Were Neanderthals biting off more than they could chew? Evidence from the temporomandibular joint of Middle and Late Pleistocene hominins

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INTRODUCTION

Neanderthal cranial form has long been considered unique among hominins, but it remains unclear what evolutionary pressures may have produced this unique morphology. One leading hypothesis is that the Neanderthal face was adapted to generating relatively high (or repetitive) forces on the anterior dentition (i.e., the anterior dental loading hypothesis (ADLH)). If Neanderthals were routinely loading their anterior teeth, then we should observe a masticatory configuration that is consistent with increased efficiency of the masticatory apparatus for extensive use of the anterior dentition. While this has been suggested to be the case by some (e.g., Spencer and Demes, 1993), others (e.g., O'Connor et al., 2005) suggest Neanderthals were unable to produce unusually high bite forces. Furthermore, recent analyses hypothesize that some Neanderthal masticatory apparatus features are linked to increased jaw gape (Rak et al., 2003; Rak and Hylander, 2014).

As the joint connecting the mandible to the cranium, the temporomandibular joint (TMJ) plays an important role in dissipating masticatory forces and governing mandibular range of motion (e.g., Hylander, 1975, 2006; Greaves, 1978). Variation in some aspects of TMJ form across primates has been suggested to be related to masticatory function (Bouvier, 1986a,b; Wall, 1999; Vinyard et al., 2003; Terhune, 2011); TMJ form may therefore be informative for understanding masticatory function in Neanderthals.

RESEARCH GOALS

1. Quantify and compare TMJ shape variation in *H. heidelbergensis*, *H. neanderthalensis*, and *H. sapiens.*
2. Test the ADLH through a comparative analysis of TMJ form. I specifically evaluate variables that may be linked to selection for increased anterior bite forces vs. increased gape.
3. Document the prevalence of TMJ osteoarthritis in Neanderthals as an indicator of masticatory stresses experienced by members of this taxon.

MATERIALS AND METHODS

Sample: 46 fossil hominins (*H. heidelbergensis*, *H. neanderthalensis*, *H. sapiens;* Table 1); Modern *H. sapiens* with different diets (Aleutian Islanders n=20; Illinois Bluff n=14)

Data collection and analysis:

- 3D landmark data analyzed using standard geometric morphometric techniques (GPA, between-group PCA, regression) were used to compare TMJ form among taxa (Fig. 1)
- Linear measures of TMJ and masticatory shape were extracted from the 3D data to test biomechanical hypotheses (Table 2); Student's t-tests were used to statistically compare Aleutian Islanders vs. Illinois Bluff and *H. heidelbergensis* vs. *H. neanderthalensis*)
- Fossil specimens were evaluated for TMJ osteoarthritis (OA) following Rando and Waldron (2012). Signs of TMJ OA: eburnation, marginal osteophytes, new bone growth, porosity, and alteration of the joint contour. Except for eburnation, two or more characters were required to diagnose OA

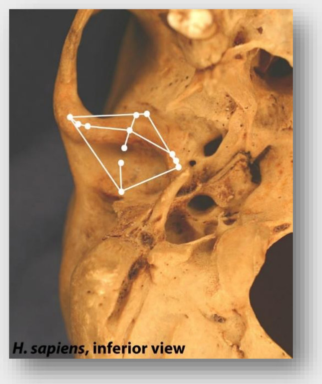


Figure 1 (Right). Three-dimensional (3D) landmarks on the glenoid fossa and corresponding wireframe diagram.

Table 2 (Below). Linear variables analyzed and their predicted variation given selection for increased bite forces vs. increased gape. The same predictions are applicable for the modern human sample, where the Aleutian Islanders are predicted to be selected for increased anterior bite forces or increased gape relative to the Illinois Bluff population.

Measurement name	Standardized for size by:	If Neanderthals had increased anterior bite forces:	If Neanderthals had increased gapes:
Temporomandibular Joint			
Articular eminence inclination	n/a	Nean>Heidel	Nean<Heidel
Preglenoid plane length	/MandLgCr		Nean>Heidel
Preglenoid length index	n/a		Nean>Heidel
Glenoid length	/MandLgCr		Nean>Heidel
Glenoid width	/MandLgCr	Nean>Heidel	Nean<Heidel
Glenoid shape index	n/a		Nean<Heidel
Condyle length	/MandLgM		Nean>Heidel
Condyle width	/MandLgM	Nean>Heidel	Nean<Heidel
Condyle shape index	n/a		Nean<Heidel
Condyle area	/MandLgM	Nean>Heidel	
Masticatory System			
Zygomatic breadth	/MandLgCr	Nean>Heidel	
Mandible length (cranium)	/Geom	Nean<Heidel	Nean>Heidel
Mandible length (mandible)	/Geom	Nean<Heidel	Nean>Heidel
Symphysis depth	/MandLgM	Nean>Heidel	
Masseter lever arm	/MandLgCr	Nean>Heidel	
Temporal fossa area	/Geom & /MandLgCr	Nean>Heidel	
TMJ height (above occlusal plane)- cranium	/MandLgCr		Nean<Heidel
TMJ height (above occlusal plane)- mandible	/MandLgM		Nean<Heidel
Condyle- M1 length	/MandLgCr		Nean>Heidel

Table 1. Fossil specimens examined for this study.

Specimen	Original/ Cast	Institution	Element
Homo heidelbergensis			
Arago 2	Cast	NMNH	Mandible
Dali	Cast	AMNH	Cranium
Kabwe	Original	BNMH	Cranium
LH 18	Cast	IHO	Cranium
Mauer	Cast	IPH	Mandible
Petralona	Cast	NMNH	Cranium
Reilingen	Original	SMFNK	Calvarium
Sima 5	Cast	AMNH	Cranium and mandible
Steinheim	Original	SMFNK	Cranium
Homo neanderthalensis			
Amud	Cast	AMNH	Cranium and mandible
Gibraltar 1	Original	BNMH	Cranium
Guattari	Original and Cast	MP	Cranium
Kebara 1	Cast	AMNH	Mandible
Krapina 5	Smith (1976)		Partial cranium
Krapina 39.1	Cast	AMNH	Temporal bone
Krapina 3	Cast	IPH	Temporal bone
Krapina 59	Cast	IPH	Mandible
Krapina 63	Smith (1976)		Mandible
Krapina 66	Smith (1976)		Mandible
La Chapelle	Original	MdH	Cranium and mandible
La Ferrassie 1	Original	MdH	Cranium and mandible
La Ferrassie 2	Original	MdH	Temporal bone
La Quina H27	Original	IPH	Temporal bone
La Quina H5	Original	MdH	Cranium and mandible
Montmaurin	Original	MdH	Mandible
Saccopastore 1	Original	Sap	Cranium
Saccopastore 2	Original	Sap	Cranium
Shanidar 1	Cast	NMNH	Cranium and mandible
Shanidar 5	Cast	NMNH	Part. cranium and temporal
Spy 1	Original	RINSB	Partial cranium
Spy 2	Original	RINSB	Part. cranium and mandible
Tabun 1	Original	BNMH	Cranium and mandible
Tabun 2	Cast	IPH	Mandible
Fossil *Homo sapiens*			
Abri Pataud	Original	MdH	Cranium and mandible
Cro Magnon	Original	MdH	Cranium and mandible
Dar es Soltan	Cast	IPH	Temporal and mandible
Jebel Irhoud	Cast	AMNH	Cranium
Kow Swamp 1	Cast	IPH	Cranium
Kow Swamp 5	Cast	IPH	Cranium and mandible
La Madeleine	Original	MdH	Mandible
Predmosti	Cast	AMNH	Cranium and mandible
Qafzeh 6	Original	IPH	Cranium
Qafzeh 9	Cast	AMNH	Cranium and mandible
Rochereil	Original	IPH	Cranium and mandible
Singa	Original	BNMH	Calvarium
Skhul V	Cast	AMNH	Cranium and mandible
Vogelherd	Schwartz and Tattersall (2002)		Cranium and mandible

RG1- Compare TMJ shape in *H. heidelbergensis*, *H. neanderthalensis*, and *H. sapiens*

- bgPC 1 (Figure 2) represents 62% of the sample variation and was significantly correlated with size (25% of shape variation, $P=0.0001$)
- bgPC 1 separated *H. neanderthalensis* and *H. heidelbergensis* from modern *H. sapiens*; fossil *H. sapiens* overlapped with both fossil hominins and modern *H. sapiens*
- Shape variation along bgPC1 was related to width vs. length of the glenoid, size of the preglenoid plane, inclination of the articular eminence, and size of the postglenoid process
- Procrustes distances among groups found significant differences between all comparisons of fossil hominins vs. modern humans, but no differences between human populations or between *H. heidelbergensis* and *H. neanderthalensis*. Fossil *H. sapiens* differed significantly from modern *H. sapiens* and the other fossil taxa

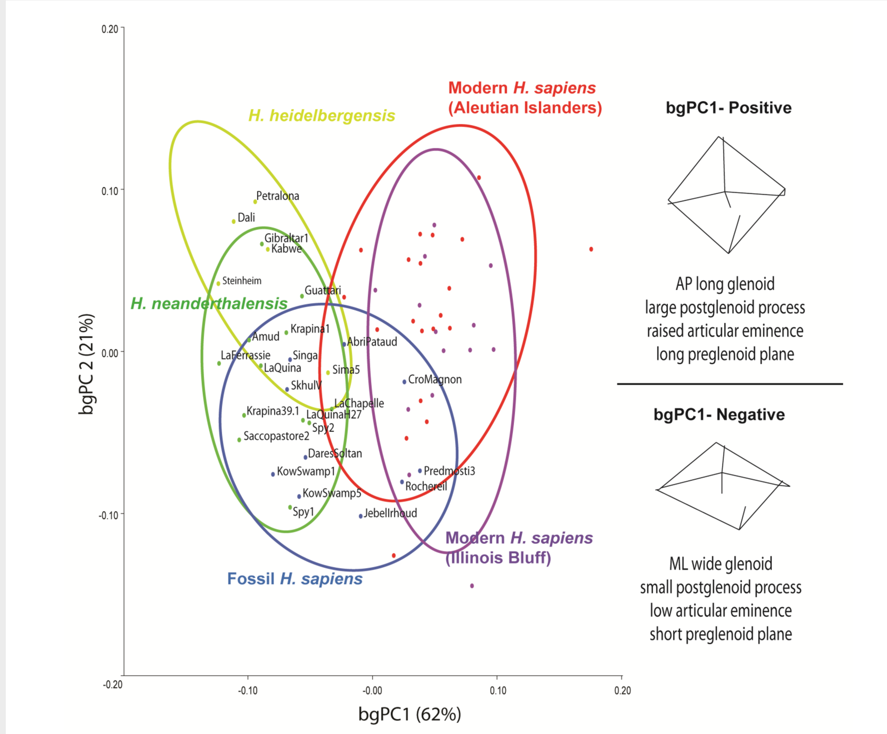
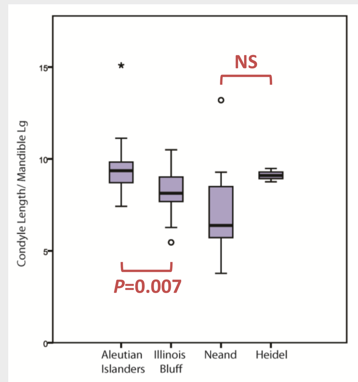


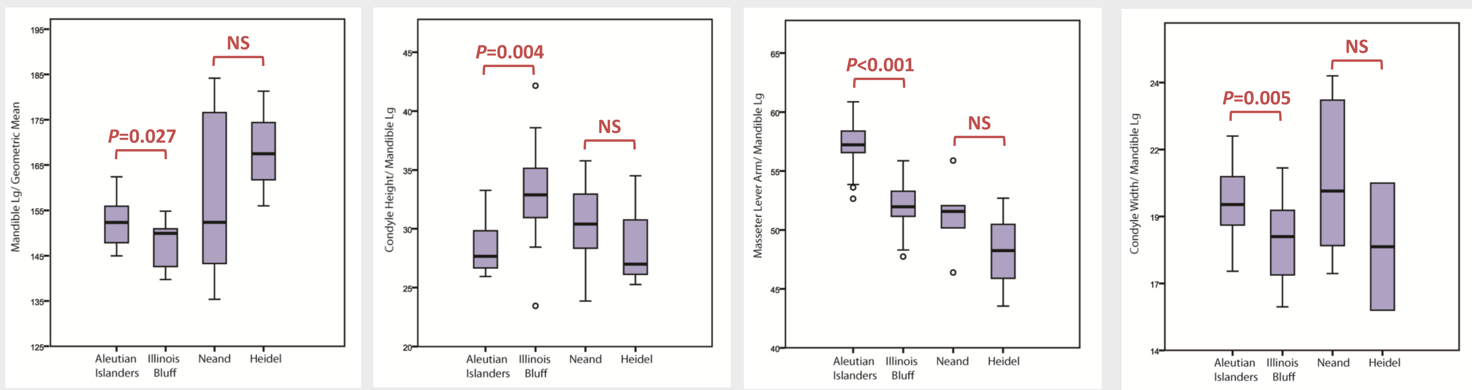
Figure 2. Between-group principal component (bgPC) plot of the glenoid fossa landmarks showing the first two axes and corresponding shape variation.

RG2- Test biomechanical hypotheses

- In the modern human sample, multiple linear variables were significantly different among groups

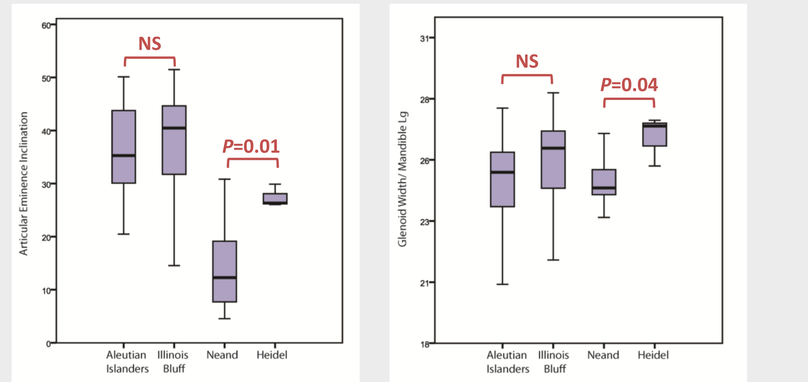
Variable	P-value	Difference	Linked to
Mandible Length	0.027	Aleutians >Illinois	increased gape
Condyle Height	0.004	Aleutians <Illinois	increased gape
Masseter Lever Arm	<0.001	Aleutians >Illinois	increased force
Condyle Width	0.005	Aleutians >Illinois	increased force
Condyle Length	0.007	Aleutians >Illinois	increased gape





- However, in the fossil sample, only two variables differed significantly between *H. heidelbergensis* and *H. neanderthalensis*

Variable	P-value	Difference	Linked to
Articular eminence inclination	0.01	*H. neanderthalensis* < *H. heidelbergensis*	increased gape
Glenoid Width	0.04	*H. neanderthalensis* < *H. heidelbergensis*	increased force

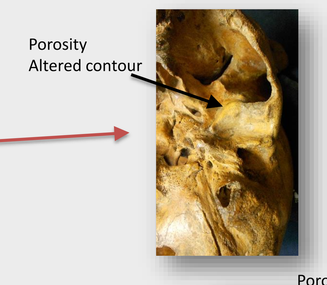


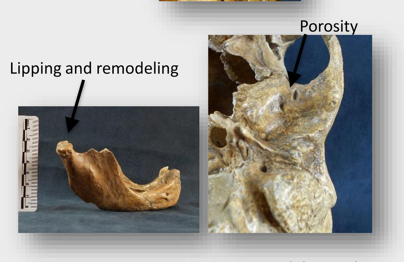
RQ3- Assess TMJ pathology in fossil hominins

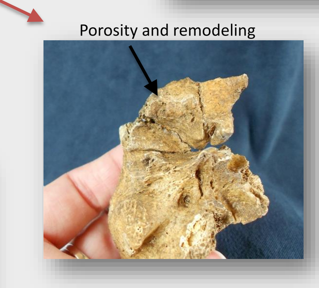
- 15 out of 46 fossils examined were identified as pathological. The most common sign of pathological changes was an altered joint contour, followed by porosity of the joint surfaces. No specimens showed signs of eburnation.

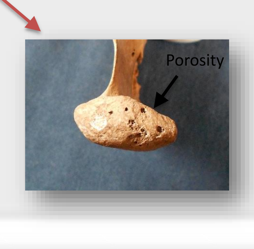
	N	Eburnation	Marginal Osteophytes	New bone growth	Porosity	Altered Joint Contour	Pathological?
H. heidelbergensis	8	0	0	1	2	4	3
H. neanderthalensis	24	0	4	2	4	10	8
Fossil *H. sapiens*	14	0	2	2	2	4	4

- Pathological specimens include:
  - *H. heidelbergensis* (3/8, 38%)
    - Kabwe
    - Mauer
    - Sima de los Huesos 5
  - *H. neanderthalensis* (8/24, 33%)
    - Amud
    - Guattari (Monte Circeo)
    - Krapina 59
    - La Chapelle-aux-Saints
    - La Ferrassie 1 (extreme remodeling)
    - La Ferrassie 2
    - La Quina H5
    - Shanidar 1 and 5
  - Fossil *H. sapiens* (4/14, 29%)
    - La Madeleine
    - Rochereil
    - Skhul V
    - Vogelherd (Stetten)









CONCLUSIONS

- The GM analysis reveals significant shape differences between the fossil and modern samples, including differences between fossil and modern *H. sapiens*. This may indicate important temporal changes in masticatory function and robusticity in humans, as has been suggested by Carlson and Van Gerven (1977).
- The shape differences between the modern and fossil taxa may reflect differences in TMJ range of motion, as more AP compressed joints likely indicate decreased sagittal sliding of the condyle (Wall, 1999). Conversely, a ML wider joint may reflect increased repetitive loading and twisting of the mandible along its long axis, which results in laterally focused stresses in the joint (Hylander, 1979, 2006; Hylander and Bays, 1979).
- The GM and linear analyses suggest few significant differences between *H. heidelbergensis* and *H. neanderthalensis* samples. Thus, there is no clear biomechanical signal that the Neanderthal masticatory apparatus is adapted for either increased anterior bite forces or increased gape.
- Pathological analysis revealed 15 fossil specimens with signs of TMJ OA. Specimens with OA were spread across all three taxa examined. Neanderthals did show a high prevalence of TMJ OA, but no more so than was observed for *H. heidelbergensis*. These results suggest that all fossil hominins considered here have a somewhat higher prevalence of TMJ OA than most contemporary humans (average = ~22%; Rando and Waldron, 2012).
- Further analyses linking the degree of dental wear directly to pathological changes in the TMJ are necessary. Recent work suggests that Neanderthals may not exhibit relatively higher degrees of anterior tooth wear than other Late Pleistocene hominins, a finding which is consistent with the result here that *H. heidelbergensis* and *H. sapiens* have similar rates of TMJ OA.
- Overall, this study provides little support for the anterior dental loading hypothesis, but does suggest that plastic changes in the TMJs of Middle and Late Pleistocene hominins are common.

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