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TITLE

Structural effects of variation in the human clavicle

SHORT RUNNING TITLE

Structural effects of clavicle variation

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ABSTRACT

Objectives: Purported evolutionary shifts in shoulder structure have been linked to changes in hominin behavior and adaptation. Researchers use clavicle morphology to infer these shifts. However, there is a lack of empirical data underlying such predictive relationships. This study investigates how clavicle morphology affects articulated shoulder girdle and upper thorax configuration in humans.

Materials and Methods: Landmarks and scalar measurements on the clavicle, scapula and ribs 1-3 were collected from three-dimensional computed tomographic scans of living humans. Covariation between disarticulated and articulated morphology was assessed using partial least squares and regression analyses.

Results: We found support for hypotheses linking combined dimensions of the clavicle, ribs, and scapula to resting protraction. Individuals with relatively short clavicles tend to exhibit protracted and elevated resting positions of the scapula. It is more difficult to predict superoinferior configuration, which is only minimally affected by clavicle curvature. Instead, the superoinferior position of the scapula on the thorax is governed equally by clavicle orientation and rib declination. Shoulder breadth is determined primarily by clavicle length, but orientation has a comparable effect. Therefore, reliable reconstructions of shoulder breadth can be established using clavicle length, together with consideration of orientation. Relationships between clavicle and thorax morphology are weaker.

Discussion: Understanding the determinants of variation in human shoulder structure informs interpretation of skeletal remains. Our investigations describe how important aspects of shoulder structure can be inferred from disarticulated clavicles and we provide the attendant predictive equations. Future work on interspecific variation will improve skeletal reconstruction for more ancient hominins.

KEYWORDS: clavicle; scapula; rib; shoulder; geometric morphometrics

MAIN TEXT

1 INTRODUCTION

Comparative studies suggest that the shoulder girdle underwent major structural changes over the course of human evolution. The shoulders of nonhuman apes are commonly described as being narrower, positioned higher above the sternum and perhaps less dorsally than in humans (Larson, 2007, 2009, 2013; Miller, 1932; Schultz, 1930, 1933, 1936, 1950; Vrba, 1979). Because humans lack morphology that is shared in common among other hominoids, parsimony-based reasoning suggests differences in shoulder breadth, height, and scapula position accumulated along the hominin lineage. Shifts in these aspects of shoulder girdle structure have been related to adaptation in modern human populations and in fossil hominins.

Shoulder breadth, height and scapula position are structural properties of the articulated skeleton. Identifying evolutionary shifts in shoulder structure requires the ability to reconstruct the articulated whole using disarticulated components. This task is particularly difficult for the shoulder girdle. It is composed of the clavicle (anteriorly) and scapula (posteriorly), with the thorax occupying the intervening space. The articular surfaces are small and flat, so they do little to constrain orientation among elements. The shoulder girdle is held together instead by soft tissue that decomposes after death. Articulated structure is therefore not apparent from simply examining skeletal remains and a predictive approach is required.

Anthropologists have conducted extensive comparisons of clavicle morphology using osteological collections, which generally lack information about the articulated skeleton. Inversely, some clinical studies have quantified shoulder configuration in living humans (Culham & Peat, 1993, 1994), but they lack detailed observations on bone morphology. Exceedingly few studies have investigated covariation between disarticulated and articulated morphology (but see Churchill, 1994a; Piontek, 1979). As a result, we currently know little about how clavicle morphology affects articulated structure.

An additional challenge lies in the potential for morphological interaction among elements. It is insufficient to consider clavicle morphology in isolation because articulated structure is potentially affected by the size, shape, position and orientation of each component (clavicle, scapula and thorax). A distinction between intrinsic and extrinsic aspects of skeletal morphology is useful in understanding how skeletal form is determined (García-Martínez, Recheis, & Bastir, 2016). Intrinsic morphology can be

observed from a disarticulated bone (i.e. size and shape), whereas extrinsic factors arise from a bone's location and orientation in articulated space. Understanding the relative importance of intrinsic and extrinsic factors is vital to shoulder reconstruction because only intrinsic morphology can be observed from skeletal remains while extrinsic factors must be inferred. Despite these challenges, clavicle morphology is regularly used to infer structural shifts and associated shifts in hominin behavior and adaptation.

1.1 Shoulder girdle reconstruction and its relevance in human evolution

Reasonably complete clavicles are known for a number of hominin species dating from the middle Pliocene onward (Carretero, Arsuaga, & Lorenzo, 1997; Carretero, Lorenzo, & Arsuaga, 1999; Alemseged et al., 2006; Churchill et al., 2013; Feuerriegel et al., 2017; Larson et al., 2007; Melillo, 2016; Ohman, 1986; Oxnard, 1968; Rosas et al., 2016; Trinkaus, 1983; Trinkaus, Holliday, & Auerbach, 2014; Trinkaus & Svoboda, 2006; Vandermeersch & Trinkaus, 1995). The size and shape of the clavicle has clearly changed, but not in a simple directional manner. The structural and functional implications of clavicle morphology are debated.

1.1.1 Shoulder height

Shoulder height is relevant to debates over adaptation in multiple hominin species, including the importance of arboreal locomotion in *Australopithecus* and *Homo* (Churchill et al., 2013; Feuerriegel et al., 2017; Hawks et al., 2017; Larson, 2007, 2013; Melillo, 2016; Ohman, 1986; Oxnard, 1968) and distance running (Bramble & Lieberman, 2004), throwing (Roach, Venkadesan, Rainbow, & Lieberman, 2013), and manipulative capabilities (Larson, 2007, 2015) in *Homo erectus*. Some authors propose that a descended shoulder evolved around 1.8 Ma. However, others argue that descent had already occurred by about 3.5 Ma (Ohman, 1986) or that the shoulder girdle remained variably elevated into the late Pleistocene (Feuerriegel et al., 2017; Rosas et al., 2016; Voisin, 2001, 2004).

Schultz (1926, 1933) was one of the first researchers to describe differences in shoulder height among hominoids, which he defined as the perpendicular distance between the suprasternal notch and the acromion (Schultz, 1929). The superoinferior position of the scapula on the thorax (scapula SI position) is another aspect of shoulder configuration that has been treated as equivalent to shoulder height. These articulated properties are commonly inferred from clavicle curvature.

The clavicle curves and twists in multiple planes. The bone's characteristic S-shape is generated by curvature in the transverse plane (as seen in superior view). The clavicle also exhibits more subtle curvature in the coronal plane (as seen in anterior view, Figure 1). In comparing coronal curvature, bone orientation is commonly standardized by positioning the acromial end parallel to the horizontal. This comparative orientation is thought to approximate articulated orientation (Ohman, 1986).

[FIGURE 1, 2 COLUMNS]

Authors differ in their descriptions of coronal curvature, but a common observation is that curvature is reduced in humans compared to non-human apes (Matiegka, 1937; Ohman, 1986; Olivier, 1951a, 1951b; Voisin, 2001, 2004, 2006a, 2006b; see Figure 1A). Coronal curvature is thought to affect shoulder height by mediating the relative positions of the acromial and sternal ends. A straighter clavicle is expected to co-occur with a more descended configuration, where medial and lateral articulations are positioned in adjacent transverse planes (Figure 1B). This hypothesis assumes that variation in shoulder height is generated primarily by coronal curvature and that extrinsic factors like bone orientation are either approximately constant or unimportant.

A rarely discussed alternative hypothesis is that shoulder height is determined by clavicle orientation, with intrinsic morphology having little effect. There is reason to believe that clavicle coronal curvature has been given unwarranted importance in reconstructing shoulder height. Although human clavicles are described as straight in a comparative context, intraspecific variation is considerable (Matiegka, 1937; Olivier, 1956). Some human clavicles approach the morphology described for non-human apes (compare Figures 1A and 1C). Quantitative measurement shows that the humans and other great apes overlap in coronal curvature and a number of fossils fall within this area of overlap or just slightly outside the human range (Melillo, 2016; Squyres & DeLeon, 2015).

Although the hypothesis linking coronal curvature to shoulder height is based on comparisons among apes (i.e. Figure 1B), it is regularly applied to interpret clavicle morphology within the hominin lineage, including in species of *Homo* (Churchill et al., 2013; Feuerriegel et al., 2017; Larson, 2007, 2009, 2013; Ohman, 1986; Rosas et al., 2016; Voisin, 2001, 2004, 2006a, 2006b). Given the overlap in human and non-human ape morphology and application to the recent hominin fossil record, it is relevant to ask whether human clavicles deviating toward ape-like coronal curvature patterns are associated with a more elevated shoulder. In other words, does the pattern accepted for among-taxa comparisons also hold at a lower taxonomic level?

1.1.2 Scapula protraction

The position of the scapula about the circumference of the thorax (resting scapula protraction) is a focal point in the debate over throwing ability in *H. erectus* (Larson, 2007, 2009, 2015; Roach & Richmond, 2015; Roach et al., 2013). It is also relevant to understanding Neanderthal anatomy. An unusual protraction angle has been suggested for Neanderthals (Rodriguez-Perez et al., 2018; Rosas et al., 2016; Vandermeersch & Trinkaus, 1995), and linked to the dorsal sulcus morphology of the axillary border that characterizes this species (Smith, 1976; Trinkaus, 2008).

[FIGURE 2, 1 COLUMN]

The idea that clavicle length and thorax shape affect scapula protraction is based in part on comparisons across primates. The short clavicle, narrow thorax and laterally positioned scapula of monkeys was contrasted with the long clavicle, broad thorax and dorsally positioned scapula of apes (Miller, 1932; Schultz, 1950). Later researchers aimed to capture interspecific variation in scapula protraction using clavicle length standardized by scapula dimensions (Ashton & Oxnard, 1964), humerus length (Larson, 2007, 2009), body size and thorax breadth (Kagaya, Ogihara & Nakatsukasa, 2010).

Within humans, a pathological condition called hypoplastic clavicle syndrome provides further support for the idea that clavicle length affects scapula position. Affected individuals exhibit abnormally short clavicles. The reduced length of the clavicle is thought to pull the scapula forward to rest in a more protracted position (Beals, 2000).

The hypothesis that shorter clavicles are associated with a more protracted scapula could have a basis in geometry (Figure 2). If the thorax is represented in cross-section as a circle, then the clavicle can be thought of as a chord constrained to intersect that circle first at a common origin along the midline (the sternoclavicular joint) and second at its lateral terminus (the acromioclavicular joint). As the chord becomes shorter, the secondary intersection must shift forward progressively to fully traverse the circle. This corresponds to a more protracted clavicle that would coincide with a shift in scapula position. However, a simple directional relationship holds only when the thorax cross-section is roughly circular (Figure 2A). If the thorax is modeled instead as an anteroposteriorly shallow ellipse, then the relationship is no longer straightforward (Figure 2B).

[FIGURE 3, 1 COLUMN]

Chan (2007) inferred scapula protraction by modeling the components of the shoulder girdle as a thoracoscapuloclavicular (TSC) triangle, with edges comprising a measure of thorax depth, a mediolateral (ML) dimension of the scapula and clavicle length (Figure 3). The law of cosines¹ was applied to calculate the angle of scapula protraction using the edge lengths.

1.1.3 Upper body dimensions

Clavicle length has been used to infer shoulder breadth and thorax dimensions. This includes reconstructions of narrow shoulders and a restricted upper thorax in australopiths (Larson, 2007; but see Haile-Selassie et al., 2016 for a contrasting interpretation), human-like dimensions in *H. erectus* (Bramble & Lieberman, 2004; Roach & Richmond, 2015) and especially broad upper bodies in Neanderthals and their predecessors or in modern human populations living in extreme environments (Carretero et al., 1999; Gomez-Olivencia et al., 2009, 2010; Rosas et al., 2016; Ruff, Niskanen, Junno, & Jamison, 2005; Trinkaus, 1983; Trinkaus et al., 2014; Weinstein, 2007, 2008; but see Voisin, 2004 for a contrasting interpretation). The former reconstructions are related to locomotor adaptations whereas the latter are taken to signal either adaptation to cold climates (Holliday, 1997; Ruff, 1991, 1994) or to increased pulmonary capacity (Churchill, 2006; Franciscus & Churchill, 2002).

Longer clavicles are typically interpreted as indicating larger upper bodies. A positive correlation is expected, but precisely how clavicle length translates to upper body dimensions is unknown (Niskanen & Ruff, 2018). Ruff et al. (2005) called attention to the fact that there is no method for estimating shoulder breadth from skeletal material. It is further unclear whether clavicle length more closely reflects thorax breadth, thorax depth, or overall size (Franciscus & Churchill, 2002).

It is intuitive to use clavicle length as a proxy for shoulder breadth and upper thorax dimensions, because the human clavicle is often depicted as horizontally oriented and spanning the thorax in a coronal plane. However, it is actually elevated from the transverse plane and retracted from the coronal plane. A simple right triangle model (Figure 4; also see Schultz, 1933) illustrates how clavicle orientation is expected to affect the relationship between bone length and the ML distance it spans (effective ML length). As the angles of elevation and retraction increase, the bone's length contributes to shifting the scapula superiorly and posteriorly and contribution to effective ML length is reduced proportionally. This

¹ $\cos \alpha = \frac{b^2+c^2-a^2}{2bc}$

model suggests that the best predictions of upper body dimensions will consider both clavicle length and clavicle orientation.

[FIGURE 4, 2 COLUMNS]

Vrba (1979) proposed a relationship between thorax depth, clavicle-scapula angle and conoid ligament position that has strongly influenced studies of the shoulder and thorax in paleoanthropology. An exercise manipulating a human scapula and clavicle is described to explain why an increase in clavicle-scapula angle (required on a deeper thorax) would be associated with a lateral shift in conoid ligament position:

“If a scapula and clavicle of modern man are oriented towards one another in the normal anatomical position, the areas of closest approach between the clavicle and coracoid are...the attachment areas of the main part of the conoid ligament... If the sternal end of the clavicle is moved forwards in the same horizontal plane, about the fulcrum of the acromioclavicular joint, the areas of closest approach of clavicle and coracoid can be seen to migrate laterally along these two bones (p. 125).”

This proposal underlies Vrba’s (1979) reconstruction of an ape-like upper thorax and scapula position in *Australopithecus africanus*. It was extended to make inferences about thorax shape using observations on the relative position of the clavicle’s conoid tubercle (the medial clavicle ratio discussed by Churchill, 1994a, 1994b)—a finding that is commonly cited in discussions of Neanderthal thorax shape (Franciscus & Churchill, 2002; García-Martínez et al., 2017; Gómez-Olivencia et al., 2010; Gómez-Olivencia et al., 2009, 2012; Holliday, 1997; Trinkaus et al., 2014).

1.2 Objectives

Hypotheses relating clavicle morphology to girdle structure are based on pathological conditions, geometric principles, or primate comparative anatomy. However, few of these proposals have been tested directly. Here, we use data derived from three-dimensional (3D) computed tomographic (CT) scans of living humans to investigate covariation between disarticulated clavicle morphology and the articulated shoulder girdle and upper thorax. The scans allow us to make detailed observations on bone morphology while the bones remain in their in-vivo positions, so that articulated and disarticulated morphology are known for each individual.

We use geometric morphometric (GM) methods to explore and visualize covariation patterns. Regression analysis is used to test existing hypotheses and to construct predictive equations. We evaluate whether the proposed associations exist within living humans and quantifying the relative importance of intrinsic and extrinsic factors in determining structural properties.

2 MATERIALS AND METHODS

2.1 Sample

The CT scans ($n = 58$) were gathered from two sources: the division of diagnostic imagery and intervention radiology at the Berufsgenossenschaftliches Klinikum Bergmannstrost in Halle, Germany and the department of medical imagery at the Hôpital Nord, CHU in Marseille, France. Scans were originally collected in the course of necessary medical care and retrieved retrospectively from hospital databases. They span the region between the neck and mid-thorax. Pixel dimensions range from 0.9 to 1.5 mm and slice interval 0.72 - 1.0 mm. Scans were anonymized, but subject sex and age are known (Supporting Information, Table S1). This study was approved by the ethics commission of the University of Leipzig, Faculty of Medicine.

Ethical considerations surrounding radiation exposure dictated a retrospective design in which patient posture and respiratory status were not explicitly standardized. This design opens the possibility that the shoulder girdle could deviate from its natural resting configuration, artificially inflating variation in our dataset and hindering detection of covariation patterns. This issue was addressed in two ways. First, our scan selection criteria minimized postural differences. All subjects are lying supine with at least one arm adducted. The skeleton was visualized to ensure that the relevant bones were free of trauma and pathology that alter natural bone morphology. We only retained scans meeting the above criteria and showing a natural shoulder posture, as judged by visualizing the body's external surface.

Second, we compared shoulder configuration measurements extracted from our sample to similar measurements reported in a clinical study of healthy females standing in a standardized posture (Culham & Peat, 1993, 1994). This comparison assessed 1) whether measurements were more variable in our sample than in a posture-standardized study and 2) whether mean values were similar between studies. Details of this comparison are provided in the Supporting Information (Text S1 and Tables S2-S3). The comparisons confirm that configuration measurements are similarly variable between studies, but a directional difference exists in measurements relating to girdle elevation/depression. We attribute

this difference to the passive influence of gravity creating a lowered configuration in standing subjects. This directional offset is not expected to impact covariation patterns. The Supporting Information also describes comparison of the two hospital samples (Text S2, Tables S4 and Figures S1-S2).

[FIGURE 5, 2 COLUMNS]

2.2 Surface models, landmarks and scalar measurements

The clavicle, scapula and ribs 1-3² were manually segmented in AVIZO software (version 9.3.0). Threshold boundaries were adjusted to best represent bone surfaces and manually edited where necessary. Surfaces were generated from the segmentations then smoothed in Geomagic Studio (2012). The landmark protocol is presented in Figure 5 and Supporting Information Table S5. Analysis and visualization of landmark data were carried out using the Morpho (Schlager, 2017) and geomorph (Adams, Collyer, Kaliontzopoulou, & Sherratt, 2017) packages in the R platform (R Development Core Team, 2008) and AVIZO. After initial placement, curve landmarks were equidistantly resampled then slid to minimize the thin-plate spline bending energy between each specimen and the Procrustes average shape (Gunz & Mitteroecker, 2013; Gunz, Mitteroecker, & Bookstein, 2005). Configurations were registered via Procrustes superimposition (Rohlf & Slice, 1990). The thin-plate spline (Bookstein, 1989) technique was used to warp surface models to represent the results of GM analyses.

We also collected a number of scalar measurements (Table 1) that isolate morphological features specified in existing hypotheses. Angles and distances were calculated from landmarks or measured directly on the image stack.

The full landmark configuration was originally collected in the in-vivo articulated position. Elements could then be virtually disarticulated to replicate the circumstance of dealing with skeletal remains. To disarticulate the clavicle from the other elements, all non-clavicle landmarks were excluded and the clavicle subset was subjected to a new round of sliding and superimposition. This procedure eliminates variation in clavicle position and orientation, so the resulting dataset only contains information about clavicle size and shape (Figure 5B, C). When the remaining non-clavicle landmarks are re-slid and

² The upper thorax was limited to ribs 1-3 because results pertaining to these ribs can be readily applied to fossils or other skeletal remains. Ribs 1 and 2 are morphologically distinct and can be identified to position with accuracy even where isolated or fragmentary. This is true of rib 3 to a lesser extent.

superimposed, the resulting configuration consists of the articulated scapula and thorax (Figure 5D, E). Articulated configurations combine information on intrinsic morphology and extrinsic factors.

In displaying GM results, meshes representing disarticulated bones are superimposed in the standard manner. Configurations are registered such that displacements are distributed evenly across all landmarks. As a result, there is no reference baseline and registration is concentrated where landmark density is highest. Articulated configurations are difficult to interpret when superimposed in the standard manner. Registration tends to be weighted toward the scapula due to greater landmark density and differences in thorax and clavicle position appear relative to the scapula. This is an undesirable artifact because here we are interested in visualizing displacements of shoulder girdle elements relative to the vertebral column. To address this issue, we took the articulated configurations depicting GM results and registered them along the vertebral landmarks. This procedure makes the vertebral column a comparative baseline for ease of visual interpretation and other displacements appear in reference to the baseline.

[TABLE 1, 2 COLUMNS]

2.3 Covariation

2.3.1 Partial least squares (PLS) analyses

The central question of our study is to what extent an isolated clavicle is informative about the configuration of the shoulder girdle. One can frame this statistically as a question of co-variation between the shape of the isolated clavicle and the remaining articulated bones. Two-block PLS is used to explore covariation when both clavicle and articulated datasets consist of landmarks. This analysis combines investigation of covariation with ordination, which makes PLS a useful tool to explore and visualize the overall pattern of covariation between two highly multivariate datasets (Mitteroecker & Gunz, 2009; Rohlf & Corti, 2000).

We perform three PLS analyses. Block one always contains the isolated clavicle and block two contains a different articulated configuration in each analysis: 1) all elements except the clavicle, 2) the articulated thorax and 3) the scapula plus midline points, which provide a reference to position the bone in articulated space. Changing the articulated configuration in block 2 provides a means to explore how each skeletal component influences covariation pattern and strength.

Covariation patterns are visualized by warping meshes to represent axis extremes. Additional results are reported in table format: singular values (SVs) relate to the proportion of covariation explained by each pair of singular axes, whereas their correlation coefficients (r_{pls}) quantify covariation strength. The likelihood of observing an r_{pls} of a given magnitude under the null hypothesis of no association was assessed by permutation ($n = 500$). Individuals in one block are shuffled randomly relative to the other block, so that the condition of no association is represented by pairing each disarticulated clavicle with the articulated configuration of a different individual (Adams & Collyer, 2016; Rohlf & Corti, 2000). The r_{pls} value is affected by landmark number, rendering comparison unreliable if analyses differ in landmark number. We therefore follow the suggestion of using a standardized Z-score to make such comparisons (Adams & Collyer, 2016).

Although PLS offers many advantages, it has properties that can be undesirable for hypothesis testing. Namely, the aspects of shape identified by the analysis are not predetermined and it is difficult to isolate the effect of a specific morphological feature.

2.3.2 Regression analyses

Regression analysis is used to directly test proposed relationships between predetermined aspects of clavicle and articulated morphology (see section 1.1). In regression analyses, clavicle morphology comprises the predictor variable(s) and response variable(s) concern the articulated structure.

Bivariate least-squares regression is used to assess relationships between two scalar measurements, for instance clavicle length and a univariate measurement of the thorax or ribs. Correlation coefficients are compared to determine which dimensions vary most closely with clavicle length. Bivariate regression is also used to assess the utility of the TSC triangle model, by quantifying the correspondence between observed measurements of scapula protraction and model predictions.

Multiple regression is used to model a univariate measurement of the articulated skeleton as the response of multivariate predictors. In cases where the predictors derive from landmark data, it was necessary to reduce dimensionality via principal components analysis (PCA). We retained all principal components (PCs) accounting for > 5% of the sample variance. In other cases, predictors include multiple scalar measurements or a combination of landmark and scalar data, which permits

investigation into the effect of one predictor with the others held constant. The overall effect size for a multiple regression model is given by the adjusted r^2 . The partial r^2 quantifies effect size of particular predictors³.

Multiple regression was used to test the hypothesis that clavicle shape affects shoulder height. We first modeled either shoulder height or glenoid SI position (defined in Table 1) as a response of clavicle shape (as represented by PCA-reduced landmark data). These models describe the effects of intrinsic clavicle morphology on articulated configuration. We next ran the multiple regressions again, adding clavicle elevation to the predictors. These more comprehensive models describe the combined effects of intrinsic and extrinsic factors on articulated configuration. Comparing models that include both intrinsic and extrinsic predictors to reduced models including only intrinsic predictors provides a way to gauge their relative effects.

We also used multiple regression to investigate whether clavicle orientation influences the relationship between clavicle length and shoulder breadth as expected (see Figure 4). A bivariate model describing the relationship between clavicle length and shoulder breadth is expanded by adding clavicle elevation and retraction as predictors in a multiple regression model. This approach was applied to quantify the effect of intrinsic morphology (clavicle length) with extrinsic factors (clavicle orientation) held constant.

Multivariate regression is used to model the effect of a univariate predictor on a landmark configuration, for instance to investigate the effect of clavicle length on girdle configuration. The full articulated landmark configuration is modeled as the response of either absolute or relative clavicle length (clavicle length / rib 2 centroid size). The overall association between predictor and response in multivariate regressions is tested using a Procrustes ANOVA (Goodall, 1991; Monteiro, 1999), as implemented with the “procD.lm” function in the geomorph package (Adams et al., 2017).

3 RESULTS

3.1 PLS results

³ partial $r^2 = \frac{\text{residual SS}_{\text{reduced}} - \text{residual SS}_{\text{full}}}{\text{residual SS}_{\text{reduced}}}$

[TABLE 2, 2 COLUMNS]

Results describing covariation between clavicle shape and different articulated configurations are presented in Table 2, Figure 6 and Supporting Information Figure S4. The strongest r_{pls} value is obtained when block two contains the scapula plus midline points. A permutation test indicates that correlations of this magnitude are unlikely to occur under the null hypothesis. Comparison of the SA 1 Z-scores indicates that effect sizes are smaller in analyses that include the upper thorax. Thus, clavicle shape co-varies most strongly with scapula shape and its articulated orientation. This is the pattern described in detail below, but covariation patterns are similar in all three analyses.

Landmark displacements for the clavicle block along SA 1 affect the relative magnitude of internal and external curves in the transverse plane (Figure 6A, C) and the magnitude of the inferior curve in the coronal plane (Figure 6B, D). These aspects of clavicle shape co-vary primarily with the shape of the scapula (Figure 6K), its SI position and tilt (Figure 6E-J). At the negative extreme, the internal curve of the clavicle is relatively pronounced (Figure 6A), with minimal curvature in the coronal plane (Figure 6B). The scapula in the corresponding articulated block is inferiorly positioned and lacks anterior tilt. In terms of its intrinsic morphology, the scapular spine and glenoid are cranially oriented and the inferior angle is medially displaced (green mesh in Figure 6K). In addition, the long axis of the glenoid is bent anteriorly to form an obtuse angle with the axillary border (Figure 6K, lateral view). The acromion and coracoid are similarly rotated, such that the acromion overhangs the glenoid and the base of the coracoid projects more anteriorly than superiorly.

At the positive extreme, the clavicle combines a relatively pronounced external curve (Figure 6C) with a single inferior curve (Figure 6D) that is concentrated at the lateral end. The scapula in the corresponding articulated block is superiorly positioned and anteriorly tilted. Within the positive articulated block, the scapula shows a transversely oriented spine and more laterally-facing glenoid (blue mesh in Figure 6K). It lacks rotation of the acromion-glenoid-coracoid complex, but in medial view the superior portion of the blade bends anteriorly, creating a pronounced “subscapular angle” (as described in Gray, 1918).

Therefore, clavicle shape co-varies primarily with scapula shape, but also imparts a small amount of information about articulated configuration. The direction of this covariation is consistent with the expectation that coronally straighter clavicles are associated with a more descended configuration. However, the more superiorly positioned scapula is associated with a clavicle showing inferior coronal curvature but no superior curve of the medial shaft (i.e. a Type 1 clavicle). This finding is inconsistent

with the expectation that the superior curvature of the medial shaft (present in Type 2 clavicles), is responsible for producing a more elevated configuration.

[FIGURE 6, 2 COLUMNS]

3.2 Regression results

3.2.1 Shoulder height

Multiple regression results showed no association between clavicle shape (represented by PCs 1-6, cumulatively accounting for 81.7% variance) and shoulder height ($F = 1.4, p = 0.25$) nor between clavicle shape and glenoid SI position ($F = 1.2, p = 0.33$). When clavicle elevation was included as a predictor, results were highly significant for both shoulder height ($F = 35.5, p < 0.001$) and glenoid SI position ($F = 4.8, p < 0.001$). The effect sizes of clavicle shape are small (partial $r^2 = 0.12$ as predictor of shoulder height, partial $r^2 = 0.11$ as predictor of glenoid SI position) compared to that of clavicle elevation (partial $r^2 = 0.81$ as predictor of shoulder height, partial $r^2 = 0.32$ as predictor of glenoid SI position). These results indicate that, in humans, extrinsic factors are the primary determinants of shoulder height. Clavicle shape by itself has a minimal effect and lacks predictive strength.

The finding that clavicle shape does not predict shoulder height or scapula SI position may seem contradictory to our PLS results (Figure 6). However, these PLS results are showing aspects of shape that co-vary maximally between intrinsic clavicle morphology on one hand and the combination of intrinsic and extrinsic articulated morphology on the other—the contributions of intrinsic and extrinsic factors are entangled in the articulated block. With the multiple regression analyses, we consider intrinsic clavicle morphology as the predictor and a single extrinsic factor is isolated as the response. Thus, the significance of the PLS results is primarily reflecting strong covariation between clavicle shape and scapula shape (see Supporting Information Text S3 and Table S6), whereas covariation between clavicle shape and scapula position is insufficiently strong on its own to be useful in a predictive capacity.

The multiple regression results also highlight that shoulder height and glenoid SI position are distinct properties of girdle configuration. Clavicle elevation accounts for 81% of the variation in shoulder height. The reason for the strong correlation is self-evident, since the predictor and response are different approaches to quantifying the relative positions of the sternoclavicular and acromioclavicular

joints. In contrast, clavicle elevation accounts for only 32% of the variation in glenoid SI position. The moderate strength of this correlation hints at other contributing factors. Rib declination and sternal position are likely important factors (Todd, 1912). Shoulder height describes the relative positions of structures within the girdle—acromioclavicular joint position relative to the sternoclavicular joint. In contrast, scapula SI position concerns shoulder height plus the superoinferior translation of the girdle relative to the vertebral column. Because sternal position determines the position of the proximal clavicle, it follows that individuals with a more inferiorly positioned sternum would also have a more inferiorly positioned scapula, if clavicle elevation were held constant.

To further explore the idea that sternal position is important in determining scapula SI position, we modeled glenoid position as the response of both clavicle elevation and rib declination. Together, these two factors account for 74% of the variation in glenoid SI position ($F = 80.5$, $r^2 = 0.74$, $p < 0.001$) and their effect sizes are roughly equal (partial r^2 clavicle elevation = 0.55, partial r^2 rib declination = 0.62). Further, bivariate regression demonstrates that clavicle elevation and rib declination are independent of each other ($F = 0.03$, $p = 0.86$). Therefore, the superoinferior position of the scapula on the thorax is determined through the combined effects of clavicle elevation and rib declination, which are themselves two independent aspects of girdle configuration.

3.2.2 Scapula protraction

Multivariate regression showed that absolute clavicle length had no effect on the configuration of the articulated shoulder girdle and upper thorax ($F = 1.1$, $p = 0.33$). However, relative clavicle length had a statistically significant effect ($F = 3.9$, $r^2 = 0.07$, $p < 0.01$). Relatively short clavicles are associated with a more protracted and elevated girdle configuration (Figure 7). A bivariate regression confirms the presence and direction of the relationship using scalar data (protraction = $89.08 \times \text{RCL} - 3.38$; $F = 13.7$, $r^2 = 0.20$, $p < 0.001$). The root mean square error (RMSE) indicates that reconstructions using this regression equation will typically have an error of 5.7 degrees. Thus, the relative length of the clavicle is informative with regard to scapula position, whereas absolute length is not.

[FIGURE 7, 1 COLUMN]

We also investigated the utility of the TSC triangle model in predicting scapula protraction. Figure 8 shows a bivariate plot of the predicted and measured angles. The predictions do not successfully approximate the observed angles, although the two values are correlated ($F = 19.5$, $r^2 = 0.25$, $p < 0.001$). If the regression equation were used to convert a predicted angle (which is overestimated to a considerable degree) to a realistic observed value, the RMSE indicates that an error of 5.4 degrees will typically be introduced.

[FIGURE 8, 2 COLUMNS]

3.2.3 Shoulder breadth

Clavicle length is a significant predictor of shoulder breadth (Table 3). The slope indicates a positive isometric relationship. However, individuals can depart considerably from expected values (RMSE = 11.9 mm, residual range: -22.0 to +30.9 mm).

The fit of the model is greatly improved when clavicle orientation measurements are added as predictors. Clavicle length has the largest effect on shoulder breadth (partial $r^2 = 0.65$), but elevation and retraction have considerable effects (both partial $r^2 = 0.48$). An increase in elevation or retraction of one degree has the effect of reducing shoulder breadth by about 1 mm, which is consistent with expectations based on a right triangle. The effective ML length of the clavicle is shorter than its maximum length (typically by about 20-30 mm in our sample). The addition of information on bone orientation does not affect the slope but more than doubles the correlation coefficient, compared to the bivariate model. Accordingly, the RMSE is sharply reduced (7.2 mm).

These results are consistent with existing hypotheses and geometry-based expectations. Shoulder breadth is determined through the interaction of clavicle length and orientation. The most accurate reconstructions of shoulder breadth will be achieved when both clavicle length and orientation are known. In cases where only clavicle length is known, the regression equation (Table 3) can be used to predict shoulder breadth with reasonable accuracy as long as orientation values are expected to fall within the typical human range. The results described here are still informative even in cases where clavicle orientation likely differed from living human values: clavicle length approximates a maximum possible shoulder breadth and the right triangle model can be used to establish a range of estimates that reflect uncertainty in clavicle orientation (i.e. 1-degree changes in orientation alter unilateral shoulder breadth by 1 mm).

[TABLE 3, 2 COLUMNS]

3.2.4 Thorax dimensions

Relationships between clavicle length and thorax dimensions are more complicated and differ depending on whether dimensions are measured from cross-sections of the articulated thorax or from disarticulated ribs. Our results show moderately strong correlations between clavicle length and rib 2 ML dimension or size. The correlation with rib 2 chord is weaker (Table 4). Anteroposterior and ML rib dimensions both scale with clavicle length at roughly $1/3$, whereas overall rib size (a measure that can be approximated by the product of AP and ML dimensions) scales isometrically with clavicle length.

Associations between clavicle length and cross-sectional measurements are much weaker. Among the cross-sectional dimensions, clavicle length is most closely associated with thorax breadth ($r^2 = 0.14$). A closer examination reveals, however, that this relationship is driven primarily by females (Supporting Information Figure S5).

We found no association between clavicle length and thorax depth. This is unexpected, given the results for rib chord. Consideration of extrinsic factors explains why clavicle length co-varies with rib chord but not thorax depth. Chord is an intrinsic dimension of a disarticulated rib, whereas cross-sectional thorax depth is an articulated dimension affected by extrinsic factors. While it is commonly accepted that rib declination reduces thorax depth, our data suggest that rib declination is actually the primary determinate of thorax depth in this sample. Rib chord alone is only very weakly related to thorax depth ($F = 4.5$, $r^2 = 0.08$, $p = 0.04$), but when declination is added as a predictor in a multiple regression model, the correlation coefficient increases to 0.77. The effect of rib declination on thorax depth is 7 times larger than rib chord (partial r^2 chord = 0.11, partial r^2 declination = 0.77). While clavicle length is related to rib chord as a byproduct of scaling with rib size, it is not related to thorax depth because this property is determined by rib declination.

[TABLE 4, 1 COLUMN]

3.2.5 Conoid tubercle position

Bivariate regression supports the idea that deeper thoraxes are associated with wider clavicle-scapula angles, regardless of whether thorax depth is represented by rib chord ($F = 4.99$, $r^2 = 0.08$, $p < 0.05$) or the cross-sectional measurement ($F = 8.4$, $r^2 = 0.13$, $p < 0.01$). However, we found no evidence that the position of the conoid tubercle varies with clavicle-scapula angle ($F = 0.79$, $p = 0.38$) nor with measures of thorax depth (second rib chord: $F = 0.56$, $p = 0.46$; cross-sectional: $F = 0.02$, $p = 0.89$). The medial clavicle ratio was actually notably invariable, showing the lowest coefficient of variation of all the scalar measurements considered in this study. These results show that deeper thoraxes require wider clavicle-scapula angles, but this information cannot be recovered from the medial clavicle ratio.

4 DISCUSSION

This study used CT scans of living humans to investigate covariation between disarticulated and articulated morphology of the shoulder girdle and upper thorax. We identified clavicle features that covary maximally with articulated configurations and tested a number of existing hypotheses that are commonly used to reconstruct the upper body from skeletal remains. A limitation of this study is that we test for the existence of the hypothesized patterns only within humans. While hypotheses based on geometric principles should hold both within and among species, hypotheses based solely on comparisons across primates are incompletely tested. Covariation patterns may not be constant at different taxonomic levels, so the absence of an association within humans does not necessarily mean that the same will be true for inter-taxon comparisons. Still, our results for living humans are clearly relevant to understanding shoulder structure in hominins—particularly because these hypotheses are regularly applied to reconstruct skeletally derived species like *Homo erectus* and Neanderthals, where disarticulated bone morphology falls within or very close to the modern human range of variation. Our investigations showed support for some of the hypotheses (Table 5).

[TABLE 5, 2 COLUMNS]

4.1 Shoulder height

One reason that researchers disagree about when shifts in shoulder height occurred is that there is no consensus about which skeletal features are informative. Clavicle coronal curvature is often discussed in this context (Churchill et al., 2013; Feuerriegel et al., 2017; Hawks et al., 2017; Larson, 2007, 2013;

Melillo, 2016; Ohman, 1986; Rosas et al., 2016; Voisin, 2001, 2004). Humans and non-human apes overlap extensively with regard to coronal curvature and here we investigate whether humans deviating toward an ape-like pattern of curvature show a more elevated configuration.

Our findings indicate that clavicle shape does not successfully predict shoulder height nor scapula SI position in humans. Instead, shoulder height is determined by extrinsic factors and intrinsic morphology has a minimal effect. Qualitative examination of the CT scans help explain this finding (Figure 9).

Although shaft curvature can generate differences in the relative positions of the sternal and acromial ends, these intrinsic effects are overshadowed by the stronger effects of bone orientation. Straight clavicles may show pronounced or minimal elevation and coronally curved clavicles can vary similarly.

[FIGURE 9, 2 COLUMNS]

Previous studies have assumed that the orientation used to compare coronal curvature either approximates in-vivo orientation or that articulated orientation is roughly constant. Given this assumption, intrinsic morphology should translate directly to shoulder height. Our investigations imply that this assumption is incorrect. Indeed, in examining the scans, it is clear that the clavicle's acromial end is not oriented parallel to the horizontal in many of our subjects—it is precisely this variation in bone orientation that is determining variation in shoulder height. Given that the magnitude of variation in clavicle elevation was found to be the same in our subjects and a sample of posture-controlled, standing subjects (Supporting Information Text S1 and Tables S2-S3), we expect that extrinsic factors have the greatest importance regardless of posture.

Shoulder height and scapula SI position are occasionally confounded in the literature, but we demonstrated here that they are distinct aspects of girdle configuration. Our results showed that clavicle elevation and rib declination together determine scapula position, with roughly equal effect sizes. Since clavicle elevation cannot be predicted from the aspects of clavicle shape considered here, attempts to reconstruct scapula position from an isolated clavicle will be imprecise. However, disarticulated ribs contain information about declination (Supporting Information Text S2, Figures S1-S2, also see García-Martínez et al., 2016). Together, these observations highlight how thorax morphology affects shoulder girdle configuration and indicate that isolated ribs can contribute to reconstructing scapula position.

The coronal curvature-shoulder height relationship among hominoids might also be less informative than traditionally thought. Coronal curvature is often dichotomized in a comparative context, which does not accurately reflect the extent of overlap revealed by quantitative analyses of this feature (Melillo, 2016; Squyres and DeLeon, 2015). Further, this variation does not correspond very closely to accepted differences in SI configuration among taxa. Some apes (particularly male orangutans and gorillas) can have straight clavicles, yet we accept that all individuals of these species exhibit elevated shoulders. Some humans can show very curved (i.e. “ape-like”) clavicles, and such morphology occurs with a descended configuration. If an among-taxa relationship is present, its predictive utility is likely limited. More work on shoulder structure in non-human apes is clearly needed, but the balance of current evidence does not support the use of clavicle coronal curvature in reconstructing shoulder height. Currently, scapular morphology appears to be a more reliable indicator of evolutionary shifts in SI configuration. This would tend to support the view that the shoulder had a lowered configuration in *Homo erectus* and its descendants (Larson, 2007, 2009, 2013; Roach, 2013), though this descent may have started much earlier (Melillo, 2015, 2016).

4.2 Scapula protraction

Scapula protraction can be predicted with reasonable accuracy using two different approaches that combine clavicle length with other skeletal dimensions. The first approach employs a simple ratio of clavicle length to rib size. Relatively short clavicles are associated with a more protracted and elevated configuration. However, absolute clavicle length had no effect.

Change in protraction is one adjustment that counteracts a deficiency in clavicle length by reducing the distance that the clavicle must span to reach the scapula. This is consistent with the previously described hypothesis. Another structural adjustment is that the girdle elements can take a more elevated configuration. This configuration may similarly reduce the distance that the clavicle must span, because it traverses the thorax more superiorly where the circumference is smaller. A superior scapula position also creates anterior tilt due to the slope of the upper thorax, which would bring the acromion closer to the sternum and similarly reduce the distance between the clavicle’s distal and proximal articulations.

The element used to standardize clavicle length is important. We use rib size in this study, whereas many observations on hominin relative clavicle length use humerus length (Churchill et al., 2013; Larson,

2007; Larson et al., 2007; Trinkaus, 1983). A convincing argument has been made against using humerus length as a standardizing dimension in the framework of inferring shoulder configuration (Roach & Richmond, 2015; Roach et al., 2013) and our investigations generally support this notion. In the model described above, the directly relevant parameters are the length of the clavicle and the size and shape of the structure it must span. Humerus length would only be useful in cases where it scales isometrically with thorax size, which is not the case for all hominins (Trinkaus et al., 2014). While previous studies reported a clavicle-rib index (Roach & Richmond, 2015), no observations of scapula protraction were reported. Indeed, empirical data describing variation in scapula position is difficult to find. In this study, we quantify this relationship and provide predictive equations. In cases where skeletal individuals exhibit clavicle-rib proportions typical of living humans, a typical scapula position can be inferred.

The TSC triangle model (Chan, 2007) provides another example of using proportions of the clavicle and thorax to reconstruct scapula protraction. Angles predicted by this model overestimated the in-vivo angle. Still, predicted and observed angles were correlated, permitting the regression equation to be used to calculate an in-vivo angle. Individuals with very high or very low predicted angles have correspondingly high or low in-vivo angles and there is little overlap when comparing the extremes (Figure 8B). Individuals falling at opposite extremes can therefore be differentiated in in-vivo protraction angle, making this model most useful in identifying individuals that fall at the extremes or outside the human range of variation.

4.3 Upper body dimensions

4.3.1 Shoulder breadth

We found support for the hypothesis that longer clavicles indicate broader shoulders in humans. We also described how increasing clavicle elevation or retraction decreases shoulder breadth. Together, these findings show how clavicle length can be used in a predictive capacity to reconstruct shoulder breadth.

The existence of a positive, isometric relationship indicates that a given difference in clavicle length will correspond directly to an equivalent difference in shoulder breadth (on average), regardless of the size or sex of an individual. However, the considerable effect of clavicle orientation means that a direct

interpretation (i.e. equating clavicle length to shoulder breadth) is contingent on the condition that variation in clavicle orientation in the theoretical skeletal population falls within intraspecific levels. In other words, two humans exhibiting a 10 mm difference in clavicle length would also tend to differ in unilateral shoulder breadth by about 10 mm. We expect the same would be true of two chimpanzees differing in clavicle length. In contrast, a 10 mm length difference between a human and chimpanzee clavicle would not correspond to the same difference in shoulder breadth, because differences in clavicle orientation between these taxa (Schultz, 1933) exceed an intraspecific level.

Application to skeletal remains necessitates considering whether there is reason to believe that clavicle orientation differed markedly from living humans. For instance, the long clavicles of Neanderthals would indicate especially broad shoulders only if orientation were within typical human values. However, some authors propose that Neanderthals retained an elevated shoulder and that their long clavicles reflect differences in shoulder height rather than breadth (Voisin, 2004). This issue further highlights the importance of reliable reconstructions of shoulder height.

4.3.2 Thorax dimensions

Clavicle length is also commonly related to various thorax dimensions, including overall size, breadth and depth (Franciscus & Churchill, 2002; Trinkaus et al., 2014; Weinstein, 2007). We found that clavicle length is correlated with all thorax dimensions except cross-sectional depth. The strongest associations occur with ML dimensions, followed closely by overall size. However, isolated rib dimensions and cross-sectional dimensions have different relationships with clavicle length. Correlation strengths are reduced when thorax cross-sectional dimensions are considered. Isolated rib measurements are commonly used as a proxy for articulated thorax dimensions, though this practice can be problematic in cases where extrinsic factors are the primary determinants of articulated dimensions (as described here for rib chord and cross-sectional thorax depth). Recent research on Neanderthal thorax morphology has described additional factors that alter rib position and orientation (Bastir et al. 2017; García-Martínez 2017).

We failed to find support for the proposal that conoid tubercle position reflects thorax depth, which contradicts previous reports of covariation in humans (Churchill, 1994a, 1994b). There are methodological differences that could account for the different findings. For instance, this study considers a sample that likely contains less geographic variation. Still, the absence of an association

between conoid tubercle position and thorax depth could be explained in a number of ways. Differences in clavicle-scapula angle could be accommodated without affecting conoid tubercle position through soft tissue differences that permit more or less separation between conoid ligament attachment sites, or through differences in the position or orientation of the coracoid process.

5 CONCLUSION

The shoulder is a complicated region of the skeleton composed of multiple freely articulating components. Shoulder structure is determined by bone size and shape (intrinsic morphology) in conjunction with their orientation and location in articulated space (extrinsic factors). However, researchers working with skeletal remains are typically restricted to making observations on intrinsic morphology alone. This makes shoulder reconstruction a challenging task.

We found that extrinsic factors have large effects on shoulder structure and upper body dimensions, in some cases comparable to or larger than the effects of bone morphology. Still, a number of articulated properties can be predicted. Clavicle length is informative about upper body dimensions. As previously thought, long clavicles reflect wide and large thoraxes, with their associated ecogeographic or respiratory implications. Clavicle length can also be used to reconstruct shoulder breadth, given considerations of clavicle orientation. Scapula protraction, a structural feature that has been related to throwing and manipulatory abilities, can be reconstructed using the combined dimensions of the clavicle, ribs and scapula.

Clavicle shape appears to be less informative. In general, clavicle shape shows weak associations with thorax shape. Further, our investigations do not support the common practice of reconstructing the SI configuration of the shoulder based on clavicle curvature. Shifts in shoulder height constitute a major reorganization of the hominin skeleton that is of great interest in understanding locomotor adaptations, but a reliable way to track these changes is still needed.

The patterns described here are relevant to understanding which parameters of the articulated skeleton can be reconstructed with the greatest accuracy using clavicle morphology. Future work investigating disarticulated-articulated covariation patterns among hominoids will extend efforts to improve

reconstruction methods. Applying these approaches to specific fossil specimens will contribute to testing specific functional hypotheses and to tracking evolutionary changes in the upper body.

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FIGURE LEGENDS

Figure 1. Clavicle coronal curvature and proposed structural effects. (A) Differences among great apes. Human clavicles are described as showing less curvature than those of non-human apes, though authors differ in their descriptions of how this difference is generated. Clavicles are shown in traditional comparative orientation, with the acromial end parallel to the horizontal. These ends are aligned at the horizontal dashed line and the black vertical lines indicate the difference in the relative position of the ends. Ohman (1986) calls attention to any curvature that affects the relative positions of the sternal and acromial ends (compare vertical line lengths), regardless of the curve's direction or location. Alternatively, Voisin (2004, 2006a, 2006b) describes the presence or absence of two curves: a superior curve of the medial shaft and an inferior curve of the lateral shaft. Non-human apes tend to exhibit both superior and inferior curves whereas the typical human clavicle shows a single inferior curve. (B) Differences in coronal curvature are thought to translate directly to differences in shoulder height. In B, the clavicle images are reduced and placed in a schematic articular context without altering orientation. The schematic individuals are aligned at the suprasternal notch (horizontal dashed line) and the vertical red lines indicate the perpendicular distance between this reference and the acromial end (i.e. shoulder height as defined by Schultz, 1929). (C) Variation within humans. Curvature of human clavicle varies in a manner that emulates among-taxon differences. Voisin follows Olivier (1951a, 1956) in organizing variation into different types according to the location and presence of superior and inferior curves. Type 2 clavicles (center-left) approximate the non-human ape pattern in possessing a superior curve medially and inferior curve laterally. Type 1 clavicles, which lack a superior curve, can be straight (left) or exhibit an inferior curve that generates a difference in the relative position ends (center-right). It is unclear whether the shape variation within humans has the same structural effects as that proposed for differences among apes. All specimens are shown in anterior view. In A and B (from left to right) Iziko South African Museum AP-5075, Harvard University Museum of Comparative Zoology 19187, Harvard University Museum of Comparative Zoology 29048, National Museum of Natural History 270807. In C (from left to right), Iziko South African Museum AP-5075, University of Witwatersrand Raymond Dart Collection 3460, Harvard University Peabody Museum 16-5-30/59382.0, Harvard University Peabody Museum 14-2-50/59255.0 (mirrored).

Figure 2. Expected relationship between relative clavicle length and scapula protraction. The clavicle is represented in superior view as a chord intersecting a circle at two points (the sternoclavicular and acromioclavicular joints). The chords are spaced at ten-degree intervals and range from 30 - 90 degrees

retraction (from the coronal plane). Shorter chords are shown in darker colors. To the right, the chords are vertically oriented and aligned to compare their lengths. (A) The thorax is modeled in cross-section as a circle and progressively more protracted orientations correspond to progressively shorter chords. (B) The upper thorax is modeled as an oval. There is comparatively little difference in chord length across different orientations. The expectation holds for the shortest chords (30-40 degrees), but the longest chord (lightest blue) is required at 50 degrees of retraction, and slightly shorter chords are compatible with either a more protracted or a more retracted orientation. Ellipses in A and B have the same area.

Figure 3. The TSC triangle model. (A) The thoracoscapuloclavicular (TSC) triangle model was described by Chan (2007). The grey ellipse represents the articulated thorax in superior view. Triangle edges (black lines) are labeled with their corresponding skeletal elements. The angle of scapula protraction to be estimated is indicated by α . Red and green lines represent coronal and midsagittal planes (respectively). (B) An articulated skeleton showing the dimensions used to represent the triangle edges in this study (clavicle length, scapula-acromion ML and rib 2 chord).

Figure 4. Expected relationships among clavicle length, orientation and upper body breadth. The mediolateral distance spanned by the clavicle, or effective ML length (EML), is the result of an interaction between clavicle length (CL) and orientation (ϑ). (A) A schematic of the body in anterior view. EML length can equal CL only at zero degrees of clavicle elevation (solid black line). With increasing clavicle elevation, EML length becomes smaller than CL. The reduction in EML is proportional to the degree of clavicle elevation, in accordance with the Pythagorean Theorem (dashed lines). (B) The same expectation holds with regard to the effect of clavicle retraction, illustrated in superior view.

Figure 5. Landmark protocol. Fixed landmarks are shown in red and curve (semi)landmarks in gold. (A) Surfaces were segmented from CT scans (left) and the full articulated configuration was measured with elements in their articulated positions (right). Bones were virtually disarticulated in various combinations for subsequent analysis. The subset of clavicle landmarks is shown in anterior (B) and superior (C) views. An articulated configuration of all non-clavicle landmarks is shown in oblique-lateral (D) and posterior (E) views. Fixed landmarks and curves are defined in more detail in the Supporting Information (Table S5). The midsagittal plane (green line in A) was best fit to the midline landmarks and the CT image stack was resampled so that one of the orthoslices paralleled the midsagittal plane. The remaining orthoslices constitute the transverse plane (blue line in A) and the coronal plane (framed in

red). Landmarks used to calculate scalar measurements (see Table 1) are labeled in grey. CL3: the inferior-most projection of the conoid tubercle, CL6: the intersection of the clavicle midline curve and the external surface of the sternal end, CL7: the intersection of the clavicle midline curve and the external surface of the acromial end, SL3: scapular spine-vertebral border junction, SL4: the inferior-most point of the inferior angle, SL8: the inferior-most point of the glenoid, SL9: the superior-most point of the glenoid, SL10: the inferolateral extent of the acromial angle, SL12: the anterolateral extent of the acromial articular surface, RL5: the medial-most point of the rib 2 head, RL 10: the anteroinferior extent of the rib 2 sternal end.

Figure 6. PLS results. Primary covariation pattern between the clavicle (block 1) and articulated scapula and midline points (block 2). The extremes of the first set of singular axes (- SA 1 and + SA 1) are shown in light green and light blue. Clavicle meshes are shown in superior (A, C) and anterior (B, D) views. The scapula is shown in articulated space in anterior (E, F, G) and oblique lateral (H, I, J) views. Articulated configurations are superimposed along the vertebral landmarks. Meshes are aligned at horizontal dashed lines. Clavicles exhibiting a relatively pronounced external curve (C) in combination with a laterally-concentrated inferior curve (D) are associated with a more elevated (F) and anteriorly tilted (I) scapula. The shape of the scapula within block 2 also varies along SA 1, as shown in inset box K where the bones in E-J are aligned at the inferior glenoid for ease of comparison (top row: posterior and lateral views, bottom row: anterior and medial views).

Figure 7. The effect of relative clavicle length on articulated configuration. The results of a multivariate regression of articulated shoulder girdle and upper thorax shape on relative clavicle length are shown in superior (A), anterior (B) and posterior (C) views. The orange and red meshes show the expected articulated configurations corresponding to the minimum and maximum values of relative clavicle length observed in our sample. Relatively short clavicles (orange) are associated with a more protracted and elevated configuration. (D) A bivariate relationship between relative clavicle length and scapula protraction also supports this association. The regression line is shown in green (protraction = $89.08 \times \text{RCL} - 3.38$, $r^2 = 0.20$).

Figure 8. Test of the TSC triangle model. (A) Bivariate relationship between the observed angle of scapula protraction and the angle predicted by the TSC model. The dashed grey line represents identity (predicted = observed) and the regression line is shown in green (observed = $0.64 \times \text{predicted} - 8.70$, $r^2 = 0.25$). The prediction does not successfully approximate the in-vivo observation, but they are

significantly correlated. (B) A box plot of the same data showing the distribution of in-vivo angles binned by predicted angle. Individuals at the extremes of the predicted angle distribution differ in observed angle. However, typical predicted angles (70 – 80°) are compatible with nearly the full range of in-vivo angles.

Figure 9. Determinants of shoulder height and scapula SI position in humans. Shoulder height is determined by clavicle orientation, whereas scapula SI position is determined by the combined effects of clavicle orientation and rib declination. Here variation in clavicle elevation is represented along the vertical axis and rib declination along the horizontal. This morphospace is populated by examples of study subjects. Skeletal structure is shown to the left and the body's external surface (mirror imaged) to the right. Horizontal dashed lines indicate positions of the suprasternal notch and the acromion. Shoulder height is indicated by the solid red vertical line. In-vivo clavicle elevation determines shoulder height directly, as a matter of geometry. Clavicle coronal curvature has minimal effect on this relationship. For example, most of these subjects show a similar pattern and magnitude of coronal curvature but they differ in clavicle elevation and therefore in shoulder height. An enlarged surface model the clavicle is shown below in standardized comparative orientation. Comparison with the scan reveals that the disarticulated orientation does not approximate in-vivo articulated orientation in most cases. Clavicle elevation is independent of rib declination, and their combined effects on scapula position can be concerted or antagonistic. The upper right quadrant shows how rib declination can counteract the effect of a very elevated clavicle. In both antagonistic quadrants, the scapula occupies the commonly-observed position (glenoid at the T1 or T2 level). The upper left and lower right quadrants show clavicle elevation and rib declination working in concert to shift the scapula to an especially superior or inferior position. C7: cervical vertebra 7, T1-3: thoracic vertebrae 1-3.