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Identification of Neandertal individuals in fragmentary fossil assemblages by means of tooth associations: The case of El Sidrón (Asturias, Spain)

Identification d'individus néandertaliens dans des assemblages fossiles fragmentaires au moyen des associations dentaires : le cas d'El Sidrón (Asturies, Espagne)

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ABSTRACT

Identification of the individuals represented in a fragmentary fossil assemblage is a key step in paleobiological research, as ensuing organism-level studies, as well as sampling strategies (e.g., DNA, isotopes, dating, etc.), may depend on the reliability of such estimates. In the human fossil record, dental remains represent the most abundant and informative material, allowing individual identification on the basis of a variety of diagnostic criteria. In this paper, we present a procedure for sequential association of the dental remains and the identification of the minimum number of individuals (MNI) represented in the 49,000-year-old Neandertal assemblage from El Sidrón (Asturias, Spain). In order to quantify the possible association errors, the 12 criteria used in this study are organised according to three levels of reliability. Following this procedure, a minimum of 13 individuals (seven adults, three adolescents, two juveniles and one infant) have been identified at El Sidrón, two of them uniquely represented by postcranial elements. A next step in this investigation foresees the development of methods for associating postcranial elements with the dentally-based identified individuals.

RÉSUMÉ

L'identification du nombre d'individus représentés dans un assemblage fossile fragmentaire est une étape clé dans les recherches paléobiologiques, étant donné que les études postérieures à l'échelle de l'organisme, mais aussi les stratégies d'échantillonnage

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(ex., ADN, isotopes, datations, etc.) peuvent dépendre de la fiabilité de ces estimations. Dans le registre humain fossile, les restes dentaires représentent le matériel le plus abondant et informatif pour l'identification des individus sur la base d'une variété de critères diagnostiques. Dans cet article, nous présentons une procédure pour l'association séquentielle d'éléments dentaires et l'identification du nombre minimal d'individus (MNI) représentés dans l'assemblage des restes néandertaliens d'El Sidrón (Asturies, Espagne), daté de 49 000 ans. Pour sécuriser les associations dentaires et identifier les erreurs possibles, les 12 critères utilisés dans cette étude ont été répartis selon trois niveaux de fiabilité. D'après cette procédure analytique, un nombre minimal de 13 individus (sept adultes, trois adolescents, deux juvéniles et un enfant) a été identifié à El Sidrón, deux d'entre eux étant uniquement représentés par des éléments postcrâniens. Une étape succédant à cette phase analytique prévoit le développement des méthodes pour l'attribution d'éléments postcrâniens à des individus identifiés uniquement par des associations dentaires.

1. Introduction

Among the currently active Middle Paleolithic excavation projects, the El Sidrón site (Asturias, Spain) has a significant place in Neandertal paleobiological studies. A number of exceptional conditions make El Sidrón a singular site. The fossil assemblage is concentrated in a small cave deposit and is composed of a large number of human skeletal remains belonging to several individuals (Rosas et al., 2006, 2012) with familial relationships (Lalueza-Fox et al., 2011). There is a limited presence of faunal remains and a relative abundance of refitting stone tools (Santamaría et al., 2010). In addition, evidence of cannibalism has been demonstrated in this sample (Rosas et al., 2006). At present, over 2300 specimens have been recovered (Fortea et al., 2003; Rosas et al., 2006, 2012). Cutting edge techniques are applied for the investigation of this assemblage, including ancient DNA sampling in the field (Fortea et al., 2008) and laboratory analyses (Lalueza-Fox et al., 2006, 2007, 2008, 2011), ultrafiltration radiocarbon datings (Torres et al., 2010; Wood et al., 2013), molecular dental calculus (Hardy et al., 2012) and morphometric analyses (Bastir et al., 2010; Rosas et al., 2008).

Fossil skeletal elements frequently appear disarticulated in the archaeo-paleontological record, even in those cases where the remains come from the same body (Haglund and Sorg, 1997; Lyman, 1994; Ubelaker, 1989; White and Folkens, 2005). Diverse sedimentary and taphonomical factors contribute to skeletal disarticulation and the scattering of the remains (Lyman, 1994). The re-assembling of the original anatomical units and the association of different fossil specimens to a single individual is a key step in taphonomical and paleobiological studies (Trinkaus et al., 2000). The El Sidrón Neandertal sample represents a good example of this widespread problem.

Several possibilities for understanding diverse cultural, taphonomic and evolutionary aspects arise when these topics are approached at organismic level. A large spectrum of analyses demands a particular strategy for sampling, which in turn requires the individual affiliation of an isolated specimen (e.g., a tooth) to be ascertained. For instance, a precise assessment of the number of individuals represented in a fossil hominin sample can yield new valuable information regarding the social structure of the group and the site function, also allowing for significant time saving when analysing individual mtDNA. Many other examples can be mentioned, such as nuclear DNA and isotopic analyses, dating, etc. Likewise, a prior characterization of the identity and biological attributes of the individuals represented in a fossil sample is required for paleodemographic studies (Bermúdez de Castro et al., 2004, 2006; Trinkaus, 1995).

Teeth are the most represented elements in the paleoanthropological record (Hillson, 1986), both because of their relative abundance within the organism and relative hardness and durability. They also preserve extremely valuable information about phylogenetic history (morphology, e.g., Bailey and Lynch, 2005; Moggi-Cecchi et al., 2006), life-history (developmental patterns, e.g., Macchiarelli et al., 2006; Smith et al., 2007), paleobiology (diet, use of the mouth, etc., e.g., Grine et al., 2006; Molnar, 1972), and individual life events (physiological stresses, e.g., Guatelli-Steinberg, 2009; Ogilvie et al., 1989). As a whole, these characteristics grant to the dentition a high degree of individual specificity. Accordingly, tooth associations are an essential component of paleobiological analyses of fossil assemblages because subsequent studies will rely upon the accuracy of these individual reconstructions (Aguirre et al., 1986; Gençturk et al., 2008; Moggi-Cecchi et al., 2006). However, the interpretation of tooth associations are largely based on the experience of the researcher (e.g., Aguirre et al., 1986; Bermúdez de Castro et al., 2004, 2006; Gençturk et al., 2008; Moggi-Cecchi et al., 2006; Wolpoff, 1979).

Given that any progress in the characterization of the paleobiological profile of the Neandertals from El Sidrón will greatly benefit from a reliable assessment of tooth associations and related number of individuals, in this study we present the procedures followed for assembling the isolated teeth.

2. Material and methods

2.1. Material

2.1.1. The site

The karstic cave of El Sidrón, with a total length of 3700 m, is situated in the "Surco Oviedo-Infiesto", a band of Mesozoic and Cenozoic sediments limited to the north and south by Paleozoic reliefs. The main gallery of the cave, called "Galería del Río", has lateral ramifications located at intervals of 50–100 m running NE-SW to north-south. All the findings come from a restricted lateral gallery inside the cave, "Galería del Osario", which is oriented north-south. Sediments are mostly sands and clays, with gravel layers indicating variations in hydraulic energy (Fortea et al., 2003; Santamaría et al., 2010).

In 1994, an exceptional set of human fossils was accidentally found and gave rise to the methodical excavation and multidisciplinary study of the site (Fortea et al., 2003). As a result, a significant archaeo-paleontological record, for the most part composed of Neandertal remains, has being recovered since 2000 (Rosas and Aguirre, 1999; Rosas et al., 2006). At present, more than 2300 human remains have been retrieved, representing several individuals whose remains are actually found commingled. All the skeletal parts are represented and some of the remains are in anatomical connection. There is also a moderate occurrence of Middle Paleolithic stone tools ($n = 415$), and very few faunal remains. Refitting of bone fragments and of 67 lithic artefacts proves unequivocally a single archaeological deposit (Santamaría et al., 2010).

The El Sidrón remains preserve ancient DNA, both mtDNA (Lalueza-Fox et al., 2005, 2006, 2011) and nuclear DNA (Krause et al., 2007; Lalueza-Fox et al., 2007, 2008). In order to avoid bone contamination with modern human DNA, and also to preserve DNA integrity by means of freezing the selected samples, a specific excavation protocol was implemented at the site (Fortea et al., 2008).

The detailed taphonomy of the site is currently under study but the following scenario can already be suggested: the remains are in a secondary position; the original deposition place occurred elsewhere (Fortea et al., 2003); and the assemblage arrived at its present location after the collapse of an upper gallery close to the "Galería del Osario" (Cañaveras et al., 2011; Sánchez-Moral et al., 2007). A multi-dating approach has been undertaken at the site, giving a consistent date of ~49,000 years for the Neandertal fossil assemblage (Torres et al., 2010; Wood et al., 2013).

2.1.2. The fossil dental sample

Coming into the 2012 field season, the El Sidrón dental sample was composed of 222 teeth. There are 108 lower teeth (61 from the left, 47 from the right side), of which 58 are enclosed in their alveoli (*in situ*) and 50 are isolated. The upper dentition is represented by 114 teeth (55 left, 59 right), of which 44 are *in situ* and 70 are isolated. There is one dental set in anatomical contact (SD-1327a to SD-1327i) though the bony support (mandible) no longer exists. Two nearly complete mandibles, two hemi mandibles and two more small mandibular fragments are preserved. In addition, two complete maxilla (which include 29 teeth in their alveoli) and three fragments of maxillae (two with four teeth each and one more with five teeth) are also preserved (Tables 1 and 2).

2.2. Methods

The study was carried out in three steps. First, the identification of the minimum number of individuals (MNI) and tooth row associations in the lower dentition. Second, the same procedure was independently followed for the upper dentition. Finally, the matching of the lower and the upper dental assemblages was considered. The number of mandibular teeth found *in situ* ($n = 58$) exceeding that of the maxillary ones ($n = 44$) was decisive in starting the analysis with the lower dentition.

The MNI was primarily established by the identification of the most common tooth. Nonetheless, other elements indicating biological age incompatible with that established from the dental remains can be used to define new individuals. For instance, the presence of postcranial elements from immature individuals not represented by dental specimens may lead to the identification of new individuals.

Individuals were assigned to one of the following five age categories adapted from Bogin (1988, 1997, 2009; see also Bogin and Smith, 1996):

- "infant" (ending at the completion of the eruption of the deciduous dentition);
- "childhood" (when the deciduous dentition is fully in occlusion);
- "juvenile" (from the time in which the first permanent molar is erupted to the loss of the second deciduous molar);
- "adolescent" (third molar eruption);
- and "adult" (the third molar is in occlusion with different degrees of wear).

Age at death for the non-adult individuals is primarily based on dental formation chronology proposed by AlQahtani et al. (2010). Among the adults, two categories have been distinguished, young and mature, based on differences in the degree of occlusal dental wear assessed following Skinner (1997). Regarding post-cranial immature remains, age at death was estimated following the epiphyseal fusion times (Scheuer and Black, 2000). The sex of the individuals was estimated using measurements of the mandibular corpus and intra-sample relative differences in canine tooth size (following Bermúdez de Castro et al., 2001, 2006; Rosas et al., 2002).

2.2.1. Order of tooth row association

For tooth row association assessment, we systematically followed the procedure summarised in Fig. 1. Starting from the most represented tooth in the sample, the reference tooth, we looked for its conjoining distal tooth (proceeding in a distal direction due to the sample composition). Once this element was identified, we looked for the antimere of the reference tooth. In searching for the antimere, we looked for a quasi identically sized and shaped specimen, as well as for its congruence in terms of wear at the available corresponding tooth class sub-sample. The next step was establishing the distal conjoining of the antimere after which we examined the reference tooth row looking for the next conjoining element. This process was reiterated.

Table 1
Complete list of dental specimens from El Sidrón (Asturias, Spain) assigned to the individuals identified so far in the sample. Assignation follows three levels of reliability (see text for details).
Tableau 1
Liste complète des spécimens dentaires d'El Sidrón (Asturies, Espagne) assignés à chacun des individus de l'échantillon identifiés à ce jour. L'attribution suit trois niveaux de fiabilité (voir les détails dans le texte).

	Level 1	Level 2	Level 3
Individual	Anatomical connection	Interproximal wear facets	Occlusal wear degree
	Fitting into the socket	Occlusal wear degree	Developmental age
	Interproximal wear facets and subvertical grooves	Developmental age	Morphology
	Occlusal wear degree	Morphology	
	Developmental age	Enamel hypoplasia	
	Morphology	Dental calculus	
	Enamel hypoplasia	Para-masticatory dental wear	
	Dental calculus	Taphonomical features	
	Other pathologies		
	Para-masticatory dental wear		
	Taphonomical features		
Adult 1			
Upper dentition	SD-1200a; LP^{4}	SD-1054; RM^{1}	
	SD-1200b; LM^{1}	SDR-141; RI^{2}	
	SD-1200c; LM^{2}	SD-1010; RC	
	SD-1200d; LM^{3}	SD-600; RP^{3}	
	SD-312; LP^{3}		
	SD-1202; LC		
	SD-441; LI^{2}		
	SD-1201; LI^{1}		
	SD-313; RI^{1}		
Lower dentition	SDR-005a; LM_{1}	SD-299a; LI_{2}	
	SDR-005b; LM_{2}		
	SDR-005c; LM_{3}		
	SDR-006a; LP_{3}		
	SDR-006b; LC		
	SDR-006c; RI_{1}		
	SDR-006d; RI_{2}		
	SDR-006e; RC		
	SDR-006f; RP_{3}		
	SDR-006 g; RP_{4}		
	SDR-006 h; RM_{1}		
	SDR-006i; RM_{2}		
	SD-1135; RM_{3}		
	SD-664; LP_{4}		
Adult 2			
Upper dentition	SD-1427b; LM^{3}	SD-1240; RI^{2}	
	SD-1427c; LM^{2}	SD-1439; LI^{1}	
	SD-1427d; LM^{1}	SD-1422; RI^{1}	
	SD-1427e; LP^{4}		
	SD-1427f; LP^{3}		
	SD-1427 g; LC		
	SD-1427 h; LI^{2}		
	SD-1427i; RC		
	SD-1427j; RP^{3}		
	SD-1427k; RP^{4}		
	SD-1427l; RM^{1}		
	SD-1427 m; RM^{2}		
	SD-1427n; RM^{3}		
Lower dentition	SDR-007a; RI_{2}	SDR-014: LI_{2}	
	SDR-007b; LP_{3}	SD-703; RI_{1}	
	SDR-007c; LP_{4}		
	SDR-007d; LM_{1}		
	SDR-007e; LM_{2}		
	SDR-007f; LM_{3}		
	SDR-007 g; C anomalous		
	SDR-007 h; C impacted		
Adult 3			
Upper dentition	SD-2200b; RP^{3}		SD-1220; LC
	SD-2200c; RP^{4}		
	SD-2200d; RM^{1}		
	SD-2200e; RM^{2}		
	SD-2200f; RM^{3}		

Table 1 (*Continued*)

	Level 1	Level 2	Level 3
Lower dentition	SD-1218b; LM$_3$ SD-1218a; LM$_2$ SD-1217c; LP$_3$ SD-1217d; LP$_4$ SD-1217e; LM$_1$ SD-1216a; RP$_3$ SD-1216b; RP$_4$ SD-1216c; RM$_1$		**SD-1222; RI$_2$** **SD-1217b: RI$_1$**
Adult 4			
Upper dentition	SD-1603; LM^1 SD-1604; LM^2 SD-1683a; RP^4 SD-1683b; RM^1	SD-1018; LC SD-1661; RC SD-1314; RM^2 SD-1662; RP^3 SD-1631; RM^3	SD-1572; LI^1 SD-1576; LP^4
Lower dentition	SD-331c; LM$_1$ SD-934; LP$_4$	SD-209; RC SD-933; LP$_3$ SD-935; LC SD-937; RP$_3$ SD-925; RP$_4$ SD-1882; LM$_2$	SD-923; RM$_3$ **SD-757; LI$_2$** **SD-599b; LI$_1$** **SD-599a; RI$_1$** **SD-355; RI$_2$**
Adult 5			
Upper dentition	SD-2010b; LM^3 SD-2010c; LM^2 SD-2010d; LM^1 SD-2010e; LP^4 SD-2010f; LP^3 SD-2010 g; LC SD-2010 h; LI^2 SD-2010i; LI^1 SD-2010j; RI^1 SD-2010k; RI^2 SD-2010l; RC SD-2010 m; RP^3 SD-2010n; RP^4 SD-2010o; RM^1 SD-2010p; RM^2 SD-2010q; RM^3		
Lower dentition	SD-1327a; RI$_2$ SD-1327b; RI$_1$ SD-1327c; LI$_1$ SD-1327d; LI$_2$ SD-1327e; LC SD-1327f; LP$_3$ SD-1327 g; LP$_4$ SD-1327 h; LM$_1$ SD-1327i; LM$_2$		
Adult 6			
Upper dentition	SD-1789: RM^2 SD-1603: RM^3 SD-1833: RM^1 SD-2040; RP^4	SD-1654; RP^3 SD-2158; LM^2 SD-2007; LM^1	SD-311; LI^1 SD-1161; LC
Lower dentition	SD-1577; LM$_1$	SD-303; LP$_4$ SD-1575; LP$_3$ SD-753; LC SD-1574; LI$_2$ SD-926; LI$_1$	SD-406; RM$_3$
Adult 7			
Upper dentition		SD-407; LM^1	SD-1707; RI^2 SD-582; RI^1 SD-639; LP^4 SD-1164; RM^3
Lower dentition	SD-920; LM$_1$ SD-928; LM$_2$	SD-936; RM$_3$ SD-657; RM$_1$	SD-921; RI$_2$
Adolescent 1			
Upper dentition	SD-915; LP^4 SD-913; LC SD-916; LM^1 SD-914; LP^3	SD-221; RC SD-1106; RP^4 SD-922; RM^1	

Table 1 (*Continued*)

	Level 1	Level 2	Level 3
Lower dentition	SD-780; LM$_1$	SD-736a; RP$_4$	SD-755; RM$_2$ SD-1019; RI$_2$ SD-278; RI$_1$ SD-927 RP$_3$
Adolescent 2			
Upper dentition	SD-411; LP^4 SDR-012; LM^1	SD-1105; RM^1 SD-551; RM^2 SD-621; RM^3 SD-741; LM^3 SD-930; LM^2 SD-50; RP^4	SD-566; RP^3 SDR-013; RI^2 SD-331a; RI^1 SD-331b; LI^1
Lower dentition	SD-756; LM$_1$ SD-540; LM$_2$	SD-1510; LM$_3$ SDR-015; RM$_1$ SD-924; RM$_3$	SD-370b; RI$_2$ SD-918; RC SD-1513; LP$_3$
Adolescent 3			
Upper dentition	SD-1221; LP^4	SD-1107; LC SD-1075; LP^3 SD-332; LM^3 SD-772; RM^3 SD-568; LI^2 SD-277; LI^1	SD-4; LM^2
Lower dentition	SD-500; LP$_4$ SD-912; LP$_3$ SD-61; LC	SD-501; RP$_4$	
Juvenile 1			
Upper dentition	SD-768; dRm^2 SD-531; RM^1 SD-1862; LM^1 SD-1863; LM^2 [a] SD-1824; RP^4 [a] SD-2020; RP^3 [a] SD-1720; RC[a] SD-1721; dRc **SD-1875; RI^1** **SD-1719; LI^1** **SD-1881; LI^2** [a]		
Lower dentition	SD-1600b; LM$_1$ SD-1600c; dLm$_2$ SD-1600d; dLm$_1$ SD-1600e; dLc SD-1600f; LI$_2$ [a,b] SD-1600 g; LC[a,b] SD-1600 h; LP$_3$ [a,b] SD-1600i; LP$_4$ [a,b] SD-1600j; LM$_2$ [a,b] SD-1660b; RM$_1$ SD-1660c; dRm$_2$ SD-1660d; dRm$_1$ SD-1660e; dRc SD-1660f; RI$_1$ SD-1660 g; RI$_2$ [a,b] SD-1660 h; RC[a,b] SD-1660i; RP$_3$ [a,b] SD-1660j; RP$_4$ [a,b] SD-1660k; RM$_2$ [a,b] SD-1716; dRi$_2$ SD-322; LI$_1$		

Specimens in bold are associated among them at a level 1. The elements found *in situ* are underlined.

[a] Unerupted tooth.

[b] Tooth included in the alveolar bone.

In the specific case of the El Sidrón sample, the reference tooth is represented by the lower left first molar (LM$_1$; $n = 10$) for the mandibular dentition and by the upper right first molar (RM^1; $n = 9$) for the maxillary one.

2.2.2. *Criteria for tooth associations*

Given the characteristics of the sample, 12 criteria were considered for tooth association, and a hierarchical classification of their reliability was established. The criteria

Table 2
Summary of individuals and dental associations identified at El Sidrón.
Tableau 2
Tableau synthétique des individus et des associations dentaires identifiés à El Sidrón.

Individual	Reference tooth/bony element	Associated skeletal specimens	Dental associations			Age	Sex
			Lower dentition	Upper dentition	Total		
Adult 1	Left M_1 SDR-005a	Mandible (SDR-005, SDR-006, SD-550a) and maxilla (SD-1200a)	3 isolated and 12 *in situ* teeth 8 right; 7 left	9 isolated and 4 *in situ* teeth 5 right; 8 left	28	Young adult	Male
Adult 2	Left M_1 SDR-007d	Hemi mandible (SDR-007, SDR-008), mandibular fragments (SD-30, SD-1095a) and maxilla (SD-1427a)	2 isolated and 8 *in situ* teeth 2 right; 8 left	3 isolated and 13 *in situ* teeth 8 right; 8 left	26	Young adult	Male
Adult 3	Left M_1 SD-1217e	Hemi mandible (SD-1217a, SD-1218) and maxilla (SD-2200)	2 isolated and 8 *in situ* teeth 5 right; 5 left	1 isolated and 5 *in situ* teeth 5 right; 1 left	16	Mature adult	Female
Adult 4	Left M_1 SD-331c	Fragment of mandible (SD-599) and fragment of maxilla (SD-1683)	11 isolated and 2 *in situ* teeth 6 right; 7 left	9 isolated and 2 *in situ* teeth 6 right; 5 left	24	Young adult	Female
Adult 5	Left M_1 SD-1327 h	Dental row found *in situ* and maxilla (SD-2010)	9 teeth *in situ* 2 right; 7 left	16 teeth *in situ* 8 right; 8 left	25	Mature adult	Female
Adult 6	Left M_1 SD-1577	Maxillary fragment (SD-1789)	7 isolated teeth 1 right; 6 left	8 isolated and 1 *in situ* teeth 5 right; 4 left	16	Mature adult	Male
Adult 7	Left M_1 SD-920		5 isolated teeth 3 right; 2 left	5 isolated teeth 3 right; 2 left	10	Mature adult	?
Adolescent 1	Left M_1 SD-780	Small maxillary fragment (SD-917)	6 isolated teeth 5 right; 1 left	3 isolated and 4 *in situ* teeth 3 right; 4 left	13	Adolescent approx. 11-12 years	Male
Adolescent 2	Left M_1 SD-756	Small mandibular fragment (SD-1510) and small maxillary fragment (SD-331a, SD-331b)	1 isolated and 7 *in situ* teeth 4 right; 4 left	10 isolated and 2 *in situ* teeth 7 right; 5 left	20	Adolescent Approx. 12-13 years	?
Adolescent 3	Left P^4 SD-1221	Small mandibular fragment (SD-912)	3 isolated and 1 *in situ* teeth 1 right; 3 left	8 isolated teeth 1 right; 7 left	12	Adolescent Approx. 12-13 years	Male
Juvenile 1	Left M_1 SD-1600b	Mandible (SD-1600a, SD-1660a, SD-2009), small maxillary fragment (SD-1875) and postcranial elements	2 isolated and 19 *in situ* teeth 11 right; 10 left	10 isolated and 1 *in situ* teeth 7 right; 4 left	32[a]	Juvenile Approx. 7.5 years	Male
Juvenile 2	Ulna SD-763b	Postcranial elements				Juvenile Approx 9-10 years	?
Infant 1	Tibia SDR-157	Postcranial elements				Infant 2-3 years	?

[a] Mixed dentition includes deciduous and permanent elements, both complete and/or in formation (see Table 1 for detailed information).

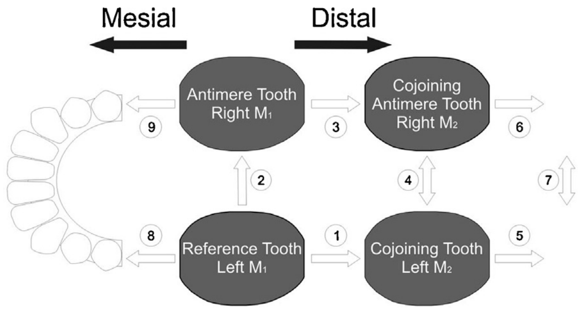

Fig. 1. Scheme for the lower dentition of the procedure followed for establishing tooth association in the El Sidrón Neandertal sample. 1: association of the element distally cojoining the reference tooth, i.e., the LM_2; 2: identification of the antimere of the reference tooth, i.e., the RM_1; 3: association of the element distally cojoining the antimere of the reference tooth, i.e., the RM_2; 4: testing the congruence between the results of steps 1 and 3; 5: association of the next contiguous tooth along the left row, i.e., the LM_3; 6: association of the next contiguous tooth along the right row, i.e., the RM_3; 7: testing the congruence between the results of steps 5 and 6. Once completed the assessment along the distal direction, the same procedure is followed in mesial direction, starting with (8) the association of the element proximally cojoining the reference tooth, i.e., the LP_4 and (9) of the element proximally cojoining the antimere of the reference tooth, i.e., the RP_4.

Fig. 1. Schéma, pour la denture inférieure, de la procédure adoptée pour établir les associations dentaires dans l'échantillon néandertalien d'El Sidrón. 1 : association de l'élément correspondant distalement à la dent de référence, i.e., la LM_2 ; 2 : identification de l'antimère de la dent de référence, i.e., la RM_1 ; 3 : association de l'élément correspondant distalement à l'antimère de la dent de référence, i.e., la RM_2 ; 4 : contrôle de la compatibilité entre les résultats des étapes 1 et 3 ; 5 : association de la dent suivante le long de la rangée dentaire gauche, i.e., la LM_3 ; 6 : association de la dent suivante le long de la rangée dentaire droite, i.e., la RM_3 ; 7 : contrôle de la compatibilité entre les résultats des étapes 5 et 6. Une fois complétées, les associations en direction distale, la même procédure est suivie en direction mésiale, à commencer par (8) l'association de l'élément correspondant proximalement à la dent de référence, i.e., la LP_4 et (9) de l'élément correspondant proximalement à l'antimère de la dent de référence, i.e., la RP_4.

below are listed in decreasing order of relevance, with the first six being the most relevant:

1. the anatomical connection (either based on the existence of a skeletal support or the topographic distribution at the site);
2. the exact fitting of a tooth in its alveolar socket;
3. the matching of interproximal wear facets:
   In order to establish a link between two isolated teeth, one of the criteria used in this study is the similarity between adjacent interproximal wear facets (Fig. 2) (Benazzi et al., 2011; Gençturk et al., 2008; Poisson et al., 2002; Rosas et al., 2006; Villa and Giacobini, 1995; Wolpoff, 1979, among the others). Apart from the size and shape of the facets, we principally considered the pattern of subvertical grooves when present. As often seen in Neandertal samples (Egocheaga et al., 2004; Poisson et al., 2002; Villa and Giacobini, 1995), a high frequency of subvertical grooves is also found in El Sidrón (Estalrrich et al., 2011). These are disposed in well-defined patterns that allow individual identification, precisely because there are no two equal subvertical groove patterns in the sample. By using scanning electron micrographs, the similarity between two presumably adjacent facets is tested by superimposing (using Adobe Photoshop©) the features of the mesial facet to the scaled and mirrored outline of the distal facet, including its subvertical grooves if present (Fig. 2). If the facets are alike, the teeth are considered to be a match;
4. the degree of occlusal wear (Skinner, 1997);
5. the developmental age and eruption stage (AlQahtani et al., 2010);
6. the tooth crown and root morphology.

This criterion is especially used for antimere identification. For size assessment, we used the bucco-lingual (BL) and mesio-distal (MD) diameters, the size and location of the cusps and crests, as well as other morphological details scored according to the ASUDAS system (Turner II et al., 1991).

There are additional criteria which have also been considered on a case by case basis. These include: 7: lineal or pitted enamel hypoplasia; 8: presence, abundance and location of dental calculus; 9: various biological features and oral pathologies (Prieto, 2005; Dean et al., 2013); 10: chipped enamel (following the score procedures by Belcastro et al., 2004); 11: pattern and abundance of instrumental or cultural striations (scratches on the labial surface of the anterior dentition related to para-masticatory activities; Bermúdez de Castro et al., 1988; Frayer et al., 2010, among the others; for El Sidrón, see Estalrrich and Rosas, 2013); 12: taphonomic features (e.g., colour, similarity in the superficial covering of calcareous deposits, etc.).

All dental macro- and micro-features were analyzed and assessed using binocular lens, optical microscope (Olympus© BX51) and ESEM (Fei Quanta 200©).

2.2.3. *Degree of reliability of the associations*

In order to better control error distribution of the associations, the degree of reliability regarding the attribution of a new tooth to a specific individual or to an anatomically-related set of dental remains has been established based on three levels of confidence (Table 1). Firstly, for practical reasons, we considered all unequivocal associations as "level 1" (criteria 1 and 2). Then, when tooth association satisfied three or more major criteria, the reliability was scored as "level 2". Finally, "level 3" indicates tooth attributions in which three or less of the major criteria were satisfied or associations relying on a process of elimination. Additional criteria help to clarify or reinforce the degree of reliability (level of the association).

When the association of a tooth to a dental row was not evident (insufficient number of matching criteria), we have considered it more parsimonious to leave the specimen unassociated rather than to create a new unit. When possible, we tried to find a correlation between an unassociated specimen and the previously identified individuals, always taking into account the greatest number of minor criteria ("level 3" of reliability).

2.2.4. *Criteria for matching upper and lower dentitions*

Occlusal fit is the principal criterion used for matching upper and lower dentitions. Additionally, secondary criteria include dental wear pattern, developmental age,

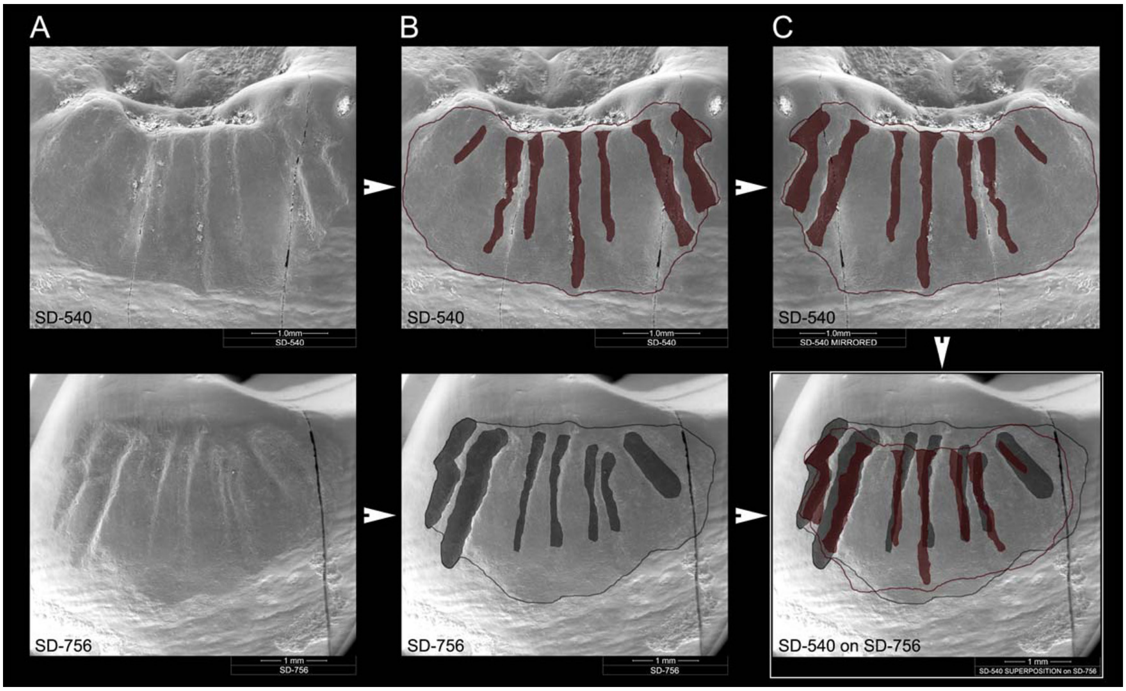

Fig. 2. Superposition of conjoint interproximal wear facets. ESEM micrographs of (A) the distal interproximal facet on the LM_1 (bottom) and the mesial facet of the LM_2 (top). B. Outlines of the two interproximal facets and of the subvertical grooves. C. Superposition of the scaled, rotated and mirrored LM_2 mesial facet outlines to the LM_1 distal figures.

Fig. 2. Superposition de facettes d'usure interproximales correspondantes. Micrographie ESEM de (A) la facette interproximale distale de la LM_1 (en bas) et de celle mésiale de la LM_2 (en haut). B. Contours des deux facettes interproximales et des sillons subverticaux. C. Superposition sur l'image de la facette distale de la LM_1 des contours de la facette mésiale de la LM_2 après étalement, rotation et effet miroir.

presence of hypoplasia lines, presence of dental calculus, colouring pattern, and texture features.

3. Results

A minimum of 13 Neandertal individuals have been identified in the El Sidrón fossil sample. Eleven of them were defined from the permanent dentition: seven adults, three adolescents and a juvenile, the latter represented also by deciduous tooth elements (Fig. 3; Tables 1 and 2). Two additional individuals, one infant and another juvenile, were determined only from postcranial remains.

3.1. Lower dentition

In the assemblage, the permanent lower left first molar (LM_1) is the most represented dental element indicating an MNI of ten (Table 2). Accordingly, the M1s have been used as reference units for assembling other isolated teeth (see methods). Amongst them, four are preserved in their respective mandibles (Adult 1 to 3 and Juvenile 1). In addition, Adult 5 was discovered during the excavations associated with a dental row consisting of 9 additional teeth (Tables 1 and 2). All but one LM_1 are fully developed and present different stages of occlusal wear (from 0 to 4–5), the remaining one, which exhibits an unfused root apex, identifies the individual Juvenile 1.

During the process of successive association of the mandibular teeth, a new individual was identified (Adolescent 3) using a set of unmatched lower teeth. Using this matching process based on the permanent mandibular teeth, eleven individuals have been identified. The age assessment of the seven adults is based on the presence of fully erupted and variably worn third molars (in six cases) and the presence of an interproximal distal wear facet on the second mandibular molar (Adult 5). Two dental assemblages are identified as adolescent individuals. The assessment of Adolescent 1 is based on the presence of a second molar lacking the interproximal distal wear facet and showing only a low degree of occlusal wear (stages 1 and 2), while Adolescent 2 is identified by an unerupted third molar (SD-1510). The tooth set that was not possible to associate with any of the reference M_{1S} (Adolescent 3) presents a slight occlusal wear (stages 1 and 2) similar to that found in the aforementioned adolescents. All of the above evidence based of the permanent tooth elements allows the identification of eleven individuals, further confirmed by the analysis of the upper dentition (see below).

3.2. Upper dentition

Among the maxillary teeth collected at El Sidrón, the upper right first molar (RM^1) is the most represented element with nine specimens recovered, four being *in situ* and five isolated (see Tables 1 and 2 and Fig. 3). One RM^1 having unclosed roots indicates the presence of a minimum of nine tooth associations. During the upper teeth

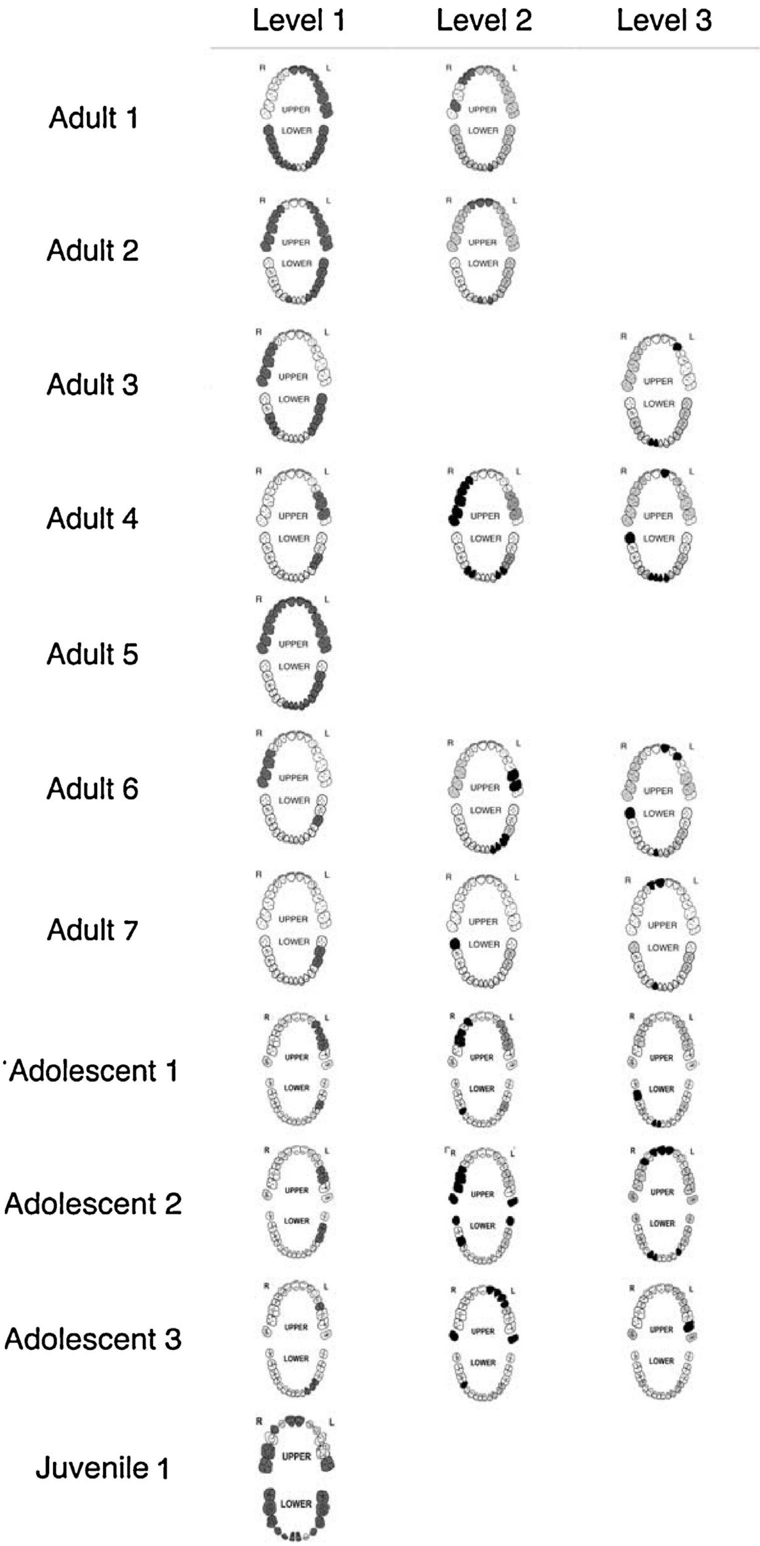

Fig. 3. Tooth associations in the El Sidrón Neandertal sample defining 11 of the 13 individuals identified so far. The different dental elements are progressively associated to the reference teeth (LM_{1s}) following three levels of reliability. See text for the description of the three levels.

Fig. 3. Associations dentaires dans l'échantillon néandertalien d'El Sidrón indiquant 11 des 13 individus identifiés à ce jour. Les différents éléments dentaires sont associés progressivement aux dents de référence (LM_{1s}) selon trois niveaux de fiabilité. Voir le texte pour la description des trois niveaux.

association process, two additional individuals were identified increasing the total number of associations to eleven.

Seven dental sets are attributed to adult individuals based on: tooth wear (stages 4 and 5), M^3 adscription (six RM^3 are completely developed and show occlusal wear) and the presence of M^2 distal wear facet. We named these individuals Adult 1 to Adult 7 (Fig. 3; Tables 1 and 2). Based on the beginning stage of root formation of two upper left third molars (LM^3) and two right third molars (RM^3), two sets were attributed to adolescent individuals. Another assemblage (left C to M^1 found in association at the site) shows a degree of occlusal wear compatible with an adolescent age (stages 1 and 2) (Table 1 and Fig. 3). The presence of a left P^4 already represented in both previously identified adolescents indicates a new individual (Adolescent 1).

Finally, another maxillary row is represented by a RM^1 with its root still under formation. While this tooth was found isolated, it can be associated to 10 additional teeth (including deciduous elements and premolar germs) based on their developmental stage (Tables 1 and 2).

3.3. *Matching of the lower and upper dentitions*

Occlusal fitting criteria of the permanent elements and the combination of the upper and lower dental associations indicate the presence of 11 individuals, whereas relative dental wear and developmental criteria had already defined seven adults. The remaining three individuals are defined as follows. Adolescent 1 is defined by one adolescent mandibular assemblage (RM_2 without distal wear facet; SD-755) fitting the maxillary assemblage displaying low occlusal wear. Adolescent 2 is defined by a second adolescent mandibular set (unerupted left M_3; SD-1510) fitting a similarly identified maxillary assemblage with incomplete M^3 roots. Finally, Adolescent 3 is represented by the mandibular assemblage displaying a low degree of occlusal wear which fits the last maxillary set compatible with an adolescent (M^3s with roots at a premature formation stage) (Fig. 3; Tables 1 and 2).

An additional juvenile individual, Juvenile 1, with which a number of postcranial elements can be securely associated (Fig. 3), has been defined by the presence of a complete mandible bearing a mixed dentition which, due to its developmental stage, cannot be assigned to any of the previously identified individuals. Duplication of postcranial elements such as ulna, radius and right V metacarpal of an immature specimen older than Juvenile 1 (following Scheuer and Black, 2000) requires the presence of Juvenile 2, a second juvenile individual. Lastly, despite a lack of any dental remains, the presence of a 1.5–3-year-old infant has been identified using a distal fragment of a right tibia (Egocheaga and Sierra, 2005; Rosas et al., 2006), a right hallux and a fifth metatarsal.

In summary, a minimum of 13 Neandertal individuals have been identified within the El Sidrón fossil assemblage. It should however be noted that an isolated slightly worn RI^2 (SD-536b) preserving its lingual crown side but not the root, cannot be associated with any of the individuals identified so far.

4. Discussion

Until the 2005 field season, eight Neandertal individuals had been identified at El Sidrón (Rosas et al., 2006). Since then, the dental sample has considerably increased and a more systematic and consistent approach for assessing the MNI has been adopted, increasing to 13 the number of ascertained individuals.

The process of tooth sequential association is greatly affected by differential tooth preservation conditions usually affecting each quadrant of the dentition. At El Sidrón, the elements from the lower dentition, notably from the left side ($n = 61$), are better represented across the individuals, while the elements of the upper dentition are essentially concentrated in five out of the 11 identified individuals. Also, the lack of maxillary elements in some dental sets (in Adult 7 and Adolescent 3) precludes a high degree of verisimilitude in upper-lower row associations.

In the assessment of the MNI in human fossil assemblages, a number of error sources can be assumed *a priori*. It is noteworthy to mention those related to the anatomical identification of dental specimens. For example, mostly due to the variable frequency of additional cusps and crests expressed at the outer surface, an unequivocal distinction between isolated M_1–M_2 and M_2–M_3 is not possible in Neandertal samples (Bailey and Hublin, 2006; Lebel and Trinkaus, 2002; Lebel et al., 2001; Maurielle et al., 2008). Nonetheless, at El Sidrón the size of the distal molar cusp (entoconid or hypoconulid) allows reliable identifications that, at least in some cases, are also supported by evidence from the interproximal facet matching (Fig. 2).

Occlusal wear asymmetry in hunter-gatherer populations (Deter, 2009; Merbs, 1983; Molnar, 1972; Molnar et al., 1983; Puech, 1981) is another source of error, especially in the case of antimere identification. Also, because it increases the difficulty of associating anterior and posterior dentitions, the commonly advanced and group-specific degree of anterior tooth wear typical of Neandertals deserves attention (Lozano et al., 2008; Puech, 1981; Ungar et al., 1997; Wallace, 1975).

Sex attributions are usually based on canine size, the most dimorphic tooth in humans and other primates (Bermúdez de Castro et al., 1993, 2001; Leutenegger, 1982; Leutenegger and Kelly, 1977; Thorén et al., 2006), as well as on mandibular size and shape. Paleogenetic evidence at El Sidrón based on Y-chromosome markers has confirmed 100% of previous sex attributions performed on morphological grounds (Lalueza-Fox et al., 2011). However, additional skeletal sites and further genetic tests still have to be considered for sexing the still unknown individuals and providing a more robust picture of the composition per sex of this Neandertal group. Similarly, age estimations have been performed so far in the perspective of tooth association. Accordingly, seven individuals presenting a moderate degree of dental wear have been identified, the maximum corresponding to stages 5-6 (Skinner, 1997). However, no cases of extreme dental wear (senile individuals) have been recorded in the sample.

Excavations at El Sidrón are planned for the coming years, and it is likely that new human specimens will be recovered in the near future. Hopefully, new material and new analyses will complete and enlarge the number of individuals reported in this study. In this perspective, a next step in our investigation will be the attribution of the isolated postcranial elements to the individuals defined on dental criteria.

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