Title: Aggressive or funerary cannibalism? Skull-cup and human bone manipulation in Cueva de El Toro (Early Neolithic, southern Iberia).

Short title: Human skull-cup and bone manipulation in Cueva de El Toro.

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ABSTRACT

Objective

We analyse the processing sequence involved in the manufacture of a skull-cup and the manipulation of human bones from the Early Neolithic of Cueva de El Toro (Málaga, Spain).

Material and methods

The Early Neolithic material studied includes human remains found in two separate assemblages. Assemblage A consists of one skull-cup, a non-manipulated adult human mandible, and four ceramic vessels. Assemblage B contains manipulated and non-manipulated human remains that appeared mingled with domestic waste. Using a taphonomic approach, we evaluate the skull-cup processing and the anthropogenic alteration of human bones.

Results

The skull-cup was processed by careful paring away of skin, fragmentation of the facial skeleton and base of the skull, and controlled percussion of the edges of the calotte to achieve a regular shape. It was later boiled for some time in a container that caused pot polish in a specific area. The other human bones appeared scattered throughout the living area, mixed with other remains of domestic activity. Some of these bones show cut marks, percussion damage for marrow extraction, and tooth/chewing marks.

Discussion

Evidence from Cueva de El Toro suggests that cannibalism was conducted in the domestic sphere, likely following ritualised practices where the skull-cup could have played a part. Interpretation of this evidence suggests two hypotheses: 1) aggressive cannibalism relates to extreme inter-group violence; and 2) funerary cannibalism is a facet of multi-stage burial practices. Similar evidence has been found in other Neolithic sites of this region and suggests that cannibalism and skull-cups were elements widespread in these communities. These practices may be linked to significant transformations associated with the end of the Early Neolithic in southern Iberia.

Keywords

Human skull-cup, Prehistoric cannibalism, Funerary practice, Neolithic, Andalusia.

INTRODUCTION

Post-mortem processing of the head as a skull-cup is present in Western Europe from the Badegoulian to the Late Neolithic (Bello, Parfitt, & Stringer, 2011; Boulestin, 2012; Boulestin & Coupey, 2015; Boulestin et al., 2009; Cáceres, Lozano, & Saladié 2007; García & Carrasco, 1981; Saladié & Rodríguez-Hidalgo, 2017). Skull-cups are post-mortem processed heads that display signs of defleshing, breakage by percussion, and careful retouching of the broken borders (Bello et al., 2011; Boulestin, 2012). Several historical and ethnographic examples indicate that heads were made into skull-cups or used as drinking cups and trophy heads (Bello et al., 2011; Boulestin, 2012). Despite the name, there is no evidence that prehistoric skull-cups were intentionally modified to serve as routine drinking vessels in prehistory. In western European prehistory, they have been considered as ritual artefacts for use in ceremonies where cannibalism was involved (Bello et al., 2011; Bello, Saladié, Cáceres, Rodríguez-Hidalgo, & Parfitt, 2015; Boulestin, 2012; Boulestin & Coupey, 2015), and some skull-cups have been associated with the processing and consumption of bodies without any symbolic connotation (Botella, 1973; Cáceres et al., 2007). Unfortunately, there are few prehistoric cases where the archaeological context is well documented (Boulestin & Coupey, 2015). This situation makes it difficult to recognise the real meaning of such objects for the community that produced and used them (Bello et al., 2011; Boulestin, 2012; Saladié & Rodríguez-Hidalgo, 2017).

The earliest evidence of skull-cups comes from the Badegoulian levels of Grotte du Placard (Charente, France), where nine crania show cut marks attributable to defleshing, breakage by percussion, and retouching of the edges, resulting in skull-cups (Henry-Gambier & Faucheux, 2012; Le Mort & Gambier, 1991). This assemblage consists of cranial and postcranial remains of 24 individuals (adults and children). Skull-cups and postcranial bone manipulation are also frequently found associated in western European prehistory (Figure 1) (Boulestin, 2012). At the Magdalenian site of Gough's Cave (Great Britain), scholars found evidence of ritual cannibalism and skull carving to make skull-cups directly dated at 14,700 BP (Andrews & Fernández-Jalvo, 2003; Bello et al., 2011, 2015). The superlative example of the association between skull cups and cannibalism is found in the Early Neolithic Linear Pottery Culture site of Herxheim (Rhineland-Palatinate, Germany). This site contains the remains of at least 1,000 individuals, many of whose bones were manipulated, showing cut marks, fractures and skull cups. Boulestin and Coupey (2015) suggest that the Herxheim remains are the result of warfare with ritualised practices in which the enemies were cannibalised, and skull-cups were systematically manufactured from the heads. Interestingly, analysis of strontium isotopes ($^{87}Sr/^{86}Sr$) indicates that some individuals came from a remote place, also supported by foreign ceramic styles found at the site (Boulestin & Coupey, 2015).

[Figure 1 here]

There are also Iberian examples of skull-cups from the Neolithic (Figure 1). Las Majólicas, Carigüela and Los Mármoles are three caves located in southern Iberia where skull-cups have been reported along with cannibalism, except in Los Mármoles (Botella, Alemán, & Jiménez-Brobeil, 2000a; Botella, Jiménez-Brobeil, Alemán, du Souich, & García, 2000b; Botella, Alemán, du Souich, Jiménez-Brobeil, & García, 2000b; García & Carrasco, 1981; Jiménez-Brobeil, Botella & Alemán, 1996; Solari, Botella, & Alemán, 2012). Bone modifications include cut marks, intentional breakage of long bones, and skull-cup manufacture. These cups have been associated with the Late Neolithic although they have not been directly dated and some of these archaeological sites preserve levels from the Early Neolithic (Martín-Socas, Camalich, Caro, & Rodríguez-Santos et al., 2018). Evidence of cannibalism and six skull-cups were also found at the Late Neolithic levels of El Mirador cave (Sierra de Atapuerca, northern Spain) (Cáceres et al., 2007). In this example, the authors consider skull-cups as the result of brain extraction for "gastronomic cannibalism" and rule out ritual practices associated with these objects. However, this hypothesis is challenged because of similarities with other assemblages where they have been interpreted as products of symbolic practices (Saladié & Rodríguez-Hidalgo, 2017).

Here, we analyse the *chaîne opératoire* involved in the manufacture of a skull-cup and the bone manipulation of human remains from Cueva de El Toro (Málaga, Spain). The item has been directly dated by radiocarbon (AMS) and situated chronologically in the Early Neolithic. This item contributes to the discussion of such objects in a well-known archaeological context, with detailed study of the anthropological evidence. Finally, we discuss the ritual and symbolic meaning of this skull-cup and manipulated human bones, according to our knowledge about the funerary practices of the early farming communities of southern Iberia.

MATERIAL AND METHODS

Material

Cueva de El Toro is located in the wide karstic mountain range of Sierra de El Torcal (Málaga, Spain). This cave shows an internal structure configured by large blocks fallen at a time before the Neolithic occupation. Thus, the original floor consists of two spaces of different heights: upper, Sector 1, and lower, Sector 2 (Figure 2). During the first quarter of the 4th millennium BCE there was a structural change, possibly as a result of a tectonic movement or collapse of the karst system, causing a general incline in the karst platform of this part of Sierra de El Torcal, towards the south (Égüez, Mallol, Martín-Socas & Camalich, 2016; Martín-Socas, Camalich, & González-Quintero, 2004). This blocked the original entrance inside the cavity, configuring a new access and a 17 m deep pit to the south of Sector 2, besides tilting its sedimentary deposit (Figure 3).

[Figure 2 here]

Five excavation campaigns have been carried out at El Toro (1977, 1980, 1981, 1985 and 1988). In Sector 1, a small gap was identified between the large slabs fallen during the collapse of the cave prior to human occupation. It has a triangular shape and the entrance is on this upper platform, separated from Sector 2. Access is difficult due to its dimensions: 0.50 m on the NS axis and 1 m on the WE axis, reaching a depth of 1.5 m. In Sector 2, a stratigraphic sequence 2.40 m in depth was identified, with four chrono-cultural phases. The two lower levels correspond to Neolithic occupation, Phases IV (Early Neolithic, 6200-5980 BP, 5280-4780 cal BC 2σ) and IIIB (Late Neolithic, 5320-5170 BP, 4250-3950 cal BC 2σ) (Martín-Socas et al., 2018). Between the two phases, a sterile deposit points to a period of abandonment of the site (Figure 3). This absence of occupation between the end of the Early Neolithic and that during the Late Neolithic has been confirmed by the absolute dates, which established a hiatus estimated at around 500 years.

[Figure 3 here]

The Early Neolithic (Phase IV) includes archaeological evidence related to domestic activities, such as cereal seeds and ovicaprid remains. Use-wear analyses of flint tools show a predominance of butchery activities, along with evidence of bone, wood, leather and clay craftwork (Rodríguez-Rodríguez, 2004; Rodríguez-Rodríguez, Martín-Socas, Camalich, & González-Quintero, 1996; Rodríguez-Rodríguez, Gibaja, Perales, & Clemente, 2013). Moreover, micromorphological analysis has identified ovicaprid coprolites from undisturbed sedimentological samples, suggesting that goats or sheep were stabled there (Égüez et al., 2016). Therefore, human occupation has been interpreted as seasonal/periodic with a pastoral emphasis in this phase (Camalich & Martín-Socas, 2013; Égüez et al., 2016; Martín-Socas et al., 2004, 2018). The Early Neolithic phase also includes human remains that were found scattered in two assemblages. Assemblage A was located in Sector 1 and consisted of one skull-cup, a non-manipulated adult human mandible, and four ceramic vessels (Figure 4). Assemblage B contains most of the human remains, mingled with domestic waste in Sector 2 (Égüez et al., 2016; Martín-Socas et al., 2018).

[Figure 4 here]

Four human bone samples were directly dated by radiocarbon techniques (AMS) and calibrated using the Oxcal 4.3 program (Bronk Ramsey, 1995, 2001), and the IntCal13 calibration curve (Reimer et al., 2013). The radiocarbon dates of the skull-cup and mandible were 5040-4850 cal BC (6060 ± 30 cal BP, Beta-365288), and 5030-4850 cal BC 2σ (6050 ± 30 BP, Beta-365287), respectively. This chronology is about the same as some two human bone specimens from Sector 2: 5080-4935 cal BC 2σ (6100 ±30 BP, Beta 498412), and 4980-4780 cal BC 2σ (5980 ± 40 BP, Beta-365292). This means that both assemblages are likely the result of the same occupational episode in the cave.

Method

Human bone fragments were identified and recorded according to skeletal element and portion. We quantified the "number of identified specimens" (NISP) as an observational unit (Lyman, 1994). In addition, we calculated the "minimum number of elements" (MNE) and the "minimum number of individuals" (MNI) according to the MNE_e (Minimum Number of Expected Elements) (Lyman, 1994). The skeletal survive rate (%survivorship) was also calculated to establish the proportion between the elements recovered and those expected (Lyman, 1994). This percentage expresses the frequency of the MNE observed and the number of elements expected (MNE_e) according to the minimum number of individuals (MNI): %survivorship= MNE/(MNE_e x MNI)x100. Age-of-death was estimated according to standard procedures (Buikstra & Ubelaker, 1994; Scheuer & Black, 2000). Molecular sex identification was carried out using sex-specific DNA markers in some isolated specimens (Fregel et al., 2018). We did not observe skeletal features to identify sex in this assemblage.

We analysed cut marks (slicing and chopping), scraping marks, percussion damage (pits, striations, notches, and adhering flakes), breakage patterns, thermo-alteration, tooth marks and chewing (Boulestin, 1999; Domínguez-Rodrigo, de Juana, Galán, & Rodríguez, 2009; Fernández-Jalvo & Andrews, 2011; Lyman, 1994; Pickering & Egeland, 2006; Saladié et al., 2013; White, 1992). Each bone was systematically examined by two experienced observers (JS and FJR) at least twice, using a Nikon SMZ 1000 binocular microscope with an 8× to 80× magnification range. Human-induced changes were examined under higher magnification using a binocular microscope (Nikon Labophot 2 and Nikon MA100) with a 50× to 100× magnification range and photographed with a Nikon SD-Fi1 camera. Images were treated with Helicon Focus v. 4.62 software. In addition, we evaluated bones with traces of indirect heat exposure at low temperature according to macroscopic (Botella et al., 2000a; Pijoan, 1997) and microscopic criteria (Bosch, Alemán, Moreno-Castilla, & Botella, 2011; Solari et al., 2015; Trujillo-Mederos, Alemán, Botella, & Bosch, 2012). Surface morphology was studied at the micrometric level using a Scanning Electron Microscopy (SEM) model JEOL JSM-7600F coupled to an EDX Oxford INCAX-Act.

Additionally, we used available ancient DNA data from El Toro site (Fregel et al., 2018) to perform kinship analyses. Concretely, we used mtDNA and Y-chromosome lineages comparison to identify direct maternal and paternal relationships, respectively. We also applied the READ software (Monroy Kuhn, Jakobsson, & Günther, 2018) to genome-wide data from Fregel et al. (2018) to infer up to second-degree relationships, including nephew/niece-uncle/aunt, grandparent-grandchild or half-siblings. The main limitation for kinship inference using READ is that very low-coverage samples (less than 0.1 X) are prone to producing false negatives. To avoid problems related to low coverage, we used SNP capture data for the MEGA array from Fregel et al. (2018), with samples coverage being higher than 0.1 X in all cases (0.15X - 0.67X).

RESULTS

The human assemblage from Cueva de El Toro comprised 101 identified specimens: 48 cranial (15 from crania, 12 from mandibles, and 21 teeth), and 53 postcranial human bone fragments (Table 1). We established a minimum number of 57 elements (9 cranial and 48 postcranial). They are well preserved with occasional traces of weathering (Behrensmeyer, 1978), infrequent trampling marks and dry breakage. We did not observe evidence of trauma on bones. Remains belonged to seven individuals as MNI (four adults and three subadults), based on the representation of mandible remains: one young adult, two female adults (molecular sex based on teeth samples), one undetermined adult, one infant aged 6 ± 2 years, one young adolescent aged 12 ± 2.5 years, and one adolescent aged 15 ± 3 years. The skeletal survival rate (%survivorship) indicates an infra-representation of limb bones, pelvis, and thorax (Table 1). In this assemblage, there was no differential effect from natural taphonomic factors because the more fragile bones were found well-preserved. For instance, most bones present were those from the hands and feet, indicating that the absence of long bones was not due to any natural taphonomic effect (Bello & Andrews, 2006; Galloway, Willey, & Snyder, 1997; Waldron, 1987).

[Table 1 here]

Human bone manipulation

The bones displayed human modifications, suggesting that corpses were processed soon after death. There was a proportion of 13.2% manipulated bones, defined mostly by cut marks and percussion damage. Cranial specimens showed modifications on 9 of 27 pieces (33.3%; MNE=4), while 5 of 53 postcranial specimens were manipulated (9.4%; MNE=4), excluding tooth marks and fire alterations.

Cut marks were detected in 11 of 101 specimens (10.9%; MNE=5) excluding teeth. They display slicing cut marks (NISP=6; MNE=4), chop marks (NISP=3; MNE=3) and scraping marks (NISP=2; MNE=1). These marks showed microscopic features indicative of cutting with stone tools such as parallel micro-striations, shoulder effect and hertzian cones (Dominguez-Rodrigo et al., 2009). Slicing cut marks were more frequent on cranial bones relating to skinning, and they appear isolated and in parallel or sub-parallel groups. We also found scraping marks on skull fragments. These marks showed features common on fresh bones soon after death (Andrews & Cook, 1985; Behrensmeyer, Gordon, & Yanagi, 1986; Bello & Soligo, 2008; Bello et al., 2011; Boulestin, 1999; Greenfield, 1999; Morales Pérez et al., 2017). Percussion damage was present in 14 of 101 specimens (13.8%; MNE=7), including human-induced fractures on fresh bone, percussion pits, lunate scars, adhering flakes and anvil striations on cranial and postcranial bones. Bone manipulation comprised skull-cup manufacture, marrow extraction from long bones and disarticulation. We also noticed a polished surface on the skull-cup.

Seven postcranial specimens display evidence compatible with tooth marks and chewing (13.2% of specimens; MNE=7). These marks include tooth pits, furrowing, crushing, saw-toothed edges, and peeling. They are located on one subadult sternal segment, and three adult ribs, two phalanges, one first metatarsal, and one metacarpal. It must be pointed out that tooth-mark identification is challenging, and much more so the species that made them, so we cannot make absolutely sure (Boulestin & Coupey, 2015; Saladié & Rodríguez-Hidalgo, 2017). These remains appear in a context of consumption and later intermixture with other waste such as faunal remains.

Fire altered the bones after soft tissue decay (NISP=35; 34.6% of specimens; Table 1). Burnt bones show variability in colour, comprising brown-grey (NISP=7), dark-black (NISP=10), and chalky-white (NISP=2). Dark-black predominance suggests that most of the burnt remains were submitted to low intensity temperatures (200°C to 550°C) for some time (Buikstra & Swegle, 1989; Gonçalves, Cunha, & Thompson, 2015; Walker, Miller, & Richman, 2008; Whyte, 2001). No evidence of warping or cracking was detected on dark-black bones, whereas this is common when bones are burnt fresh (Buikstra & Swegle, 1989; Depierre, 2014; Gonçalves et al., 2015; Guillon, 1987; Herrmann & Bennett, 1999; Spennemann & Colley, 1989; Symes, Smith, & Berryman, 1996; Walker et al., 2008; Whyte, 2001). Chalky-white burnt bones, displaying longitudinal cracks on the surface, often indicate high temperatures (>600º/800ºC) maintained for some time. These features may point to combustion of fresh corpses or bones surrounded by muscle, and fatty marrow (Bontrager & Nawrocki, 2008; Buikstra & Swegle, 1989; Symes et al., 1996). Some heterogeneous combustion damage could also be due to burning fresh corpses, such as cranial fragment TCT85-46757. However, these fire alterations could also derive from various episodes of burning documented in Sector 2 (Égüez et al., 2016). In cannibalism, meat is usually processed after defleshing, which implies that the bones are not necessarily affected by fire (Saladié & Rodríguez-Hidalgo, 2017).

Other types of thermoalteration were also noted on the skull-cup and other bones: a mandible, a hand phalanx, and two foot phalanges (NISP=6; MNE=5; 5.9% of specimens). They look smooth, vitreous, more yellowish, and better preserved. These traits may indicate that some bones were boiled, because similar macroscopic features have been observed in experimental and archaeological cases, including Neolithic assemblages in Iberia (Botella et al., 2000a; Cáceres et al., 2007; Saladié & Rodríguez-Hidalgo, 2017; Solari et al., 2012; White, 1992). In the following all the bones with human-induced alterations are described:

1. **Assemblage A. Sector 1.**

Skull-cup

This is a human calvaria represented by the frontal and both parietal bones (Figure 5). It shows anthropogenic modification with evidence of cut marks, percussion damage, polish and boiling. The frontal bone is the most modified, since only the posterior area is preserved. The left parietal bone is largely conserved in the region over the superior temporal line, while the right portion is preserved above both inferior temporal lines, one cm under the stephanion, all the anterior area and the whole coronal suture. The occipital bone is absent due to dislocation.

[Figure 5 here]

Cut marks were present only on the ectocranial surface. We counted 74 slicing cuts ranging between 8.36 and 42.97 mm in length. They ran both parallel and perpendicular to the sagittal line, divisible into ten groups: three on the frontal bone (Figure 6b), four on the right parietal bone (Figure 6a) and three on the left parietal bone. There were cut marks in areas far from muscle attachments, on the squama of the frontal and on the parietals on both sides of the sagittal suture. These marks point to careful removal of soft tissues covering the calvaria. None of the incisions overlaps on the edges of the cracks or fractures, and when they are in close proximity, they are separated by percussion damage. This evidence suggests that the skull was first skinned and then carved.

[Figure 6 here]

The next stage involved controlled percussion resulting in an irregular fracture edge, with semi-circular or trapezoidal notches that have reflected and stepped endings produced by the carving (Figure 7). The points of impact are better defined on the external face than the internal, where there was deeper nick-scarring, besides diffuse irregular fractures. This indicates that percussion was conducted from the outside towards the inside of the calvaria.

[Figure 7 here]

In areas where the force applied was insufficient to fracture the bone, partial collapse and micro-pits were generated on the external face (Figure 8). These impacts also produced two large cracks, one almost on the midline of the frontal bone (Figure 8a) and one on the third posterior part of the left parietal bone. In both cases, the maximum width of the crack is located on the outer perimeter, suggesting this is the origin of an impacted fracture from where fissures subsequent irradiated, coinciding with the location of the respective apices. In the frontal area behind the crack the edges overlap. This requires plasticity, which is characteristic of fresh bone. The distribution of impact damage and flaking is indicative of meticulous controlled shaping of the broken edges to obtain the desired shape.

[Figure 8 here]

The skull-cup surface appears smooth and slightly vitreous when exposed to direct light. These macroscopic features have been observed when bones are boiled (Solari et al., 2015; Trujillo-Mederos, Bosch, Pijoan, & Mansilla, 2016). Micrographs obtained by scanning electron microscopy (SEM) showed a microscopic morphology constituted by ordered fibrils, with a smooth dense surface where the pore openings are obstructed, indicating diffusion and degradation of collagen fibrils (Figure 9). Macroscopic and microscopic features suggest that the artefact was subjected to low-temperatures and exposure to boiling water for some time (Bosch et al., 2011; Solari et al., 2015; Trujillo-Mederos et al., 2012). These anthropogenic manipulations have also been described in various cannibalism assemblages in Iberia, such as Malalmuerzo and El Mirador (Botella el al., 2000a,b; 2003: Cáceres et al., 2007; Saladié & Rodríguez-Hidalgo, 2017; Solari et al., 2012).

[Figure 9 here]

Additionally, there is a well-defined area in the frontal zone where use-wear is superimposed on technical traces. It describes a segment of approximately two centimetres along the edge on the outer side. This edge is rounded, in contrast to the other fractured areas (Figure 10). The surface shows a micro-topography, slightly convex and smooth, with higher reflectivity. There are long, thin striations in the polished area, oriented perpendicular and/or slightly oblique to the edge. They are not abundant, but they indicate a complex motion perpendicular to the contact area. The combination of these use-wear features suggests that a circumscribed segment was in contact with a soft, lightly abrasive material (Évora, 2015; Sidéra & Legrand, 2006).

[Figure 10 here]

2. **Assemblage B. Sector 2.**

Cranial bone fragments

A cranial fragment was found in Sector 2 that refits the skull-cup (TCT81-40858-2), including its modifications during processing (Figure 11). There are also two other cranial fragments (Figure 12) displaying cut marks and percussion damage consistent with skull-cup shaping, but they do not refit (TCT88-1540-4 and TCT81-40858-1). Another parietal fragment (TCT85-46757), carrying a portion of the parietal-occipital suture, shows parallel cut marks and low-intensity fire damage (Figure 13a). Moreover, the fragment TCT81-41038-1 shows cut marks on the ectocranial surface (Figure 13b) aimed at removing the scalp from the cranium (Botella et al., 2000b; Saladié et al., 2015; White, 1992). These fragments do not display boiling damage.

[Figure 11 here]

[Figure 12 here]

[Figure 13 here]

A left mandibular ramus (TCT88-1405-1) displays cut marks, effects of boiling, and crushing damage on the condyle, consistent with percussion or chewing (Figure 14a) (Saladié et al., 2013; White, 1992). This set of manipulations could derive from cutting the masseter muscle, further suggesting separation of the mandible from the cranium (Bello et al., 2011; Le Mort & Gambier 1991; Santana et al., 2012; White, 1992). Additionally, a right mandibular ramus (TCT85-46642-2) shows transversal breakage with two notches and an adhering flake, although cut marks were not observed on this bone (Figure 14b). Percussion damage observed on mandibular rami suggest they were intentionally fractured to extract marrow (Bello et al., 2011; 2015; Boulestin & Coupey, 2015; Fernández-Jalvo & Andrews, 2011).

[Figure 14 here]

Postcranial bone fragments

We found a left unfused proximal diaphysis of a subadult femur (TCT80-10705) that displays a chopping mark on the femoral neck (Figure 15). This mark suggests detachment of the femur from the *ossa coxae* and cutting of the ilio-femoral ligament (Bello et al., 2015; Mariotti et al., 2009; Villa, 1992). The femur also shows longitudinal and curved breakage, along with adhering flakes. This pattern suggests that this bone was intentionally manipulated, and is consistent with cracking for marrow extraction (Bello et al., 2015; Boulestin, 1999; Villa & Mahieu, 1991; Villa, Courtin, & Helmer, 1988; Villa et al., 1986; White 1992). The outer surface shows exfoliation, which could be heat induced (White, 1992).

[Figure 15 here]

A shaft fragment of tibia (TCT88-1540-3) shows percussion damage, including longitudinal and oblique fractures, notches and percussion pits. These features can be interpreted as a manipulation for marrow extraction (Boulestin, 1999; Bello et al. 2015; Villa & Mahieu, 1991; Villa et al., 1986, 1988; White, 1992).

Slicing cut marks are in two groups on a right talus neck (TCT81-41038-2), near the tibiotalar joint, showing a perpendicular orientation to the long axis of the bone (Figure 16). They are likely associated with cutting both talonavicular and anterior talofibular ligaments, during tibiotarsal disarticulation of the foot from leg (Bello et al., 2015). Such cut marks are observed in cannibalism assemblages (Boulestin & Coupey, 2015).

[Figure 16 here]

We observed one tooth pit (6.8 x 5.6 mm) and tooth marks on the distal epiphysis of a first metatarsal (TCT85-46039-2), which also showed an oblique fracture on the shaft (Figure 17a). This bone displays fire damage with black and brown hues. A third metacarpal (TCT85-46285-2) also shows two tooth pits, one on the proximal epiphysis and other on the distal epiphysis, showing associated fractures at the distal epiphysis (Figure 17b). Proximal (TCT85-46007-1) and intermediate (TCT85-46642-1) hand phalanges show crenulated edges at their proximal epiphyses (Figure 17c). There is a rib with shallow scores on the internal surface and two pits at the proximal end (Figure 17d), and another fragment with notches and splintering (Figure 17e). Moreover, we noticed shallow peeling on a rib which was fractured when fresh (Figure 17f). Lastly, a subadult sternal segment (TCT80-19967) showed various tooth marks as double arch punctures in crenulated edges, notches, and two isolated pits (Figure 18).

[Figure 17 here]

[Figure 18 here]

Kinship analysis

MtDNA haplogroups for the skull-cup sample (TOR.5) and the mandible (TOR.11) from Assemblage A were J2b1a and K1a2a, respectively (Fregel et al., 2018), rejecting a direct maternal relationship. One sample from Assemblage B (TOR.12) belongs to the same haplogroup as the skull cup, although the haplotype motif is different, and the possibility of a direct maternal link is unlikely (Supplementary Figure 1). However, two samples from Assemblage B share the same mtDNA lineage (TOR.6 and TOR.7), indicating a possible maternal relationship. Unfortunately, only the skull cup had enough Y-chromosome coverage to perform a reliable classification into haplogroups, and direct paternal relationships could not be tested. Finally, after kinship analysis using READ software, we determined that the skull-cup did not have any familial relationship (up to the second degree) with either the mandible in Assemblage A or any of the samples from Assemblage B. READ analysis results suggest that samples TOR.6 and TOR.7 had a first degree relationship ($P0 = 0.144 \pm 0.002$) (Supplementary Figure 2). This result, coupled with mtDNA and molecular sex analyses (Fregel et al., 2018), indicates that they could have had either a mother-daughter or sister relationship.

DISCUSSION

Archaeological evidence suggests that El Toro cave was occupied by a small human group during the Early Neolithic (5280-4780 Cal BC 2σ). During this period, a skull cup was made and the remains of at least seven individuals were processed shortly after their death, including features compatible with cannibalism (see below for discussions on what type). These manipulated bones mixed with domestic residues, as well as remnants from carving the skull, suggest that this manipulation occurred in the domestic area. Kinship analyses of the human remains did not show any relationship between the skull cup and the other individuals, at least up to the second degree. However, two samples from Assemblage B show a first degree relationship suggesting that these practices involved various members of the same family.

El Toro skull-cup

Anthropogenic post-mortem processing of one head was conducted to obtain a specific shape by controlled percussion and careful removal of soft tissue. There are no evisceration cut marks on the inner surface of the calotte. We did not find the cranial bones that had been removed, such as facial, temporal, sphenoid and zygomatic bones. Consequently, we cannot describe the entire processing of the head to transform it into a skull-cup, but we can see the result, which is enough to establish the main *chaîne opératoire*.

Parallel, oblique and perpendicular sagittal cut marks on the frontal and parietal bones away from muscle attachments indicate scalp removal. This process must have taken place before decay of soft tissue, which is compatible with removal shortly after death (Bello et al., 2011; Boulestin & Coupey, 2015; Haglund, 1991). The distribution of cut marks indicates scrupulous cleaning of the skull. Then the calotte was subjected to careful systematic breakage by percussion to remove facial, temporal, sphenoid and zygomatic bones, and fine retouching of the broken edges to make them more regular, leaving the controlled damage visible. We have also documented one fragment in Sector 2 that refits with the occipital-parietal edge of the skull-cup. This evidence suggests that the skull-cup was processed in Sector 2, where domestic activities took place, along with other body manipulations.

Moreover, the missing pieces suggest that the first stage of the cup-making process was performed elsewhere.

The skull-cup also displays some macroscopic and microscopic indicators of boiling. Boiled skull-cups have also been reported in El Mirador and Carigüela assemblages (Cáceres et al., 2007; Solari et al., 2015). We also observed wear owing to contact at the shaped edge of the skull-cup with a material that was soft, lightly abrasive and humid. The delineation of wear, its size and position conform a pattern that can be interpreted as "pot polish". It occurs when bones are boiled in pottery vessels whose inner surface is abrasive, leading to polished facets (White, 1992:122). Pot polish has also been reproduced in experimental analyses using ceramic vessels (Dixon et al., 2010; Kopp & Graham, 2011; White, 1992:121-122). It has been reported in several cannibalism assemblages such as in the Late Neolithic site at El Mirador (Cáceres et al., 2007), in American Southwest sites (Hurlburt, 2000; Turner & Turner, 1995, 1999; White, 1992), and in survival cannibalism from the 19th century (Dixon et al., 2010; Mays & Beattie, 2016). This feature has also been considered as an effective means of recognizing boiling and cannibalism in archaeological material (Hurlbut, 2000; White, 1992). As seen in the El Toro skull-cup, entire bone surfaces are not pot-polished because it depends upon their shape and how long they circulate in the cooking vessel, the rate of movement and the roughness of the vessel's inner surface (Dixon et al., 2010; Kopp & Graham, 2011; White, 1992:124). Furthermore, pot-polish faceting was located at the retouched edges of the skull-cup, indicating that boiling was conducted after attaining the final shape. This process would probably have been aimed at cleaning the bone and finishing skull-cup processing.

The skull-cup appeared next to a mandible from another contemporary deceased individual without evidence of anthropic manipulation. The absence of manipulation marks on the mandible suggests it was not processed shortly after death, in contrast to the skull. Ancient DNA analysis demonstrates that the skull and the mandible do not belong to the same individual and that they are not related, at least up to the second degree. This set of evidence was located in a separate cache from the habitat area, indicating a special treatment differentiated from the other human bones, and raises the possibility of a ritualised context, perhaps linked to handling practices accorded to certain human bones.

Other examples of skull-cups in southern Iberia suggest that this practice may have been widespread among the first farming communities. Two skull-cups have been documented (one had been boiled) at Carigüela cave (Botella et al., 2000b,2003; García & Carrasco, 1981), one at Las Majólicas (Boulestin, 2012), and other at Cueva de Los Mármoles (Jiménez-Brobeil et al., 1996), also showing evidence of cicatrised trauma on frontal and left parietal bones. The processing sequence for these skull-cups is similar to the El Toro skull-cup, with skinning and shaping by later percussion. At Carigüela and Las Majólicas, there are also signs of bone manipulation linked to cannibalism, including skinning marks on the skulls, disarticulation traces on the limb bones, defleshing, boiling and breakage (Botella, 1973; Botella et al., 2000b, 2003; García & Carrasco, 1981). These skull-cups have been allocated to the end of the Neolithic, although there are no direct radiocarbon dates or rigorous stratigraphic contexts associated with these remains. This hinders establishing a clear chronological relationship with the Cueva de El Toro specimen. Nevertheless, these caves were occupied during the Early Neolithic and there are some available radiocarbon dates from this period (Carrasco & Martínez-Sevilla, 2014). Furthermore, there were no skull-cups found in Malalmuerzo cave, but anthropogenic manipulation linked to cannibalism has also been documented there as attested by cut marks, boiling, and breakage of human bones (Botella et al., 2000b). The human bone assemblage of Malalmuerzo provides one radiocarbon date from the Early Neolithic (5373-5079 cal BC, 6295±45 BP; Carrasco & Martínez-Sevilla, 2014). It means that we should not rule out that these skull-cups and cannibalism examples belong to the Early Neolithic. Moreover, there are other manipulated skulls in the Neolithic of southern Iberia that were not processed as skull-cups. These examples also come from Carigüela, Las

Majólicas and Malalmuerzo, where along with the manipulated postcranial remains, there are also skulls that were skinned and deliberately broken. These remains suggest that not all skulls were selected to be transformed into skull-cups.

[Figure 19 here]

Cannibalism at Cueva de El Toro

If bone manipulation evidence from Cueva de El Toro is considered the result of cannibalism, the main challenge is to provide an explanation of why cannibalism occurred at Cueva del Toro. The available osteological record allows a range of hypotheses based on ethnographical and archaeological evidence. According to anthropological data, cannibalism can be classified into three categories: survival, aggressive and funerary (Boulestin & Coupey, 2015; Fausto, 2007; Kantner, 1999; Saladié & Rodríguez-Hidalgo, 2017; Sanday, 1986). We should also consider that the two individuals from Assemblage B show a first degree relationship. It means that cannibalism was carried out in a family context where the bodies of relatives were eaten as result of multi-stage funerals, or El Toro inhabitants ate members of the same family from another group, indicating acts of extreme violence against enemies. In both cases, it could be a ritualised cannibalism with ceremonies where the skull-cup might have played a role.

Considering the first hypothesis, survival cannibalism has not been proposed so far in the Neolithic of southern Iberia, and there is no evidence of starvation in the archaeological or osteological record. Nevertheless, farming populations could have been sensitive to environmental variation and crop failure during the implantation of the Neolithic, and plague pandemics affected Neolithic populations in Europe (Rascovan et al., 2018). The archaeological record indicates a scarcity of human occupation from the end of the Early Neolithic to the beginning of the Late Neolithic (ca. 4500-4200 BC, Martín-Socas et al., 2018). It represents a decline in both the density of archaeological sites and the number of radiocarbon dates, as well as the abandonment at sites with stratigraphic sequences, as at El Toro, Los Murciélagos at Zuheros and Los Castillejos (Camalich & Martín-Socas, 2013; Cámara, Afonso, & Molina, 2016; Martín-Socas et al., 2018). This change has been interpreted as a consequence of a new territorial organisation model where hunter-gatherers and farmers shared open-air settlements (Martín-Socas et al., 2018). So far, no evidence suggests that cannibalism was due to a starvation crisis, but the decline in occupation density at that time could also be considered as an indicator of a population collapse and the emergence of social tension.

The second hypothesis, aggressive cannibalism, has previously been considered (Jiménez-Brobeil et al., 2009). It is based on the lack of careful treatment of the cannibalised remains such as at Carigüela and Malalmuerzo (mixed with domestic waste as in El Toro), and a high frequency of cranial injuries are indicators of inter-personal violence (Jiménez-Brobeil et al., 2009). Cranial remains from this period display a high frequency of traumatic injuries (11.5%), which is also higher than in the Copper Age (4.7%), and similar to the Bronze Age (12.3%) (Jiménez-Brobeil et al., 2009), when warrior elites emerged (Aranda, Montón, & Jiménez-Brobeil, 2009). The injuries of Neolithic males show a higher frequency than female individuals, and injuries are predominantly located at the frontal and left side of the crania. This evidence points to significant social tension and hostility in the Early Neolithic of southern Iberia (Jiménez-Brobeil et al., 2009).

This hypothesis nevertheless reveals some problems. Scattered human bones do not necessarily indicate a lack of reverential attitudes toward the dead, since unburied remains are frequently found dispersed after secondary burial practices (Hutchinson & Aragon, 2002; Weiss-Krejci, 2013). Furthermore, these cranial remains display non-fatal traumatic injuries since individuals survived the violent conflict, and not all can be definitely attributed to intentional violence (Jiménez-Brobeil et al., 2009). This injury pattern has been considered the result of face-to-face confrontations and suggests that open inter-group fighting or warfare were not common practices (Delgado, Alberto, & Velasco, 2018; Milner, 1999; Smith, 2003; Steadman, 2008). As a result, it could be related to non-lethal violence for resolving conflicts, without intending to kill the enemy (Paine, Mancinelli, Ruggieri, & Coppa, 2007; Scott & Buckley, 2014; Walker, 1997). Although it is clear that violence played a role in the Neolithic populations, it does not necessarily indicate warfare and subsequent aggressive cannibalism. Moreover, no cannibalised remains from southern Iberia display clear evidence of violence that may associate these remains with enemies (Botella et al., 2000b; Jiménez-Brobeil et al., 2009). Neither mass graves nor simultaneous burials have so far been documented that could be related to massacres or warfare such as in Herxheim (Boulestin & Coupey, 2015) or Schöneck-Kilianstädten (Meyer, Lohr, Gronenborn, & Alt, 2015) from the Linearbandkeramik Culture (LBK) in Central Europe.

Funerary cannibalism (in terms of endocannibalism) has been suggested for the cannibalised remains of Malalmuerzo, Majólicas and Carigüela caves (Botella et al., 2000b; Solari et al., 2012). This hypothesis has not been fully developed since there is no explication of the reasons behind this behaviour, and its relationship with other burial practices. Botella et al. (2000b; 2003) and Solari et al. (2012) have allocated these remains to the last phase of the Neolithic (which is called "advance" and situated in the IV millennium BC by them), but no direct radiocarbon dates and detailed contextual evidence have been given to support this chronological assignment. As already mentioned, we should consider the fact there is archaeological evidence allocated to the Early Neolithic in these caves, including directly dated human remains in Malalmuerzo, indicating that an older chronological allocation could be more likely. Jiménez-Brobeil (1990) indicates that primary burials were located in this cave, although there is no direct dating or stratigraphic relationship of this evidence with the area where the cannibalised remains appeared. It precludes considering if there was any relationship between cannibalised bones and primary deposits in Malamuerzo.

Marks from marrow extraction, cutting and probably tooth marks identified on bones from El Toro indicate that cannibalism occurred there during its Early Neolithic occupation period. However, several bones, such as ribs, phalanges and vertebrae, showed no evidence of human-induced modifications. The cut marks rate was 10.9% of specimens (18.7 on cranial and 3.77% on postcranial specimens), which was lower than in other cannibalism assemblages from Prehistory (Saladié & Rodríguez Hidalgo, 2017). Hand and foot bones show tooth/chewing marks as in cannibalism assemblages such as Gough's Cave (Bello et al., 2015), Malalmuerzo (Solari et al., 2012), Herxheim (Boulestin & Coupey, 2015) and Mancos (White, 1992). If we consider that tooth marks and chewing at El Toro were caused by humans (6.9% of specimens), the proportion affected is lower compared with some assemblages such as El Mirador (48.1%) (Cáceres et al., 2007) and Gough's Cave (53%) (Bello et al., 2015; 2016), but higher than others such as Les Perrats (1.08%) (Boulestin, 1999), Malalmuerzo (3.9%) (Solari et al., 2012), and Herxheim (0.89%) (Boulestin & Coupey, 2015). Also, when carnivorous animals consume corpses the extremities of the limbs are little affected, except in unusually intensive scavenging (Haglund, 1991). Thus, we cannot rule out that some tooth marks found on human bones were the result of medium-sized or small carnivores. For instance, tooth and chewing marks on the subadult sternal segment can be interpreted as carnivore rather than human action. Carnivorous animals usually consume corpses in a centrifugal pattern and the sternum area is frequently affected in gaining access to the internal organs (Haglund, 1991).

On comparing the skeletal survival rate (%survivorship) from El Toro with other skeletal assemblages showing evidence of anthropogenic manipulation, including cannibalism and secondary burials, El Mirador presented the most similar values (Figure 19). It is obvious the representation difference between the cranial and postcranial skeleton in El Toro and El Mirador. The %survivorship also shows differences from secondary funerary assemblages with deliberate manipulation of the corpses. Vertebrae, and hand and foot bones are also commonly underrepresented in cannibalism contexts

(Bello et al., 2015; Boulestin et al., 2009; Boulestin & Coupey, 2015; Saladié & Rodríguez-Hidalgo, 2017), while at El Toro hands and feet were well-represented. Furthermore, percussion damage for marrow extraction does not explain the low representation of limb bones in this cave, because they are also well represented in cannibalism assemblages where this action was frequent, usually fractured for marrow extraction.

The presence of manipulated human bones in Sector 2 suggests that the corpses were handled in the habitat area. It means that body parts could have been consumed at the cave. However, the infra-representation of limb bones and other skeletal regions suggests that some body parts were collected and transferred from Sector 2 to a new so far unknown location. This set of evidence only describes part of the treatment that was given to the bodies, since the final destination of most of the bones remains to be discovered. Similar behaviour in the Neolithic site of Fontbrégoua (France) has been described, recently dated at 5450-4800 cal BC 2σ (Le Bras-Goude, Binder, Zemour, & Richards, 2010). There, archaeologists reported different treatments in the deposition of human bones, along with cannibalism and ritual treatment of the skulls (Villa, 1992; Villa et al., 1986). This evidence has also been interpreted as war cannibalism between different groups, these remains likely being war trophies (Courtin, 2000). Near Fontbrégoua, the Early Neolithic sequence of the Grotte de l'Adaouste contains remains of five individuals displaying bone manipulation such as cut marks and intentional fractures (Mafart, Baroni, & Onoratini, 2004). In this case, bone manipulation is considered a consequence of burial practices rather than cannibalism, since human remains were not treated the same as faunal remains. Furthermore, Mafart et al. (2004) suggest that Grotte de l'Adaouste and Fontbrégoua assemblages display the same regional funeral ritual, part of the same cultural identity.

In southern Iberia, Early Neolithic funerary deposits include primary burials such as at Cueva de los Murciélagos (Valdiosera et al., 2018), Cueva de la Mujer (García-Sánchez & Jiménez-Brobeil, 1985), Cerro Virtud (Montero, Rihuete, & Ruiz et al., 1999), and Sima de La Maquila (Mengíbar, Muñoz, & González, 1981), along with secondary deposits found at different caves (Botella et al., 2000b, 2003; Carrasco et al., 2014; Díaz-Zorita, Costa, & García-Sanjuán, 2012; Martín-Socas et al., 2018). These records point to a wide variability of archaeological contexts where human remains played a role, and where primary and secondary depositions are documented along with cannibalism. This evidence also highlights the significant relationship between caves and burial practices, including specific paraphernalia and material culture associated with funerary rituals (Carrasco Rus et al., 2014; Martín-Socas et al., 2018). Some scholars have argued that caves were used exclusively as funeral spaces with a clear ritual and worship function during this time (Carrasco & Martínez-Sevilla, 2014; Carrasco, Morgado, & Martínez-Sevilla, 2016). Nevertheless, several archaeological examples provide clues to a more complex and diverse management of cave-use as polyfunctional spaces, as in El Toro, including simultaneous habitat, stock-pen, craftwork and human bone manipulation (Martín-Socas et al., 2018). This means that distinguishing between funerary and aggressive cannibalism remains a challenge, given the extremely complex nature of some caves used in the Early Neolithic. Unfortunately, we have no precise evidence about the archaeological contexts where cannibalism appears in southern Iberia to establish comparisons with El Toro beyond taphonomic aspects of the osteological record. More research must be done to understand the archaeological contexts where these bones were found, as far as possible, and reinforce the radiocarbon series of the osteological collections from these sites according to the minimum number of individuals.

It is premature to offer a comprehensive explanation for the evidence of cannibalism in the Early Neolithic of southern Iberia. Evidence from El Toro suggests that cannibalism was conducted in the domestic area, likely following ritualised practices where skull-cups may have played a part. The composition of the deposit where the skull-cup was found suggests that this was a special feature with a significant meaning for the inhabitants of Cueva de El Toro. This skull-cup was made soon after the individual's death, which could be linked to the cannibalistic practices detected in the domestic area. The reasons for cannibalism at El Toro remain unresolved but two main hypotheses seem to be the most convincing: 1) Aggressive cannibalism relates to the emergence of social tension and inter-group violence; and 2) Funerary cannibalism is a facet of multi-stage funerary practices in caves. These hypotheses also affect the explanation of the relationship between the skull-cup and the inhabitants of Cueva de El Toro: it may be a trophy-head that belonged to an enemy, from the same or another group, or otherwise a relic of a preeminent member of this group. Ethnohistoric and ethnographic records highlight that most skull-cups are linked with aggressive cannibalism against enemies, and only a few examples with funerary practices (Boulestin, 2012). Even then, we should not rule out other kinds of behaviour in Prehistory, when funerary practices were highly diverse and complex.

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FIGURE LEGENDS

Figure 1. Location map of the sites with skull-cups in Western European prehistory.

Figure 2. Map of Cueva de El Toro and excavation area, indicating both sectors and the Sector 1 entrance.

Figure 3. Stratigraphic sequence of Cueva de El Toro.

Figure 4. Skull-cup, the non-manipulated mandible and the four ceramic vessels found at Sector 1.

Figure 5. Skull-cup from Cueva de El Toro; (a) anterior view; (b) right lateral view (c) left lateral view; (d) posterior lateral left view.

Figure 6. Image and drawing to show the location of cut marks. (A) Cut marks recorded on left parietal bone (x8) and detail (x30). The image shows a portion of one of the cut marks, displaying some micro-striations (white arrows) at the base and a V-shaped section with a shoulder effect (black arrows). (B) Detail of another cut mark (x60): the lower edge is regular, while the upper shows flaking due to retouching with another stone tool.

Figure 7. (a) Zones of the skull-cup: (1) external view (2) internal view; Zone 1: single parietal foramen; Zone 2: cut marks; Zone 3: percussion line. Zone 4: (A) polish (B) percussion pit. (b) Views of the modified edges of the skull-cup in Zone 3; (c) Exocranial and (d) Endocranial views showing the modified edges. The arrows indicate percussion impact.

Figure 8. (a) Detail of Zone 4 B: conchoidal impact fracture (x10); (b) Cut marks made previous to shaping (18x); (c) Cut marks and micro-pits in the external table (25x).

Figure 9. SEM images obtained at a magnification of x500 (a) and x 2,500 (b). Morphology constituted by ordered fibrils, with a smooth dense surface owing to indirect heat treatment (boiling).

Figure 10. Location of the worn section and use-wear features: rounded edge; a wavy, almost bright surface; scarce perpendicular and oblique striations.

Figure 11. Posterior view of the skull-cup. The left parietal fragment with a section of lambdoid suture that refitted with the skull-cup. (A) cut marks; (B) percussion damage.

Figure 12. (a) TCT88-1540-4 and (b) TCT40858-1. Both specimens show cut marks (black arrows), and percussion damage (white arrows).

Figure 13. (a) TCT85-46757. Cut marks on the bone. Fire-damage shows colour changes such as a brown colouring on most of the surface and black hues on some edges of the fragment. Fat wrapping or cracking was not observed. (b) TCT81-41038-1. Parietal fragment shows intensive crossed thin and overlapping scraping marks on the ectocranial surface, including several groups of parallel and sub-parallel incisions in varying directions.

Figure 14. (a) TCT88-1405-1. Cut marks are located on the mandibular ramus, displaying chopping and slicing cut marks (A and B) from the posterior to lingual surface. There is also crushing damage on the condyle. (b) TCT85-46642-2. There are small notches and (A) an adhering flake.

Figure 15. The chopping mark is located on the medial surface of the femoral neck (black arrow). It shows a perpendicular orientation to the long axis of the diaphysis. It has a smooth wall, marking an angle of 45° and a V-shaped kerf. There are several conchoidal scars on the diaphysis and epiphysis (white arrows), and two adhering flakes on the epiphysis (white circle).

Figure 16. Pronounced cut marks showing overlapping incisions in both groups.

Figure 17. Tooth and chewing marks.

Figure 18. Tooth and chewing marks on the sternum.

Figure 19. Skeletal survival rate (%survivorship) in assemblages with human-induced manipulation including cannibalism and secondary burial practices (Boulestin & Coupey, 2015; Bello et al., 2015; Robb et al., 2015; Santana et al., 2015).

Supplementary Figure 1. Phylogenetic tree of complete mtDNA sequences from El Toro. Number along links refers to nucleotide changes, whereas “@” and parenthesis indicates back mutations and recurrent mutations within lineages, respectively. Recurrent mutations as 309iC, 315iC and 16519 have not been taken into account.

Supplementary Figure 2. READ kinship estimates for El Toro individuals. (A) Sorted non-normalised average P0 values for all pairwise comparisons between El Toro samples. The solid horizontal line indicates the median value used for normalisation and dashed lines show the cutoffs used to classify the related individuals. The grey areas around dashed lines indicate 95% confidence intervals for the cutoffs. (B) A histogram of the non-normalised average P0 values. Vertical dashed and solid lines are the same as in Figure S2A.