Journal of Human Evolution 95 (2016) 55–67

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

Adult Neandertal clavicles from the El Sidrón site (Asturias, Spain) in the context of *Homo* pectoral girdle evolution

Antonio Rosas [a, *], Francisco Javier Rodriguez-Perez [a], Markus Bastir [a], Almudena Estalrrich [a], Rosa Huguet [b, c], Antonio García-Tabernero [a], Juan Francisco Pastor [d], Marco de la Rasilla [e]

[a] *Group of Paleoanthropology MNCN-CSIC, Department of Paleobiology, Museo Nacional de Ciencias Naturales-CSIC, Calle José Gutiérrez Abascal 2, 28006 Madrid, Spain*
[b] *Institut Català de Paleoecologia Humana i Evolució Social (IPHES), Campus Sescelades URV (Edifici W3), Unidad Asociada al CSIC, 43007 Tarragona, Spain*
[c] *Universitat Rovira i Virgili, Avda. Catalunya, 35, 43002 Tarragona, Spain*
[d] *Museo Anatómico, departamento de Anatomía Humana, Universidad de Valladolid, Calle Ramón y Cajal 7, 47005 Valladolid, Spain*
[e] *Área de Prehistoria, Department of History, Universidad de Oviedo, Calle Teniente Alfonso Martínez s/n, 33011 Oviedo, Spain*

ARTICLE INFO

Article history:
Received 27 July 2015
Accepted 10 March 2016
Available online 3 May 2016

Keywords:
Pleistocene
H. neanderthalensis
Collarbone morphology
Geometric morphometrics
Trait polarity

ABSTRACT

We undertook a three-dimensional geometric morphometric (3DGM) analysis on 12 new Neandertal clavicle specimens from the El Sidrón site (Spain), dated to 49,000 years ago. The 3DGM methods were applied in a comparative framework in order to improve our understanding of trait polarity in features related to *Homo* pectoral girdle evolution, using other Neandertals, *Homo sapiens*, *Pan*, ATD6-50 (*Homo antecessor*), and KNM-WT 15000 (*Homo ergaster/erectus*) in the reference collection. Twenty-nine homologous landmarks were measured for each clavicle. Variation and morphological similarities were assessed through principal component analysis, conducted separately for the complete clavicle and the diaphysis. On average, Neandertal clavicles had significantly larger muscular entheses, double dorsal curvature, clavicle torsion, and cranial orientation of the acromial end than non-Neandertal clavicles; the El Sidrón clavicles fit this pattern. Variation within the samples was large, with extensive overlap between *Homo* species; only chimpanzee specimens clearly differed from the other specimens in morphometric terms. Taken together, our morphometric analyses are consistent with the following phylogenetic sequence. The primitive condition of the clavicle is manifest in the cranial orientation of both the acromial and sternal ends. The derived condition expressed in the *H. sapiens* + Neandertal clade is defined by caudal rotation of both the sternal and acromial ends, but with variation in the number of acromia remaining in a certain cranial orientation. Finally, the autapomorphic Neandertal condition is defined by secondarily acquired primitive cranial re-orientation of the acromial end, which varies from individual to individual. These results suggest that the pace of phylogenetic change in the pectoral girdle does not seem to follow that of other postcranial skeletal features.

1. Introduction

Clarifying whether the features frequently observed in Neandertal populations originated in the last common ancestor of Neandertals and *Homo sapiens* or only in the lineage leading to Neandertals (since divergence) may provide insight into morphofunctional evolution in Pleistocene hominins. Many derived features in the postcranial skeleton may be morphological consequences of body-form divergences; pelvis breadth, thorax shape, and the pectoral girdle seem to be involved in these divergences in one way or another. The Neandertal torso is large and deep (Bastir et al., 2015), traditionally perceived as a body form specialized for cold weather (Vandermeersch and Trinkaus, 1995; Churchill, 1996). The upper thorax of modern humans differs in shape from that of Neandertals, which shows more anteriorly projecting upper ribs during inspiration (Bastir et al., 2015). This in turn implies a reconfigured spatial arrangement of the pectoral girdle. In this context, study of the configuration of the clavicle through three-

* Corresponding author.
E-mail address: arosas@mncn.csic.es (A. Rosas).

http://dx.doi.org/10.1016/j.jhevol.2016.03.005
0047-2484/

dimensional geometric morphometric (3DGM) analysis may help characterize variations in form and elucidate its potential covariation with other elements of the pectoral girdle.

Clavicle length is one of the characteristics that originally enabled researchers to distinguish Neandertal anatomy from that of anatomically modern humans (Boule, 1911; Churchill, 1994; Holliday, 1997; Larson, 2013; see Trinkaus et al., 2014 for a complete review). Supposedly, a long clavicle allows for a broad thorax. As a consequence of an enlarged chest, Vandermeersch and Trinkaus (1995) and Churchill (1996) suggested that Neandertal scapulae were positioned more laterally, with a horizontal scapular spine and a distinctive axillary-border morphology, along with more anteriorly directed tall and narrow glenoid fossae (Churchill and Trinkaus, 1990). Later, Larson (2007) suggested that the relatively long clavicles of Neandertals were also products of large chest size, as they were needed to bridge the longer distance from the sternum to the acromion. A distinctive scapulo-humeral joint shape has also been reported (Carretero et al., 1997; Lari et al., 2015). Nonetheless, Trinkaus et al. (2014) recently downplayed this evidence on the basis that relative clavicle length, appropriately scaled to body mass, maintains a constant relationship across species of the genus *Homo* (sensu stricto), and thus paleobiological inferences based on the study of clavicle length should be avoided.

In contrast, other experts have determined that in addition to the size of the clavicle, its shape discriminates among groups of *Homo*. Independent of length, clavicle morphology potentially yields insight into *Homo* paleobiology and evolution. For instance, Voisin (2004) stated that the Neandertal clavicle reflects the special architecture of the Neandertal shoulder, which is characterized by a high scapula in relation to the thorax. In a broader context, clavicular curvature on the dorsal view is related to shoulder position (Voisin, 2001, 2004, 2006a,b, 2008, 2010). The vast majority of hominin species (except *H. sapiens*) normally exhibit clavicles with two curvatures on the dorsal view: one inferior, at the lateral extremity, and one superior, at the medial extremity. The morphology of these type-II clavicles is related to a scapula that is positioned high relative to the rib cage. By contrast, most modern humans harbor clavicles with a single curvature (type I) due to the low position of the scapula in relation to the thorax (Voisin, 2001, 2004, 2008, 2010); 75% of Neandertal clavicles are type II, but this morphology appears in only 15% of modern human clavicles (Voisin, 2001).

The collarbone also displays a morphological characteristic that is rarely mentioned in the literature: clavicular twist (Ashton and Oxnard, 1964; Oxnard, 1984; Aiello and Dean, 1990). This twist is defined by the line of the anterior border and is related to the orientation of the acromial end (Oxnard, 1984). Generally, modern humans exhibit low torsion, while non-human hominoids and other primates present a cranially oriented acromial end (Oxnard, 1984; Aiello and Dean, 1990). Such torsion is also evident in the hominin fossil record (Oxnard, 1984; Carretero et al., 1999; Churchill et al., 2013), together with a diaphysis twist that is marked in some Neandertals (Vandermeersch and Trinkaus, 1995; Carretero et al., 1997).

The shape of the midshaft cross section is also relevant to the morphological evolution of the human clavicle. Hominin species preceding *H. sapiens* exhibit an elliptical midshaft cross section with a low midshaft index (<80; [minimum diameter/maximum diameter] $\times$ 100); these clavicles have been designated as platicleidic (Carretero et al., 1997, 1999). In contrast, in modern humans, the cross section at midshaft is circular, with mesocleidic morphology and a midshaft index of 80–120 (McCown and Keith, 1939; Trinkaus, 1983; Carretero et al., 1997, 1999). It has been reported that 88% of *Homo neanderthalensis* clavicle fossils present a flattened diaphysis. In most cases, this flattening is dorsoventral (Vandermeersch and Trinkaus, 1995; Carretero et al., 1997, 1999), but some craniocaudal examples have been described that are consistent with the elliptical cross section reported for Neandertals (Trinkaus, 1983; Vandermeersch and Trinkaus, 1995; Carretero et al., 1997, 1999; Mersey et al., 2013).

Despite large variations in clavicle dimensions, the anatomy of isolated clavicles seems to indicate systematic differences among *Homo* species. However, the phylogenetic pattern of this variation remains largely unexplored. Three-dimensional geometric morphometric analysis of the clavicle as part of the pectoral girdle may shed new light onto this problem. Discovery of new, well-preserved clavicle remains from the ~49 ka (thousands of years old) El Sidrón site (Northern Spain) (Rosas et al., 2006, 2012) encouraged us to use a comparative framework to explore several questions. Do the new El Sidrón clavicle remains fit the characteristic form of Neandertal clavicles? Are there significant differences in clavicle size and shape between Neandertals and modern humans? If so, which features provide information about classification and what is the phylogenetic trait polarity of these features? Although we recognize the difficulty in establishing functional relationships through the study of isolated anatomical elements, we sought to evaluate these features in the context of the evolution of the *Homo* pectoral girdle. Thus, this investigation evaluated the new Neandertal clavicles from the El Sidrón site in comparison with samples of Neandertal, modern human, and chimpanzee clavicles and ATD6-50 (*Homo antecessor*) and KNM-WT 15000 (*Homo ergaster/erectus*) specimens. Using 3DGM methods complemented with classic measurements, we sought to determine the main form differences among clavicles from human species in order to improve our understanding of trait polarity in features related to *Homo* pectoral girdle evolution. Identification of so-called "Neandertal features" in European Lower Pleistocene populations, particularly those attributed to *H. antecessor* from TD6 (Atapuerca), has renewed interest in trait polarity (Martinón-Torres et al., 2007; Bermúdez de Castro et al., 2015; Gómez-Robles et al., 2015). Determining which of these features are uniquely derived (autapomorphies) and which are inherited from previous ancestors (Bermúdez de Castro et al., 2012, 2015; Rosas et al., 2015) is a key issue in the resolution of the *Homo* evolutionary model.

2. Material and methods

2.1. The El Sidrón site

El Sidrón is a karst system located in Asturias, Spain (Fortea et al., 2003; Rosas et al., 2006; de la Rasilla et al., 2011). Since 2000, samples ~49 ka have been recovered from this site (Wood et al., 2013), constituting the most complete Neandertal sample from the Iberian Peninsula (Rosas et al., 2006, 2012). The remains were in a secondary position; the original deposit, worn out by erosion, is thought to have been either on the surface or in an upper karst level (Fortea et al., 2003). All skeletal parts are preserved, and there is a moderate occurrence of Middle Paleolithic stone tools at the site (Rosas et al., 2006; Santamaria et al., 2010). The remains of at least 13 individuals were present at the site: one infant, two juveniles, three adolescents, and seven adults (Rosas et al., 2012, 2013).

2.2. Conservation and inventory of the clavicle material

A total of 12 clavicle fragments have been recovered from the El Sidrón site, representing eight clavicles: five left and one right adult clavicles, one indeterminate fragment and two clavicles from juvenile 1 (Rosas et al., 2013) that were not included in the current analysis (Table 1), as only the adult specimens were considered. The