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1 New Neandertal wrist bones from El Sidrón, Spain (1994-2009)

2

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1 **Abstract**

2 Twenty-nine carpal bones of *Homo neanderthalensis* have been recovered from the site
3 of El Sidrón (Asturias, Spain) during excavations between 1994–2009, alongside ~2500 other
4 Neandertal skeletal elements dated to ~49,000 years ago. All bones of the wrist are
5 represented, including adult scaphoids ($n = 6$), lunates ($n = 2$), triquetra ($n = 4$), pisiforms ($n =$
6 2), trapezia ($n = 2$), trapezoids ($n = 5$), capitates ($n = 5$), and hamates ($n = 2$), as well as one
7 fragmentary and possibly juvenile scaphoid. Several of these carpals appear to belong to the
8 complete right wrist of a single individual. Here we provide qualitative and quantitative
9 morphological descriptions of these carpals, within a comparative context of other European
10 and Near Eastern Neandertals, early and recent *Homo sapiens*, and other fossil hominins,
11 including *Homo antecessor*, *Homo naledi*, and australopiths.

12 Overall, the El Sidrón carpals show characteristics that typically distinguish Neandertals
13 from *Homo sapiens*, such as a relatively flat first metacarpal facet on the trapezium and a more
14 laterally oriented second metacarpal facet on the capitate. However, there are some distinctive
15 features of the El Sidrón carpals compared with most other Neandertals. For example, the
16 tubercle of the trapezium is small with limited projection, while the scaphoid tubercle and
17 hamate hamulus are among the largest seen in other Neandertals. Furthermore, three of the six
18 adult scaphoids show a distinctive os-centrale portion, while another is a bipartite scaphoid with
19 a truncated tubercle. The high frequency of rare carpal morphologies supports other evidence of
20 a close genetic relationship among the Neandertals found at El Sidrón.

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23

1 **1. Introduction**

2 The El Sidrón Cave site (Asturias, Spain) has yielded over 2500 Neandertal (*Homo*
3 *neanderthalensis*) skeletal elements from at least 13 individuals, making it the largest sample of
4 this taxon in the Iberian Peninsula (Fortea et al., 2003; Rosas et al., 2006, 2015; Bastir et al.,
5 2010). These remains were recovered from the El Sidrón karst system and have been dated to
6 49,000 years ago based on direct radiocarbon dating of a Neandertal bone fragment (Wood et
7 al., 2013), as well as electron spin resonance, optically stimulated luminescence, and amino
8 acid racemisation of the Neandertal remains and surrounding sediments (de Torres et al.,
9 2010). The total sample represents seven adults, three adolescents, two juveniles, and one
10 infant, and all skeletal elements are represented (Rosas et al., 2006, 2013). Geological,
11 archaeological, and paleontological evidence suggests that these individuals likely represented
12 a contemporaneous social group of Neandertals (Rosas et al., 2006; Santamaria et al., 2010).
13 Genetic analyses confirm that these individuals represented a small, patrilocal community with
14 low genetic diversity (Lalueza-Fox et al., 2010). Congenital defects are also present in the
15 sample and likely reflect the low genetic diversity within this social group (Dean et al., 2013;
16 Ríos et al., 2015).

17 Several morphological studies of the El Sidrón Neandertals have been conducted,
18 including analyses of the crania (Rosas et al., 2008; Bastir et al., 2010; Pena-Melian et al.,
19 2011), dentition (Rosas et al., 2006, 2013; Dean et al., 2013), ribs (Bastir et al., 2015, 2017),
20 clavicles (Rosas et al., 2016), humeri (Rosas et al., 2015) and tali (Rosas et al., 2017). Among
21 the preserved Neandertal remains at El Sidrón are multiple hand bones, including carpals,
22 metacarpals, and phalanges that were discovered between 1994 and 2009. Like the whole El
23 Sidrón sample, the hand remains were recovered from a restricted area in the Galeria del
24 Osario within the El Sidrón cave system (Fig. 1). The carpals, metacarpals, and phalanges were
25 found mixed with the rest of the skeletal elements without any special distribution (F5, F7, F8,
26 F9, G6, and G8 m² of the archaeological excavations; Fig. 1). Although the handedness of the
27 El Sidrón individuals has been addressed through analyses of their dentitions, showing a right-
28 hand preference (Estalrich and Rosas, 2013), the hand bones have not yet been described.
29 Here we describe and analyze the El Sidrón carpals, including 29 specimens representing all
30 eight carpal elements, and compare them with those of other European and Near Eastern
31 Neandertals, recent and early *Homo sapiens*, other *Homo* taxa, and australopiths.

32 33 **2. Materials and methods**

1 All of the El Sidrón carpal bones were compared qualitatively and quantitatively to a
2 sample of female and male recent modern humans (*H. sapiens*), including Europeans, small-
3 bodied Khoisan, and skeletally robust Tierra del Fuegians, and a sample of fossil hominins
4 (Table 1). The morphometric variables used for the comparative analyses are listed in Tables
5 2–9 and images of these measurements are provided in the box-and-whisker plots (see below)
6 and elsewhere (Kivell and Begun, 2009; Begun and Kivell, 2011; Kivell et al., 2013a, b). All
7 measurements were collected by one of us (TLK) on original specimens or surface models of
8 original specimens, apart from the following specimens: the Shanidar 4 and La Chapelle
9 capitates and the Regourdou 1 triquetrum, pisiform, and hamate, for which measurements were
10 derived from surface models of casts. Measurements on 3D surface models were taken in
11 Avizo® 6.3 (FEI Visualization Sciences Group). Furthermore, data for some Shanidar carpals
12 and all of the early *H. sapiens* Dolní Věstonice specimens were obtained from Trinkaus (1983)
13 and Sladek et al. (2000), respectively. Table 1 provides the details and sources of the
14 comparative sample.

15 Since body mass is typically not available for fossil specimens or most extant specimens
16 in comparative collections, each morphometric variable was divided by a geometric mean
17 derived from a subset of variables on each carpal bone to adjust for carpal size (i.e., to create
18 shape ratios; Mosimann, 1970; Jungers et al., 1995). For all carpals, a geometric mean was
19 derived from the maximum mediolateral (ML) breadth, dorsopalmar (DP) height, and
20 proximodistal (PD) length of the bone, unless otherwise stated. We investigated variation in the
21 shape ratios (with sexes pooled) visually via box-and-whisker plots and principal components
22 analysis (PCA) using a variance-covariance matrix. We used Spearman's rank correlation to
23 test for potential significant correlations between the geometric mean and shape ratios (only
24 significant correlations are reported). All statistical analyses were conducted in PAST.3.14
25 (Hammer et al., 2001).

26

27 **3. Anatomical description of the El Sidrón carpal bones**

28

29 *3.1. Scaphoids (Table 2, Fig. 2)*

30 SD-744 right scaphoid *Preservation*. This bone is largely complete and generally well-preserved
31 apart from the distomedial region. There is a large fragment missing from the distomedial border
32 that reaches proximally to the capitate facet. Much of the capitate articular surface is eroded but
33 trabeculae are not exposed. Small fragments are missing from the proximopalmar portion of the
34 capitate facet and distal and medial regions of the tubercle.

1 *Morphology.* This scaphoid is large both DP and PD. The tubercle is long and robust, especially
2 at its base. The trapezium-trapezoid articulation extends almost to the tip of the tubercle and the
3 relatively flat trapezium facet is distinguished from the smaller trapezoid facet by a slight
4 concavity and change in orientation. The radial facet is DP taller than it is PD long and mildly
5 convex throughout. There is a deep groove between the radial and trapezoid facets. The
6 borders of the lunate facet are poorly defined, but it is PD narrow and DP tall and extends along
7 the proximomedial edge of the scaphoid to roughly the middle of the capitate facet. The
8 capitate facet is oval-shaped, being DP taller than it is PD long, and shallowly concave.

9

10 SDR-064 left scaphoid *Preservation.* This bone is largely complete, but there are large
11 fragments missing from the middle and distal portions of the capitate facet and the base of the
12 tubercle, exposing trabeculae in some regions. Portions of the dorsal and palmar borders of the
13 capitate facet are preserved such that the maximum dimension of the articular surface is clear.
14 The remainder of the bone is well-preserved.

15 *Morphology.* The morphology of this scaphoid is similar to that described for SD-744 but with
16 some important differences. There is a small, semi-circular projection roughly midway along the
17 distal border of the scaphoid body that is similar to a morphological condition found rarely in
18 modern humans and described here as a distinct os centrale portion (Leboucq, 1884; Dwight,
19 1907; Virchow, 1929). What is preserved of the capitate facet suggests that it is slightly more
20 concave than SD-744. The trapezium facet morphology is similar to SD-744, but what is
21 preserved of the trapezoid facet suggests that the articular surface was concavo-convex.

22

23 SD-96 right scaphoid *Preservation.* This bone is largely complete, apart from a large fragment
24 missing from the proximolateral half of the bone, exposing trabeculae. There is also a crack
25 running PD through the capitate and trapezoid facets at roughly the midline. Small fragments
26 are missing from the proximolateral border of its truncated tubercle, the distolateral corner of the
27 capitate facet, and from the most lateral point of the trapezoid facet, exposing trabeculae.

28 *Morphology.* This specimen differs from the other El Sidrón scaphoids in that the tubercle is
29 truncated at its base, 6.6 mm from the most palmar extent of the capitate facet. The tubercle
30 ends with a smooth, flat, square-shaped facet, measuring 8.3 mm in PD length and 11.0 mm in
31 ML breadth, that is mostly palmarly and slightly laterally oriented. This morphology is consistent
32 with a bipartite scaphoid that has been described in modern humans, in which separate
33 ossification centers have been retained as separate bones in adulthood (Dwight, 1907). An
34 associated separate tubercle or equally unusual trapezium have not yet been found at the El

1 Sidrón site. This unusual morphology alters the trapezium-trapezoid articulation as well; they
2 are not continuous, unlike in the other scaphoid specimens. What is presumed to be the
3 trapezium facet is complete (although it likely continued onto the associated portion of the
4 bipartite scaphoid), small, and triangular shaped, measuring 9.8 mm in PD length and 6.0 mm in
5 DP height. It is oriented at a strong angle to the truncated tubercle facet, such that it is primarily
6 medially oriented. There is a deep sulcus and change in orientation distinguishing it from the
7 trapezoid facet, which is relatively flat and appears “raised” from the body of the scaphoid. The
8 trapezoid articulation is more distopalmarly oriented and measures 12.5 mm in maximum DP
9 height and 8.8 mm in ML breadth. The radial and capitate facets are relatively PD longer than
10 that of the other El Sidrón scaphoids, such that the overall shape is more round rather than
11 oval-shaped. The distal border of the capitate facet is “open” (Tocheri, 2007), despite the
12 idiosyncratic morphology. The lunate facet is poorly defined but also appears to be distinct from
13 the other scaphoids in being limited to the dorsal portion of the scaphoid, rather than extending
14 along the proximal border of the scaphoid.

15

16 SD-110 right scaphoid fragment, possibly juvenile *Preservation*. This specimen is most likely a
17 proximodorsal fragment of a right scaphoid, preserving a portion of the lunate facet and the
18 proximodorsal borders of the capitate and radial facets. The entire preserved surface, apart
19 from the lunate facet, is porous and the facets are poorly defined.

20 *Morphology*. This fragment measures 13.2 mm in DP height, 9.9 mm in PD length, and 7.1 mm
21 in ML breadth. This bone is identified as a scaphoid fragment based on the preservation of
22 slightly concave articular surface, a medially and proximally oriented articular facet, and a
23 convex laterally oriented facet that are consistent with capitate, lunate, and radial articular
24 surfaces, respectively. Its small size, poorly defined facets, and porous cortex together suggest
25 that this specimen could be juvenile. This morphology is consistent with human scaphoid
26 development between 6–10 years of age (Baker et al., 2005; Kivell, 2007). However, the bone is
27 ML thick at the capitate-radial facet border, suggesting it could be from a small adult but with a
28 strongly eroded surface.

29

30 SD-258 left scaphoid *Preservation*. This bone is complete and well-preserved. There are small
31 fragments missing from the distomedial corner of the tubercle base and the proximal border of
32 the capitate facet, exposing trabeculae. There is a crack exposing trabeculae along the non-
33 articular area between the radial facet and tubercle of the scaphoid’s proximal surface.

1 *Morphology.* This bone is most similar in its morphology to that described above for SDR-064,
2 primarily because it also preserves a small, semi-circular projection or distinct os centrale
3 portion along the distal border of the scaphoid. This morphology is better preserved in SD-258
4 than in SDR-064. The projection acts to “close” the distal border of the capitate facet (Tocheri,
5 2007) more so than in the other El Sidrón scaphoids that lack this morphological feature and
6 makes the capitate facet appear more deeply concave. This projecting os centrale portion also
7 creates a unique morphology of the trapezoid facet. Distally, the trapezium and trapezoid facets
8 are continuous and each measures 13.4 mm and 11.1 mm in their maximum dimension (DP
9 height), respectively. However, the trapezoid articular area is strongly concavo-convex and can
10 be divided into three regions: (1) it is distinguished from the trapezium facet by a concavity at
11 the palmar-lateral region, (2) a mildly convex and distally oriented dorsomedial portion, and (3) a
12 generally flat and more laterally oriented dorsolateral region that extends onto the projecting os
13 centrale portion. The scaphoid tubercle is extremely robust, especially at its base, and less
14 proximally oriented than SDR-064.

15
16 SD-679b left scaphoid fragment *Preservation.* This specimen preserves only the dorsal half of
17 the scaphoid, including the lunate facet, most of the radial and capitate facets apart from their
18 proximal borders, and part of the trapezoid facet. The scaphoid is broken dorsal to the base of
19 the tubercle, exposing trabeculae. There is a fragment missing from the proximal border of the
20 radial facet that distorts the full extent of the lunate facet.

21 *Morphology.* The preserved morphology of this specimen measures 18.1 mm in DP height, 15.1
22 mm in PD length, and 8.0 mm in ML breadth. The morphology preserved in this specimen is
23 most similar to SD-258 because it has a projection or distinct os centrale portion along its distal
24 border. There is an indentation between the radial facet and os centrale portion that
25 accentuates its projection distally. The preserved area of the trapezoid facet is distolaterally
26 oriented and generally flat.

27
28 SD-1243 left scaphoid *Preservation.* This scaphoid is complete and well-preserved, apart from a
29 small fragment missing from the distal border of the capitate facet and erosion of the cortex from
30 most of the trapezoid facet and non-articular region between the radial and capitate facets,
31 exposing trabeculae.

32 *Morphology.* The overall morphology of SD-1243 is similar to that described for SD-744,
33 although it is absolutely smaller in its DP and PD dimensions. The distal border of the capitate
34 facet is not complete, but the preserved morphology and relatively small trapezoid facet suggest

1 that this border is “open” (Tocheri, 2007) and that this specimen did not have a small, distal
2 projection like that of SDR-064, SD-258, and SD-679b.

3 4 *3.2 Lunates (Table 3, Fig. 3)*

5 SD-85 right lunate *Preservation*. This bone is complete and well-preserved. There are small
6 fragments of cortex missing from the palmar-medial edge of the capitate facet and the palmar
7 border of the triquetrum facet.

8 *Morphology*. This lunate is ML broad, making its breadth relatively equal with its DP height and
9 PD length and giving the bone an overall round shape. The scaphoid facet is positioned roughly
10 at the DP midline of the lunate’s lateral side. The scaphoid facet is flat, DP short and PD narrow,
11 and primarily laterally oriented at a roughly 90° angle to the capitate facet. The palmar portion of
12 the scaphoid facet is more distally oriented than the dorsal portion, such that it can be seen from
13 the distal view of the bone. The distal articulation has separate facets for the capitate and
14 hamate that blend into one another; the hamate facet is distinguished by a slightly more medial
15 orientation, measuring 9.7 mm in DP height and 4.4 mm in ML breadth. The triquetrum facet is
16 generally flat and rectangular in shape. The radial facet dominates the proximal view of the
17 lunate. It is ML broad and continuously convex both DP and ML.

18
19 SD-1011a right lunate *Preservation*. This bone is complete and well-preserved, apart from
20 erosion of the cortex on its medial side, obscuring the full extent of the triquetrum facet, a thin
21 fracture running DP roughly through the sagittal midline of the radial facet, a crack in the cortex
22 along the dorsomedial edge of the radial facet, exposing trabeculae, and damage to the non-
23 articular cortex of the palmar surface.

24 *Morphology*. This bone is slightly larger in absolute size than SD-85, but its overall morphology
25 is identical, apart from a few minor differences. The palmar portion of the scaphoid facet is
26 slightly more distally oriented and the hamate facet is also more distinct from the capitate facet
27 by being slightly more medially oriented than in SD-85.

28 29 30 *3.3 Triquetra (Table 4, Fig. 4)*

31 SD-1227 left triquetrum *Preservation*. This bone is almost complete and generally well-
32 preserved. It is missing the most medial portion of the body, truncating the medial edges of the
33 pisiform and hamate facets, although the overall size of the morphology can be confidently
34 estimated. The cortex is eroded at the palmar and dorsal corners of the hamate facet’s lateral
35 edge.

1 *Morphology.* This bone is squat in its overall shape, being DP tall but ML narrow, such that the
2 overall shape in distal or proximal view is roughly that of a right-angled triangle. The lunate facet
3 is oriented at a right angle to the hamate facet, and is flat and triangular-shaped (the palmar
4 portion is PD longer and then tapers dorsally). The hamate facet, like the overall shape of the
5 triquetrum body, is ML short and DP tall. It is mildly concave DP and mildly convex at the
6 dorsomedial border. The pisiform facet is positioned approximately 3.0 mm from the lateral edge
7 of the triquetrum body, and is flat, palmarly oriented, and oval-shaped (slightly ML broader than
8 it is PD long). The non-articular proximomedial surface is excavated by a deep pit for the ulnar
9 collateral ligament attachment.

10

11 SD-58 right triquetrum *Preservation.* This triquetrum is missing most of its proximal and medial
12 cortical surface and part of the lateral surface, exposing trabeculae. The cortex is eroded from
13 the proximopalmar portion of the lunate facet, and the proximal and lateral borders of the
14 pisiform facet are not preserved, while the hamate facet is generally complete.

15 *Morphology.* The preserved morphology of this bone is virtually identical in size and shape to
16 that described above for SD-1227.

17

18 SD-1022a left triquetrum *Preservation.* This bone is missing a large fragment from its palmar-
19 medial corner such that none of the pisiform facet is preserved. The lunate and hamate facets
20 are generally complete and most of the non-articular proximal surface is preserved.

21 *Morphology.* This bone is slightly smaller in absolute size than other triquetra in the El Sidrón
22 sample, but the morphology is similar to that described for SD-1227. Morphological differences
23 include a more rectangular-shaped lunate facet and that the non-articular bulbous portion of the
24 palmar-lateral corner of the proximal surface is not as pronounced. Although much of the palmar
25 and medial portions of the triquetrum are missing, the preserved morphology indicates a
26 similarly stout overall shape as seen in SD-1227 and SD-58 (but unlike SD-1813, see below).

27

28 SD-1813 right triquetrum *Preservation.* This triquetrum is missing most of its palmar-lateral
29 portion, such that the palmar portion of the lunate and hamate facets is not preserved, but is
30 otherwise complete.

31 *Morphology.* The morphology of this triquetrum differs from that of the remaining El Sidrón
32 triquetra in several aspects. The overall shape of the triquetrum body is ML broader and DP
33 shorter. The hamate facet is also ML broader and appears DP shorter, and is slightly more
34 dorsally oriented than the hamate facets of the other triquetra. The medial border of the hamate

1 facet curves sharply onto a smooth medial surface of the triquetrum body. Although much of the
2 palmar-lateral surface is eroded, it is clear that the pisiform facet is more medially positioned on
3 the triquetrum body and is slightly more medially oriented (rather than directly palmarly
4 oriented). The lunate facet is slightly more PD convex, but the preserved morphology suggests
5 a generally triangular-shaped facet as in the other triquetra.

6 7 *3.4 Pisiforms (Table 5, Fig. 4)*

8 SD-29 right pisiform *Preservation*. This bone is complete and well-preserved, apart from erosion
9 of the cortex on the lateral, non-articular surface that exposes trabeculae.

10 *Morphology*. This pisiform is considered to be from the right side based on siding methods
11 outlined in Baker et al. (2005). This bone is pea-shaped. The triquetrum facet is well-defined,
12 oval-shaped (longer PD and shorter ML), mildly concave throughout its PD length, and
13 proximally positioned on the dorsal surface of the pisiform body.

14
15 SD-646 right pisiform *Preservation*. This bone is complete and well-preserved. The cortex is
16 eroded from the dorsal surface of the non-articular region and distal edge of the triquetrum
17 facet, and from the distal half of the lateral side, exposing trabeculae.

18 *Morphology*. This bone is slightly larger and more robust than SD-29, but otherwise the
19 morphology is identical.

20 21 *3.5 Trapezia (Table 6, Fig. 5)*

22 SD-373 right trapezium *Preservation*. This bone is complete and perfectly preserved.

23 *Morphology*. This trapezium has a saddle-shaped (concave ML and convex DP) first metacarpal
24 (Mc1) facet that is broad and relatively flat. The trapezium tubercle is not robust and does not
25 project strongly either palmarly or laterally. Similarly, the sulcus for the flexor carpi radialis
26 tendon is shallow. The scaphoid facet is large and rectangular-shaped compared to the smaller
27 trapezoid facet. Both facets are ML broader than they are DP tall. The Mc2 facet is rectangular
28 in shape, being PD longer than it is DP tall, and faces distomedially.

29
30 SD-2019 right trapezium *Preservation*. This bone is missing its tubercle, but is otherwise
31 complete and well-preserved. The cortex is eroded at the proximal edge of the non-articular
32 dorsal surface and at the junction of the scaphoid and trapezoid facets, exposing trabeculae.

33 *Morphology*. The preserved morphology of this bone is identical to that described for SD-373.
34 Although the tubercle is missing, the preserved base of the tubercle suggests that it was likely

1 small like that of SD-373, and the flexor carpi radialis tendon sulcus is similarly shallow. The
2 Mc1 facet is less well-defined along its palmar border but is clearly expanded and of the same
3 general morphology as that described in SD-373.

4 5 *3.6 Trapezoids (Table 7, Fig. 6)*

6 SD-28 right trapezoid *Preservation*. This bone is complete and well-preserved apart from
7 erosion of the cortex at the dorsal edge of the lateral Mc2 facet and at the dorsal junction
8 between the trapezium and scaphoid facets, exposing trabeculae.

9 *Morphology*. This bone has an expanded non-articular palmar surface and an overall “boot-
10 shape.” The Mc2 articulation is relatively flat, such that the articular surface is primarily distally
11 oriented and there is no distinct ridge between the (larger) medial and lateral sides of the facet.
12 A flat, well-defined trapezium facet occupies most of the lateral surface. Proximally, the
13 scaphoid facet is large, mildly concave, roughly triangular-shaped, and DP taller than it is ML
14 broad. Medially, SD-28 has two capitate facets; a smaller dorsal facet and larger palmar facet
15 that measure 3.6 mm and 6.1 mm in PD length and 4.3 mm and 4.9 mm in DP height,
16 respectively. The capitate facets are separated by a deep attachment for the capitotrapezoid
17 interosseous ligament. In dorsal view, the non-articular surface is diamond-shaped, being
18 roughly equally broad in its PD length and ML breadth.

19
20 SD-94 right trapezoid fragment *Preservation*. The specimen preserves the dorsolateral portion
21 of a right trapezoid. The dorsodistal portion of the trapezium facet, dorsolateral portion of the
22 lateral Mc2 articulation, and the majority of the non-articular dorsal surface is preserved.

23 *Morphology*. The limited morphology that is preserved in this specimen is similar to that
24 described for SD-28, although its overall size is smaller. The preserved morphology measures
25 10.7 mm in DP height, 11.9 mm in PD length, and 10.9 in ML breadth.

26
27 SD-104 left trapezoid fragment *Preservation*. This specimen preserves only the dorsal non-
28 articular surface and dorsal border of the scaphoid facet.

29 *Morphology*. The shape of the dorsal surface is similar to that described for SD-28. The overall
30 size is smaller than SD-28 and more similar to SD-94.

31
32 SD-529 right trapezoid *Preservation*. This bone is complete and generally well-preserved, but
33 the cortex is slightly abraded such that the articular facets on the proximal and medial sides are
34 not well-defined.

1 *Morphology.* This trapezoid is substantially smaller than SD-28, but its overall morphology is very
2 similar. The few differences in morphology include a less expanded non-articular palmar portion
3 (although the overall boot-shape is clear) and an Mc2 facet that is even flatter than in SD-28,
4 with little variation in the orientation of the medial and lateral portions of the facet. The medial
5 trapezoid surface is PD short and is slightly abraded, but it does not appear to have a separate
6 dorsal capitate facet as in SD-28. The palmar half of the medial side is dominated by an
7 expanded, rectangular shaped capitate facet measuring 6.3 mm in DP height and 4.0 mm in PD
8 length.

9

10 SD-1022b left trapezoid *Preservation.* This bone preserves the dorsal and lateral portions of a
11 left trapezoid, but the cortex is strongly abraded, obscuring much of the morphology. Most of
12 the lateral portion of the scaphoid facet, the proximal portion of the trapezium facet, and the
13 dorsolateral corner of the Mc2 facet are preserved, but none is complete.

14 *Morphology.* The preserved morphology of SD-1022b and its overall size is similar to that
15 described for SD-28.

16

17 *3.7 Capitates (Table 8, Fig. 7)*

18 SD-1034 left capitate *Preservation.* This bone is complete and perfectly preserved apart from a
19 crack at the most proximomedial extent of the scaphoid facet on the capitate head and erosion
20 of the cortex at the most dorsal border of the lunate facet, exposing trabeculae.

21 *Morphology.* This is a robust and squat capitate, appearing DP tall and ML broad for its PD
22 length, with minimal capitate “waisting.” The palmar portion of the capitate body is robust. The
23 lateral portion of the non-articular dorsal surface is strongly indented, creating a “scooped”
24 dorsal outline in sagittal view. The lunate and scaphoid articular regions are clearly defined,
25 such that the lunate facet is flat in its dorsal outline and slightly medially oriented, while the
26 scaphoid facet is round in dorsal view and laterally expanded. In proximal view, the lunate facet
27 is DP shorter than the scaphoid facet. In lateral view, the scaphoid facet extends distally to the
28 PD midline of the capitate’s body, and its dorsal portion is continuous with a small, dorsal
29 trapezoid facet, measuring 5.5 mm in PD length and 3.3 mm in DP height. The dorsal trapezoid
30 facet is separated by a non-articular sulcus from a larger palmar trapezoid facet, measuring 4.7
31 mm in PD length and 6.9 mm in DP height. The dual dorsal and palmar trapezoid facets are
32 consistent with dual capitate facets present on the right SD-28 trapezoid.

33 The Mc2 facet can be clearly seen in lateral view. It is a single, large articulation that
34 extends most of the DP height of the capitate body and is DP concave. The palmar half of the

1 facet is more distally oriented than the dorsal half, but overall the facet is primarily laterally
2 oriented. The Mc2 facet angle, defined as the angle between the Mc2 and Mc3 facets
3 (Niewoehner et al., 1997; their “CMC2A”), is approximately 71°, reflecting a primarily laterally
4 facing facet. In distal view, the Mc3 articulation is triangular in outline and generally smooth,
5 with a slight concavity at the palmar-medial edge. The dorsolateral corner of the Mc3 facet is
6 truncated, convex, and more proximally oriented, making room for a short styloid process on the
7 base of the Mc3.

8 In medial view, that hamate facet is PD concave and is divided into two parts; the
9 proximal $\frac{3}{4}$ is separated from the distal $\frac{1}{4}$ by a narrow non-articular region, such that the
10 hamate articulation is connected only via a thin strip along the dorsal border.

11

12 SD-557 right capitate *Preservation*. This bone is complete and generally well-preserved apart
13 from the lateral side. There is a fragment missing from the palmar-lateral border of the scaphoid
14 facet and much of the cortex is abraded at the most distal extent of the scaphoid articular
15 surface. A large fragment is missing from the lateral border of the Mc3 articulation such that all
16 of the Mc2 facet and (potential) dorsal trapezoid facet are missing, and part of the palmar
17 trapezoid facet is obscured.

18 *Morphology*. This bone is slightly smaller in overall size compared with SD-1034, but otherwise
19 the preserved morphology is very similar. Its smaller size is likely accentuated by its poorer
20 preservation, and the size variation between SD-557 and SD-1034 is consistent with bilateral
21 asymmetry within a single individual. This specimen better preserves the distodorsal extent of
22 the proximal articulation than in SD-1034. The lunate facet does not extend far distally onto the
23 dorsal surface, and relative to the hamate facet, the lunate facet is more medially oriented such
24 that its distal border runs obliquely across the dorsal surface of the capitate.

25

26 SDR-063 left capitate *Preservation*. This specimen preserves only the medial and proximal
27 regions of a left capitate. All of the capitate head is preserved, apart from the most distal extent
28 of the scaphoid articulation on the lateral side. Medially, the proximal $\frac{3}{4}$ of the hamate facet and
29 most of the non-articular palmar region of the body is preserved.

30 *Morphology*. This bone is slightly smaller in overall size than SD-1034 and SD-557. The
31 preserved morphology is generally similar to that described for SD-1034, but with a few subtle
32 distinctions. In lateral view, there is a deep and PD longer non-articular region dividing the
33 palmar scaphoid and trapezoid articular regions. The palmar trapezoid facet is less expansive; it
34 is a narrow oval-shaped facet, measuring 2.6 mm in PD length and an estimated 5.2 mm in DP

1 height. The capitate is broken along the dorsal edge of the trapezoid facet, but the preserved
2 morphology appears to be the full extent of the facet. Only the palmar 1/3 of the Mc2 facet is
3 preserved (measuring 5.5 mm in PD length and 5.3 mm in DP height), but it is more laterally
4 oriented than the slightly more distally oriented morphology of SD-1034. The oblique, medially
5 oriented distodorsal border of the lunate facet is more pronounced than that of SD-557.

6
7 SD-400 right capitate head *Preservation*. This specimen preserves only the majority of the
8 capitate head and a small portion of the palmar non-articular surface. There is a large fragment
9 missing from the palmar surface of the scaphoid facet and a fracture running obliquely through
10 the proximopalmar portion of the hamate facet.

11 *Morphology*. The preserved morphology suggests that this specimen was roughly the same size
12 as SD-1034 and SD-557. The limited preserved morphology is identical to that described for
13 SD-1034.

14
15 SD-632a left capitate *Preservation*. This specimen preserves only the dorsal portion of the
16 capitate and is broken (and refitted) obliquely across the approximate PD midline of the capitate
17 body. Most of the dorsal surface is preserved, albeit the cortex is eroded in some areas, as well
18 as the dorsal portions of the proximal head, hamate, and metacarpal facets, and the non-
19 articular surface on the lateral side. There is general abrasion of the lateral capitate surface
20 obscuring some of the articular morphology.

21 *Morphology*. This bone is slightly smaller in overall size than SDR-063. The preserved
22 morphology is generally similar to that described for SD-1034. Abrasion of the lateral surface
23 makes it impossible to determine if there is a separate dorsal articulation for the trapezoid. Most
24 of the Mc2 facet is preserved, measuring 9.3 mm in DP height and 4.9 mm in PD length (but it is
25 not complete), and mildly concave DP. It is primarily laterally oriented, with a Mc2 facet angle of
26 approximately 58°, but more distally oriented than the morphology preserved in SDR-063 or SD-
27 1034. Part of the palmar trapezoid facet is also retained, measuring 3.1 mm in DP height and
28 4.2 mm in PD length, although the full extent of this facet or its potential continuity with the
29 scaphoid articular surface cannot be determined.

30 31 *3.8 Hamates (Table 9, Fig. 8)*

32 SD-742 right hamate *Preservation*. This specimen preserves the hamulus and proximal half of
33 the hamate body. The palmer border of the distal metacarpal articulation is also preserved.

1 *Morphology.* This hamate has a robust and palmarly extended hamulus relative to the size of
2 the hamate body. The hamulus extends almost exclusively palmarly, with little distal extension
3 beyond what is preserved of the hamate body. Only the proximal half of the capitate facet is
4 preserved and is generally flat, except for a slight concavity at the palmar border. The proximal
5 portion of the triquetrum facet is DP and ML convex and is slightly dorsally oriented. There is no
6 clear distinction between the triquetrum and lunate articular surfaces. Distally, the Mc5 facet is
7 more medially oriented than the Mc4 facet. The preserved palmar portions of the metacarpal
8 articulation suggest that the Mc4 facet is ML broader and more concave (both DP and ML) than
9 the narrower and flatter Mc5 facet. The Mc5 facet extends onto the hamulus and therefore
10 projects further palmarly than does the hamate body.

11

12 SDR-158 left hamate hamulus *Preservation.* This specimen preserves only the hamulus and
13 part of the distal metacarpal articulation, but the cortex is strongly abraded in most areas.

14 *Morphology.* The limited preserved morphology of this specimen is similar to that described for
15 SD-742. Abrasion of the distal articular surfaces prohibits determining the relative size of the
16 Mc4 and Mc5 facets. The hamulus measures 15.2 mm in DP height.

17

18 *3.9 Minimum number of individuals*

19 The minimum number of individuals based on the largest sample of any carpal element—the
20 scaphoid—is six adults and possibly one juvenile. Examination of all El Sidrón carpals revealed
21 that several specimens from the F8 square and two specimens from the F7 square (Fig. 1) were
22 of a similar size and morphology and articulated well together. These specimens, including two
23 antimeres, are interpreted as likely being associated with a single individual and are referred to
24 together as “Hand 1” (Fig. 9). The right scaphoid (SD-744), trapezium (SD-373), trapezoid (SD-
25 28), and capitate (SD-557) are confidently attributed to the same individual as their articular
26 surfaces are all well matched. The right lunate (SD-85), triquetrum (SD-58), and hamate (SD-
27 742), as well as their antimeres (left SD-1227 triquetrum and SD-1034 capitate), are associated
28 with Hand 1 with reasonable certainty due to poor preservation of the capitate facet on the SD-
29 742 hamate and the more ambiguous articular morphology of the lunatoscapoid and
30 lunatotriquetrum facets. Although the size and preservation of the right SD-29 pisiform matches
31 that of the remaining carpals, the flat articulation between the pisiform and triquetrum makes
32 this association more questionable. Some of the carpals of Hand 1 also articulate well with left
33 and right metacarpals also recovered from El Sidrón but that are not described in this study.

34

1 **4. Comparative morphology**

2 **4.1 Scaphoid**

3 A geometric mean of scaphoid size was derived from the DP height and ML breadth of
4 the scaphoid body, and DP height and PD length of the radial facet to maximize the
5 comparative fossil sample. Box-and-whisker plots of scaphoid shape ratios show that, relative to
6 most other Neandertals, the El Sidrón scaphoids are relatively ML narrow but PD long and DP
7 tall (Fig. 10). In this way, the El Sidrón scaphoids are generally similar to the relative
8 proportions of *Australopithecus* sp. (StW 618), *Australopithecus sediba* (MH2), and *H. naledi*
9 (U.W. 101-807, -1639, and -1726), but also fall within the range of variation seen in *H. sapiens*.
10 There is also substantial overlap and variation across the entire comparative sample for each
11 metric. The El Sidrón scaphoid's capitate facet is PD longer than most other Neandertals, apart
12 from Regourdou 1 and the Shanidar median, while the radial facet is relatively DP taller than
13 most other Neandertals, and most similar to Tabun 1 and Kebara 2 (Fig. 10). Together, the El
14 Sidrón scaphoid shape ratios are similar to those of other Neandertals, but the overall
15 morphology is not identical to any one Neandertal specimen in particular.

16 A principal components analysis (PCA) including six scaphoid shape ratios (Table 10)
17 allowed for all fossil specimens to be included, apart from SD-744 and the fragmentary scaphoid
18 specimens SD-110 and -679b. The first two principal components explain 71.7% of the total
19 variance (Table 10). The first PC generally separates small-bodied recent humans from other
20 modern humans and most fossil taxa in having a relatively PD longer capitate facet and DP
21 taller height of the scaphoid but shorter DP height of the radial facet (Fig. 11). The separation of
22 small-bodied recent humans from other modern humans along PC1 suggests that, despite using
23 shape ratios, size may still account for some of the variation across the samples. Spearman's
24 rank correlation coefficient revealed that only the relative PD length of the capitate facet, which
25 loaded heavily on PC1, was significantly (negatively) correlated with the scaphoid's geometric
26 mean ($r_s = -0.359$, $p = 0.006$). Regourdou 1 and most Shanidar specimens (apart from Shanidar
27 3) are distinct in grouping with small-bodied humans. The second PC distinguishes *H. naledi*
28 and *Australopithecus* sp. StW 618 with relatively DP taller but ML narrower scaphoid bodies
29 from the Shanidar scaphoids with the opposite morphology. All other fossils specimens
30 generally fall within the modern human range of variation. Most of the El Sidrón scaphoids fall
31 within the center of the recent human distribution and are most similar to early *H. sapiens*
32 (Qafzeh 9 and Arene Candide 2). Specimen SD-96, the bipartite scaphoid, falls out next to the
33 Tabun 1 Neandertal, but still within the human distribution (Fig. 11).

1 Like other Neandertals (McCown and Keith, 1939; Trinkaus, 1982, 1983; Vилlemeur,
2 1994), the El Sidrón scaphoids differ primarily from *H. sapiens* in having a more robust tubercle
3 (Fig. 12). Trinkaus (1983) noted that the tubercle projection of the Shanidar Neandertals was
4 within the upper limits of variation among other Near Eastern and European Neandertals. The El
5 Sidrón scaphoids display even greater absolute and relative (scaphoid tubercle projection/DP
6 height of scaphoid body) tubercle projection than that of the Shanidar specimens and, in this
7 aspect, are most similar to Amud 1 (Fig. 12). A large, projecting scaphoid tubercle, in
8 combination with large tubercles on the trapezium and hamate, has been interpreted as
9 reflecting a deeper carpal tunnel to accommodate well-developed digit flexor tendons and an
10 increased mechanical advantage for many of the extrinsic muscles of the wrist and intrinsic
11 muscles of the thumb and fifth digit (Trinkaus, 1983; Niewoehner, 2006).

12 Tocheri (2007) highlighted the “open” distal border of the scaphoid’s capitate facet that
13 typically distinguishes *H. sapiens* and Neandertals from African apes, and results in a smaller,
14 more rectangular articulation with the trapezoid. The smaller scaphoid-trapezoid joint reflects
15 the derived boot-shaped human/Neandertal trapezoid and the relatively parallel radial
16 carpometacarpal joints that are better able to accommodate high joint reaction forces from
17 loading of the thumb (Tocheri et al., 2003, 2008; Tocheri, 2007). The more closed distal border
18 of the capitate facet in the El Sidrón scaphoids with a distinctive os centrale region differs from
19 the typical morphology of modern humans, but would likely still permit similar mechanical
20 advantages of accommodating joint stress as the “open” distal border. The trapezoid facet
21 extends to the edge of the os centrale portion and thus would allow for the larger medial
22 articular area for the capitate on both the scaphoid and trapezoid. In addition, the El Sidrón
23 trapezoids show the typical derived morphology of Neandertals and modern humans that
24 distinguishes them from African apes (see below).

25 26 *4.2 Scaphoid anomalies*

27 The El Sidrón scaphoid sample represents a minimum of seven individuals, of which at
28 least three individuals retain a distinct os centrale portion and there is one example of a bipartite
29 scaphoid (Fig. 2). These unusual morphologies have been documented in recent humans and
30 are generally explained as genetic and/or developmental anomalies (e.g., Dwight, 1907; Bogart,
31 1932; Waugh and Sullivan, 1950; Holt and Oram, 1960; Poznanski et al., 1970). In humans, all
32 carpal mesenchymal and cartilaginous condensations, including one for a separate os centrale,
33 appear between the sixth and seventh week in utero (O’Rahilly, 1949; Scheuer and Black, 2000;
34 Hita-Contreras et al., 2012). The cartilaginous os centrale is fully fused with the scaphoid by the

1 ninth week of prenatal life (O’Rahilly, 1954; Čihák, 1972; Hita-Contreras et al., 2012). Thus, at
2 birth, the entirely cartilaginous human scaphoid has an adult-like shape with a fully-fused os
3 centrale (Kivell and Begun, 2007). Indeed, in humans, the “open” distal border of the capitate
4 facet may reflect a reduced os centrale cartilaginous precursor prior to ossification of the
5 scaphoid postnatally. Neandertals typically show the same ‘distally-open’ capitate facet that is
6 found in humans (although the Shanidar 3 scaphoid is an exception; Tocheri, 2007).

7 Although developmental anomalies in the human carpus are rare, the two most common
8 anomalies are a separate os centrale and bipartite scaphoid (Waugh and Sullivan, 1950). A
9 separate os centrale can occur as a well-developed, independent bone or as an incompletely
10 separated bony fragment of the scaphoid (Leboucq, 1884; Dwight, 1907; Bogart, 1932; Wood-
11 Jones, 1942; Waugh and Sullivan, 1950). The morphology of the El Sidrón scaphoids is most
12 similar to the latter condition, described as “persistence du central” by Leboucq (1884:101) or a
13 “partially marked-off” os centrale by Dwight (1907:5; Fig. 13). The occurrence of a separate or
14 incompletely separated os centrale occurs in only 0.48% to 3.13% of humans (Pfitzner, 1895;
15 Virchow, 1929). A bipartite scaphoid is even more rare among recent humans, with reports
16 ranging from 0.13–0.60% of humans (Gruber, 1866; Pfitzner 1895; Codman and Chase, 1905;
17 Bogart, 1932; Waugh and Sullivan, 1950). Although a bipartite scaphoid can result from trauma
18 (Louis et al., 1976), several have noted it as a developmental anomaly (Pfitzner, 1895; Dwight,
19 1907; Faulkner, 1928; Doman and Marcus, 1990), particularly when the articular surfaces
20 between the separate portions are smooth (Todd, 1921). The occurrence of the scaphoid
21 anomalies in the El Sidrón sample is extraordinarily high by recent human standards: 43% of
22 seven scaphoids show a distinct os centrale portion and 14% show a bipartite scaphoid.

23 24 4.3 Lunate

25 Box-and-whisker plots of lunate shape ratios reveal that Neandertals have a ML broad
26 but PD short lunate that is distinct from that of *H. sapiens* (apart from the Dolní Věstonice
27 sample), and that the El Sidrón lunates show the extreme of this morphology (Fig. 14). In this
28 way, the El Sidrón lunates are most similar to Shanidar 3 and 4, as well as *Au. sediba* MH2 and
29 *Australopithecus cf. afarensis* KNM-WT 22944-J. A comparison to the published mean values
30 of the Sima de los Huesos (SH) lunates ($n = 8$) shows that the El Sidrón sample is both PD
31 longer (El Sidrón mean = 13.7 [standard deviation (SD) = 0.99] vs. SH mean = 12.1 [SD = 0.91])
32 and ML broader (El Sidrón mean = 15.6 [SD = 0.71] vs. SH mean = 13.9 [SD = 0.88]; Arsuaga
33 et al., 2015). The El Sidrón specimens have particularly large distal (including articulations for
34 the capitate and hamate) and radial facets, being both ML broader and DP taller than most

1 other Neandertals. In this way, El Sidrón is most similar to Kebara 2 and Amud 1 among
2 Neandertals and is generally smaller than early *H. sapiens* (although the Dolní Věstonice
3 sample is highly variable). The relatively large radial facet is shared with australopiths, while the
4 exceptionally DP tall distal facet in the El Sidrón lunates overlaps only with recent *H. sapiens*.

5 Results of a PCA of seven lunate shape ratios (Table 10) are shown in Figure 15.
6 Spearman's rank correlation coefficient revealed that the DP height of the capitate facet ($r_s = -$
7 $0.342, p < 0.001$) was significantly negatively correlated with the geometric mean. The first two
8 components explain 57.8% of the total variance (Table 10). The first PC generally separates the
9 Dolní Věstonice early *H. sapiens* and Tabun 1 from recent humans, while other Neandertals,
10 including El Sidrón, and australopith fossils fall within the extreme left of the recent human
11 distribution. Thus, these fossils have a relatively ML broader but DP shorter lunate body, and
12 DP shorter radial facet compared to most recent humans. The second PC generally divides the
13 fossil sample into two groups; most Neandertals and australopiths have a relatively short PD
14 length of the lunate body but DP tall radial facet, with the El Sidrón and KNM-WT 22944-J
15 lunates showing the extreme of this morphology, while most early *H. sapiens*, *Au. afarensis*, *H.*
16 *naledi*, and the Tabun 1 and Neandertal 1 Neandertals show the opposite morphology.
17 Altogether, the El Sidrón lunate morphology falls out as most similar to the KNM-WT 22944-J
18 (*Au. cf. afarensis*) lunate (Ward et al., 1999), *Au. sediba*, and the Kebara 2 and Shanidar
19 Neandertals (Fig. 15).

20 The El Sidrón lunates have a lunatohamate articulation (Fig. 3), like many other
21 Neandertals (i.e., Tabun 1, Shanidar 3, Amud 1, Neandertal 1, and Kebara 2 in this study). A
22 lunatohamate articulation is common in recent humans (65–71% of individuals; Pfitzner, 1895;
23 Marzke et al., 1994), although its frequency is less common than is found in African apes
24 (Marzke et al., 1994). Contact between the lunate and hamate disrupts the continuity of the
25 roughly “ball-and-socket” (formed by proximal and distal carpal rows) midcarpal joint in neutral
26 position. The presence of lunatohamate joint in recent humans is often associated with
27 pathological cartilage erosion (Viegas et al., 1990). This pathology, in combination with the
28 higher frequency of this trait in African apes, suggested to Marzke and colleagues (1994) that
29 perhaps a lunatohamate articulation was primitive for hominins but that the frequency of this
30 feature was decreasing in recent humans. This hypothesis is consistent with the presence of a
31 lunatohamate articulation in most of the Neandertals studied here and the presence of a
32 lunatohamate articulation in *Ardipithecus ramidus* (6/500-34; TLK, pers. obs.). However, a
33 lunatohamate joint is not found in preserved specimens of *Au. afarensis* (AL 444-3; Ward et al.,

1 2012), *Au. sediba* (MH2), or *H. naledi* (Kivell et al., 2011, 2015), suggesting that its presence
2 and any potential functional or pathological significance in fossil hominins was variable.

3 4 4.4 *Triquetrum*

5 The El Sidrón triquetra show two, albeit subtle, variations in morphology; SD-1813 is
6 more similar to several other Neandertals and the Swartkans specimen SKX 3498, while the
7 SD-58, -1022a, and -1227 are generally more similar to recent humans. Quantitative analyses
8 also demonstrate this morphological variability (although SD-58 was excluded from all
9 quantitative analyses due to poor preservation). Box-and-whisker plots show that SD-1022a and
10 SD-1227 have a much narrower ML breadth but slightly taller DP height of the triquetrum body
11 and taller DP height of the hamate facet compared to most other Neandertals and, in this
12 aspect, are most similar to *H. sapiens* (Fig. 16). In contrast, SD-1813 falls out at the extremes of
13 the El Sidrón variation, with a much broader ML and shorter DP triquetrum body and broader
14 ML hamate facet, which together make it more similar to other Neandertals (Fig. 16). The broad
15 shape of SD-1813 also appears to be similar to the Sima de los Huesos (SH) triquetra ($n = 7$),
16 although images of the SH triquetra have not yet been published (Arsuaga et al., 2015). The
17 SD-1813 ML breadth (16.4 mm) and PD length (8.3 mm) are more similar to the published
18 mean values of the SH triquetra (ML breadth mean = 16.1 [SD = 1.6]; PD length mean = 9.0
19 [SD = 0.8]; Arsuaga et al., 2015) than the narrower SD-1022a and -1227 specimens (ML
20 breadth mean = 13.8 [SD = 1.1]; PD length mean = 10.3 [SD = 1.5]). All the El Sidrón triquetra
21 also have a relatively short PD length of the lunate facet, overlapping only with recent humans
22 and being much shorter compared to all other fossil taxa.

23 Results of a PCA of seven shape ratios (Table 10) are shown in Figure 17. The first two
24 PCs explain 58.8% of the total variance (Table 10), but all fossils fall within the range of
25 variation of recent humans. The second PC separates the El Sidrón specimens SD-1022a and -
26 1227, with relatively narrow ML but tall DP triquetrum bodies and narrow ML hamate facets,
27 from all other fossils, including SD-1813. SD-1813 falls out at the opposite extreme on PC2,
28 closest to the Kebara 2 Neandertal. Together, all El Sidrón triquetra fall either outside or at the
29 extremes of recent human variation.

30 31 4.5 *Pisiform*

32 Box-and-whisker plots show that the shape of the El Sidrón pisiforms is PD short like
33 that of other Neandertals and *H. sapiens*, and distinct from the long pisiform body of *Au.*
34 *afarensis* (Fig. 18). The El Sidrón pisiforms are generally similar to those of most other

1 Neandertals in having a relatively narrower ML breadth but taller DP height of the pisiform body
2 compared with the typical morphology of *H. sapiens*. The El Sidrón pisiforms are distinguished
3 by a relatively long PD triquetrum facet, which is similar to Kebara 2, the Tabun specimens, and
4 *H. sapiens* (Fig. 18).

5 A PCA of five pisiform shape ratios (Table 10) reveals substantial variation in pisiform
6 morphology across fossil taxa, and most fall outside the range of variation of the recent human
7 samples (Fig. 19). The first two PCs explain 70.6% of the total variation (Table 10). On the first
8 PC, most Neandertals either fall to the left extreme of or outside of the range of variation in
9 recent humans in having a shorter PD and narrower ML length of the triquetrum facet. On PC2,
10 the El Sidrón pisiforms are similar to most other Neandertals, apart from Shanidar 5 and Tabun
11 1, in having a relatively narrow ML breadth of the pisiform body and longer PD length of the
12 triquetrum facet.

13 The El Sidrón pisiforms are generally similar to other Neandertals and *H. sapiens* in
14 being substantially reduced in length compared to other primates and *Au. afarensis* (Bush et al.,
15 1982). Thus, the El Sidrón (and Neandertals in general) pisiform likely functions in a similar way
16 to that described in humans. A short pisiform reduces the mechanical advantage for the flexor
17 carpi ulnaris and abductor digiti minimi muscles, but may help to facilitate palmar grip and
18 opposition between the thumb and fifth digit (Marzke et al., 1992; Young, 2003; Lovejoy et al.,
19 2009). The relatively flat, long PD triquetrum facet is consistent with the corresponding, oval-
20 shaped pisiform facet on the triquetrum (Fig. 4), and suggests substantial sliding of the pisiform
21 on the triquetrum during various wrist movements, as documented through in vivo analyses in
22 humans (Moojen et al., 2001).

23

24 4.6 Trapezium

25 To maximize the comparative fossil sample, a geometric mean was calculated from the
26 maximum DP height of the trapezium body, PD length of the Mc1 facet, and ML breadth of the
27 scaphoid facet. Box-and-whisker plots of trapezium shape ratios reveal that the El Sidrón
28 trapezia have a relatively short PD length and, especially, DP height of the trapezium body
29 compared with most other Neandertals. In this way, the El Sidrón trapezia are most similar to
30 Kebara 2 and *H. sapiens* (Fig. 20). The Mc1 facet of the El Sidrón specimens is especially ML
31 broad compared with other Neandertals, but all Neandertals overlap with the range of variation
32 seen in *H. sapiens* and all are narrower than the Mc1 facets of *H. habilis* OH7 and *Au. afarensis*
33 (Fig. 20). The Mc1 facet of El Sidrón trapezia are similar to most other Neandertals in being
34 relatively DP flat but still saddle-shaped (Kimura, 1976; Trinkaus, 1982, 1989; Trinkaus et al.,

1 1991; Niewoehner, 2006; Marzke et al., 2010). The flatness of this articulation was originally
2 interpreted as limiting mobility at the trapeziometacarpal joint in Neandertals relative to humans
3 (Musgrave, 1971; Vlček, 1975). However, it is now generally thought to reflect an increase in
4 articular surface area and thus greater ability of the joint to cope with axially directed joint
5 reaction forces during thumb use (Trinkaus, 1989; Trinkaus et al., 1991; Niewoehner, 2001;
6 Marzke et al., 2010), while at the same time resulting in a more unstable trapeziometacarpal
7 joint that would have been more reliant on interosseous ligaments for effective joint function
8 (Marzke et al., 2010).

9 The El Sidrón SD-373 trapezium has a notably small tubercle compared to that of other
10 Neandertals, as well as the Sima de los Huesos hominins (Arsuaga et al., 2015). Comparison of
11 the tubercle projection ratio (tubercle projection/breadth of Mc1 facet*100 [Trinkaus, 1983])
12 shows that the SD-373 has the relatively smallest tubercle compared with all other Neandertals
13 in our sample and is most similar to *H. sapiens* in this respect (Fig. 21). Although the El Sidrón
14 trapezia also have relatively broad Mc1 facets, which would influence the tubercle projection
15 ratio, the cross-sectional size (tubercle length * tubercle thickness [Trinkaus, 1983]) of the SD-
16 373 tubercle is also small compared to other Neandertals (Fig. 21). Previous researchers have
17 noted the large and projecting trapezium tubercles typical of most Neandertals (Trinkaus, 1982,
18 1983; Niewoehner 2006), and although the El Sidrón scaphoids have remarkably robust
19 tubercles (see above), the trapezia do not.

20 21 4.7 Trapezoid

22 Box-and-whisker plots of trapezoid shape reveal that the most well-preserved El Sidrón
23 trapezoids (SD-28 and -529) are relatively ML broad but PD short compared with most other
24 Neandertals and *H. sapiens*, overlapping with only the La Ferrassie specimens and *H. naledi*
25 (Fig. 22). However, the remainder of the quantified morphology is generally similar to that of
26 other Neandertals and *H. sapiens*, including the DP height of the trapezoid body and PD length
27 of the palmar surface, both of which demonstrate substantial intra- and interspecific variation.

28 A PCA of six shape ratios (Table 10) shows that both El Sidrón trapezoids fall outside
29 the range of variation of the extant *H. sapiens* sample (Fig. 23). The first two PCs explain 62.7%
30 of the total variance (Table 10). On PC1, both El Sidrón specimens have a relatively shorter PD
31 length of the trapezoid body (dorsal surface) but DP taller height of the trapezium facet, and in
32 these aspects are most similar to *H. naledi* (UW 101-1581), as well as Kebara 2, La Ferrassie 1,
33 and Qafzeh 8, all of which also fall outside the recent human range of variation. On PC2, both El

1 Sidrón specimens show a relatively short PD length of the palmar surface compared to most
2 other Neandertal and *H. sapiens* specimens (Fig. 23).

3 The overall morphology of the El Sidrón trapezoids is derived like that of other
4 Neandertals and *H. sapiens* and distinctly different from the wedge-shaped trapezoid of African
5 apes (Lewis, 1989; Tocheri et al., 2005; Tocheri, 2007) and *Homo floresiensis* (Tocheri et al.,
6 2007). The El Sidrón trapezoids are “boot-shaped” with an expanded non-articular palmar
7 surface, although this surface is relatively short compared to other Neandertals. The
8 comparatively flat and distally oriented Mc2 articulation and the large scaphoid articulation are
9 both similar to that of other Neandertals and *H. sapiens* and are distinct from the articular
10 morphology of *H. floresiensis* and African apes (Tocheri et al., 2005, 2007). SD-28 and SD-529
11 (the only two El Sidrón trapezoids preserving the medial side) have a large palmar capitate
12 facet, and SD-28 also preserves a small dorsal capitate facet. This dual-facet morphology is
13 consistent with the El Sidrón capitate morphology (SD-1034), but differs from the single,
14 expanded palmar capitate facet that typically occupies most of the palmar region of the
15 trapezoid in other Neandertals (e.g., Kebara 2), as well as *H. sapiens* (Tocheri, 2007; Tocheri et
16 al., 2007) and *H. naledi* (Kivell et al., 2015).

17 18 4.8 Capitate

19 Box-and-whisker plots of capitate shape ratios show that the El Sidrón capitates are
20 relatively PD short but ML broad compared to most other Neandertals (Fig. 24). In this way, the
21 El Sidrón capitates most closely resemble the Neandertal 1, Kebara 2, and Tabun 1 specimens,
22 but also *H. sapiens* and some australopiths. A relatively narrow ML breadth of the capitate body
23 in Neandertals has been noted previously as being distinct from modern humans (Villemeur,
24 1994; Niewoehner et al., 1997), but there appears to be more variation in this feature across
25 Neandertals than previously recognized. The ML breadth of the capitate’s proximal facet in the
26 El Sidrón sample is intermediate among the variation seen in Neandertals, but also overlaps
27 with *H. sapiens* and *Au. afarensis* (Fig. 24). The El Sidrón capitates are similar to those of other
28 Neandertals in having a relatively short DP height of the distal Mc3 facet, which is similar to that
29 of *H. naledi* and many australopiths, but distinct from the typically taller morphology found in
30 recent humans (Niewoehner et al., 1997; but contra Niewoehner, 2006).

31 A PCA of seven capitate shape ratios (Table 10) reveals a clear clustering of fossil
32 hominins along the first PC, although most fall within the range of recent human variation (Fig.
33 25). The first two PCs explain 63.4% of the total variance (Table 10). Most fossil hominin
34 specimens are clustered on the left of the plot, with a ML broad Mc3 facet and DP short

1 proximal facet, while most recent humans, as well as early *H. sapiens* Arene Candide 2,
2 Neandertal La Ferrassie 1, and cf. *Au. afarensis* KNM WT 22944-H, show the opposite
3 morphology. On PC2, Neandertal (as well as australopiths and early *H. sapiens*) specimens
4 span the breadth of the morphological variation, with El Sidrón SD-557, La Chapelle, and
5 Neandertal 1 capitates having relatively narrower ML but taller DP distal facets compared to the
6 remaining Neandertal specimens, including SD-1034 (Fig. 25). However, given that SD-557 and
7 SD-1034 are considered to be likely antimeres from the same individual, this suggests that
8 morphological variation across the sample is actually quite small, at least for the shape ratios
9 included in this analysis. Spearman's rank correlation coefficient revealed that the DP height (r_s
10 = -0.233, $p = 0.026$) and ML breadth ($r_s = -0.520$, $p < 0.001$) of the capitate's proximal facet, the
11 former of which loaded highly on PC1, were significantly negatively correlated with the
12 geometric mean.

13 The El Sidrón capitate's Mc2 facet is a single, continuous, and DP curved facet, similar
14 to other Neandertals, *H. sapiens*, and other hominins (e.g., Johanson et al., 1982; McHenry,
15 1983; Lorenzo et al., 1999; Ward et al., 1999, 2001). The Mc2 facet angle could be measured in
16 two El Sidrón capitates and is relatively laterally oriented (58° and 71°), each falling out at the
17 extreme ranges of other Neandertals (range 44°–75° degrees; Table 11). This orientation is
18 distinct from the more distal-facing Mc2 facet typical of *H. sapiens* (Niewoehner et al., 1997;
19 Table 11).

20

21 4.9 Hamate

22 To accommodate the preservation of the SD-742 hamate, a geometric mean was
23 calculated from the PD length of the hamate body, maximum DP height of the hamate, and ML
24 breadth of the distal facet. Box-and-whisker plots of hamate shape ratios show that SD-742 has
25 a relatively short PD length of the hamate body, overlapping only with the Shanidar specimens,
26 while the remaining Neandertal sample, other hominins, and all *H. sapiens* are relatively longer
27 (Fig. 26). SD-742 has a larger, more palmarly projecting hamulus than most other Neandertals,
28 as well as the Sima de los Huesos hominins (Arsuaga et al., 2015), *H. sapiens*, and other
29 hominins. This is confirmed by a comparison of the hamulus projection index (=hamulus
30 height/total height of hamate body * 100), following Trinkaus (1982, 1983), showing that SD-742
31 has the most projecting hamulus of any other known Neandertal (Table 12). The hamulus cross-
32 sectional area (PD length * ML breadth of the hamulus) of the El Sidrón hamates is intermediate
33 among Neandertals (Table 12), but larger than that of *H. sapiens* and most other hominins.
34 Relative to hamate size, the ML breadth of the hamate body and the distal articular surface in

1 SD-742 is intermediate among Neandertals and within the range of variation of *H. sapiens* (Fig.
2 26). Niewoehner (2006) described a ML expansion of the metacarpal articulation in Neandertals
3 relative to recent humans. However, in this analysis all Neandertals fall within the range of
4 variation seen in recent humans and, indeed, most Neandertals (apart from the Shanidar
5 specimens) are relatively narrower than early and recent *H. sapiens* median values (Fig. 26). It
6 is important to note that this discrepancy between our findings and those of Niewoehner (2006)
7 may be the result of methodological differences (linear measurements vs. geometric
8 morphometric analysis). The Mc5 facet is relatively narrower than the Mc4 facet, as in many
9 other Neandertals (Niewoehner 2006).

10 A PCA of six hamate shape ratios (Table 10) reveals a large range of variation in
11 hamate morphology (Fig. 27). Spearman's rank correlation coefficient revealed that the DP
12 height of the hamate body ($r_s = -0.206$, $p = 0.016$) was significantly negatively correlated with the
13 geometric mean. The first two PCs explain 70.4% of the total variance. PC1 separates most
14 Neandertal specimens (apart from Kebara 2), including El Sidrón SD-742, from the majority of
15 early and recent *H. sapiens* in having a relatively DP tall maximum height of the hamate but PD
16 short hamate body. PC2 separates Neandertals SD-742 and Shanidar 4 and 5 from the
17 remaining Neandertal sample in having a relatively taller DP capitate facet and shorter PD
18 length of the hamate body. However, there is substantial variation in hamate morphology,
19 including intraspecific (e.g., within *H. naledi*) or inter-individual (e.g., Dolní Věstonice) variation,
20 that makes it difficult to define distinct morphological patterns across taxa based on the hamate
21 shape variables included in this analysis.

22

23 **5. Discussion and conclusions**

24 The recovered carpal bones from El Sidrón provide further insight into the morphological
25 variation of the Neandertal hand, as well as the close genetic relationship among the El Sidrón
26 individuals. The 29 carpals described here represent a minimum of seven individuals, of which
27 one may be a juvenile between the ages of 6–10 years old. This assessment is consistent with
28 previous morphological and paleogenetic analyses of the El Sidrón demographics indicating the
29 presence of seven adults (at least three females and three males) and a juvenile (Juvenile 1)
30 aged 6–8 years old (Lalueza-Fox et al., 2010; Rosas et al., 2012; Estalrich and Rosas, 2013).
31 Among the new El Sidrón carpals, several articulate well together or are considered antimeres
32 with reasonable certainty, and are therefore considered to be associated with same adult
33 individual (Hand 1). The Hand 1 carpals are generally the largest within the sample, suggesting

1 that the carpus may be that of a male individual, although the size variation within the sample is
2 limited.

3 Qualitative and quantitative comparative analyses reveal that the El Sidrón carpals
4 generally fall out as most similar to Near Eastern Neandertals, especially Kebara 2 (but also the
5 Tabun and Shanidar specimens), rather than other European Neandertals. A similar result was
6 found in a morphometric analysis of the mandible, revealing that the El Sidrón specimens
7 showed greater similarities with “southern” Neandertals (including Kebara, Tabun, and
8 Shanidar, among others) than with “northern” Neandertals (e.g., La Ferrassie, Le Moustier;
9 Rosas et al., 2006). Thus, the carpal morphology provides further support for the hypothesis
10 that there were southern and northern morphs of Neandertals (Rosas et al., 2006). That being
11 said, the El Sidrón specimens also show several morphological features that are thought to
12 generally distinguish all Neandertals from *H. sapiens* (e.g., Trinkaus, 1982, 1983, 2016;
13 Niewoehner et al., 1997; Niewoehner, 2006). These features include large, palmarly projecting
14 tuberosities on the scaphoid and hamate (but not the trapezium, see below), a relatively flat (but
15 still saddle-shaped) trapezium-Mc1 articulation, a more laterally facing Mc2 facet and ML broad
16 Mc3 facet on the capitate, and a relatively small and ML flatter Mc5 facet compared to the Mc4
17 articulation on the hamate. The presence of these features suggests that the El Sidrón wrist
18 functioned in much the same way as has been interpreted for other Neandertals (Trinkaus,
19 1982, 1989, 2016; Niewoehner et al., 1997; Niewoehner 2006). For example, the relatively flat
20 trapezium-Mc1 is better able to accommodate larger axially directed forces from a robust,
21 powerful thumb compared with recent humans, while the capitate-metacarpal articulations
22 would allow recent human-like Mc2 rotation but would be less able to resist obliquely oriented
23 forces during manipulation (Trinkaus, 1989, 2016; Niewoehner et al., 1997; Niewoehner, 2001,
24 2006; Marzke et al., 2010).

25 The El Sidrón carpals also differ from other Neandertals in having a remarkably small
26 trapezium tubercle with limited projection, a capitate Mc3 facet that is DP short (rather than tall),
27 and a relatively ML broad (rather than narrow) distal capitate body (contra Trinkaus, 1983;
28 Villemeur, 1994; Niewoehner et al., 1997; Niewoehner, 2006). Indeed, this comparative analysis
29 reveals that a DP short Mc3 facet is typical of all Neandertals in our sample (with El Sidrón
30 being particularly short), and that this feature is likely primitive, being shared with *Au. cf.*
31 *afarensis*, *Au. sediba*, and *H. naledi* (Fig. 24). It is only recent *H. sapiens* that have, on average,
32 a notably taller Mc3 facet on the capitate. Similarly, our analysis shows that Neandertals
33 typically have a ML broad distal capitate body, with only the La Chapelle and Le Ferrassie
34 specimens being notable exceptions. In this way, Neandertals (with El Sidrón being particularly

1 broad) have capitates that are just as ML broad for their size as australopiths, *H. naledi*, and *H.*
2 *sapiens*. The absence of a robust and palmarly projecting trapezium tubercle in El Sidrón
3 suggests that there may be more variability in Neandertal tubercle morphology than previously
4 recognized. Trinkaus (2016) also recently discussed the great degree of variability in the
5 hamate hamulus morphology among Neandertals and other later *Homo* species.

6 When looking at the Hand 1 carpus together (with the caveat that these bones were not
7 found associated in situ), this individual has the most robust and most palmarly projecting
8 scaphoid tubercle and hamate hamulus within our comparative Neandertal sample. However,
9 the trapezium's tubercle has the smallest cross-sectional area and is by far the least projecting
10 relative to other Neandertals (Fig. 21). In the El Sidrón Hand 1, the extreme palmar projection of
11 the scaphoid and hamate tuberosities would increase the depth of the carpal tunnel to
12 accommodate hypertrophied extrinsic flexor tendons (Trinkaus, 1982, 2016). However, the
13 limited projection and relative gracility of the trapezium tubercle suggest that the mechanical
14 advantage for the intrinsic pollical muscles (i.e., opponens pollicis and flexor pollicis brevis
15 muscles) may have been reduced compared with other Neandertals. The size of the tuberosities
16 may also reflect hypertrophy of the muscles that attach to them (e.g., Ward et al., 1999; Orr et
17 al., 2013; Trinkaus, 2016a), in which case the intrinsic pollical muscles of the El Sidrón
18 Neandertals may have been smaller and more similar in size to those of *H. sapiens*. However,
19 the relationship between bony (enthesal) morphology and muscle size within the hand has
20 been recently brought into question (Williams-Hatala et al., 2016).

21 The El Sidrón capitate (SD-1034) and trapezoid (SD-28) associated with Hand 1 share
22 both a palmar and dorsal articulation, which differs from the single, expanded palmar capitate-
23 trapezoid facet that is typical in other Neandertals (e.g., Kebara 2) and *H. sapiens* (Tocheri,
24 2007; Tocheri et al., 2007), as well as *H. naledi* (Kivell et al., 2015). A distinct dorsal trapezoid-
25 capitate facet is present on the *H. antecessor* ATD6-24 capitate and has been interpreted as a
26 transitional morphology between the dorsal trapezoid-capitate articulation of australopiths
27 (McHenry, 1983; Lorenzo et al., 1999) and the more palmarly positioned facet typical of humans
28 (Lewis, 1989; Tocheri, 2007). However, the preserved morphology of SD-529 trapezoid
29 suggests it only has a palmar trapezoid-capitate articulation, demonstrating variability in this
30 morphology within the El Sidrón population. Furthermore, a dual-facet morphology is found in
31 some Neandertals, including Tabun 1 and possibly Skhul IV (McCown and Keith, 1939) and
32 Amud 1 (Endo and Kimura, 1972), and occasionally in modern humans (Lewis, 1989; Tocheri,
33 2007). A dual trapezoid-capitate facet is also found in *Au. sediba* (Kivell et al., 2011) and *Au.*
34 *afarensis* (TLK, pers. obs.), demonstrating that variability in this articulation goes back much

1 further into human evolutionary history than previously considered. Interestingly, Tocheri (2007)
2 has noted that in modern humans that display a dual capitate-trapezoid articulation, this
3 morphology is also correlated with a less distally open capitate facet on the scaphoid and a
4 more triangular-shaped scaphoid joint on the trapezoid. Within the associated El Sidrón carpals
5 of Hand 1, the SD-28 trapezoid has a more triangular-shaped scaphoid facet and the SD-744
6 scaphoid has a more closed distal border of the capitate facet than is typical of *H. sapiens*
7 (Tocheri, 2007), supporting a correlated morphological pattern across these radial carpals.

8 Analyses of lunate shape reveal that all Neandertals have relatively ML broad but PD
9 short lunates, falling outside the range of variation seen in early and recent *H. sapiens* (apart
10 from the Dolní Věstonice sample, which is highly variable). This is likely a primitive condition
11 retained in Neandertals as they share this shape with australopiths, while *H. sapiens* appear
12 derived in having relatively ML narrower but PD longer lunates (Fig. 14). The shape of the
13 Neandertal triquetrum is similarly broad ML relative to that of most early and recent *H. sapiens*,
14 and in this respect Neandertals are most similar to australopiths (Fig. 16). Interestingly, the El
15 Sidrón triquetrum sample shows two subtle morphological variants: SD-1813 is similar to other
16 Neandertals, as well as SKX 3498 from Swartkrans, in being relatively broad ML, as well as
17 short DP (Kivell, 2011; Figs. 16 and 17). In contrast, the two specimens associated with Hand 1
18 (SD-58 and SD-1227) show the opposite extreme of this morphology, being narrow ML and tall
19 DP, with a more stout triquetrum shape that is more similar to *H. sapiens* (as well as African
20 apes; Kivell, 2011). The combination of both a relatively broad ML lunate and triquetrum would
21 potentially increase the radiolunate articulation (indeed, the El Sidrón lunates have relatively
22 broad radial facets, but Neandertals overall are generally within the range of variation seen in *H.*
23 *sapiens*), as well as accentuate the role of the pisiform, shifting the pisiform distomedially to
24 increase the flexion and adduction moment arm of the flexor carpi ulnaris muscle (Kivell, 2011).
25 Kivell (2011) previously interpreted similarities between the SKX 3498 and Neandertal
26 triquetrum shape as either symplesiomorphic, since *Ar. ramidus* also has a relatively broad
27 triquetrum (Lovejoy et al. 2009), or, less likely, suggesting that SKX 3498 may be more likely
28 attributed to early *Homo* than to *Au. robustus*. However, finding these two, albeit subtle,
29 triquetrum morphs within a single, closely related Neandertal population at El Sidrón suggests
30 that this variation in triquetrum morphology may have limited functional or taxonomic
31 significance.

32 When looking more broadly across all Neandertals in relation to early and recent *H.*
33 *sapiens*, *H. naledi*, earlier *Homo*, and australopith species, our analyses reveal that there is both
34 greater variation within Neandertals and greater similarity across hominins in carpal shape than

1 perhaps previously recognized. This may be partly due to the fact that many studies have
2 focused only on the morphological differences between Neandertals and *H. sapiens* (e.g.,
3 Trinkaus, 1982, 1983; Niewoehner et al., 1997, Niewoehner, 2001, 2006) or comparisons
4 across other late *Homo* species (e.g., Lorenzo et al., 1999; Mersey et al., 2013; Trinkaus,
5 2016a). Many aspects of Neandertal carpal shape overlap with the range of variation that we
6 see in early and recent *H. sapiens*, including small-bodied humans, as well as other *Homo* and
7 australopiths. A broader hominin perspective can shed light on the polarity of particular
8 Neandertal features or reveal that they are not necessarily “Neandertal features” at all.

9

10 *Scaphoid developmental anomalies and implications for El Sidrón demography*

11 The most distinctive feature of the El Sidrón carpals is the high frequency of rare
12 morphology and/or developmental anomalies within the scaphoid sample (Figs. 2 and 13). The
13 El Sidrón scaphoid sample shows a high frequency of a distinctive os centrale projection, with
14 three of the seven individuals represented by the scaphoid sample showing this idiosyncratic
15 morphology. Interestingly, a similar distinctive os centrale portion is found in the Neandertal
16 Krapina 200.1 left scaphoid (Trinkaus, 2016b), the Shanidar 3 left and right scaphoids (Tocheri,
17 2007; Fig. 13) and a cast of the Shanidar 4 left scaphoid, although this idiosyncratic morphology
18 has not been discussed in previous descriptions of these carpal bones to our knowledge
19 (Trinkaus, 1982, 1983, 2016b). We also document the first occurrence of a bipartite scaphoid in
20 Neandertals, with the El Sidrón sample representing a much higher prevalence (i.e., 14% of
21 seven individuals) than the <1% frequency documented in recent humans (Gruber, 1866;
22 Pfitzner, 1895; Codman and Chase, 1905; Bogart, 1932; Waugh and Sullivan, 1950). Although
23 these developmental anomalies likely had little impact on wrist function (Faulkner, 1928; Doman
24 and Marcus, 1990), they have not yet been found in any other Neandertal to our knowledge.
25 Other carpal anomalies have been identified in the La Ferrassie 2 Neandertal, showing a
26 coalition between the right lunate and triquetrum (Oberlin and Sakka, 1989), and the Shanidar 4
27 hand preserves a connection between the trapezoid and Mc2 (Trinkaus, 1983) that may also
28 represent an anomalous coalition (M. Tocheri, pers. comm.).

29 A high prevalence of developmental anomalies in the carpus is consistent with previous
30 documentation of congenital defects in other areas of the skeleton among the El Sidrón
31 individuals. Ríos and colleagues (2015) documented a congenital posterior and anterior cleft in
32 two of the three atlases known in the El Sidrón sample, which occur at a much higher frequency
33 (at least 8% for each congenital cleft) than is documented in recent humans (<4% frequency for
34 a posterior cleft and <1% for an anterior cleft). Furthermore, Dean and colleagues (2013)

1 described a pathological retention of a mandibular deciduous canine in two male individuals
2 (Adult 2 and Adolescent 3) that were maternally related, sharing the same mitochondrial DNA
3 (Lalueza-Fox et al., 2011; López-Valverde et al., 2012). Together, the high prevalence of
4 otherwise rare skeletal morphology is consistent with paleogenetic evidence showing that the
5 Neandertal individuals at El Sidrón represented a closely related group (Lalueza-Fox et al.,
6 2011). Combining the high frequency of scaphoid anomalies with those of the cervical vertebrae
7 and dentition, all of which likely had little effect on function or fitness, may also signal endogamy
8 or inbreeding (Raikkonen et al., 2013; Ríos et al., 2015) within the small hominin populations of
9 the Pleistocene (Bittles and Black, 2010; Castellano et al., 2014).

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4 **Figure legends**

5
6 Figure 1. Map of El Sidrón Osario Gallery. Map showing excavated area and location that each
7 carpal bone was recovered. Gray squares indicate areas from which carpals were recovered;
8 the star indicates the square (F8) from which most of the carpals were recovered, including
9 specimens thought to be associated with the same individual (black text, see discussion of
10 Hand 1 in the main text). Specimens SD-1011, SDR-063, SDR-064, and SDR-158 do not have
11 a known context. For a complete map of cave system and location of El Sidrón within Spain,
12 see Rosas et al. (2006).
13

14 Figure 2. The El Sidrón scaphoids. All specimens show adult morphology, apart from the SD-
15 110 fragment that may be juvenile. All specimens are presented in medial view (left), showing
16 the capitate facet; distal view (middle), showing the trapezoid-trapezium articulation; and
17 proximal view (right), showing part of the radial facet. Palmar is towards the top of the page.
18 Fossil specimens enclosed in boxes are in different views: SD-96 image in box shows palmar
19 view of bipartite articular surface and SD-679b image in box shows radial view to highlight the
20 distinct os centrale portion. Black arrows indicate the truncated tubercle and articular surface of
21 a bipartite scaphoid (SD-96) and asterisks indicate the distinct os centrale portion in SDR-064,
22 SD-258, and SD-679b. All scaphoids are from the left side except SD-96, -110, and -744 that
23 are right. All scaphoids are scaled to the same 1 cm scale. “Hand 1,” here and in Figures 3–9,
24 refers to specimens that are thought to be associated to the same individual (see text).
25

26 Figure 3. The El Sidrón lunates. Both specimens are presented in, from left to right, distal view,
27 showing the capitate and hamate facets; proximal view, showing the radial facet; medial view,
28 showing triquetrum facet; and palmar view, showing non-articular surface. Distal is towards the
29 top of the page in the palmar view, while palmar is towards the top of the page in all other views.
30 Both lunates are from the right side and scaled to the same 1 cm scale.
31

32 Figure 4. The El Sidrón triquetra and pisiforms. The triquetra (left) are presented in, from left to
33 right, lateral view, showing the lunate facet; distal view, showing the hamate facet; and palmar
34 view, showing the pisiform facet. SD-1227 (left side) and SD-58 (right side) are likely antimeres
35 from the same individual and possibly associated with Hand 1. SD-1022a is a left and SD-1813

1 is from the right side. The pisiforms (right) are presented in dorsal view, showing the triquetrum
2 facet, and medial view of the non-articular surface. SD-29 is possibly associated with Hand 1
3 and both pisiforms are from the right side. All carpals are scaled to the same 1 cm scale.

4
5 Figure 5. The El Sidrón trapezia. Both trapezia are from the right side and shown in, from left to
6 right, distal view, showing the first metacarpal facet; palmar view, showing the trapezium's
7 tubercle; dorsal view of non-articular surface; and proximal view, showing the scaphoid facet.
8 SD-2019 is missing its tubercle. Both bones are scaled to the same 1 cm scale.

9
10 Figure 6. The El Sidrón trapezoids. Trapezoids shown in, from left to right, palmar and dorsal
11 views of the non-articular surface (for which distal is towards the top of the page); proximal view,
12 showing scaphoid facet; distal view, showing second metacarpal facet; and lateral view,
13 showing trapezium facet (for which palmar is towards the top of the page). SD-94 image in box
14 shows bone in distolateral view to highlight its best-preserved morphology. SD-104 and SD-
15 1022b are left and all other specimens are from the right side. All bones are scaled to the same
16 1 cm scale.

17
18 Figure 7. The El Sidrón capitates. Capitates shown in, from left to right, palmar and dorsal views
19 of the (mostly) non-articular surface (for which distal is towards the top of the page); proximal
20 view, showing the lunate and scaphoid articulation; distal view, showing the third metacarpal
21 facet; medial view, showing the hamate facet; and lateral view, showing the scaphoid, trapezoid,
22 and second metacarpal facets (for which dorsal is towards the top of the page). SD-557 and
23 SD-400 are right and all other specimens are from the left side. All bones are scaled to the
24 same 1 cm scale.

25
26 Figure 8. The El Sidrón hamates. Hamates shown in, from left to right, distal view of metacarpal
27 articulation; medial view, showing triquetrum facet; lateral view, showing capitate facet (for
28 which dorsal is towards the top of the page); and palmar and dorsal views of the non-articular
29 surface (for which proximal is towards the top of the page). SD-742 is from the right side and
30 SD-158 is from the left side. All bones are scaled to the same 1 cm scale.

31
32 Figure 9. El Sidrón Hand 1 articulated right carpus. Carpals that articulate well together and are
33 likely to be from a single individual include right SD-744 scaphoid, SD-85 lunate, SD-58
34 triquetrum, SD-29 pisiform, SD-373 trapezium, SD-28 trapezoid, SD-557 capitate, and SD-742

1 hamate. Top row, carpus shown in palmar view, including the medial carpals with pisiform (left),
2 complete carpus excluding the pisiform (middle), and lateral carpals (right), highlighting the
3 expanded non-articular palmar surface of the trapezoid (right). Bottom row, medial carpus
4 shown in dorsal view (left), complete carpus in distolateral view (middle), and lateral carpals in
5 dorsolateral view (right).

6

7 Figure 10. Clockwise from top left, box-and-whisker plots of scaphoid shape ratios showing
8 relative size (i.e., divided by a geometric mean) of the dorsopalmar (DP) height of the scaphoid
9 body, mediolateral (ML) breadth of the scaphoid body, proximodistal (PD) length of the capitate
10 facet, and DP height of the radial facet. Inset images show how each metric was measured. All
11 Neandertal specimens are highlighted in gray. Recent human ('humans') and small-bodied
12 human ('s-b humans') samples are as described in Table 1. The El Sidrón sample includes SD-
13 96, -258, -744, -1243, and SDR-064; *Australopithecus sediba* sample includes UW 88-158;
14 *Homo naledi* sample includes UW 101-807, -1639, and -1726. Dolni Vest. = Dolní Věstonice.
15 See Table 1 for details of remaining fossil sample.

16

17 Figure 11. Principal component analysis of scaphoid shape. Recent human sample shown in
18 dark gray dots and small-bodied populations in light gray dots; early *Homo sapiens* indicated by
19 green triangles, *Homo neanderthalensis* by blue/purple squares, and australopiths by crosses.
20 Human and fossil sample composition the same as described in Table 1 and Figure 10, apart
21 from El Sidrón SD-744, which was excluded due to poor preservation of capitate facet. Are =
22 Arene Candide 2, Bar = Barma Grande 2, Dolni = Dolní Věstonice, Oha = Ohalo II, Qaf =
23 Qafzeh 9, Keb = Kebara 2, LaF = LaFerrassie 1, Reg = Regourdou 1, Tab = Tabun 1-152, MH2
24 = *Australopithecus sediba*, StW = *Australopithecus* sp. StW 618.

25

26 Figure 12. Neandertal scaphoid tubercle projection. Bar chart showing (A) absolute tubercle
27 projection (mm), as defined by Trinkaus (1982, 1983), in a sample of Neandertals in comparison
28 to recent humans (Europeans and Amerindians) and (B) relative tubercle projection, expressed
29 as a ratio of the scaphoid tubercle projection relative to the dorsopalmar height of the scaphoid
30 body, across Neandertals. All comparative data from Trinkaus (1983). Error bars represent
31 standard deviation. 'LaFerrassie' includes LaFerrassie 1 and 2 specimens; 'Shanidar' includes
32 Shanidar 3, 4, 6, and 8 specimens.

33

1 Figure 13. Comparative anomalous scaphoid shape. Examples of anomalous scaphoid
2 morphology with a distinctive os centrale portion (*) similar to that found in the El Sidrón
3 scaphoids: (A) image adapted from Dwight (1907) of a recent human scaphoid with a “partly
4 marked off” os centrale in medial view, (B) images adapted from Leboucq (1884) of a recent
5 human scaphoid with a “persistance du central” in medial and distal views, (C) surface models
6 of the Shanidar 3 Neandertal left (fragmentary) and right scaphoids in medial (above) and distal
7 (below) views. Surface models of Shanidar 3 generously provided by M. Tocheri.

8

9 Figure 14. Clockwise from top left, box-and-whisker plots of lunate shape ratios showing relative
10 size (i.e., divided by a geometric mean) of the mediolateral (ML) breadth of the lunate body,
11 proximodistal (PD) length of the lunate body, dorsopalmar (DP) height of the distal facet, and
12 ML breadth of the radial facet. Inset images show how each metric was measured. All
13 Neandertal specimens are highlighted in gray. Human and small-bodied (s-b) human samples
14 the same as described in Table 1. The El Sidrón sample includes SD-85 and -1011a; *Homo*
15 *naledi* sample includes UW101-418b, -1546, and -1732; *Australopithecus sediba* is UW 88-159;
16 *Australopithecus afarensis* is AL 444-3. Dolni Vest. = Dolní Věstonice; cf. *Austral.* = cf. *Au.*
17 *afarensis* KNM-WT 22944-J. See Table 1 for further details of fossil sample.

18

19 Figure 15. Principal component analysis of lunate shape. Recent human sample shown in dark
20 gray dots and small-bodied populations in light gray dots; early *Homo sapiens* indicated by
21 green triangles, *Homo neanderthalensis* by blue/purple squares apart from El Sidrón (red
22 squares), and australopiths by crosses. Human and fossil sample composition the same as
23 described in Table 1 and Figure 13. Are = Arene Candide 2, Bar = Barma Grande 2, Dolni =
24 Dolní Věstonice, Qaf = Qafzeh 9, Tian = Tianyuan 1, Amud = Amud 1, Keb = Kebara 2, Nean =
25 Neandertal 1, Shan = Shanidar 3 and 4, Tab = Tabun 1-162', MH2 = *Australopithecus sediba*,
26 AL-444 = *Australopithecus afarensis* AL 444-3.

27

28 Figure 16. Box-and-whisker plots of triquetrum shape ratios. Relative size (i.e., divided by a
29 geometric mean) of the mediolateral (ML) breadth and dorsopalmar (DP) height of the
30 triquetrum body. All Neandertal specimens are highlighted in gray. Inset images show how each
31 metric was measured. Details of human, small-bodied (s-b) human, and fossil samples are in
32 Table 1. El Sidrón sample includes SD-1022a, -1227 (both associated with Hand 1), and -1813.
33 SD-1813 falls out at the extremes of the range of variation for both ratios, with the largest ML
34 breadth but shortest DP height of triquetrum body. SKX 3498 is affiliated with either

1 *Australopithecus robustus* or early *Homo*. *Homo naledi* specimen is UW101-1727 and
2 *Australopithecus sediba* is UW 88-159.

3
4 Figure 17. Principal component analysis of triquetrum shape. Recent human sample shown in
5 dark gray dots and small-bodied populations in light gray dots; early *Homo sapiens* indicated by
6 green triangles, *Homo neanderthalensis* by blue/purple squares apart from El Sidrón (red
7 squares), and australopiths by crosses. Human and fossil sample composition the same as
8 described in Table 1. Are = Arene Candide 2, Bar = Barma Grande 2, Oha = Ohalo II, Qaf =
9 Qafzeh 8 and 9, Amud = Amud 1, Keb = Kebara 2, Reg = Regourdou 1, Tab = Tabun 1-154,
10 MH2 = *Australopithecus sediba*, SKX = SKX 3498 *Australopithecus robustus* or early *Homo*.

11
12 Figure 18. Clockwise from top left, box-and-whisker plots of pisiform shape ratios showing
13 relative size (i.e., divided by geometric mean) of proximodistal (PD) length of pisiform body,
14 mediolateral (ML) breadth of pisiform body, PD length of the pisiform's triquetrum facet, and
15 dorsopalmar (DP) height of pisiform body. Inset images show how each metric was measured.
16 All Neandertal specimens are highlighted in gray. Details of human, small-bodied (s-b) human,
17 and fossil samples are in Table 1. El Sidrón sample includes SD-29 and SD-646;
18 *Australopithecus afarensis* is AL 333-91; Dolni = Dolní Věstonice.

19
20 Figure 19. Principal component analysis of pisiform shape. Recent human sample shown in
21 dark gray dots and small-bodied populations in light gray dots; early *Homo sapiens* indicated by
22 green triangles, *Homo neanderthalensis* by blue/purple squares apart from El Sidrón (red
23 squares), and australopiths by crosses. Human and fossil sample composition the same as
24 described in Table 1. The El Sidrón sample includes SD-29 (falling out closer to Kebara 2) and
25 SD-646. Dolni = Dolní Věstonice, Oha = Ohalo II, Qaf = Qafzeh 8 and 9, Amud = Amud 1, Keb
26 = Kebara 2, Reg = Regourdou 1, Shan = Shanidar 5, Tab = Tabun 1-157 and Tabun IV, AL 333
27 = AL 333-91 *Australopithecus afarensis*.

28
29 Figure 20. Clockwise from top left, box-and-whisker plots of trapezium shape ratios showing
30 relative size (i.e., divided by a geometric mean) of the dorsopalmar (DP) height of trapezium
31 body, proximodistal (PD) length of trapezoid facet, mediolateral (ML) breadth of first metacarpal
32 facet (Mc1), and PD length of Mc1 facet. Inset images show how each metric was measured. All
33 Neandertal specimens are highlighted in gray. Details of human, small-bodied (s-b) human, and
34 fossil samples are in Table 1. Are = Arene Candide 2; Oha = Ohalo II; Qaf = Qafzeh 9; El Sid =

1 El Sidrón, including SD-373 and -2019; Keb = Kebara 2; *H. nal* = *Homo naledi*, including
2 UW101-916 and -1731; OH 7 = *Homo habilis* FLK-NN-Q; *Au. Afar* = *Australopithecus afarensis*
3 AL 333-80.

4

5 Figure 21. Trapezium tubercle morphology. (A) Tubercle cross-sectional area (mm^2) calculated
6 as tubercle length x tubercle thickness, following Trinkaus (1983) and (B) tubercle projection
7 ratio, calculated as the tubercle projection/length of the first metacarpal facet * 100. All
8 comparative data from Trinkaus (1983) and Niewoehner (2006), apart from El Sidrón SD-373,
9 Shanidar 3, Regourdou 1, and Arene Candide 2 ('Arene Can.'). SD-373 has a relatively small
10 tubercle of the trapezium compared with most other Neandertals. Note that Trinkaus (1983)
11 reports a larger tubercle cross-sectional area of 98 mm^2 for Regourdou 1, and "length" of the
12 first metacarpal facet in this study is equivalent to "breadth" of this facet used to calculate the
13 tubercle index in Trinkaus (1983).

14

15 Figure 22. Clockwise from top left, box-and-whisker plots of trapezoid shape ratios showing
16 relative size (i.e., divided by a geometric mean) of the dorsopalmar (DP) height of trapezoid
17 body, proximodistal (PD) length of trapezoid's palmar surface, mediolateral (ML) length of the
18 trapezoid's dorsal surface, and PD length of the trapezoid's dorsal surface. Inset images show
19 how each metric was measured. All Neandertal specimens are highlighted in gray. Details of
20 human (hum), small-bodied (s-b) human, and fossil samples are in Table 1. El Sidrón sample
21 includes SD-28 and -529; *Homo naledi* sample includes UW101-1581 and -1782. La Ferr = La
22 Ferrassie, Arene = Arene Candide 2, Ohalo = Ohalo II.

23

24 Figure 23. Principal component analysis of trapezoid shape. Recent human sample shown in
25 dark gray dots and small-bodied populations in light gray dots; early *Homo sapiens* indicated by
26 green triangles, *Homo neanderthalensis* by blue/purple squares apart from El Sidrón (red
27 squares). Human and fossil sample composition the same as described in Table 1 and Figure
28 22. *Homo naledi* specimen UW 101-1581 falls out closest to the El Sidrón trapezoids.

29

30 Figure 24. Clockwise from top left, box-and-whisker plots of capitate shape ratios showing
31 relative size (i.e., divided by a geometric mean) of the proximodistal (PD) length of the capitate
32 body, mediolateral (ML) breadth of the capitate body, dorsopalmar (DP) height of the third
33 metacarpal (Mc3) facet, and ML breadth of the proximal facet. Inset images show how each
34 metric was measured. All Neandertal specimens are highlighted in gray. Details of human,

1 small-bodied (s-b) human, and fossil samples are in Table 1. El Sidrón sample includes SD-557
2 and -1034, *Homo naledi* sample includes UW101-930 and -1730, *Australopithecus sediba* is
3 mean of UW-105 and -156 from MH2, *Australopithecus afarensis* is AL 333-40,
4 *Australopithecus africanus* is TM 1526.

5
6 Figure 25. Principal component analysis of capitate shape. Recent human sample shown in
7 dark gray dots and small-bodied humans in light gray dots; early *Homo sapiens* indicated by
8 green triangles, *Homo neanderthalensis* by blue/purple squares apart from El Sidrón (red
9 squares), and australopiths by crosses. Human and fossil sample composition the same as
10 described in Table 1 and Figure 24. Are = Arene Candide 2, Oha = Ohalo II, Qaf = Qafzeh 9,
11 Barma = Barma Grande 2, Tian = Tianyuan, Keb = Kebara 2, Moula = Moula-Guercy M-F1-461,
12 Dolni = Dolní Věstonice 15, Shan = Shanidar 4, Tab = Tabun 1, Nean = Neandertal 1, MH2 =
13 *Australopithecus sediba*, KNM = cf. *Australopithecus afarensis* KNM-WT 22944-H, AL 333 =
14 *Australopithecus afarensis* AL 333-40.

15
16 Figure 26. Clockwise from top left, box-and-whisker plots of hamate shape ratios showing
17 relative size (i.e., divided by a geometric mean) of the proximodistal (PD) length of hamate
18 body, dorsopalmar (DP) height of hamate, including and excluding the hamulus, and
19 mediolateral (ML) breadth of the hamate's distal metacarpal facets. All Neandertal specimens
20 are highlighted in gray. Details of human, small-bodied (s-b) human, and fossil samples are in
21 Table 1. El Sidrón sample includes SD-742; *Homo naledi* sample includes UW 101-1640 and -
22 1729; *Australopithecus sediba* is mean of UW 88-95 and -106 from MH2; *Australopithecus*
23 *afarensis* is AL 333-50; KNM-WT 22944-I is cf. *Australopithecus afarensis*.

24
25 Figure 27. Principal component analysis of hamate shape. Recent human sample shown in dark
26 gray dots and small-bodied humans in light gray dots; early *Homo sapiens* indicated by green
27 triangles, *Homo neanderthalensis* by blue/purple squares apart from El Sidrón (red squares),
28 and australopiths by crosses. Human and fossil samples composition the same as described in
29 Table 1 and Figure 26. Are = Arene Candide 2, Ohalo = Ohalo II, Dolni = Dolní Věstonice 3 and
30 15, Qaf = Qafzeh 9, Keb = Kebara 2, Reg = Regourdou 1, Shan = Shanidar 4 and 5, MH2 =
31 *Australopithecus sediba*, KNM = cf. *Australopithecus afarensis* KNM-WT 22944-I, AL 333 *Au.*
32 *afarensis* AL 333-50.

33
34

1 **Tables**

2 Table 1. Comparative extant and fossil sample for each carpal bone.^a

Species	Site/specimen	Age	Sex	Scaphoid	Lunate	Triq	Pisiform	Trpzm	Trpzd	Capitate	Hamate
Male/female											
Recent <i>Homo sapiens</i>	European, Africans, Tierra del Fuegians			72/70	68/69	67/68	6/5	9/7	8/8	83/84	54/54
	small-bodied Khoisan			5/11	5/11	5/11	4/9	5/11	5/11	12/13	5/11
Left/right											
<i>Homo neanderthalensis</i>	Europe										
	El Sidrón	49 Ka	?	3/2	0/2	2/2	0/2	0/2	0/2	2/3	1/1
	Feldhofer Neandertal 1	40 Ka	?	-	1/0*	-	-	-	-	1/0*	-
	La Chapelle	56–47 Ka	M	-	-	-	-	-	-	1/0*	-
	Regourdou 1	~70 Ka	?	1/1*	-	1/0*	1*	-	-	-	0/1*
	Kiik-Koba 1	~70 Ka	M	-	-	-	-	-	1/0 ^g	-	-
	La Ferrassie 1	74–68 Ka	M	1/0*	-	1/0 ^b	-	1/1*	1/0*	0/1*	-
	La Ferrassie 2	74–68 Ka	F	-	-	-	-	-	1/1 ^b	0/1 ^b	-
	Moula-Guercy M-F1-461 ^b	120–100 Ka	?	-	-	-	-	-	-	1/0	-
	Krapina 200 ^c	~130 Ka	?	-	-	-	-	-	-	0/1	-
	Near East										
	Amud 1	50–41 Ka	M	-	1/1	1/1	1/1	-	1/1 ^b	1/0	-
	Shanidar 3	50–45 Ka	M	0/1*	1/1*	-	-	0/1*	-	-	1/0*
	Shanidar 4	>45 Ka	M	1/1 ^d	1/0 ^d	-	-	-	-	1/0*	1/0 ^d
	Shanidar 5 ^d	>45 Ka	M	-	-	-	0/1	-	-	-	0/1
Shanidar 6 ^d	~75–50 Ka	F	0/1	-	-	-	-	-	-	-	
Shanidar 8 ^d	?		0/1	-	-	-	-	-	-	-	
Kebara 2	61–59 Ka	M	1/1	1/1	1/0	1/1	1/0	1/0	1/0	1/0	
Tabun 1	~122 Ka	F	1/0	1/0	1/0	1/0	-	1/0	1/0	1/0	
Tabun 3	?	?	-	-	-	-	-	-	-	0/1	
Tabun IV	?	?	-	-	-	0/1	-	-	-	-	
Early <i>Homo sapiens</i>	Europe										

Arene Candide 2		M	1/1	1/1	1/0	-	1/1	1/1	1/1	1/1
Barma Grande 2	26–23 Ka	M	1/1	1/1	1/1	-	-	-	1/1	1/1
Dolni Vestonice 3 ^e	29–27 Ka		1/0	0/1	-	-	-	-	-	1/0
Dolni Vestonice 14 ^e	29–27 Ka	M	0/1	1/0	-	0/1	-	-	-	-
Dolni Vestonice 15 ^e	29–27 Ka	F	-	0/1	-	-	-	-	0/1	0/1
Dolni Vestonice 16 ^e	29–27 Ka	M	1/1	1/0	-	-	-	-	0/1	-

Near East

Ohalo II	23–19 Ka	M	1/1	1/0	1/0	1/1	1/1	1/1	1/1	1/1
Qafzeh 9	100–80 Ka	F	1/1	1/1	0/1	1/1	0/1	1/1	0/1	0/1
Qafzeh 8	100–80 Ka	?	-	-	0/1	0/1	-	0/1	-	-
Skhul V	130–100 Ka	M	-	1/0 ^h	1/0 ^h	-	-	-	0/1	-
Skhul IV	130–100 Ka		-	-	1/1 ^h	1/0 ^f	-	1/0 ^h	-	-

Asia

Tianyuan 1*	~40 Ka		-	0/1*	-	-	-	-	0/1*	-
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Other hominins

<i>H. antecessor</i>	ATD6-24 and 23 ^f Hand 1 + isolated specimens	~730 Ka	?	-	-	-	-	-	1/0	1/0
<i>H. naledi</i>		?	?	1/2	1/2	0/1	-	1/1	0/2	2/1
<i>H. habilis</i>	OH 7 FLK-NN-Q	1.75 Ma	?	-	-	-	-	0/1	-	-
<i>Au. afarensis</i>	AL 333 and AL 444	3.2 Ma	?	-	0/1	-	1/0	0/1	-	0/1
<i>Au. sp.</i>	StW 618	3–2 Ma	?	1/0	-	-	-	-	-	-
<i>Au. cf. afarensis</i>	KNM WT 22944 ^g	3.5 Ma	?	-	1/0	-	-	-	-	1/0
<i>Au. sediba</i>	MH2	1.98 Ma	F	0/1	0/1	0/1	-	-	-	1/1
<i>Au. africanus</i>	TM 1526	3–2 Ma	?	-	-	-	-	-	-	0/1
<i>Au. robustus/early Homo</i>	SKX 3498	~1.5 Ma	?	-	-	0/1	-	-	-	-

1 ^aFor recent human sample, male and female sample sizes are provided. For fossil hominin sample, species, and specimen, date and
2 left and right bones are provided. Triq = triquetrum, trapzm = trapezium, trpzd = trapezoid

3 ^b Data from Mersey et al. (2013)

4 ^c Data from Heim (1982)

5 ^d Data from Trinkaus (1983)

6 ^e Data from Sladek et al. (2000)

7 ^f Data from Lorenzo et al. (1999)

8 ^h Data from Endo and Kimura (1972)

- 1 ^g Measurements taken from cast
- 2 *Measurements taken from surface model

1 Table 2. Scaphoid metric data (mm).^a

Specimen Side	SD-744 ^c	SDR-064 ^d	SD-96 ^e	SD-110 ^f	SD- 258 ^d	SD-679b ^d	SD- 1243
	R	L	R	R?	L	L	L
Measurement							
Max. breadth	28.7	26.8	25.7	-	26.5	-	28.2
Max. height	17.5	[17.0]	17.0	-	15.8	-	14.6
Max. length	[13.4]	[12.8]	[13.7]	-	13.2	-	12.7
Height of radial facet	[14.7]	14.0	15.8	-	13.7	[12.6]	13.1
Breadth of radial facet	17.7	17.4	[18.0]	-	17.4	[18.5]	18.5
Height of lunate facet	[14.0]	12.5	[7.3]	-	10.2	[11.2]	[11.7]
Length of lunate facet	10.9	10.4	[3.0]	-	9.5	-	[10.7]
Breadth of capitate Facet		[15.8]	15.4	-	15.2	-	15.3
Height of capitate facet	[11.8]	[13.5]	12.7	-	12.6	[12.7]	11.6
Height of trapezium- Trapezoid facet	20.0	21.5	12.5	-	21.4	-	-
Length of trapezium- Trapezoid facet	[10.6]	-	9.8	-	10.8	-	[9.6]
Tubercle projection ^b	[15.8]	[15.8]	-	-	13.9	-	15.7
Minimum thickness ^b	5.5	[5.5]	4.3	4.2	4.4	4.5	4.4

2 ^a Here and in Tables 2–8, “breadth” always refers to the mediolateral dimension, ‘height’ refers
 3 to the dorsopalmar dimension, and ‘length’ refers to the proximodistal dimension. R = right side,
 4 L = left side, max. = maximum, ‘-’ indicates that preservation prohibited measurement or a
 5 confident estimation of that measurement; ‘[x]’ indicates estimated values.

6 ^b Measurements following Trinkaus (1982, 1983)

7 ^c Associated with Hand 1

8 ^d Preserves a distinct ‘os centrale’ portion

9 ^e Bipartite tubercle

10 ^f Possibly juvenile

11

12

1 Table 3. Lunate metric data (mm).^a

	Specimen	SD-85 ^b	SD-1011a
	Side	R	R
Measurement			
Max. length		13.0	14.4
Max. height		17.3	17.8
Max. breadth		15.1	16.1
Height of scaphoid facet		8.3	11.7
Length of scaphoid facet		3.7	5.5
Height of distal facet ^c		15.5	15.6
Breadth of distal facet ^c		12.0	11.8
Height of radial facet		15.8	17.1
Breadth of radial facet		15.2	16.2
Height of triquetrum facet		7.8	[10.0]
Length of triquetrum facet		7.0	8.6

2 ^a Abbreviations the same as in Table 1

3 ^b Associated with Hand 1

4 ^c Includes both capitate and hamate facets

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1 Table 4. Triquetrum metric data (mm).^a

Specimen	SD-1227 ^b	SD-58 ^b	SD-1022a	SD-1813
Side	L	R	L	R
Measurements				
Max. breadth	[14.5]	[14.0]	[13.0]	16.4
Max. height	14.6	14.6	[14.3]	13.2
Max. length	11.3	-	9.2	[8.3]
Height of lunate facet	9.4	[8.9]	8.5	-
Length of lunate facet	[7.1]	[7.0]	6.9	[7.3]
Breadth of hamate facet	[11.9]	12.0	-	14.0
Height of hamate facet	11.7	10.2	[9.7]	-
Breadth of pisiform facet	[8.3]	[7.9]	-	[8.9]
Length of pisiform facet	7.7	[7.0]	-	[7.3]

2 ^a Abbreviations the same as in Table 1

3 ^b Associated with Hand 1

4

5

6

7

1 Table 5. Pisiform metric data (mm).^a

2

	Specimen	SD-29 ^b	SD-646
	Side	R	R
Measurement			
Max. breadth		8.9	10.4
Max. height		11.0	11.6
Max. length		15.3	15.6
Length of triquetrum facet		10.4	[10.4]
Breadth of triquetrum facet		7.8	8.6

3 ^a Abbreviations the same as in Table 1

4 ^b Potentially associated with Hand 1

5

6

7

1 Table 6. Trapezium metric data (mm).^a

	Specimen Side	SD-373 ^c	SD-2019
		R	R
Measurement			
Max. length		24.2	-
Max. height		14.3	14.2
Length of Mc1 facet		14.5	14.2
Breadth of Mc1 facet		12.3	13.5
Length of trapezoid facet		7.9	11.2
Height of trapezoid facet		8.7	8.7
Breadth of scaphoid facet		10.8	10.5
Length of scaphoid facet		9.1	9.0
Tubercle length ^b		11.1	-
Tubercle thickness ^b		4.1	-
Tubercle projection ^b		3.2	-

2 ^a Abbreviations the same as in Table 1

3 ^b Metric as defined in Trinkaus (1983)

4 ^c Associated with Hand 1

5

6

7

8

1 Table 7. Trapezoid metric data (mm).^a

	Specimen^b	SD-28 ^c	SD-529	SD-104
	Side	R	R	L
Measurement				
Max. length		20.2	16.2	-
Max. height of palmar surface		8.6	6.1	-
Max. breadth of dorsal surface		13.5	12.6	12.2
Max. height of dorsal surface		13.2	11.8	11.6
Height of trapezium facet		15.1	12.9	-
Length of trapezium facet		9.0	9.9	-
Height of Mc2 facet		17.4	14.4	-
Breadth of Mc2 facet		12.1	11.7	-
Height of scaphoid facet		12.4	9.8	-
Breadth of scaphoid facet		10.4	9.8	-

2 ^a Abbreviations the same as in Table 1

3 ^b Preserved metric data for fragmentary specimens SD-94 and SD-1022a provided in text

4 ^c Associated with Hand 1

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1 Table 8. Capitate metric data (mm).^a

	Specimen	SD-1034 ^b	SD-557 ^b	SDR-063	SD-400	SD-632a
		Side	L	R	L	R
Measurement						
Max. length		24.1	22.4	-	-	-
Max. height		21.1	21.2	-	-	-
Max. breadth		17.6	[16.4]	-	-	-
Height of hamate facet		9.8	10.0	[9.4]	-	-
Length of hamate facet		17.2	17.5	[17.3]	-	15.7
Breadth of proximal facet		12.9	12.8	12.4	12.6	[12.1]
Height of proximal facet		14.4	13.2	12.1	[14.0]	-
Breadth of capitate "neck"		11.1	11.2	10.0	-	-
Height of Mc3 facet		16.1	16.1	-	-	-
Dorsal breadth of Mc3 facet		16.4	-	-	-	[14.0]
Height of Mc2 facet		15.2	-	-	-	-
Length of Mc2 facet		5.3	-	-	-	-

2 ^a Abbreviations the same as in Table 1

3 ^b Likely associated with Hand 1

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1 Table 9. Hamate metric data (mm).^a

	Specimen Side	SD-742 ^c	SDR-158
		R	L
Measurement			
Max. length (incl. hamulus)		[20.0]	-
Max. length of hamate body		[17.7]	-
Max. height (incl. hamulus)		[28.0]	-
Max. height of hamate body		[12.5]	-
Max. breadth		[15.7]	-
Height of capitate facet		[11.2]	-
Breadth of Mc4 facet		[8.8]	-
Breadth of Mc5 facet		[5.5]	-
Hamulus length ^b		12.0	[11.8]
Hamulus thickness ^b		6.0	5.9
Hamulus projection ^b		14.3	15.2

2 ^a Abbreviations the same as in Table 1

3 ^b As described by Trinkaus (1983)

4 ^c Likely associated with Hand 1

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Table 10. Results of principal component analysis for each carpal bone.^a

Shape variable	PC1	PC2	Shape variable	PC1	PC2
Scaphoid	42.5%	29.3%	Trapezoid	39.1%	23.6%
Height of capitate facet	0.68	-0.26	Height of trapezium facet	0.75	0.40
Length of scaphoid body	0.57	0.58	Length of dorsal surface (body)	-0.47	0.20
Length of radial facet	-0.39	0.14	Breadth of dorsal surface (body)	0.32	-0.11
Breadth of scaphoid body	0.15	-0.66	Length of palmar surface	-0.60	0.85
Length of capitate facet	0.13	0.27	Length of trapezium facet	0.21	0.25
Height of radial facet	-0.14	0.26	Height of trapezoid body	0.07	-0.05
Lunate	33.6%	24.3%	Capitate	35.6%	27.8%
Breadth of lunate body	-0.51	0.29	Breadth of Mc3 facet	-0.58	0.69
Height of lunate body	0.43	0.21	Height of proximal facet	0.41	0.35
Height of radial facet	0.42	0.53	Breadth of capitate body	-0.35	0.02
Height of capitate facet	0.36	0.36	Height of Mc3 facet	0.36	0.55
Breadth of radial facet	-0.37	0.25	Breadth of proximal facet	0.33	0.14
Breadth of capitate facet	-0.31	0.37	Length of capitate body	0.31	0.19
Length of lunate body	0.17	-0.52	Height of capitate body	0.21	-0.18
Triquetrum	33.4%	25.4%	Hamate	45.5%	24.9%
Height of hamate facet	0.85	-0.11	Max. height of hamate body	-0.81	0.15
Height of lunate facet	0.46	0.16	Length of hamate body	0.36	-0.60
Breadth of hamate facet	0.19	0.70	Breadth of distal facet	0.30	0.36
Height of triquetrum body	0.17	-0.43	Height of capitate facet	0.24	0.62
Breadth of triquetrum body	-0.08	0.53	Breadth of hamate body	0.23	0.31
Length of triquetrum body	-0.06	-0.04	Height of hamate body	0.12	0.05
Length of lunate facet	-0.01	0.11			
Pisiform	44.0%	26.6%			
Length of triquetrum facet	0.66	0.50			
Breadth of triquetrum facet	0.57	0.14			
Breadth of pisiform body	0.38	-0.66			
Height of pisiform body	-0.22	0.45			
Length of pisiform body	-0.22	0.30			

^a The percentage of variance explained for the first (PC1) and second (PC2) principal components and the loadings of each shape variable (i.e., metric/geometric mean) on each PC is given for each carpal bone. Shape variables are ordered from highest to lowest

overall loading on PC1, and for each, height, length, and breadth refers to the dorsopalmar, proximodistal, and mediolateral dimensions, respectively.

Table 11. Capitate's Mc2 facet angle, relative to the Mc3 (following Niewoehner et al., 1997).^a

Taxon	Specimen/population	Capitate's Mc2 angle (SD)
<i>Homo sapiens</i>	Amerindians (<i>n</i> = 41)	46 (7.0)
		Range 31–58
	European (<i>n</i> = 53)	39 (8.9)
		Range 19–58
<i>Homo neanderthalensis</i>	Amud 1	50
	Kebara 2	56
	Krapina	65
	La Chapelle	54
	Shanidar 4	44
	Tabun 1	64
	La Ferrassie 1	75
	La Ferrassie 2	72
	El Sidrón SD-1034	71
	El Sidrón SD-632a	58
<i>Homo heidelbergensis</i>	Sima de los Huesos (<i>n</i> = 6)	59.7 (6.1)
<i>Homo antecessor</i>	ATD6-24	48

^a All comparative data taken from Niewoehner et al. (1997) except that of *Homo heidelbergensis* (Arsuaga et al., 2015) and *Homo antecessor* (Lorenzo et al., 1999).

Table 12. Comparison of hamate hamulus shape.^a

Taxon	Sample/specimen	Hamulus cross-sectional area (mm²)	Hamulus projection index
<i>Homo sapiens</i>	Recent humans	40.2 (9.2) ^b	-
	Euroamericans (<i>n</i> = 25)	47.2 (14.1) ^c	42.0 ^c
	Afroamericans (<i>n</i> = 21)	55.4 (11.5) ^c	40.9 ^c
Early <i>H. sapiens</i>	Dolni Vest. 3	38.25 ^d	34.6 ^d
	Dolni Vest. 15	37.41 ^d	33.7 ^d
	Qafzeh 8	54.5 ^b	[36.9] ^b
	Qafzeh 9	61.0	38.7
	Ohalo II	-	41.4
	Arene	-	38.7
	Caviglione	-	39.2 ^b
	Tianyuan 1	-	40.0
	Range	37.4–61.0	33.7–41.4
<i>Homo neanderthalensis</i>	SD-742	72.0	[51.1]
	SD-158	[69.6]	-
	Shanidar 3	[79.4] ^b	47.7 ^b
	Shanidar 4	87.5 ^b	45.7 ^b
	Shanidar 5	74.8 ^b	43.3 ^b
	Regourdou 1	82.8 ^b	49.6
	Amud 1	98.0 ^b	45.4 ^b
	La Ferrassie 2	57.8 ^b	43.8 ^b
	Tabun 1	52.8 ^b	48.1 ^b
	Tabun 3	-	45.8
	Kebara 2	84.2	45.9
	Range (excl. El Sidron)	52.8–98.0	43.0–49.6
<i>Homo heidelbergensis</i>	Sima de los Huesos (<i>n</i> = 3)	62.1 (2.5) ^c	45.8 ^c
<i>Homo antecessor</i>	ATD6-23	52.9 ^c	[38.2] ^c
<i>Homo naledi</i>	UW 101-1729	50.8	39.7
<i>Australopithecus sediba</i>	UW 88-106	45.6	39.6
<i>Australopithecus afarensis</i>	AL 333-50	51.8	28.7

Au. cf. afarensis

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90.9

37.2

^a Hamulus cross-sectional area (hamulus PD length x hamulus ML breadth) and hamulus projection index (hamulus projection/maximum height of the hamate) in *Homo sapiens*, Neandertals, and other hominins.[x] = estimated values.

^b Data from Trinkaus (1983)

^c Data from Lorenzo et al. (1999)

^d Data from Sladek et al. (2000)