict masticatory muscle PCSA in modern humans and in several species of macaques. She found that bony measures of the temporalis, masseter, and medial pterygoid were only weakly correlated with their respective PCSAs. Antón (1994b, 1996b) therefore concluded that bone proxies are better suited for testing hypotheses related to relative rather than absolute force production, and that they should be used with care, particularly when applied to fossil remains. Given that our "raw PCSAs" were quite similar, although not identical, to those used in her studies, her cautionary remarks apply to the present study.

Because a reliable method for its measurement does not yet exist, deriving realistic values for muscle-force magnitude is a problem common to most biomechanical analyses. There are clearly additional difficulties when attempting to do so for fossil hominids. Cadaver studies can determine which skeletal measures, if any, predict muscle PCSA in recent humans, but will these same measures hold for fossils? Assuming they do, is the value of intrinsic muscle strength the same? And finally, are there differences in internal muscle architecture that may affect force production? Given the relatively close phylogenetic relationship between the archaic and modern humans used in the present study, the answer to the first two questions is most likely yes. In an attempt to answer the third question, Antón (1996a) examined the tendon-associated features of masticatory muscles in Neandertal and recent modern human crania. She found bony evidence that the anterior portion of the temporalis and the deep portion of the masseter were larger and more defined in Neandertals than in modern humans. Considering fiber orientation, which is predominantly vertical in the anterior temporalis and lateral in the deep masseter, our results can be reconciled with her findings: the vertical force component of temporalis and the lateral force component of masseter were proportionately larger in the Neandertals than in the recent humans.

Together with the generally good agreement of our results with published values of bite force (Table 2), we take this as evidence that our method captured the most important aspects of masticatory force production. We attribute this to: the use of multiple points, recorded with a three-dimensional digitizer, to establish each model parameter; the consideration of both the cranium and mandible in our analysis; and carrying out calculations in three dimensions. While these steps also served to minimize measurement and calculation error, we recog-

nize that the potential error associated with our estimation of muscle-force magnitude remains. This error can be mitigated, however, if the results concerning force-production capability are viewed in a relative framework. That is, since each specimen was subject to the same assumptions and simplifications, differences between specimens are primarily a reflection of true differences in force magnitudes rather than of methodology. Alternatively, this error can be completely eliminated if only muscle mechanical advantages are considered, although we feel valuable information is eliminated by doing so.

Discussion of results and comparison with previous studies

In the introduction, we posed four questions related to certain aspects of the ADLH. We will discuss the results of our study in the context of those questions and, when possible, compare our results with previous work.

Force-production capability

In contrast to the expectation set forth by the ADLH, our results indicate that Neandertals were not capable of generating significantly larger anterior dental loads compared with early modern and recent modern humans. In fact, the primary dichotomy in all measures of force-production capability was not between Neandertal and modern specimens, but rather between large, robust vs. small, gracile specimens. Estimates of incisal bite force, muscle force, and condylar reaction force magnitudes were very similar among the largest Pleistocene specimens, Skhul 5 and the Neandertals (Table 5; Figs. 5, 7). Further, several recent humans with comparably large geometric means had equally large force estimates. Most pertinent to the ADLH, the incisal bite force magnitude of all three Neandertals was exceeded by Skhul 5 and Ohalo 2 and, in the case of La Chapelle-aux-Saints and La Ferrassie 1, by several Ohlone males. Therefore, the assumption that Neandertals were generating exceptionally heavy anterior dental loads compared with both early modern and recent modern humans appears unwarranted. We note that Bonferroni corrections to the pairwise comparisons noted at the bottom of Tables 3–8 only serve to further minimize force magnitude and other differences between the Neandertals and the comparative sample, and that our discussion of uncorrected values (above) is thus actually conservative with respect to this question.

Our results for force-production capability do not agree completely with those of Antón (1990, 1994b). While our muscle force and condylar force estimates were similar to hers, our bite force estimate was 44% higher (Table 10). This difference results from two factors. First, Antón (1990, 1994b) combined the force vectors of the masseter and medial pterygoid, assuming the same lever arm for both. Second, she
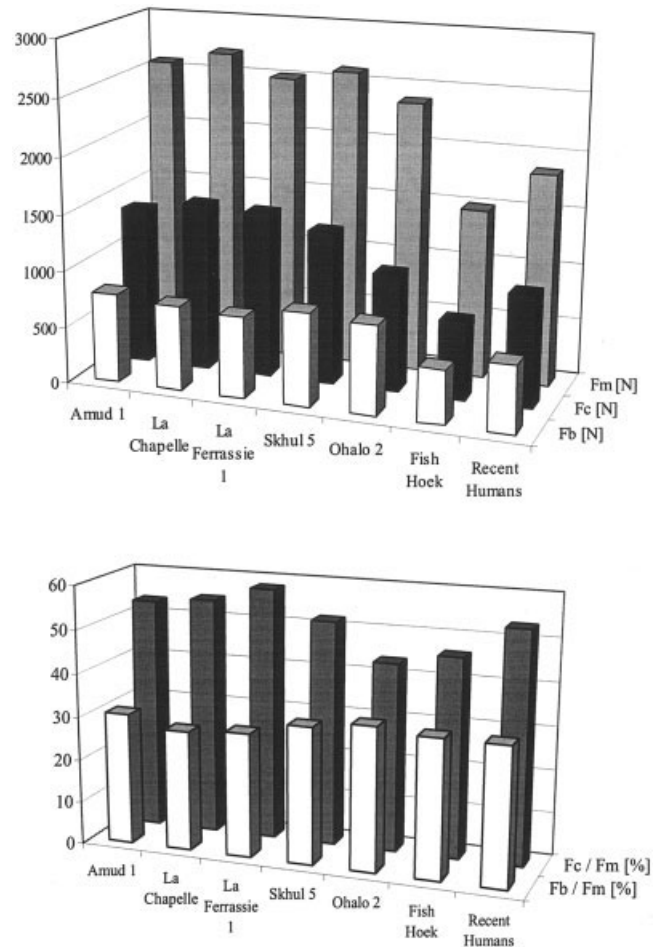

Fig. 7. Bar graph illustrating force magnitudes (top) and force ratios (bottom) for bilateral incisal biting for each Pleistocene individual and recent combined sample. Large values for muscle force resultant (Fm) and condylar reaction (Fc) forces are evident for Neandertals and Skhul 5. In contrast, Neandertal bite force values (Fb) are not remarkable. Bottom graph illustrates slightly lower values of force production efficiency (i.e., force ratios) for Neandertals.

moved the combined vector closer to the condyle without preserving its angular effect on the system. Both of these simplifications reduced the moment generated by the masseter and medial pterygoid about the condyle, resulting in artificially low values of bite force (and higher values of condylar reaction force). The net effect is disproportionately greater in Neandertals than in recent humans due to the magnitude of lever arms in these muscles. This study does not support the low Fb found for Amud 1 by Antón (1990, 1994b); however, it should be noted that this fossil is still modeled here as producing less bite force per muscle force (Table 6) than our modern sample and a relatively large amount of condylar reaction force. Thus, her conclusion that Neandertal facial architecture may not be a result of high-magnitude occlusal loads is supported here by our enhanced dataset, although the increased comparative sample size suggests there is less difference in efficiency than she suggested (see below).

TABLE 10. Comparison of results for Neandertals with previous work

	Force-production capability (Newtons)		
	Fm	Fc	Fb
Anton (1990, 1994b)[1] (n = 1)	2,240	1,500	550
Present study[2] (n = 1)	2,587	1,385	790
% difference	+15%	−8%	+44%

	Force-production efficiency	
	Fb/Fm	Fc/Fm
Anton (1990, 1994b)[1] (n = 1)	0.245	0.670
Present study[2] (n = 1)	0.305	0.535
% difference	+6%	−14%

	MA_{MASS}	MA_{MPT}	MA_{TEMP}
Spencer and Demes (1993)[3] (n = 8)	0.626	0.456	0.461
Present study[4] (n = 3)	0.338	0.347	0.246
% difference	−29%	−11%	−22%

[1] Amud 1 only; Fm was recalculated from results of Anton (1990, 1994b) to correspond with our definition (i.e., sum of muscle force magnitudes rather than magnitude of their vector sum).
[2] Amud 1 only.
[3] Average of Amud 1, La Chapelle 2, La Ferrassie 1, Monte Circeo 1, Saccopastore 1, Gibraltar 1, Tabun C1, and Shanidar 1.
[4] Average of Amud 1, La Chapelle 2, and La Ferrassie 1.

Force-production efficiency

We found that Neandertals were neither considerably more nor less efficient at generating anterior dental loads compared with early modern and recent modern humans. In fact, our results suggest that the masticatory system in the genus *Homo* scales such that force-production efficiency is maintained across a considerable range of size and robusticity. While muscle, bite, and condylar reaction force magnitudes increased predictably with the geometric mean, the ratios of these force magnitudes remained relatively constant (Table 9; Figs. 6, 7). Similarly, muscle and bite force lever arms were positively correlated with the geometric mean, but the ratios of the two, or muscle mechanical advantages, were not (Table 9).

There was a trend, although not statistically significant, toward decreasing efficiency with increasing size (Table 9; Fig. 6). Interestingly, Hylander (1985) observed that body-size increase in macaques is associated with a decreased ability to generate masticatory muscle force and an increased level of recruitment of balancing-side muscle force. Subsequent studies (Hylander et al., 1998, 2000), however, did not find this size relationship. Nonetheless, given the rather prognathic lower faces and consequently long bite force lever arms of the larger Pleistocene individuals in our study, this trend for decreased efficiency with larger overall facial size is not unexpected. We propose that their substantial medial pterygoids compensated for their increased prognathism, thereby allowing them to operate with a similar efficiency as the less prognathic specimens. This interpretation is supported by the work of Weijs and Hillen (1986), who found that the cross-sectional area of medial pterygoids in recent humans was most strongly correlated with measures of mandibular length. This also underscores the importance of considering muscle size as well as muscle leverage; an increase in the former can compensate for a decrease in the latter.

Considering the differences in force magnitudes, our force ratios for Amud 1 differed predictably from those of Antón (1990, 1994b) (Table 10). Because our bite force estimate was considerably higher than hers, our bite to muscle force ratio (Fb/Fm) was also higher. Similarly, because our condylar reaction force estimate was lower, so too was our condylar reaction to muscle force ratio (Fc/Fm). Amud 1 appeared considerably more efficient at incisal biting in the present analysis than in the previous, for the same reasons given above.

A comparison of our estimates of muscle mechanical advantage (MA) with those of Spencer and Demes (1993) reveals two important differences (Table 10). First, our values are considerably smaller. Second, while Spencer and Demes (1993) found the masseter to have a considerably larger MA than the temporalis and medial pterygoid, we instead found the medial pterygoid and masseter to have a comparable MA (both larger than the temporalis MA). These differences do not result from differences in the biomechanical models used. To borrow terminology from Spencer (1998), we employed an "unconstrained" lever model of mastication, whereas Spencer and Demes (1993) employed a "constrained" lever model. Briefly, the former places no restrictions on muscle activity, whereas the latter assumes that there is a zone in which balancing-side muscle activity must decrease as the bite point moves posteriorly (for a detailed description of this model, see Spencer and Demes, 1993; Spencer, 1998). However, as this zone corresponds roughly to the molar region, there is essentially no difference between the two models for incisal biting; neither predicts the experimentally observed reduction in muscle activity for anterior biting. We feel that the differences in MA values are instead due to the use by Spencer and Demes (1993) of anteroposterior muscle position rather than muscle lever arm to calculate MA; geometry informs us that the former will always be greater than the latter.[3] Further, they used only one point, the anteriormost cranial attachment point, to assess muscle position; in essence, they characterized the leverage of each muscle by the cranial position of its anteriormost fiber. In contrast, we used the line-of-action of a centroidal fiber to characterize muscle leverage, an approach that accounts for muscle origin, insertion, and distribution.

---

[3] The anteroposterior muscle position, muscle lever arm, and muscle line-of-action form a right triangle, with anteroposterior muscle position as the hypotenuse (Fig. 2).

Despite the differences in absolute values of MA, we find several points of agreement with Spencer and Demes (1993). Their results, like ours, showed that the temporalis and masseter operated less efficiently in Neandertals than in recent humans during incisal biting, while the medial pterygoid operated with nearly the same efficiency. Measures of overall system efficiency (i.e., unweighted and weighted averages of muscle MA) were also lower in Neandertals than in recent humans. Compared with early *Homo*, however, they found Neandertals to have slightly larger values of MA for all three muscles. Because Spencer and Demes (1993) did not evaluate overall size, we can only speculate that this slight increase in efficiency may be related to a modest decrease in overall craniofacial size from early *Homo* to Neandertals (Trinkaus, 1987, 2003; Franciscus, 1995; Franciscus and Trinkaus, 1995). Our differing conclusions regarding the ADLH result primarily from the difference in our comparative samples.

Differential loading patterns of the condyles

As expected, the balancing-side condyle was more heavily loaded than the working-side in all specimens during nonsymmetric biting. As evidenced by the ratio of the two reaction forces (Table 8), this differential loading was the least pronounced in Neandertals. That is, the total condylar reaction force was more evenly distributed between the two condyles in Neandertals than in early modern or recent modern humans, due to their relatively wider intercondylar distance. The fact that intercondylar distance affects the load distribution on the condyles (with relatively wide intercondylar distance being advantageous) is consistent with observations by Hylander (1975, 1977) in humans, and Smith (1978) across anthropoids. Osborn (1996), using a linear programming model to study how changes in the mandible affect unilateral maximum bite forces, also found that increased intercondylar distance resulted in more evenly distributed loads between the two condyles. Because the ratio of the distance between the incisors to distance between the condyles is relatively small in Neandertals, the nonsymmetric biting case approaches the symmetric biting case, in which the left- and right-side condylar reaction forces must be equal. Because condylar reaction forces were typically high in Neandertals (Table 5), this may have prevented the balancing-side condyle from being overloaded during unilateral biting.

It should be noted that the large intercondylar distance in Neandertals is functionally and developmentally related to their wide cranial bases, the latter a symplesiomorphy shared with earlier *Homo*. In light of the above, it is possible that Neandertal cranial base and intercondylar widths, in particular, may have been mechanically constrained to a greater degree than other aspects of their more derived craniofacial morphology.

Craniofacial size and implications for the ADLH

It is not difficult to accept that some Neandertal features are, at least in part, related to masticatory biomechanics. The difficulty comes in describing precisely which specific features these are, and what specific aspect(s) of masticatory biomechanics they may be related to. Perhaps to avoid this difficulty, the ADLH has historically been set forth in rather broad terms: force generation, force dissipation, high-magnitude loading, and repetitive loading have all been implicated (often simultaneously) in Neandertal facial architecture. We feel more precise language is required, since each of these aspects of masticatory biomechanics requires a different biomechanical model and/or approach in order to be properly examined, and each may have resulted in different adaptive responses. Force generation can be treated with rigid body mechanics (e.g., the present study; Antón, 1990, 1994b; Spencer and Demes, 1993), while force dissipation must be treated with deformable body mechanics. This can be done computationally using finite element analysis or experimentally using in vivo and in vitro strain gages (Hylander et al., 1991; Hylander and Johnson, 1997). High-magnitude loading can be examined with either rigid or deformable body mechanics, depending on whether the ability to generate loads or the ability to dissipate loads is at issue. Repetitive loading requires a more complicated approach; finite-element models that incorporate bone-remodeling algorithms were able to clarify the tissue response to cyclical loads (Beaupré et al., 1990a,b), but this represents adaptations in an individual through developmental plasticity rather than evolutionary adaptations in a lineage. Given the multiple interpretations of the ADLH, we do not (indeed cannot) fully reject it on the basis of this study.

We do, however, challenge the direct association of high-magnitude anterior dental loads and Neandertal facial architecture. The amount of incisal bite force the Neandertals were able to generate under optimal muscular conditions was not significantly greater than that generated by recent humans, and was approximately equal to that generated by Skhul 5 and Ohalo 2. Nor did the Neandertals appear considerably more (or less) efficient at generating anterior dental loads; because their muscle positions were not particularly mechanically advantageous, their increased muscle size appeared only to maintain, rather than improve, force-production efficiency. Studies that investigated the relationship between bite force and craniofacial morphology in recent humans (Waltimo et al., 1994; Tuxen et al., 1999; Raadsheer et al., 1999) demonstrated that facial features typically associated with high bite forces (e.g., reduced facial height) are, in fact, not those that characterize Neandertal facial morphology. Further, several studies showed that overall craniofacial size has a greater influence on bite force than individual features (Raadsheer et al., 1996,

1999), and the fact that large bite forces are produced by large (not necessarily high) faces is consistent with our results.

Given the relationship between overall size and bite force production documented here, and the slight decrease in Neandertal facial size relative to Middle Pleistocene hominids (Franciscus, 1995; Franciscus and Trinkaus, 1995; Trinkaus, 2003), we argue that Neandertals likely also underwent a modest decrease in force production relative to their Middle Pleistocene precursors. If this same relationship between masticatory forces and overall size exists for Middle Pleistocene hominids as it does across the wide range of variation exhibited by Neandertals, early modern humans, and recent humans, an evolutionary trend toward a *decrease* in generated masticatory forces should be expected from the Middle to Late Pleistocene.

Although we did not specifically examine the issue of force dissipation, we are of the opinion that if Neandertals were not generating exceptionally heavy anterior dental loads, then it is unlikely that certain of their features were adaptations to dissipate them. We instead feel that at least some of their features (e.g., lateral condylar tubercles) may represent adaptations to dissipate muscle and condylar reaction forces, which *were* exceptionally heavy.

The absence of significantly higher levels of anterior bite force among Neandertals indicates that increased dental attrition on the anterior teeth is more likely a result of repetitive use. This could occur either as the result of repetitive vertical occlusal forces at low loads, which can have a large effect on bone remodeling (Lanyon and Rubin, 1984), or more obliquely oriented wear that induces incisor beveling (Ungar et al., 1997). Selection for larger anterior tooth dimensions to resist such low and more frequent forces, and the associated attrition, may have also been an important factor in Neandertal facial morphology, rather than dissipation of high anterior tooth loads. Larger incisor crowns are significantly correlated with larger roots, periodontal ligaments, and vertical alveolar bone dimensions in Neandertals and recent humans (Smith and Paquette, 1989). Thus larger faces may simply result from the need to maintain large anterior teeth. It is noteworthy in this regard that while robust australopithecines appeared to have been capable of producing exceptionally high molar bite forces relative to other Plio-Pleistocene hominids and extant hominoids, bite force per unit molar crown area is roughly isometric across all extant and extinct hominoids (Demes and Creel, 1988). The higher bite forces estimated for robust australopithecines were necessary for force equivalency across much larger molar crown areas, the latter likely related to resisting high enamel attrition and processing a higher-volume, low-quality diet. In both of these cases, selection on crown size seems primary, with scaled bite-force production following as a secondary accommodation.

The results of this analysis may help explain the unique muscle-scarring patterns found among Neandertals. Muscle-scarring patterns observed by Antón (1996a) reveal that Neandertals exhibit a higher frequency of postorbital ridging as opposed to tubercles that mark modern humans. Her results, coupled with the nonsignificantly different values for temporalis forces found in this study, may indicate functional differences for the anterior region of the Neandertal temporalis. Furthermore, the relatively high forces generated by the medial pterygoid muscle documented here may, in part, explain the unique morphology of the medial aspect of the Neandertal mandibular ramus. Although there is considerable debate with regard to the medial pterygoid tubercle as a Neandertal autapomorphy (e.g., Rak et al., 1994; Creed-Miles et al., 1996; Richards et al., 2003), the force generated by the Neandertal medial pterygoid may result in the unique *complex* of features including gonial inversion and truncation, and a higher frequency of the medial pterygoid tubercle. We stress, however, that such alterations are best seen as accommodative responses to maintain functional levels of force and efficiency, and not as indicators of enhanced biomechanical capacity.

If biomechanics do not underlie variation in the facial skeleton in later Pleistocene *Homo* to the degree previously argued, then this lessens one important aspect of environmental influence on facial architecture. This, in turn, lends increased credibility to using facial traits for phylogenetic analysis. Whether this argument can be extended to other periods of hominid evolution remains to be seen. In early Plio-Pleistocene hominids, craniofacial homoplasies may indeed be due to the commonality of postcanine megadontia and masticatory functional convergence (McHenry, 1996). We suggest, however, that the methods employed in the present analysis might fruitfully be extended to specimens from this time period to more fully test this idea. With respect to later Pleistocene *Homo*, we conclude that masticatory biomechanical adaptation is not the primary factor underlying the evolution of Neandertal facial architecture, and that continued exploration of alternative factors (i.e., climatic, respiratory, and especially developmental and/or stochastic mechanisms) seems warranted.

ACKNOWLEDGMENTS

LITERATURE CITED

Antón SC. 1990. Neandertals and the anterior dental loading hypothesis: a biomechanical evaluation of bite force production. Kroeber Anthropol Soc Pap 71–72:67–76.

Antón SC. 1994a. Mechanical and other perspectives on Neandertal craniofacial morphology. In: Corruccini RS, Ciochon RL, editors. Integrative paths to the past. Englewood Cliffs: Prentice Hall. p 677–695.

Antón SC. 1994b. Masticatory muscle architecture and bone morphology in primates. Ph.D. thesis, University of California (Berkeley).

Antón SC. 1996a. Tendon-associated bone features of the masticatory system in Neandertals. J Hum Evol 31:391–408.

Antón SC. 1996b. Cranial adaptation to high attrition diet in Japanese macaques. Int J Primatol 17:401–427.

Baragar FA, Osborn JW. 1987. Efficiency as a predictor of human jaw design in the sagittal plane. J Biomech 20:447–457.

Beaupré GS, Orr TE, Carter DR. 1990a. An approach for time-dependent bone modeling and remodeling—theoretical development. J Orthop Res 8:651–661.

Beaupré GS, Orr TE, Carter DR. 1990b. An approach for time-dependent bone modeling and remodeling-application: a preliminary remodeling simulation. J Orthop Res 8:662–670.

Blanksma NG, van Eijden TMGJ. 1990. Electromyographic heterogeneity in the human temporalis muscle. J Dent Res 69:1686–1690.

Brace CL. 1962. Cultural factors in the evolution of the human dentition. In: Ashley Montagu MF, editor. Culture and the evolution of man. New York: Oxford. p 343–354.

Brace CL. 1963. Structural reduction in human evolution. Am Nat 97:39–49.

Brace CL. 1995. Biocultural interaction and the mechanism of mosaic evolution in the emergence of "modern" morphology. Am Anthropol 97:711–721.

Brace CL, Ryan AS, Smith BH. 1981. Comment on: "Tooth wear in La Ferrassie man." Curr Anthropol 22:426–430.

Brand RA, Crowninshield RD, Wittstock CE, Pedersen DR, Clark CR, van Krieken FM. 1982. A model of lower extremity muscular anatomy. J Biomech Eng 104:304–310.

Braun S, Bantleon HP, Hnat WP, Freudenthaler JW, Marcotte MR, Johnson BE. 1995. A study of bite force, part 1: relationship to various physical characteristics. Angle Orthod 65:397–372.

Brothwell DR. 1975. Adaptive growth rate changes as a possible explanation for the distinctiveness of the Neanderthalers. J Archaeol Sci 2:161–163.

Coberly MB. 1973. The archaeology of the Ryan Mound, site Ala-329, a central California village site. University of Northern Colorado, Museum of Anthropology occasional publications in anthropology, archaeology series 4. Greenley: University of Northern Colorado.

Coon CS. 1962. The origin of races. New York: Knopf.

Couture C. 1993. Changements de position du massif facial et de l'articulation temporomandibulaire dans la lignée néandertalienne. Organisation crânio-maxillo-faciale des néandertaliennes. C R Acad Sci [II] 316:1627–1633.

Creed-Miles M, Rosas A, Kruszynski R. 1996. Issues in the identification of Neandertal derivative traits at early post-natal stages. J Hum Evol 30:147–153.

Dean JS, Throckmorton GS, Ellis E, Sinn DP. 1992. A preliminary study of maximum voluntary bite force in pre-orthognathic surgery patients. J Oral Maxillofac Surg 50:2395–1288.

Demes B. 1987. Another look at an old face: biomechanics of the Neandertal facial skeleton reconsidered. J Hum Evol 16:297–303.

Demes B, Creel N. 1988. Bite force, diet, and cranial morphology of fossil hominids. J Hum Evol 17:657–670.

Franciscus RG. 1995. Later Pleistocene nasofacial variation in western Eurasia and Africa and modern human origins. Ph.D. thesis, University of New Mexico.

Franciscus RG. 1999. Neandertal nasal structures and upper respiratory tract "specialization." Proc Natl Acad Sci USA 96:1805–1809.

Franciscus RG. 2003. Internal nasal floor configuration in *Homo* with special reference to the evolution of Neandertal facial form. J Hum Evol 44:701–729.

Franciscus RG, Trinkaus E. 1988. The Neandertal nose. Am J Phys Anthropol 75:209–210 [abstract].

Franciscus RG, Trinkaus E. 1995. Determinants of retromolar space presence in Pleistocene *Homo* mandibles. J Hum Evol 28:577–595.

Gay T, Rendell J, Majoureau A, Maloney FT. 1994 Estimating human incisal bite forces from the electromyogram/bite-force function. Arch Oral Biol 39:111–115.

Glitsch U, Baumann W. 1997. The three-dimensional determination of internal loads in the lower extremity. J Biomech 30:1123–1131.

Greaves WS. 1978. The jaw lever system in ungulates: a new model. J Zool (Lond) 184:271–285.

Grün R, Stringer CB. 1991. Electron spin resonance dating and the evolution of modern humans. Achaeom 33:153–199.

Hannam AG. 1969. The response of periodontal mechanoreceptors in the dog to controlled loading of the teeth. Arch Oral Biol 14:781–791.

Hannam AG, Wood WW. 1989. Relationships between the size and spatial morphology of human masseter and medial pterygoid muscles, the craniofacial skeleton, and jaw biomechanics. Am J Phys Anthropol 80:429–445.

Haxton HA. 1944. Absolute muscle force in the ankle flexors of man. J Physiol 103:267–273.

Heim J-L. 1976. Les hommes fossiles de La Ferrassie I: le gisement. Les squelettes adultes (crâne et squellete du tronc). Arch Inst Paleontol Hum [Lond] 35:1–331.

Herzog W, Read LJ. 1993. Lines of action and moment arms of the major force-carrying structures crossing the human knee joint. J Anat 182:213–230.

Hettinger T. 1961. Physiology of strength. Springfield, IL: Charles C. Thomas.

Hiiemae K. 1971. The structure and function of the aw muscles in the rat (*Rattus norvegicus* L.) III. The mechanics of the muscles. Zool J Linn Soc 50:111–132.

Howell FC. 1951. The place of Neanderthal man in human evolution. Am J Phys Anthropol 9:379–416.

Howell FC. 1952. Pleistocene glacial ecology and the evolution of "classic Neandertal" man. Southwest J Anthropol 8:377–410.

Hublin J-J. 1990. Le peuplements paléolithiques de l'Europe: un point de vue paléobiogéographique. Mem Mus Prehist France 3:29–37.

Hublin J-J. 1998. Climatic changes, paleogeography, and the evolution of the Neandertals. In: Akazawa T, Aoki K, Bar-Yosef O, editors. Neandertals and modern humans in western Asia. New York: Plenum Press. p 295–310.

Hublin J-J. 2000. Modern-nonmodern hominid interactions: a Mediterranean perspective. In: Bar-Yosef O, Pilbeam D, editors. The geography of Neandertals and modern humans in Europe and the greater Mediterranean. Peabody Museum bulletin 8. Cambridge, MA: Harvard University Press. p 157–182.

Hylander WL. 1975. The human mandible: lever or link? Am J Phys Anthropol 43:227–242.

Hylander WL. 1977. The adaptive significance of Eskimo cranio-facial morphology. In: Dahlberg AA, Graber TM, editors. Oral-facial growth and development. The Hague: Mouton. p 129–170.

Hylander WL. 1978. Incisal bite force direction in humans and the functional significance of mammalian mandibular translation. Am J Phys Anthropol 48:1–7.

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

Hylander WL. 1992. Functional anatomy. In: Sarnat BG, Laskin DM, editors. The temporomandibular joint: a biological basis for clinical practice, 4th ed. Philadelphia: W.B. Saunders. p 60–89.

Hylander WL, Johnson KR. 1985. Temporalis and masseter function in humans and macaques during incision. Int J Primatol 6:286–322.

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

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

Hylander WL, Ravosa MJ, Ross CF, Johnson KR. 1998. Mandibular corpus strain in primates: Further evidence for a functional link between symphyseal fusion and jaw-adductor muscle force. Am J Phys Anthrpol 107:257–271.

Hylander WL, Ravosa MJ, Ross CF, Wall CE, Johnson KR. 2000. Symphseal fusion and jaw-adductor muscle force: An EMG study. Am J Phys Anthropol 112:469–492.

Jensen RH, Davy DT. 1975. An investigation of muscle lines of action about the hip: a centroid line approach vs. the straight line approach. J Biomech 8:103–110.

Jurmain RD. 1990. Palelepidemiology of a central California prehistoric population from CA-Ala-329: dental disease. Am J Phys Anthropol 81:333–342.

Kikuchi M, Korioth TWP, Hannam AG. 1997. The association among occlusal contacts, clenching effort, and bite force distribution in man. J Dent Res 76:1316–1325.

Koolstra JH, van Eijden TM. 1995. Biomechanical analysis of jaw-closing movements. J Dent Res 74:1564–1570.

Koolstra JH, van Eijden TM, Weijs WA, Naeije M. 1988. A three-dimensional mathematical model of the human masticatory system predicting maximum possible bite forces. J Biomech 21:563–576.

Lahr MM. 1996. The evolution of modern human diversity: a study of cranial variation. Cambridge: Cambridge University Press.

Lahr MM, Wright RVS. 1996. The question of robusticity and the relationship between cranial size and shape in *Homo sapiens*. J Hum Evol 31:157–191.

Lanyon LE, Rubin CT. 1984. Static vs. dynamic loads as an influence on bone remodelling. J Biomech 17:897–905.

Larsen CS. 1985. Dental modification and tool use in the western Great Basin. Am J Phys Anthropol 67:393–402.

Lucas PW, Peters CR, Arrandale SR. 1994. Seed-breaking forces exerted by orang-utans with their teeth in captivity and a new technique for estimating forces produced in the wild. Am J Phys Anthropol 94:365–378.

Maughan RJ, Watson JS, Weir J. 1983. Strength and cross-sectional area of human skeletal muscle. J Physiol [Lond] 338:37–49.

McGill SM, Norman RW. 1986. Partitioning of the L4–L5 dynamic moment into disc, ligamentous, and muscular components during lifting. Spine 11:666–678.

McHenry HM. 1996. Homoplasy, clades, and hominid phylogeny. In: Meikle WE, Howell FC, Jablonski NG, editors. Contemporary issues in human evolution. San Francisco: California Academy of Sciences. p 77–92.

Mercier N, Valladas H, Bar-Yosef O, Vandermeersch B, Stringer CB, Joron JL. 1993. Thermoluminescence date for the Mousterian burial site of es-Skhul, Mt. Carmel. J Archaeol Sci 20:169–174.

Møller E. 1966. The chewing apparatus. An electromyographic study of the action of the muscles of mastication and its correlation to facial morphology. Acta Physiol Scand 69 [Suppl 280]:1–229.

Molnar S. 1972. Tooth wear and culture: a survey of tooth function among some prehistoric populations. Curr Anthropol 13:511–526.

Moratto MJ. 1984. California archaeology. Orlando: Academic Press.

Nadel D, Hershkovitz I. 1991. New subsistence data and human remains from the earliest Levantine Epipaleolithic. Curr Anthropol 32:631–635.

Nadel D, Carmi I, Segal D. 1995. Radiocarbon dating of Ohalo II: archaeological and methodological implications. J Archaeol Sci 22:811–822.

Nygaard E, Houston M, Suzuki Y, Jorgensen K, Saltin B. 1983. Morphology of the brachial biceps muscle and elbow flexion in man. Acta Physiol Scand 117:287–292.

Osborn JW. 1996. Features of human jaw design which maximize the bite force. J Biomech 29:589–595.

Osborn JW, Baragar FA. 1985. Predicted pattern of human muscle activity during clenching derived from a computer assisted model: symmetric vertical bite forces. J Biomech 18:599–612.

Osborn JW, Baragar FA. 1992. Predicted and observed shapes of human mandibular condyles. J Biomech 25:967–974.

Paphangkorakit J, Osborn JW. 1997a. The effect of pressure on a maximal incisal bite force in man. Arch Oral Biol 42:11–17.

Paphangkorakit J, Osborn JW. 1997b. Effect of jaw opening on the direction and the magnitude of human bite force. J Dent Res 76:561–567.

Paphangkorakit J, Osborn JW. 1998. Effects of human maximum bite force of biting on a softer or harder object. Arch Oral Biol 43:833–839.

Pitman MI, Peterson L. 1989. Biomechanics of skeletal muscle. In: Nordin M, Frankel VH, editors. Basic biomechanics of the musculoskeletal system. Philadelphia: Lea & Febiger. p 89–111.

Ponce de León MS, Zollikofer CPE. 2001. Neanderthal cranial ontogeny and its implications for late hominid diversity. Nature 412:534–538.

Pruim GJ, de Jongh HJ, ten Bosch JJ. 1980. Forces acting on the mandible during bilateral static bite at different bite force levels. J Biomech 13:755–763.

Raadsheer MC, Kiliaridis S, Van Eijden TM, Van Ginkel FC, Prahl-Anderson B. 1996. Masseter muscle thickness in growing individuals and its relation to facial morphology. Arch Oral Biol 41:323–332.

Raadsheer MC, Van Eijden TM, Van Ginkel FC, Prahl-Anderson B. 1999. Contributions of jaw muscle size and craniofacial morphology to human bite force magnitude. J Dent Res 78:31–42.

Rak Y. 1986. The Neanderthal: a new look at an old face. J Hum Evol 15:151–164.

Rak Y, Hylander WL. 2003. Neanderthal facial morphology and increased jaw gape. Am J Phys Anthropol [Suppl] 36:174.

Rak Y, Kimble WH, Hovers E. 1994. A Neandertal infant from Amud Cave, Israel. J Hum Evol 26:313–324.

Richards GD, Jabbour RS, Anderson JY. 2003. Medial mandibular ramus. Ontogenetic, idiosyncratic, and geographic variation in recent *Homo*, great apes, and fossil hominids. BAR Int Ser 1138:1–113.

Ross CF, Hylander WL. 2000. Electromyography of the anterior temporalis and masseter muscles of owl monkeys (*Aotus trivirgatus*) and the function of the postorbital septum. Am J Phys Anthropol 112:455–468.

Schulz P. 1977. Task activity and anterior grooving in prehistoric California Indians. Am J Phys Anthropol 46:87–92.

Sergi S. 1962. The Neanderthal Palaeanthropi in Italy. In: Howells WW, editor. Ideas on human evolution: selected essays, 1949–1961. Cambridge, MA: Harvard University Press. p 500–506.

Sinn DP, De Assis E, Throckmorton GS. 1996. Mandibular excursions and maximum bite forces in patients with temporomandibular joint disorders. J Oral Maxillofac Surg 54:671–680.

Smith RJ. 1978. Mandibular biomechanics and temporomandibular joint function in primates. Am J Phys Anthropol 49:341–350.

Smith FH. 1983. Behavioral interpretations of changes in craniofacial morphology across the archaic/modern *Homo sapiens* transition. BAR Int Ser 164:137–209.

Smith FH. 1985. Continuity and change in the origin of modern *Homo sapiens*. Z Morphol Anthropol 75:197–222.

Smith FH. 1991. The Neandertals: evolutionary dead ends or ancestors of modern people? J Anthropol Res 47:219–238.

Smith FH, Paquette SP. 1989. The adaptive basis of Neandertal facial form, with some thoughts on the nature of modern human origins. In: Trinkaus E, editor. The emergence of modern humans: biocultural adaptations in the Later Pleistocene. Cambridge: Cambridge University Press. p 181–210.

Sokal RR, Rohlf FJ. 1981. Biometry, 2nd ed. New York: W.H. Freeman & Co.

Spencer MA. 1998. Force production in the primate masticatory system: electromyographic tests of biomechanical hypotheses. J Hum Evol 34:25–54.

Spencer MA, Demes B. 1993. Biomechanical analysis of masticatory system configuration in Neandertals and Inuits. Am. J Phys Anthropol 91:1–20.

Stewart TD. 1959. Restoration and study of the Shanidar 1 Neanderthal skeleton in Baghdad. Yrbk Am Philos Soc 1958. p 274–278.

Stringer CB. 1996. Current issues in modern human origins. In: Meikle MH, Howell FC, Jabolonski N, editors. Contemporary issues in human evolution. San Francisco: California Academy of Sciences. p 115–133.

Stringer CB, Hublin JJ, Vandermeersch B. 1984. The origin of anatomically modern humans in Western Europe. In: Smith FH, Spencer F, editors. The origins of moderns humans: a world survey of the fossil evidence. New York: Alan R. Liss. p 51–135

Stringer CB, Grün R, Schwarcz HP, Goldberg P. 1989. ESR dates for the hominid burial site of Es Skhul in Israel. Nature 338: 756–758.

Tate GS, Throckmorton GS, Ellis E, Sinn DP. 1994. Masticatory performance, muscle activity and occlusal force in pre-orthognathic surgery patients. J Oral Maxillofac Surg 52:476–481.

Throckmorton GS. 1985. Quantitative calculations of temporomandibular joint reaction forces—II. The importance of the direction of the jaw muscle forces. J Biomech 18:453–461.

Throckmorton GS, Throckmorton LS. 1985. Quantitative calculations of temporomandibular joint reaction forces—I. The importance of the magnitude of the jaw muscle forces. J Biomech 18:445–452.

Throckmorton GS, Finn RA, Bell WH. 1980. Biomechanics of differences in lower facial height. Am J Orthod 77:410–420.

Trainor PG, McLachlan KR, McCall WD. 1995. Modeling of forces in the human masticatory system with optimization of the angulations of the joint loads. J Biomech 28:829–843.

Trinkaus E. 1983. The Shanidar Neandertals. New York: Academic Press.

Trinkaus E. 1987. The Neandertal face: evolutionary and functional perspectives on a recent hominid face. J Hum Evol 16: 429–443.

Trinkaus E. 2003. Neandertal faces were not long; modern human faces are short. Proc Natl Acad Sci USA 100:8142–8145.

Tuxen A, Bakke M, Pinholt EM. 1999. Comparative data from young men and women on masseter muscle fibres, function and facial morphology. Arch Oral Biol 44:509–518.

Ungar PS, Fennell KJ, Gordon K, Trinkaus E. 1997. Neandertal incisor beveling. J Hum Evol 32:407–421.

van Eijden TM, Blanksma NG, Brugman P. 1993. Amplitude and timing of EMG activity in the human masseter muscle during selected motor tasks. J Dent Res 72:599–606.

van Spronsen PH, Weijs WA, Valk J, Prahl-Andersen B, Van Ginkel FC. 1989. Comparison of jaw muscle bite-force cross-sections obtained by means of magnetic resonance imaging and high resolution CT scanning. J Dent Res 68:1765–1770.

Vitti M, Basmajian JV. 1977. Integrated actions of masticatory muscles: simultaneous EMG from eight intramuscular electrodes. Anat Rec 187:173–189.

Waltimo A, Nyström M, Könönen M. 1994. Bite force and dentofacial morphology in men with severe dental attrition. Scand J Dent Res 102:92–96.

Waugh LM. 1937. Influence of diet on the jaw and face of the American Eskimo. J Am Dent Assoc 24:1640–1647.

Weijs WA, Hillen B. 1985a. Cross-sectional areas and estimated intrinsic strength of the human jaw muscles. Acta Morphol Neerl Scand 23:267–274.

Weijs WA, Hillen B. 1985b. Physiological cross-section of the human jaw muscles. Acta Anat (Basel) 121:31–35.

Weijs WA, Hillen B. 1986. Correlations between the cross-sectional area of the jaw muscles and craniofacial size and shape. Am J Phys Anthropol.70:423–431.

Weis-Fogh T, Alexander RM. 1977. The sustained power output from striated muscle. In: Pedry TJ, editor. Scale effects in animal locomotion. London: Academic Press. p 511–525.

Wolpoff MH. 1996. Human evolution. New York: McGraw-Hill.

Yaroch LA. 1996. Shape analysis using the thin-plate spline: Neanderthal cranial shape as an example. Yrbk Phys Anthropol 39:43–89.

Zajac FE. 1989. Muscle and tendon: properties, models, scaling, and application to biomechanics and motor control. Crit Rev Biomed Eng 17:359–411.

APPENDIX

Bilateral biting analysis

The magnitude of the total bite force and the two-dimensional (2D) components of the total condylar reaction force can be solved for in a sagittal plane, using the 2D equations of static equilibrium. With the appropriate substitutions, these equations take the following form:

$$F_B = [F_{MASS} d_{MASS} + F_{MPT} d_{MPT} + F_{TEMP} d_{TEMP}]/d_B$$

$$F_{C,Y} = F_{B,Y} + F_{MASS,Y} + F_{MPT,Y} + F_{TEMP,Y}$$

$$F_{C,Z} = F_{B,Z} + F_{MASS,Z} + F_{MPT,Z} + F_{TEMP,Z}$$

where F_{MASS}, F_{MPT}, and F_{TEMP} are the magnitudes of masseter, medial pterygoid, and temporalis, respectively; d_{MASS}, d_{MPT}, d_{TEMP}, and d_B are the lever arms of masseter, medial pterygoid, temporalis, and the bite force, respectively; $F_{i,Y}$ is the y-component of force F_i; and $F_{i,Z}$ is the z-component of force F_i.

Unilateral biting analysis

By applying the principle of superposition, the solution to the symmetric biting analysis can be used in a frontal projection to solve for the working-side condylar reaction force ($F_{C,WORK}$) and the balancing-side condylar reaction force ($F_{C,BAL}$) during nonsymmetric biting. The principle of superposition states that the summed input of given variable is equal to their summed output. First, we solve for the condylar reaction forces during "antisymmetric" biting. This case is a purely mathematical construct (note that no muscle forces are acting) that serves only as a link between the two physiological biting cases. Letting w_C be the bicondylar width and w_B be the distance between incisors (or molars); summing moments about any point, we find:

$$F_{CZ,ANTI} = 0.5 F_B (w_B/w_C).$$

Referring to Figure 3, we see that the antisymmetric case superimposed on the symmetric case yields the nonsymmetric. Adding the solutions:

$$F_{C,WORK} = 0.5\ F_{C,Z} - F_{CZ,ANTI}$$
$$= 0.5\ F_{C,Z} - 0.5\ F_B\ (w_B/w_C)$$
$$F_{C,BAL} = 0.5\ F_{C,Z} + F_{CZ,ANTI}$$
$$= 0.5\ F_{C,Z} + 0.5\ F_B\ (w_B/w_C).$$

It is apparent from these equations that the working-side, or chewing-side, condylar reaction force is less than the balancing-side condylar reaction force during unilateral chewing; we also note that when $w_B = 0$ (i.e., when the bite force is in the midsagittal plane), the unilateral nonsymmetric case reduces to the bilateral symmetric case, in which the two condylar reaction forces are equal.