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The Neanderthal lower arm

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ABSTRACT

Neanderthal forearms have been described as being very powerful. Different individual features in the lower arm bones have been described to distinguish Neanderthals from modern humans. In this study, the overall morphology of the radius and ulna is considered, and morphological differences among Neanderthals, Upper Paleolithic *Homo sapiens* and recent *H. sapiens* are described.

Comparisons among populations were made using a combination of 3D geometric morphometrics and standard multivariate methods. Comparative material included all available complete radii and ulnae from Neanderthals, early *H. sapiens* and archaeological and recent human populations, representing a wide geographical and lifestyle range.

There are few differences among the populations when features are considered individually. Neanderthals and early *H. sapiens* fell within the range of modern human variation. When the suite of measurements and shapes were analyzed, differences and similarities became apparent. The Neanderthal radius is more laterally curved, has a more medially placed radial tuberosity, a longer radial neck, a more antero-posteriorly ovoid head and a well-developed proximal interosseous crest. The Neanderthal ulna has a more anterior facing trochlear notch, a lower M. brachialis insertion, larger relative midshaft size and a more medio-lateral and antero-posterior sinusoidal shaft. The Neanderthal lower arm morphology reflects a strong cold-adapted short forearm. The forearms of *H. sapiens* are less powerful in pronation and supination. Many differences between Neanderthals and *H. sapiens* can be explained as a secondary consequence of the hyper-polar body proportions of the Neanderthals, but also as retentions of the primitive condition of other hominoids.

Introduction

From the well-pronounced muscle attachment sites on their upper limb bones, it is suggested that Neanderthals had very powerful forearms (Trinkaus and Churchill, 1988). There are several features in the lower arm bones that distinguish Neanderthals from modern humans (Fischer, 1906; Patte, 1955; Trinkaus and Churchill, 1988; Aiello and Dean, 1990; Vandermeersch and Trinkaus, 1995; Pearson and Grine, 1997). The Neanderthal radius has been described as more laterally curved than that of humans (Fischer, 1906; Patte, 1955; Vandermeersch and Trinkaus, 1995; Carretero et al., 1999; Czarnetzki, 2000).

Increased curvature of the radius results in a greater distance between the ulna and the radius, which increases the distance between the insertions of the M. pronator quadratus and the M. pronator teres. Increased curvature moves the lines of action further away from the axis of pronation and supination, and therefore enhances the power arms of these muscles. African apes are less curved than other mammals (Swartz, 1990). Swartz (1990) suggests that this is due to the long bones of primates being longer than those of other mammals and that this produces larger bending stresses during normal locomotion. Experimental work has demonstrated the need for normally functioning muscles in order for normal bone curvature to develop (Lanyon, 1980). Higher degrees of radial curvature in anthropoids have been explained as the result of an increase in size and functional importance of the supinator musculature, but in gibbons curvature was not affected by differential muscle mass (Swartz, 1990). Compared with humans, however, apes have a higher degree of lateral curvature (Aiello and Dean, 1990). The higher degree of lateral curvature in African apes (Martin and Saller, 1959; Knussman, 1967 in Swartz, 1990) and a more lateral insertion of the M. pronator teres increases the lever advantage of the lower arm (Aiello and Dean, 1990).

The lateral subtense of the radius of the Neanderthals is remarkable (Fischer, 1906; Botez, 1926 in Patte, 1955; Vandermeersch and Trinkaus, 1995; Carretero et al., 1999; Czarnetzki, 2000). The supinator crest of the radius is strongly

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developed. Neanderthals also possess a more medially positioned radial tuberosity (Trinkaus and Churchill, 1988). This position is a measure of the lever advantage of the M. biceps brachii and the range of action over which this muscle can operate as a supinator. In apes, the radial tuberosity is also positioned more medially and gives them a greater mechanical advantage of the M. biceps brachii in supination (Aiello and Dean, 1990). If the radial tuberosity is placed more antero-laterally, as it is in modern humans, then the power advantage is lost during the final phases of supination (Trinkaus and Churchill, 1988; Aiello and Dean, 1990; Pearson and Grine, 1997). The radial subtense, supinator crest and position of the radial tuberosity may indicate that Neanderthals closely resemble earlier hominins in the morphology and strength of the radius, and that the Neanderthal forearm and elbow was especially strong during pronation and supination (Trinkaus and Churchill, 1988).

Neanderthals have been described as having a pronounced posterior subtense in the ulna (Fischer, 1906). In comparison with the African apes, hominins, including modern humans, have a more anterior facing trochlear notch (Drapeau, 2004, 2008). The Neanderthal proximal ulna, however, has been described as having an even more anterior facing trochlear notch than modern humans (Trinkaus and Churchill, 1988). Trinkaus and Churchill (1988) propose that this would not have limited the range of movement but was rather an expression of different habitual behavior, such as the increased use of forearms with the elbow flexed. A more anterior facing trochlear notch was also observed in the *Australopithecus afarensis* ulna, A.L. 438-1a, from Hadar, Ethiopia (Drapeau et al., 2005). It is unknown what kind of habitual behavior results in this morphology. The M. pronator quadratus crest in Neanderthals is very pronounced and also suggests a more muscular forearm, although the interosseous crest is poorly developed and the shaft is relatively narrow (Trinkaus and Churchill, 1988; Aiello and Dean, 1990).

In addition to reportedly having more laterally curved radii and posteriorly curved ulnae, Neanderthals have a suite of characteristics that, when considered independently, may occur in modern human populations, but that, as a suite, set apart the Neanderthals as a group that is distinct from modern humans (Boule and Vallois, 1952; Trinkaus, 1983; Hublin, 1989; Stringer, 1992; Hublin et al., 1996). Many post-cranial characters have been interpreted as the result of the Neanderthal hyper-polar body shape and muscular hypertrophy (Patte, 1955; Vlček, 1961; Rak and Arensburg, 1987; Tompkins and Trinkaus, 1987; Holliday and Trinkaus, 1991; Ruff and Walker, 1993; Ruff et al., 1993; Walker and Leakey, 1993; Ruff, 1994; Trinkaus et al., 1994, 1998; Vandermeersch and Trinkaus, 1995; Pearson and Grine, 1997; Churchill, 1998; Trinkaus and Ruff, 1999; Pearson, 2000a; Holliday and Ruff, 2001; Shackelford and Trinkaus, 2002; Majó et al., 2003; Weaver, 2003; Thompson and Nelson, 2005; Shackelford, 2007; De Groote, 2011). Some characteristic Neanderthal post-cranial features may be primitive retentions in Neanderthals (Trinkaus, 1981, 1983), whereas others may be autapomorphic traits or phenotypic adaptations to a particular environmental or functional environment (Howell, 1957; Pearson, 2000a,b; Pearson and Lieberman, 2004; Churchill, 2005, 2006; Pearson et al., 2006; Trinkaus, 2006; Weaver, 2009; De Groote, 2011). The aim of this study is to describe Neanderthal forearm morphology, particularly the morphological differences in the radius and ulna of Neanderthals and modern humans, and to understand the functional relevance of these differences.

Table 1
List of modern humans in the sample.

Population	*N*	Absolute latitude	Collection	Location
African American	12/14	n/a	African-Americans Terry Collection	Smithsonian, Washington
Alaskan Aleutian Isl.	7/10	71	Aleutian Islands Collection	Peabody, Harvard
Alaskan Point Hope	12/13	68	Alaskan Inuit	NHM, New York
Andaman	11/11	11	College of Surgeons Collection	NHM, London
Arizona	18/19	36	Canyon del Muertos	NHM, New York
Australian	7/10	30	College of Surgeons Collection	NHM, London
Bantu	1/0	7	Republic of Congo	RBINS, Brussels
Belgian Medieval	18/20	50	Spy and Gutschoven	RBINS, Brussels
Belgian Mesolithic	1/0	50	Abri des Autours	RBINS, Brussels
Belgian Neolithic	23/15	50	Furfooz, Maurenne, Hastière, Dinant	RBINS, Brussels
Chinese	4/7	35	Chinese Cemetary, Karluk Quad Alaska	Smithsonian, Washington
Colorado Native	2/3	43	Montezuma County, Colorado	Peabody, Harvard
Czech Medieval	34/33	49	Moravian Empire Collection	NHM, Prague
Danish Medieval	10/11	55	Sankt Bendtskirke, Ringsted	University, Copenhagen
Danish Neolithic	19/10	55	Korshoj Adby, Guldhoj, Borreby	University Copenhagen
Egyptian	5/5	26	Egyptian Dynasty	NHM, Paris
English Medieval	16/12	54	Scarborough	NHM, London
English Urban	19/20	51	Spitalfields 18th-19thC	NHM, London
French Medieval	5/4	49	Villebourg, St. Gabriel	NHM, Paris
French Neolithic	3/0	48	Valée du Petit Morin	NHM, Paris
Greenland Inuit	14/13	69	Tuqutut, Ilutalik, Uunartoq, Ilorsuit	University, Copenhagen
Kazach Medieval	0/7	47	Southern Volga Region	St. Petersburg
Khoikhoi	9/8	28	Oxford Collection	NHM, London
Lapland	22/15	67	Russian Saami	Moscow State Univ.
Natufian	11/9	32	Mallaha	University, Tel Aviv
New Mexico	8/8	31	Aztec Ruins	NHM, New York
Ohio	14/12	40	Madissonville, Ohio	Peabody, Harvard
Peru	3/6	11	Ancon (Lima)	NHM, Paris
Pygmy	1/3	7	Lituri Central Africa	RBINS, Brussels
Russian Eskimo	14/14	66	Siberian Peninsula, Ekveni	Moscow State University
Russian Mesolithic	7/6	58	Vasilievski	St.-Petersburg
Siberia	14/14	66	Sibstey, Salehard Siberia	Moscow State University
South Dakota	14/12	45	Campbell County, Ohae Reservoir	Moscow State University
Tasmanian	2/2	42	Tasmania	NHM, London, Brussels
Tierra del Fuego	1/1	54	Tierra del Fuego, Argentina	NHM, Vienna

N = Radius/Ulna.