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Evidence of habitual behavior from non-alimentary dental wear on deciduous teeth from the Middle and Upper Paleolithic Cantabrian region, Northern Spain

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A R T I C L E I N F O

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A B S T R A C T

The use of 'teeth as tools' (non-masticatory or cultural-related dental wear) has largely been employed as a proxy for studying of past human behavior, mainly in permanent dentition from adult individuals. Here we present the analysis of the non-masticatory dental wear modifications on the deciduous dentition assigned to eight Neanderthal and anatomically modern human subadult individuals from Mousterian to Magdalenian technocultural contexts in the Cantabrian region (Northern Spain). Although preliminary, we tentatively suggest that these eight subadults present activity-related dental wear, including cultural striations, chipped enamel, toothpick grooves, and subvertical grooves. We also found evidence of habitual dental hygienic practices in the form of toothpicking on a deciduous premolar. Orientation of the cultural striations indicates similar handedness development as in modern children. Taken together, these dental wear patterns support the participation of young individuals in group activities, making them potential contributors to group welfare. This study potentially adds new evidence to the importance of the use of the mouth in paramasticatory activities or as a third hand throughout the Pleistocene, which can be confirmed with a more specific reference sample.

1. Introduction

1.1. Non-masticatory behavior during human evolution

One of the proxies used for the study of past human behavior is the analysis of the non-masticatory, cultural or activity-related dental wear, characteristic of the genus *Homo* since its appearance (Koby, 1956; Molnar, 1972; Brace, 1975; Puech, 1981; Frayer and Russell, 1987; Formicola, 1988; Lukacs and Pastor, 1988). For example, several specimens of early *Homo* present toothpick grooves on the interproximal sides of the teeth, suggesting that grass stalks were intensively employed as a tool for removing food particles retained between the teeth and, therefore, it is considered one of the earliest human cultural habits—in this case, related to oral hygiene (Frayer and Russell, 1987; Formicola, 1988, 1991; Turner and Cacciatore, 1998; Ungar et al., 2001; Hlusko, 2003; Estalrrich et al., 2020).

The majority of research has been focused toward the study of non-masticatory dental wear mostly on Middle and Late Pleistocene fossil hominins, noticing an increase of the use of the mouth in non-masticatory tasks during the Middle and Late Pleistocene (Koby, 1956; Molnar, 1972; Brace, 1975; Puech, 1981; Lukacs and Pastor, 1988; Bermúdez de Castro et al., 1988; Lalueza-Fox and Frayer, 1997; Lozano et al., 2008; d'Incau et al., 2012; Krueger and Ungar, 2012; Volpato et al., 2012; Fiorenza and Kullmer, 2013; Willman, 2016; Estalrrich et al., 2017a). Only recently research has begun to include samples of early modern humans to explore the broad behavioral picture and evolutionary developmental patterns (Clement et al., 2009; Fiorenza et al., 2011; Krueger, 2011; Sarig et al., 2016; Willman, 2016).

Since dental wear is a cumulative process (Lucas, 2004), most of the studies dealing with non-masticatory dental wear on past populations include only adult individuals (Molnar et al., 1983; Bonfiglioli et al., 2004; Lorkiewicz, 2011; Molnar, 2008, 2011). In

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fact, non-masticatory dental wear features have been defined in adult individuals (de Lumley, 1973; Bermúdez de Castro et al., 1988; Belcastro et al., 2004; Scott and Winn, 2011). However, these features in young individuals with mixed dentition have also been described (e.g., Lozano et al., 2008 for Atapuerca Sima de los Huesos; Estalrrich and Rosas, 2013 and 2015 for El Sidrón Neanderthals). A juvenile Neanderthal individual (around 7.5 years old) from El Sidrón cave (Estalrrich and Rosas, 2013, 2015) displays the same dental wear features (same morphology and distribution) in both permanent and deciduous teeth (number, in this case, depends on tooth type). These features were also comparable to the features from the adult individuals of the same group (Estalrrich and Rosas, 2013, 2015) and similar to the marks broadly described for Neanderthals and other hominins from archaeo-paleontological samples.

Besides having a prolonged immature phase—by the insertion of a life history stage called childhood (when the deciduous dentition is fully in occlusion, spanning from years 2.5–3.5 to the 6th) between infancy (ending at the completion of the eruption of the deciduous dentition between 2.5 and 3.5 years) and juvenility (from the time in which the first permanent molar is erupted to the loss of the deciduous fourth premolar, spanning from years 6th to 12th approximately) after the appearance of *Homo erectus* (Bogin and Smith, 1996, 2012; Bogin, 1997)—little is known about the behavior of immature individuals from highly encephalized human species. After the appearance of *H. erectus* one of the main constraints to dig into their past behavior is the scarcity of juvenile and child skeletal remains in the Middle and Late Pleistocene record (probably the main factor behind why the majority of activity related dental wear studies have dealt only with adult individuals), as well as the difficulties in identifying byproducts of their activities (Shea, 2006).

Due to the scarcity of non-masticatory dental wear studies on immature individuals, herein we present the analysis of these dental wear modifications in Neanderthal and anatomically modern human (AMH) deciduous teeth from the Cantabrian region (Northern Spain). We aim to explore: (1) whether the subadult individuals from Mousterian to Magdalenian cultural contexts (>45 to 12,000 uncal BP) show dental wear related to habitual behavior as their adult counterparts; and (2) if so, how this could be interpreted in terms of behavioral development and their possible role within the social group organization.

1.2. Non-masticatory dental wear modifications

Cultural or instrumental striations The striae appear on the labial surface on the anterior teeth (central and lateral incisors, and canine teeth), in both maxillary and mandibular dentition. In some cases, this feature has also been described on the first permanent premolars (Lozano et al., 2008). Each striae measured between 1 and 4 mm in length and between 20 and 100 μm in width (Lalueza-Fox and Frayer, 1997; Estalrrich and Rosas, 2015). These striations present the same morphological features as described for the cutmarks on the bone (Shipman and Rose, 1984)—i.e., Hertzian cones, grooves with a V-shaped section, linear and parallel borders, and microscratches at the bottom (Bermúdez de Castro et al., 1988; Lozano-Ruíz et al., 2004; Estalrrich and Rosas, 2013)—although some of these features could be worn away in vivo through dietary abrasion and the repetition of non-masticatory behaviors (Frayer et al., 2010). Instrumental striations could easily be distinguished from dietary microwear mainly due to their larger size (dietary scratches are between 50 and 200 μm in length and width does not exceed 5 μm), low number, and preferred orientation (Ungar and Grine, 1991; Lalueza-Fox, 1992; Lozano et al., 2008; Estalrrich and Rosas, 2013).

The striations are associated with the use of the anterior teeth as a third hand or also known as ‘stuff-and-cut’ behavior (Brace, 1975), associated with food or leather preparation or preprocessing food items (e.g., cutting meat held between teeth). This modification has been described in several modern human populations, such as the Chalcolithic individuals from Pakistan (Lukacs and Pastor, 1988), Canadian Inuit, Aleuts, Australian Aborigines, Fueguians, Tasman, Arikara, Illinois Bluff and Puye groups (Merbs, 1983; Molnar et al., 1983; Green et al., 1998; Bax and Ungar, 1999; Lozano et al., 2008), as well as in Middle and Late Pleistocene hominins from the sites of La Quina (Martin, 1923), L'Hortus (de Lumley, 1973; Estalrrich and Rosas, 2015), Shanidar (Trinkaus, 1983), Krapina (Lalueza-Fox and Frayer, 1997), Regourdou (Volpato et al., 2012), Mauer (Lalueza-Fox and Pérez-Pérez, 1994), Spy (Estalrrich and Rosas, 2015), El Sidrón (Estalrrich and Rosas, 2013, 2015), and Sima de los Huesos (Bermúdez de Castro et al., 1988; Lozano-Ruíz et al., 2004; Lozano et al., 2008). Even as earlier as 1.8 Ma in Olduvai Gorge, OH-65 present those same striations (Frayer et al., 2016). The above mentioned cases suggest a more likely similar etiology for these labial or cultural striations.

Chipped enamel Chipped enamel is produced due to pressure caused as a result of paramasticatory activities or due to hard particles ingested with food, resulting in antemortem fractures affecting just the enamel or both the enamel and dentine (Merbs, 1983; Belcastro et al., 2004; Bonfiglioli et al., 2004; Scott and Jolie, 2008; Scott and Winn, 2011), depending on the force applied. Chipped enamel related to extramasticatory activities may appear on the incisal edge of each anterior tooth. The fractures that appear on the occlusal face of molar and premolar teeth are supposed to be linked to a masticatory function (Belcastro et al., 2004). All fractures produced antemortem have a smooth appearance, with the edges of the fracture rounded (Belcastro et al., 2004; Scott and Winn, 2011).

In modern hunter-gatherer populations chipped enamel on the anterior dentition is related to retouching the stone tool cutting edge (Turner and Cadien, 1969; Merbs, 1983; Belcastro et al., 2004; Lozano et al., 2008). This dental wear feature has been also found on several specimens from the Middle and Late Pleistocene (Wallace, 1975; Lozano-Ruíz et al., 2004; Estalrrich and Rosas, 2015; Willman, 2016; Belcastro et al., 2018; Krueger et al., 2019), including some deciduous teeth from the Krapina (Belcastro et al., 2018), l'Hortus and El Sidrón (Estalrrich and Rosas, 2015) Neanderthals.

Toothpick grooves Toothpick grooves are modifications located on the mesial and distal surfaces between two adjacent teeth, commonly premolars and molars, and, at a lower frequency, on incisors and canines (Formicola, 1988, 1991; Frayer, 1991; Ravy et al., 1996; Ungar et al., 2001; Estalrrich et al., 2017b). The surface of the grooves shows numerous parallel buccolingually oriented microstriations (Grine et al., 2000; Ungar et al., 2001; Hlusko, 2003; Bouchneb and Maureille, 2004; Lozano et al., 2013; Estalrrich et al., 2017b).

Extensive toothpicking activity leads to the generation of a toothpick groove. This dental modification has been found in different prehistoric populations including early *Homo* (Boaz and Howell, 1977; Frayer and Russell, 1987; Ungar et al., 2001; Hlusko, 2003; Estalrrich et al., 2020), Middle Pleistocene hominins (Bermúdez de Castro et al., 1997; Sun et al., 2014), Neanderthals (Siffre, 1911; Frayer and Russell, 1987; Bouchneb and Maureille, 2004; Lozano et al., 2013; Estalrrich et al., 2017b), and AMH (Ubelaker et al., 1969; Brown and Molnar, 1990; Turner and Cacciatore, 1998; Teegen and Schultz, 2002; Ricci et al., 2016; Willman, 2016).

Toothpicking is a cumulative process during the individual's life, and is accepted as the oldest human habit, typically associated with dental hygiene (Frayer and Russell, 1987; Ungar et al., 2001; Hlusko, 2003; Estalrrich et al., 2017b), and sometimes as the result of a therapeutic or palliative activity (Lozano et al., 2013).

Subvertical grooves inside interproximal facets. Subvertical grooves are small furrows located on the interproximal wear facets (the latter produced by tooth-to-tooth contact; Wolpoff, 1971; Lucas, 2004), and they usually display a subvertical orientation radiating from the occlusal surface. The grooves are semicircular in cross-section, with no microstriations, appear from one to eight in number and 0.1–0.5 mm in width, and have been described across the whole permanent dentition (Villa and Giacobini, 1995; Estalrrich et al., 2011). The grooves from one facet mirror the grooves from the adjacent facet (Estalrrich et al., 2011), so this circumstance has been used to group isolated teeth (Gençturk et al., 2008; Rosas et al., 2013).

Subvertical grooves have been observed primarily in Neanderthals (Giacobini et al., 1984; Antunes and Santinho Cunha, 1992; Villa and Giacobini, 1995; Poisson et al., 2002; Egocheaga et al., 2004; Rosas et al., 2006; Estalrrich et al., 2011). This trait has also been described in other fossil and extant hominins, such as *Homo habilis* (Puech and Cianfarani, 1988), early *Homo* (Brink et al., 2012), Middle Pleistocene hominins (Pérez-Pérez et al., 2003), early modern humans (Vandermeersch, 1981; Sarig et al., 2016), and AMH (Kaidonis et al., 1992). The etiology of this modification is not well known, but it seems to be due to a multifactor combination of biomechanical, non-masticatory and dietary preferences (Poisson et al., 2002; Egocheaga et al., 2004; Estalrrich et al., 2011).

1.3. Differences between deciduous and permanent enamel

There are differences between deciduous and permanent enamel regarding their mechanical properties that could have potential implications for the comparative proposes undertaken in this study.

While the enamel of deciduous teeth is thinner than the permanent enamel, it has a higher density of enamel rods (Hillson, 1996; Grine, 2005; De Menezes Oliveira et al., 2010; Mahoney, 2010; Lynch, 2013). This could mean that it is softer and more easily worn off. However, not all is just about the enamel per se. Other factors such as flow rate due to smaller salivary glands could also affect the resistance of deciduous enamel to cracks and erosion (Ashley et al., 1991). Another critical factor affecting both the physical and chemical characteristic of enamel is known as the posteruptive maturation, in which the enamel surfaces accumulate fluoride and metal ions, becoming harder and less porous (Fanning et al., 1954; Driessens et al., 1982; Hicks et al., 2004; but see Lynch, 2013 for a complete review). This factor is time-dependent, and deciduous teeth remain in the mouth for a short time, so they will be likely less influenced by this factor.

Despite these differences, there is currently no consensus concerning to what extent it could affect for example dietary-related occlusal and buccal microwear characterization between deciduous and permanent teeth (Krueger, 2016; Mahoney et al., 2016; Kelly et al., 2020; Hernando et al., 2020).

Regarding our study on the paramasticatory dental wear, we recognize that a comparative sample of known and inferred non-masticatory behaviors in deciduous teeth is not currently available. Nevertheless, this study represents a glimpse apropos the possible type of non-masticatory dental wear in deciduous teeth.

1.4. Background of the archeological sites studied

The sample from Axlor cave (Dima, Biscay) preserves a long and rich Middle Paleolithic sequence, first identified and described by Barandiarán (1980). The two deciduous teeth (Table 1) here studied were found on undisturbed Mousterian layers IV and V excavated during the 1970s and assigned to *Homo neanderthalensis* by Gómez-Olivencia et al. (2020) and González-Urquijo et al., 2021. Recent radiocarbon dates on level IV (Table 1) indicates that this level goes beyond the radiocarbon limit with dates >49,300 BP (OxA-32428) and >49,900 BP (OxA-32429; Marín-Arroyo et al., 2018). The specimens are housed at the Arkeologi Museoa in Bilbao.

El Castillo Cave (Puente Viesgo, Cantabria) contains more than 20 archeological stratigraphic layers, beginning in the Acheulean and ending in the Bronze Age (Cabrera Valdés et al., 2005). There are over 150 cave paintings already catalogued, including hand stencils, red disks and engravings of deer. In a phase of the 'Aurignacian-delta' from Obermaier's excavation campaign in 1912, a mandible with two deciduous teeth (Castillo C, see Table 1), recently dated to 24,720 ± 210 uncal BP has been ascribed to the Gravettian technocomplex (Garralda et al., 2019). Besides, three deciduous teeth (Table 1; Garralda, 2006) were recovered from Level 18b (Transitional Aurignacian) recently dated between 46,000 ± 2400 and 45,800 ± 2300 uncal BP (Wood et al., 2018). According to Garralda et al. (1992; see also Garralda, 2006), the variability of the human teeth can be found in both the Neanderthal lineage and that of AMH, but their archaic characteristics made the authors considered them as Neanderthals. We assign them to *H.* cf. *neanderthalensis*. The specimens are curated at the Museo de Prehistoria y Arqueología de Cantabria (MUPAC) in Santander.

Las Caldas Cave (Priorio, Oviedo, Asturias) is located in the middle valley of the Nalón River, in a setting widely occupied from the end of the Pleistocene until the Late Glacial Maximum containing a rich archeological record of the Solutrean and Magdalenian cultures (Corchón, 2017; Haber-Uriarte and López-Lázaro, 2017; Jones et al., 2021). Within Level XI, dated to 13,755 ± 120 uncal BP (Table 1) and associated to the Lower Magdalenian culture, one tooth belonging to a subadult individual was studied. The specimen is curated at Museo Arqueológico de Asturias in Oviedo.

Tito Bustillo cave (Ribadesella, Asturias) was inhabited by humans who produced Magdalenian artifacts. It has an abundant record of cave paintings representing horses, deer, ox, marine mammals and even human figures (Moure, 1997; Balbín and Alcolea, 2014). Here, the two teeth (Table 1) studied were recovered during the 1975 field season (Garralda, 1976) in Level 1c dated around 14,440 ± 100 uncal BP (Balbín and Alcolea, 2014). The specimens are housed at Museo Arqueológico de Asturias in Oviedo.

Santa Catalina cave (Lekeitio, Biscay) was excavated between 1982 and 2000. Three archeological levels were identified: Upper Magdalenian (Level III), Final Magdalenian (Level II) and Azilian (Level I; Berganza Gochi and Arribas Pastor, 2014). Within the Magdalenian levels, three human teeth were recovered. Two of them are deciduous teeth (Table 1) found in the Upper Magdalenian (Level III), being the level dated between 10,360 ± 90 and 12,425 ± 90 uncal BP (Berganza Gochi and Arribas Pastor, 2014; the complete set of chronology data for Level III is provided on Table 1). The specimens are housed at the Arkeologi Museoa in Bilbao.

2. Materials and methods

The sample analyzed in this study comprises the subadult individuals from several cave sites located along the Cantabrian region (Las Caldas and Tito Bustillo in Asturias, El Castillo in Cantabria, and Santa Catalina and Axlor in Biscay) from the Mousterian, Aurignacian, Gravettian and Magdalenian cultures, with a total number of 12 teeth recovered (Table 1).

Age at death for the individuals has been estimated based on the standards of tooth development (AlQahtani et al., 2010). Age at death for the left dI^1 (AX.5b.299.31.64.17) from Axlor cave (Dima, Biscay) was previously estimated in 6–8 years old (Gómez-

Table 1
Sample considered in this study, indicating site, technological context, chronology (when available), taxonomic assignment, subadult dental remains recovered, and estimated age at death. The calibrations have been done using IntCal20 (Reimer et al., 2020) calibration curve in OxCal v. 4.3 (Bronk Ramsey 1998, 2009).

Site	Cultural period (Level)	Sub-unit	Lab reference	Chronology ^{14}C ka BP	Chronology ^{14}C ka cal BP	Assignment	Catalog No.	Teeth	Age at death	Reference
Santa Catalina (Biscay)	Upper Magdalenian (Level III)	29C	Ua-24653 (AMS)	10360±90	12606-11837	*H. sapiens*	SC. C8. L31H. 1883	R dP_4	Juvenile (10 yr)	Albisu-Andrade et al. (2014); Berganza Gochi and Arribas Pastor (2014)
		29C	Ua-42320 (AMS)	12146±98	14798-13786					
		29E	Ua-24654 (AMS)	11225±80	13304-12934					
		29F	Ua-24655 (AMS)	12345±85	1483-14082		SC. B6. L30F. 815	L dP_4	Juvenile (10 yr)	
		31H	Ua-13876 (AMS)	12405±95	14971-14142					
		31J	Ua-13877 (AMS)	12425±90	14990-14165					
Tito Bustillo (Asturias)	Magdalenian (Level 1c)	–	OxA-6261 (AMS)	14440±100	17951-17326	*H. sapiens*	1975 1C	R dP^4; L I^1 (unerupted)	Child (5.5–7.5 yr)	Garralda (1976)
Las Caldas (Asturias)	Magdalenian (Level IX)	–	Ua-10188 (AMS)	13370±110	16410-15750	*H. sapiens*	4759	R dP_4	Juvenile (<10.5 yr)	Haber-Uriarte and López-Lázaro (2017)
El Castillo (Cantabria)	Gravettian (Unit 18)	–	OxA-26613 (AMS)	24720 ± 210	29503-28504	*H. sapiens*	Castillo C	R dP_3; R dP_4	Child (4–5 yr)	Obermaier (1925); Garralda, 2006;
	Transitional Aurignacian/Aurignacian-delta (Level 18b)	–	OxA-21973 (Ultrafiltered) OxA-21972 (Ultrafiltered)	45800±2300 46000±2400	-45427 -45655	*H.* cf. *neanderthalensis*	292, 924 492	L dI^1; L dP_4 dLP^3 (unerupted)	Child (4.5–6.5 yr) Infant (1.5 yr)[a]	Wood et al. (2018); Garralda et al. (2019)
Axlor (Biscay)	Mousterian Level IV	299 300	OxA-32428 (Ultrafiltered) OxA-32429 (Ultrafiltered)	>49300 >49900	– –	*H. neanderthalensis*	AX.IV. 283.103	L dP^4	Child (4.5–6.5 yr)	Barandiarian (1971); Marín-Arroyo et al. (2018); Gómez-Olivencia et al. (2020)
	Mousterian Level V	–				*H. neanderthalensis*	AX.5b. 299.31.64.17	L dI^1	Child (6–8 yr)	

Abbreviations: L = left; R = right.
[a] Individual represented by an unerupted tooth, no dental wear present and thus not studied here.

Olivencia et al., 2020). In our opinion, the root is being naturally resorbed, so we consider this individual to be younger than 6.5 years (based on the tables AlQahtani et al., 2010), and thus considered this individual as a child. The left dP^4 (AX.IV.283.103) was assigned to a 10–11 years old individual (Gómez-Olivencia et al., 2020) based on modern standards. Since the root of this tooth is broken it was not possible to know if it was in the resorption phase or not. Still, the thickness of the root at the cervix could indicate that the resorption was not advanced, meaning that the individual was younger than 10 years (juvenile).

Castillo C mandible has been assigned to an individual between 4 and 5 years old, due to the presence of all the deciduous dentition in occlusion (only right dP_3 and dP_4 were preserved) and the development of the permanent dentition in their respective alveoli (Garralda et al., 2019). We considered this individual as a child. Besides, two teeth left dI^1 (catalogue number 924) and left dP_4 (catalogue number 292) were assigned to a child between 4.5 and 6.5 years, based on the state of the root (according to AlQahtani et al., 2010). The last tooth is a left dP^3 (catalogue number 492), still in formation. It has been estimated to belong to an individual younger than 1.5 years old (an infant; according to the atlas proposed by AlQahtani et al., 2010).

A right dP_4 (catalogue number 4759) found within level XI from Las Caldas cave was assigned to a juvenile individual younger than 10.5 years old (according to AlQahtani et al., 2010) and advanced occlusal wear (Haber-Uriarte and López-Lázaro, 2017).

A dP^4 and a left I^1 still in formation, both from Tito Bustillo cave and with catalogue number 1975 1C from the Magdalenian level could belong to the same individual. We estimated the age between 5.5 and 7.5 years (based on AlQahtani et al., 2010), considering this individual as a child.

The two deciduous teeth from the Upper Magdalenian level III from Santa Catalina cave are a right dP_4 (SC. C8. L31H. 1883) and a left dP_4 (SC. B6. L30F. 815). Both individuals were estimated to be, approximately, 10 years of age and assigned to the juvenile category (Albisu Andrade et al., 2014).

All the specimens were inspected and photographed with a binocular lens up to 80× of magnification. For the samples from Axlor, Santa Catalina and Castillo C, the preservation of the fossils prevented any manipulation, so the study was performed at their respective museum facilities. For the specimens from El Castillo isolated teeth, Las Caldas and Tito Bustillo, it was possible to perform high-resolution replicas of the teeth and then, to the study of dental modifications with a Leica DVM6 Digital Microscope (Leica Microsystems, Heerburgg, Switzerland) at the EvoAdapta Group facilities of the University of Cantabria.

High-resolution replicas of the dentition were prepared following conventional procedures (Bromage, 1987; Teaford and Oyen, 1989; Martínez-Maza et al., 2011; Estalrrich and Rosas, 2015). The museums' curators previously cleaned and prepared all teeth. Teeth were molded using Coltène/Whaledent President Jet Polyvinylsiloxane dental impression material, and then molds were cast using Epotek 301 high-resolution epoxy and hardener and allowed to dry before analysis.

The absence or presence of the cultural striations was recorded. In case of presence, it was also recorded in which tooth appeared, the number of striations according to the orientation (right-oblique, left-oblique, horizontal, vertical) in that tooth (following Lozano-Ruíz et al., 2004; Estalrrich and Rosas, 2013). Chipped enamel was scored following the three-stage scale proposed by Belcastro et al. (2004), which consists of: 1 = small crack affecting only the enamel; 2 = square irregular lesion with enamel deeply involved; 3 = affecting seriously both dentine and enamel. For toothpicking grooves, we recorded absence/

Table 2
Non-masticatory dental wear traits present on the sample.

Site	Cultural period	Teeth	Occlusal wear[a]	Cultural striations	Chipped enamel	Toothpick grooves	Subvertical grooves
Santa Catalina (Biscay)	Upper Magdalenian (Level III)	R dP_4	4	N	N	Y (degree 2)	N
		L dP_4	3	N	1M 1D	Y (degree 1)	N
Tito Bustillo (Asturias)	Magdalenian (Level 1c)	R dP^4	4	N	1M	Y (degree 2–3)	Y
Las Caldas (Asturias)	Solutrean (Level 11b)	R dP_4	4/5	N	1M	N	Y
El Castillo (Cantabria)	Gravettian (Unit 18)	R dP_3	2	N	1M	N	N
	Transitional Aurignacian/ Aurignacian	L dI^1	3/4	9RO 1LO 1V	1M 1Lab	N	N
	- delta (Level 18b)	L dP_4	3/4	N	1M	N	N
Axlor (Biscay)	Mousterian Level IV	L dI^1	3	7RO 3H	1M	N	N
	Mousterian Level V	L dP^4	4/5	N	N	Y (degree 1)	Y

Abbreviations: L = left; R = right; RO = right-oblique; LO = left-oblique; H = horizontal; V = vertical; M = mesial; D = distal; Lab = labial; Y = yes; N = no.
[a] Following occlusal wear degree scale proposed by Skinner (1997).

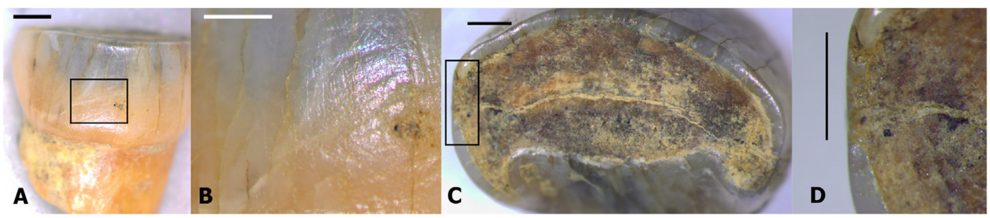

Figure 1. Non-masticatory dental wear traits studied on left dI^1 (AX.5b.299.31.64.17) Mousterian child from Axlor: A) Cultural or instrumental striations (outlined with a square); B) Detail of the cultural striation; C) Chipped enamel on the incisal mesial edge (outlined with a square); D) Detail of the chipped enamel. Scale bar = 1 mm.

presence, and in this last situation, the degree of groove development using a five-stage scale proposed by Estalrrich et al. (2017b). In the case of the subvertical grooves, only absence/presence was recorded.

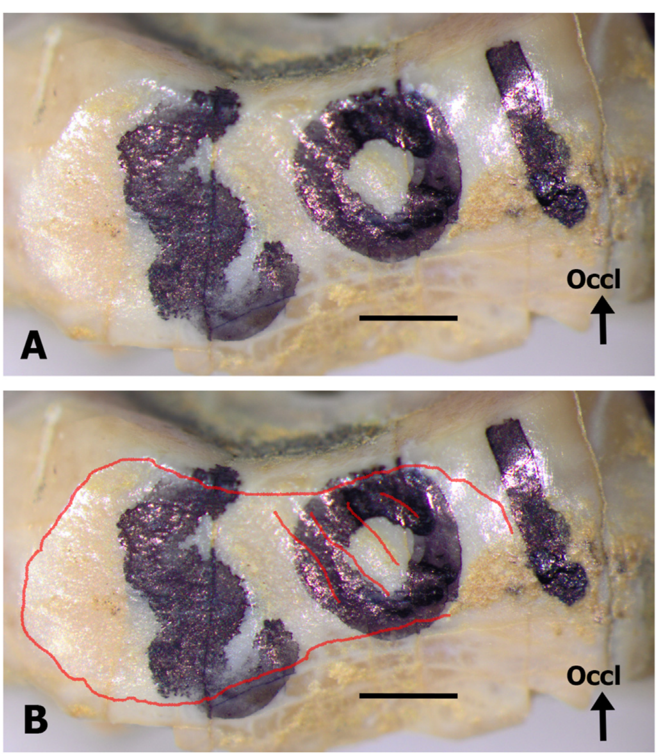

Figure 2. Subvertical grooves on the distal facet of left dP^4 (AX.IV.283.103) Mousterian juvenile from Axlor: A) Complete distal facet showing the subvertical grooves; B) The interproximal facet's shape and central axis of the subvertical grooves are outlined. Scale bar = 1 mm. Occl = occlusal.

3. Results

Detailed information of the non-masticatory dental traits retrieved is provided in Table 2. In the Mousterian (Neanderthal) sample from Axlor, we found cultural striation and chipped enamel (Fig. 1) on the deciduous incisor (a child) and traces of toothpicking and well-developed subvertical grooves (Fig. 2) on the deciduous premolar (a juvenile). Regarding the Transitional Aurignacian from El Castillo sample, the infant individual has an unerupted tooth, so no dental wear was found. The other two deciduous teeth (from a child) present few non-masticatory dental wear traits. The deciduous incisor has cultural striations (Fig. 3A and B) predominantly right-oblique oriented, and two cases of small chipped enamel, while the deciduous dP_4 only presents chipped enamel.

The Gravettian child from El Castillo, Castillo C, has very little record of paramasticatory dental wear. The interproximal sides between dP_3 and dP_4 present the expected interproximal contact facets without subvertical grooves. The mesial side of the dP_3 was broken at some point and was recently reconstructed by Garralda et al. (2019) but shows a slight trace of chipped enamel on the occlusal surface of the dP_4.

The Magdalenian right dP_4 from the juvenile individual from Las Caldas shows chipped enamel on the medial-occlusal side and subvertical grooves on its mesial interproximal facet.

Finally, both Magdalenian juveniles Santa Catalina and the Magdalenian child from Tito Bustillo display chipped enamel, bigger (following Belcastro et al., 2004 grading scale) than in the other Magdalenian specimen from Las Caldas, and toothpick grooves (Fig. 3C). Also, we recorded subvertical grooves on the interproximal contact facets of the right dP^4 from Tito Bustillo cave.

4. Discussion

Activity-related or non-masticatory dental wear has been associated with habitual activities on recent modern humans and it is also frequently found on fossil human species (e.g., Molnar, 1972; Puech, 1981; Merbs, 1983; Lukacs and Pastor, 1988; Bermúdez de

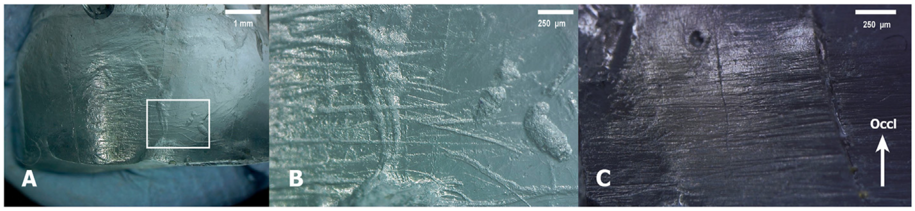

Figure 3. Non-masticatory dental wear traits on high-resolution epoxy replicas from Middle and Upper Paleolithic anatomically modern humans. A) Cultural or instrumental striations from El Castillo Transitional Aurignacian left dI^1 (catalog number 924); B) Detail of the cultural striation from A; C) Toothpick groove on the distal side from Magdalenian Tito Bustillo right dP^4 (Catalog number 1975 1C) showing the characteristic parallel fine microstriations. Occl = occlusal.

Castro et al., 1988; Frayer, 1991; Molleson, 1994; Belcastro et al., 2004; Scott and Jolie, 2008; Lozano et al., 2008; Berbesque et al., 2012; Estalrrich and Rosas, 2015). However, this type of cultural behavior has not been thoroughly addressed in subadult individuals (Lozano-Ruíz et al., 2004; Lozano et al., 2008; Estalrrich and Rosas, 2013, 2015). Including subadult individuals in these analyses is relevant not only to investigate the role they may have played within their group, but to understand the development of learning during the evolution of our genus. One example of this attempt comes from El Sidrón Juvenile 1 Neanderthal, who exhibits the same activity-related dental wear as the adults from the group, and in both deciduous and permanent teeth (Estalrrich and Rosas, 2013, 2015). This indicates that: (1) activity-related dental wear could be recorded on deciduous teeth as well as in permanent teeth; and (2) the role of this individual within the El Sidrón Neanderthal group might be that of an apprentice while performing different activities, as is the case of juveniles from modern hunter-gatherer societies (Bogin, 1999; Marlowe, 2005; Hewlett et al., 2011; Lew-Levy et al., 2017). In fact, ethnographic studies in modern hunter-gatherers have shown that learning of a variety of skills and knowledge starts as early as during infancy (Hewlett et al., 2011; Hewlett and Roulette, 2016), and by the time they are about ten years old, they can provide up to 50% of their own food intake (Hewlett et al., 2011).

The Transitional Aurignacian dental wear identified in the immature individuals of this study indicates habitual use of the mouth in activities other than mastication. Only a single dental wear trait from all the analyzed, chipped enamel, shows a constant presence in all the cultural facies appearing both on the anterior and posterior dentition. Chipped enamel on the anterior dentition (both dI^1s from the Mousterian level IV at Axlor and the Transitional Aurignacian Level 18B at El Castillo) could have been generated when the children manipulated or broke some items harder than tooth enamel. In the case of adult individuals, it has been documented that the use of the anterior dentition to prepare skins for clothing or to correct or reshape the stone tool cutting edge could leave chipped enamel (Gould, 1968; Merbs, 1983; Turner and Cadien, 1969; Molnar, 1972; Lukacs and Pastor, 1988; Belcastro et al., 2004; Scott and Winn, 2011). It is not possible, however, to discern if these Neanderthal children (plausible for El Castillo individuals) performed the mentioned activities, but a similar behavior could be behind these marks.

Instead, the chips found on the posterior dentition (deciduous premolars from all the sites and technocultural contexts) might have originated during mastication, due to the dust and grit introduced with the food, as well as the physical properties of the food itself (Constantino et al., 2010; Scott and Winn, 2011). A similar case of chipped enamel on deciduous teeth has been found on a left dP_3 of an early *Homo sapiens* from Sibudu Cave, South Africa (Riga et al., 2018), where an antemortem chip was located on the distobuccal corner on the occlusal surface. These chips on the posterior dentition provide us with information regarding the food preparation techniques utilized by past populations. Our results show a predominant incidence on the Magdalenian juveniles. Such predominance might be linked to increasing food abrasiveness. In fact, through microwear texture analysis, El Zaatari and Hublin (2014) found that individuals from a Magdalenian context have significantly higher mean values of complexity (Asfc) compared with individuals from the preceding Gravettian and Aurignacian contexts. The authors suggest that the Magdalenian diet was more varied and had higher abrasive loads than earlier contexts. Also, Scott and Winn (2011) noted that the use of grinding stones to process grains adds fine-grained particles in the product, increasing tooth wear. Depending on the nature of the stone, larger particles could be detached from it and during mastication, the occlusal dental surface could be chipped. The grit also makes the food more abrasive, wearing down the tooth faster (El Zaatari, 2010; Lucas et al., 2014).

Toothpicking grooves have been described as the oldest human habit, as they appear throughout the genus *Homo* (Frayer and Russell, 1987; Formicola, 1991; Ungar et al., 2001; Hlusko, 2003; Sun et al., 2014; Estalrrich et al., 2020). In our study, we found mainly incipient grooves, with multiple fine parallel microstriations located on the enamel below the interproximal contact facet and running buccolingually (grade 2 of Estalrrich et al., 2017b). Toothpick grooves were only found on the deciduous posterior dentition of Magdalenian juveniles from Tito Bustillo (Asturias) and Santa Catalina (Biscay), and the Neanderthal deciduous premolar from Axlor site. This is the first time such a trait has been found on deciduous human teeth in the Cantabrian Region. The evidence retrieved from the Neanderthal deciduous molar from Axlor is similar to the case found in Hortus II/III Neanderthal (Estalrrich et al., 2017b), as well as in other adolescent Neanderthals from El Sidrón cave (Estalrrich et al., 2017b). As it has been previously demonstrated (Hlusko, 2003; Bouchneb and Maureille, 2004; Estalrrich et al., 2017b), grass stalks were the material used to clean the interproximal spaces, leaving the microstriations behind, and, with time, developing into a deep groove. Our results indicate that the need for teeth cleaning was a well-established habit in human behavior since childhood, and that grass stalks were presumably used for probing purposes.

Cultural or instrumental striations have been identified on both dI^1s from the Transitional Aurignacian Level 18b from El Castillo and the Mousterian Level IV from Axlor. Since this tooth type is the only one belonging to the anterior dentition found on the sample, and cultural striations appear mainly on the anterior dentition, this result is not surprising. As indicated above, cultural striations appear on both fossil and extant humans, allowing a common etiology ('stuff-and-cut'; Molnar, 1972). For this reason, these striations can also be used as a proxy for the identification of handedness in fossil individuals (Bermúdez de Castro et al., 1988; Lalueza-Fox and Frayer, 1997; Lozano-Ruíz et al., 2004; Lozano et al., 2008, 2017; Volpato et al., 2012; Estalrrich and Rosas, 2013; Frayer et al., 2016). The presence of a majority of right-oblique oriented striations is characteristic of right-handed individuals, so it is highly probable that both the Mousterian and Transitional Aurignacian children were also right-handed individuals. According to their estimated age at death between 4.5 and 6.5 years old (following AlQahtani et al., 2010), the ontogenetic development for handedness of these individuals matches the modern children's pattern: manual laterality preference, when performing complex tasks and bimanual actions, appears around four years of age (Sacrey et al., 2012) and it is set around seven years of age (Fennell, 1986). If we consider these two individuals as Neanderthals, the results of handedness fall perfectly within the estimated right-handedness frequency for Neanderthals, with a 93% (Uomini, 2011; Volpato et al., 2012; Estalrrich and Rosas, 2013). They further corroborate the shared ontogenetic development of handedness with modern humans, implying its plausible presence in their common ancestor (Frayer et al., 2012).

Subvertical grooves on the interproximal contact facets have also been recovered. This trait is frequent in Neanderthals and archaic *Homo* (Villa and Giacobini, 1995; Poisson et al., 2002; Egocheaga et al., 2004; Estalrrich et al., 2011; Dąbrowski et al., 2013; Sarig et al., 2016). Since the etiology of these traits seems to be multifunctional (food properties, use of the mouth as a third hand, mesial drift of the teeth or microstructure of the tooth enamel), we cannot be confident about its implications for understanding fossil human behavior. However, it is remarkable that few examples of subvertical grooves have been reported for AMH populations (Villa and Giacobini, 1995) and in early *H. sapiens* from Qafzeh (Vandermeersch, 1981) and Qesem Cave (Sarig et al., 2016). It is noteworthy that our results come from only juvenile individuals and their deciduous teeth. Besides informing us on the presence of this trait during the Mousterian and Magdalenian in Northern Spain, it is the first time subvertical grooves have been reported for the deciduous dentition, which has the potential to provide clues about their origin and significance for the study of human behavior, as they appear in both Neanderthals and anatomically modern humans both permanent and deciduous teeth.

To sum up, we have identified a large number of non-masticatory dental wear traits on the child and juvenile individuals here studied, who present the same features of activity-related dental wear as adults (Molnar, 1972; Merbs, 1983; Lukacs and Pastor, 1988; Molleson, 1994; Belcastro et al., 2004; Lozano-Ruíz et al., 2004; Scott and Jolie, 2008; Lozano et al., 2008; Lorkiewicz, 2011; Molnar, 2011; d'Incau et al., 2012; Estalrrich and Rosas, 2013, 2015; Willman, 2016; Estalrrich et al., 2017b) and subadults (including infants, children, juveniles and adolescents; Lozano-Ruíz et al., 2004; Estalrrich and Rosas 2013, 2015), both from the Middle and Upper Paleolithic previously described by the above cited authors.

It has been documented that to become proficient and independent hunters and gatherers, children (even from a young age) from modern hunter-gatherer societies learn the skills and knowledge from the adults, adolescents and older children of the group, and even participate in group activities (Bogin, 1999; Marlowe, 2005; Hewlett et al., 2011; Lew-Levy et al., 2017). Thus, in light of the evidence, it is possible that the Middle and Upper Paleolithic children from the Cantabria region also participated in the group activities to acquire the olders' skills which might have been a guarantee for them to be integrated and also, cover their own living and feeding necessities.

5. Conclusions

The analysis of non-masticatory dental wear on 12 deciduous teeth belonging to eight individuals from the Mousterian to the Magdalenian technocultural contexts in the Cantabrian region has provided insight into the behavior of these individuals. Chipped enamel is the only trait present along the complete chronological sequence and appears on the deciduous premolars indicating that these young individuals were exposed to strong occlusal forces, included grit particles within their food, or both. Subvertical grooves on the interproximal facets appear on deciduous teeth, on Neanderthal individuals from the Mousterian and AMH from the Magdalenian. Toothpicking grooves appear on a Neanderthal children from Axlor and on the Magdalenian individuals from Santa Catalina and Tito Bustillo sites, indicating that teeth cleaning was a common task, probably using grass stalks as probing material. Cultural striations from the Transitional-Aurignacian juvenile from El Castillo and the Mousterian child from Axlor indicate the use of small sharp material for the preparation of food or other items, as well as a preferential use of the right hand to perform such activities, as previously reported for Neanderthal individuals (both adult and immature).

Our results indicate that the children and juvenile individuals studied herein present the same activity-related dental wear features as those reported for adult *H. sapiens* and *H. neanderthalensis*, and also similar to those of Middle Pleistocene humans (Lozano et al., 2008; Sun et al., 2014), despite the known differences between the deciduous and permanent enamel. In addition, the characteristics of their non-masticatory dental wear (low number and small features) suggest that these children and juveniles could have been learning the proficient skills. If that is the case, the length of learning could have spanned at least childhood and juvenility, a similar length in learning process as in modern hunter-gatherers. And, thus, their role within the group could be extrapolated as similar: learning from more experienced individuals from the group to become skilled performers.

Declaration of competing interest

The authors have no competing interests to declare.

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