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Morphological and morphometric study of the hominin dental casts from Grotta-Riparo di Uluzzo C (Apulia, southern Italy)

Francesca Seghi[1] | Rita Sorrentino[2] | Shara E. Bailey[3] | Erica Piccirilli[1] | Antonino Vazzana[1] | Eugenio Bortolini[1] | Owen A. Higgins[1,4] | Giulia Marciani[1,5] | Medica A. Orlando[6] | Enza E. Spinapolice[7] | Adriana Moroni[5,8] | Stefano Benazzi[1]

[1]Department of Cultural Heritage, University of Bologna, Ravenna, Italy
[2]Department of Biological, Geological and Environmental Sciences, University of Bologna, Bologna, Italy
[3]Department of Anthropology, Center for the Study of Human Origins, New York University, New York, USA
[4]Department of Odontostomatological and Maxillofacial Sciences, University of Rome "La Sapienza", Rome, Italy
[5]Department of Physical Sciences, Earth and Environment, R.U. of Prehistory and Anthropology, University of Siena, Siena, Italy
[6]Museo Civico di Paleontologia e Paletnologia "Decio de Lorentiis", Maglie, Lecce, Italy
[7]Department of Ancient World Studies, University of Rome "La Sapienza", Rome, Italy
[8]Centro Studi sul Quaternario, Sansepolcro, Arezzo, Italy

Correspondence
Francesca Seghi, Department of Cultural Heritage, University of Bologna, Via degli Ariani 1, 48121 Ravenna, Italy.
Email: francesca.seghi2@unibo.it

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Abstract

Objectives: Grotta-Riparo di Uluzzo C (Apulia, southern Italy) is a pivotal site for investigating the evolution of the Middle Paleolithic and the earliest phases of the Upper Paleolithic in southern Italy, as the extensive stratigraphic record of this site includes a thick Mousterian sequence followed by the Uluzzian. Here, we investigate the taxonomic affinity of seven unpublished deciduous human teeth retrieved from the site of Uluzzo C in 1960.

Materials and Methods: The teeth are represented by seven plaster dental casts, which are housed at the Museo Civico di Paleontologia e Paletnologia in Maglie (Lecce, Apulia). The location of the original specimens remains unknown, rendering these casts the only human remains evidence yielded by Uluzzo C to date. Based on occlusal-view photographs and digital models of the casts, we examined the external morphology and morphometry of the teeth, comparing them to *Homo sapiens* and *H. neanderthalensis* samples. Through geometric morphometric methods and statistical analyses, we analyzed the crown outline of the deciduous molars.

Results: The teeth show morphological and morphometric features that are variably found in *H. neanderthalensis*, *H. sapiens*, or both. Specifically, crown outline analysis shows that all molars fall within *H. neanderthalensis* variability, except for Uluzzo 853 (lower right deciduous first molar), which falls within *H. sapiens* variability.

Discussion: This study provides the first taxonomic assessment of the hominin teeth from Uluzzo C. The results contribute additional insights into the Paleolithic peopling of southern Italy during a crucial period marked by the persistence of post-Tyrrhenian Neanderthal techno-complexes and the arrival of *H. sapiens*.

KEYWORDS
dental casts, geometric morphometrics, *Homo sapiens*, Neanderthal

1 | INTRODUCTION

Southern Italy has yielded few, albeit very important, fossil remains attributable to *H. neanderthalensis* (hereafter: Neanderthal) and *H. sapiens* dating to the crucial period between 45 and 40 ka BP (MIS3). This period marks the phase in which the two human groups coexisted in Europe, before the final demise of Neanderthals around 40 ka years ago (Benazzi et al., 2015; Benazzi, Douka, et al., 2011; Douka et al., 2014; Higham et al., 2014; Hublin et al., 2020; Marciani et al., 2020). Currently remains exclusively consist of deciduous teeth from the sites of Grotta del Cavallo, in Apulia (one tooth from Mousterian and two teeth from Uluzzian deposits; Benazzi, Douka, et al., 2011; Fabbri et al., 2016; Moroni et al., 2018; Palma di Cesnola & Messeri, 1967) and Roccia San Sebastiano, in Campania (one tooth from Mousterian and one tooth from Uluzzian deposits; Oxilia et al., 2022). These and other southern sites (e.g., Grotta-Riparo di Uluzzo C, Grotta Bernardini, Serra Cicora, Grotta di Castelcivita, and Grotta della Cala) are crucial for understanding the replacement of Neanderthals by *H. sapiens* in Italy between 45 and 40 ka BP, as they document this phase based on both cultural and/or anthropological evidence (Arrighi et al., 2020; Benini, Boscato, & Gambassini, 1997; Gambassini, 1997; Marciani et al., 2020; Martini et al., 2018; Spinapolice et al., 2022).

In addition to the extraordinary discovery in Apulia of the famous "Uomo di Altamura," more than 130 ka years old (Profico et al., 2023), other sites in southern Italy that have yielded Neanderthal remains are: Grotta di Santa Croce (a femur; Mallegni et al., 1987), Fondo Cattie (one tooth; Borgognini Tarli, 1983), and Grotta delle Tre Porte (one tooth; Benazzi et al., 2013; Blanc, 1961) in Apulia; Archi (a juvenile mandible; Mallegni & Trinkaus, 1997) in Calabria; Grotta del Poggio (a tooth; Messeri, 1975), Grotta Taddeo (four teeth; Benazzi, Viola, et al., 2011; Messeri & Palma di Cesnola, 1976), and Riparo del Molare (a juvenile mandible; Mallegni & Ronchitelli, 1989) in Campania. Some of these sites are fundamental for reconstructing the Middle Paleolithic culture in the Mediterranean area, as they show multi-layered anthropic deposits from MIS6 (i.e., Grotta del Poggio; Gambassini, 1995) and post-Tyrrhenian MIS5 (i.e., Grotta del Cavallo, Riparo del Molare; Boscato et al., 2002; Zanchetta et al., 2020). These deposits attest to significant cultural changes including the introduction of new technological production strategies, such as the Levallois (Carmignani et al., 2021).

Such findings testify to the presence of Neanderthals in southern Italy from at least 130 ka years ago until the arrival of *H. sapiens* around 44–43 ka (Douka et al., 2014). Considering Grotta del Cavallo (Nardò, Lecce, Apulia), where the Uluzzian techno-complex was described for the first time by Palma di Cesnola (Palma di Cesnola, 1965, 1966, 1993), anthropological evidence clearly attests to the transition between Neanderthals and *H. sapiens*. Indeed, in this site, an incisor from the latest Mousterian deposit was attributed to a Neanderthal individual (Fabbri et al., 2016), while the two deciduous molars found in the earliest Uluzzian layers were attributed to *H. sapiens* (Benazzi, Douka, et al., 2011).

Grotta-Riparo di Uluzzo C (Nardò, Lecce, Apulia), located in Uluzzo Bay, very close to Grotta del Cavallo (Figure 1a,b), has been documented for its stratigraphic sequence, lithic assemblages and faunal remains, which were excavated between 1964 and 1966, and 2015 and 2018 (Borzatti von Löwenstern, 1963, 1964, 1965; Borzatti von Löwenstern & Magaldi, 1966; Silvestrini et al., 2022; Spinapolice

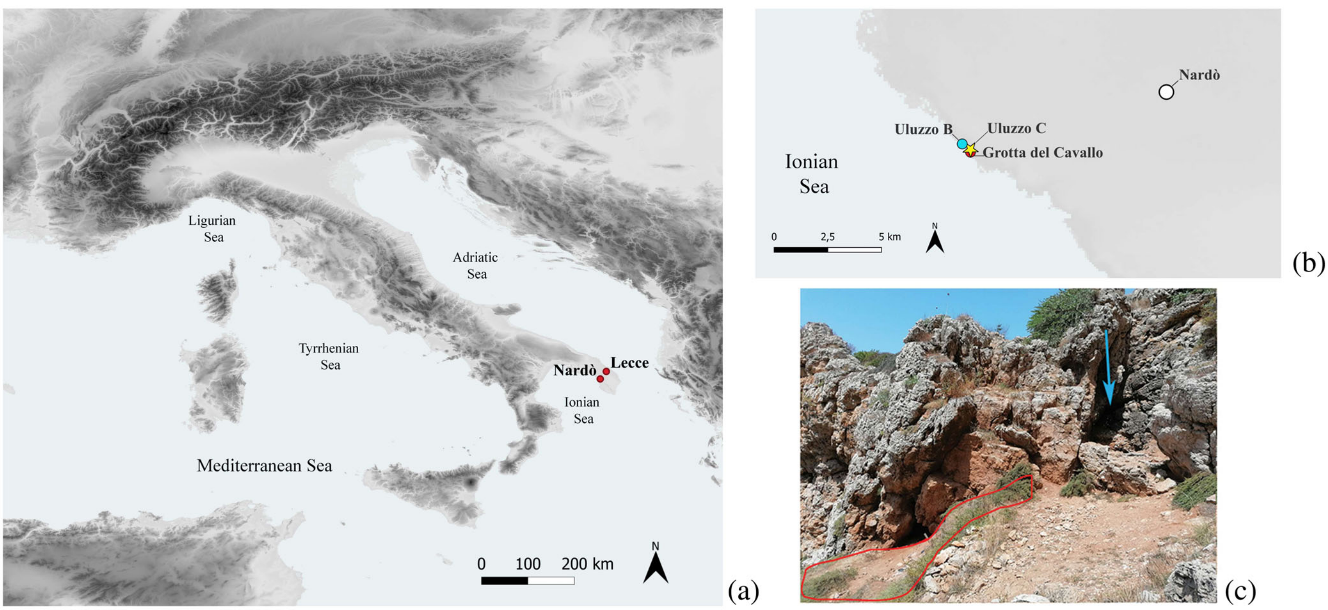


FIGURE 1 Grotta-Riparo di Uluzzo C. (a) Map of Italy with Nardò (Apulia) highlighted by the red dot. (b) Detailed view of Uluzzo Bay with the three sites described by Carlo Cosma: Grotta del Cavallo (red dot), Grotta-Riparo di Uluzzo C (yellow star), and Grotta di Uluzzo B (blue dot). (c) The external deposit is highlighted by the red line. The inner cave is highlighted by the blue arrow. Map was created with QGIS 3.36 and raster files were obtained from Jarvis et al. (2008).

et al., 2022). Recent reassessment of the faunal and lithic material from this site led to the rediscovery of the casts of seven human tooth crowns at the Museo Civico di Paleontologia e Paletnologia "Decio De Lorentiis" in Maglie (Lecce, Apulia). The original teeth were found in 1960 in the deposit of the shelter (Figure 1c; Cosma, 1960). The complex and, in some respects, mysterious history of these teeth is described in detail below. The aim of this study is to analyze the size and shape of these dental remains using the available casts to assess the minimum number of individuals (MNI) and their taxonomic attribution to either *H. sapiens* or Neanderthal.

1.1 | Grotta-Riparo di Uluzzo C and the research history

Grotta-Riparo di Uluzzo C (also called "Grotta Cosma," after the name of its discoverer) is located in Uluzzo Bay, on the Ionian coast (Nardò, Lecce, Apulia, southeastern Italy), about 15 m above sea level.

The site was visited and formally described for the first time by Carlo Cosma (a member of the Gruppo Speleologico Salentino) in 1960. Stratigraphic excavations started in 1964 by the Istituto Italiano di Preistoria e Protostoria (IIPP), under the scientific direction of Prof. Edoardo Borzatti von Löwenstern (Borzatti von Löwenstern, 1963, 1964, 1965; Borzatti von Löwenstern & Magaldi, 1966) and they continued until 1966. Since 2015, the site has been the subject of reinvestigation involving the Universities of Bologna and Roma "La Sapienza." Currently, the site consists of a narrow central hall (the present cave) with a smaller cavity on the right side (Silvestrini et al., 2022; Spinapolice et al., 2022) and of an adjacent shelter (Figure 1c). The cave and the shelter were originally part of a much larger cavity, the vault of which is now almost completely collapsed. Professor Edoardo Borzatti von Löwenstern carried out the excavations in the central hall. The deposit includes a ca. 6.40 m thick continental sequence lying atop a marine deposit (layer L). The continental succession identified by Borzatti von Löwenstern includes (in stratigraphic order): a thick Mousterian sequence (spits 21–6 corresponding to layers H–E) followed, after a discontinuous thin layer of volcanic sediments (layer γ), by the Uluzzian (layers D–C) and Romanellian occupations (layer A), which are separated from each other by sterile sediments (layer B), with the latter containing a basal layer of pomiceous sand (layer β). At the very top of the sequence there is also evidence of a disturbed Bronze Age occupation (Figure 2; Borzatti

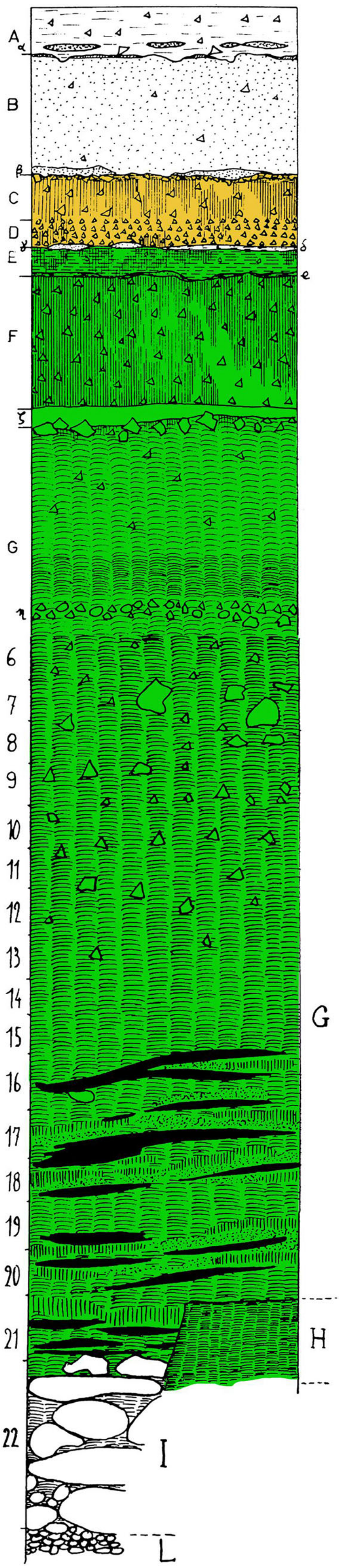
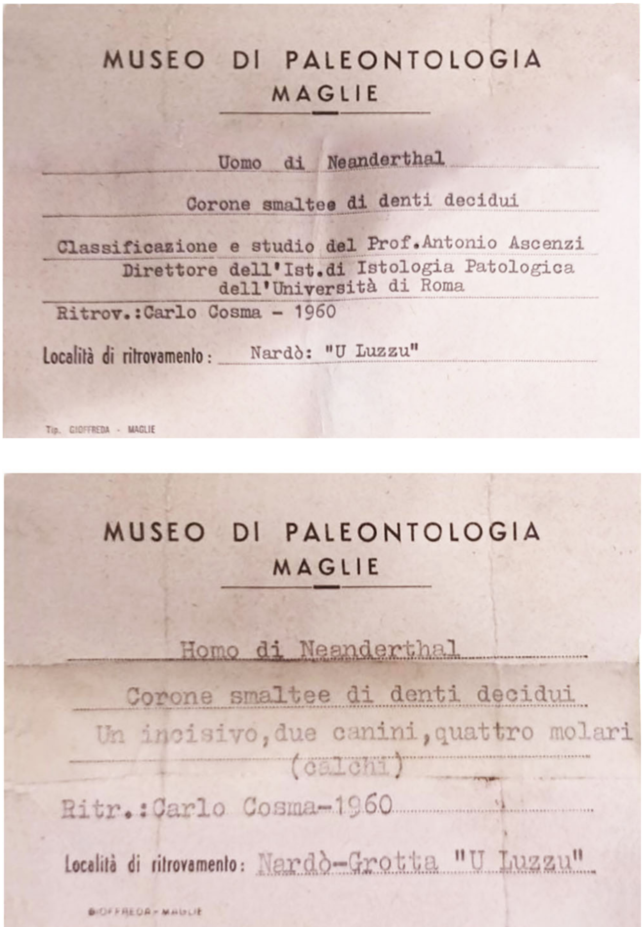


FIGURE 2 Stratigraphic sequence of Grotta-Riparo di Uluzzo C: A, Romanellian; B, sterile; C–D, Uluzzian (in yellow); E, Mousterian with some Uluzzian inclusions; F–H, Mousterian (in green); I, large rock blocks smoothed by wave motion and showing traces of bioerosion (lithodomes); and L, cemented marine beach (modified after Borzatti von Löwenstern, 1965, Borzatti von Lowerstern, 1966).


MUSEO DI PALEONTOLOGIA
MAGLIE
Uomo di Neanderthal
Corone smaltee di denti decidui
Classificazione e studio del Prof.Antonio Ascenzi
Direttore dell'Ist.di Istologia Patologica
dell'Università di Roma
Ritrov.:Carlo Cosma - 1960
Località di ritrovamento: Nardò: "U Luzzu"
Tip. CIOFFREDA - MAGLIE

MUSEO DI PALEONTOLOGIA
MAGLIE
Homo di Neanderthal
Corone smaltee di denti decidui
Un incisivo,due canini,quattro molari
(calchi)
Ritr.:Carlo Cosma-1960
Località di ritrovamento: Nardò-Grotta "U Luzzu"
CIOFFREDA - MAGLIE

FIGURE 3 Original tags found with the dental casts housed at the Museo Civico di Paleontologia e Paletnologia "Decio de Lorentiis", Maglie (Lecce), Italy.

von Löwenstern, 1965; Borzatti von Löwenstern & Magaldi, 1966). The continental deposit directly rests on a layer (layer I) of large limestone rock blocks smoothed by wave motion and exhibiting signs of bioerosion (lithodomes). This layer, in turn, overlies a cemented marine beach (layer L). During recent research, optically stimulated luminescence (OSL) dating was obtained from Mousterian layers F and G (46 ± 4.0 ka and 42 ± 2.7 ka, respectively), and Uluzzian layers C and D (42.7 ± 2.6 ka and 38.1 ± 2.2 ka, respectively). OSL and C^{14} dating are also available from layer B (OSL 22.4 ± 2 ka and C^{14} 25.310 ± 77 BP; Spinapolice et al., 2022). There is, instead, no absolute chronology for the lowermost Mousterian layers (spits 21–6). So far, the only points of reference for spits 21–6 are the U/Th dates obtained from the nearby Grotta del Cavallo, where the base of layer M, overlying a deposit fully comparable with layers I and L of Uluzzo C, is dated to 116 ± 0.7 ka and 117 ± 0.7 ka. This provides a post-Tyrrhenian chronology for the entire Mousterian occupation of Grotta del Cavallo (Zanchetta et al., 2020; for a different view see Sarti & Martini, 2020) and most probably also of Uluzzo C.

At Uluzzo C, an external deposit characterized by the same stratigraphic sequence as the cave is present in the shelter. The surface of this deposit is sloping toward the sea, possibly because it was washed-out over time. However, the remaining layers appear to be *in situ* and the seven human teeth described in this study were discovered by Carlo Cosma at the very top of this external deposit, together with a large quantity of Mousterian artifacts, during his survey of Uluzzo Bay in 1960. In his 1960 report, Cosma clearly described the karstic cavities he visited, which were later named Uluzzo A (Grotta del Cavallo), Uluzzo C (Grotta-Riparo di Uluzzo C or Grotta Cosma), and Uluzzo B (Grotta di Uluzzo) by Prof. Arturo Palma di Cesnola and Prof. Edoardo Borzatti von Löwenstern (Palma di Cesnola, 1961). This description (Cosma, 1960) shows that lithic artifacts, bones, and *"six distinctly human teeth"* were recovered from the external deposit of Uluzzo C (Figure 1c; Translated from Italian into English).

The details provided by Cosma refer to the site of Uluzzo C, and in particular to its external deposit (Figure 1c). In 1960, Cosma hypothesized that the teeth could be attributed to a Neanderthal individual and suggested their transfer to the Istituto Italiano di Paleontologia Umana for study. Today, the location of the original teeth is unknown, and only the casts of the human tooth crowns, housed at the Museo Civico di Paleontologia e Paletnologia "Decio De Lorentiis" in Maglie (Lecce, Apulia), are available. These were rediscovered during the revision of the whole set of materials from past excavations carried out at Uluzzo C. The casts undoubtedly represent the teeth found by Carlo Cosma, as they were found associated with their original tags indicating the name of the discoverer, the place and year of discovery, and a brief description (Figure 3). It should be noted that there are seven tooth casts, as opposed to the six teeth that are mentioned in Cosma's text. Unfortunately, we have not found any information in the literature that could explain this discrepancy. It must be highlighted that the exact layer in which the teeth were retrieved is unknown, and we are unable to ascribe even an approximate relative age to these remains as they could come from any of the layers of the Uluzzo C deposit. However, their age can be reasonably circumscribed between MIS5d-MIS3 (around 117 and 40 ka). In addition, based on Cosma's description of the finds, we are confident that future fieldwork research will help to further circumscribe their stratigraphic provenance.

2 | MATERIALS AND METHODS

2.1 | The dental plaster casts

The seven plaster casts of the human tooth crowns housed at the Museo Civico di Paleontologia e Paletnologia "Decio de Lorentiis" in Maglie are the subjects of the present study. Although working with casts differs from working on real teeth due to potential shrinkage over time, it has been shown that the size differences between plaster casts and real teeth are negligible (Bailey & Tryon, 2023; Hubbard et al., 2022). Moreover, although the casts were made after 1960 (when the original teeth were discovered by Cosma), they were made with great attention to anatomical details to closely replicate the original teeth. The pursuit of reliability as study materials is further evidenced by the precision with which each cast was painted in a brown shade, paying particular attention to nuances in cavities and depressions, adding further levels of accuracy to the replication process (Figure 4). Unfortunately, in some cases, the casts do not allow us to

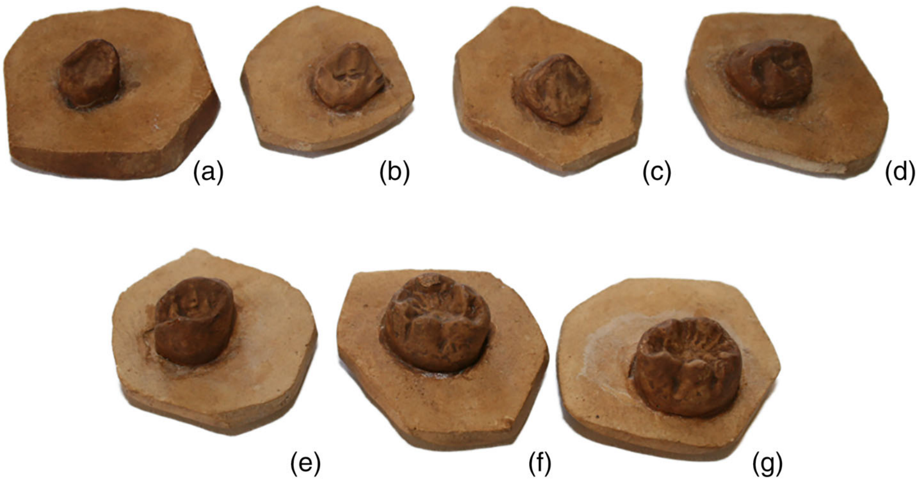


FIGURE 4 Dental plaster casts of Uluzzo C housed at the Museo Civico di Paleontologia e Paletnologia "Decio De Lorentiis" in Maglie (Lecce, Apulia): Uluzzo 850 (a), Uluzzo 851 (b), Uluzzo 852 (c), Uluzzo 853 (d), Uluzzo 854 (e), Uluzzo 855 (f), and Uluzzo 856 (g).

determine if the entire crown was formed (e.g., the upper lateral incisor, see Section 3.1 for more information), which limits the accuracy of any age estimates.

2.2 | Virtual acquisition and optimization of the dental casts

The virtual acquisition of the seven casts was performed at the Museo Civico di Paleontologia e Paletnologia "Decio De Lorentiis" in Maglie using a high-resolution 3D blue light handled scanner Artec Space Spider (Artec 3D, San Diego, California, USA). The casts were scanned with a resolution of 0.1 mm, a 3D point accuracy of 0.05 mm and a 3D accuracy over distance of 0.05 mm + 0.3 mm/m, a volume capture zone of 2.000 cm^3, a linear field of view HxW of 90 × 70 mm (closest range) and 180 × 140 mm (furthest range), and an angular field of view HxW of 30 × 21°. The texture resolution is 1.3 mp with a data acquisition speed of 1 mLn points/s and a 3D exposure time of 0.0002 s. The 3D models of the dental casts were then optimized in Geomagic Design X (3D Systems Software, Rock Hill, South Carolina, US) to refine the triangles in the edges, close the holes in the surfaces, and remove the plaster cast bases.

2.3 | Dental morphology

First, the tooth class of each specimen was identified (Hillson, 1996). The description of the crown morphology was based on the original casts, high-resolution occlusal images, and digital models. The assessment of non-metric trait expression is based on Hanihara (1961), the Arizona State University Dental Anthropology System (ASUDAS; Turner II et al., 1991), Bailey and Hublin (2006), Bailey et al. (2011), Harvati et al. (2015), Tillier (1979) and Toussaint et al. (2010). In addition to comparisons with data in the literature, unpublished data recorded on Neanderthals (N), early *H. sapiens* (EHS), Upper Paleolithic *H. sapiens* (UPHS), and recent *H. sapiens* (RHS) deciduous teeth were also evaluated (Bailey, unpublished data). The list of the individuals used in the comparative samples is shown in Table S1.

2.4 | Metric comparison

Maximum mesiodistal (MD) and buccolingual (BL) crown diameters were measured directly from the digital models in Geomagic Design X (3D Systems Software, Rock Hill, South Carolina, US). These measurements were compared to those of N, EHS, UPHS, and RHS, obtained from literature (Arnaud et al., 2016; Bailey & Hublin, 2006; Becam & Chevalier, 2018; Benazzi, Fornai, et al., 2011; Bermúdez de Castro et al., 2017; Frayer, 1978; Hershkovitz et al., 2016; Riga et al., 2018; Romandini et al., 2020; Toro-Moyano et al., 2013; Zanolli et al., 2012).

2.5 | Geometric morphometrics and statistical analyses

The geometric morphometrics (GM) analysis of the crown outlines was carried out following published protocols (Bailey et al., 2016; Bailey et al., 2020; Benazzi, Douka, et al., 2011; Benazzi et al., 2012). Each digital model was aligned and rotated in Geomagic Design X (3D Systems Software, Rock Hill, South Carolina, USA), with the cervical plane parallel to the xy-plane of the Cartesian coordinate system and rotated around the *z*-axis, in order to have the lingual aspect parallel to the *x*-axis. Once each digital model was oriented, the crown outline was extracted and saved as an .igs file. The teeth from the right side were mirror-imaged, because the teeth in our comparative sample were either from the left side or mirror-imaged to represent the left side. The extracted crown outline of each tooth was centered on its centroid in Rhinoceros v.5 (Robert McNeel & Associates, Seattle, WA). The outline was subdivided by 24 pseudo landmarks, obtained from the same number of equiangularly spaced radial vectors originating from the centroid. The first radius was buccally directed and oriented parallel to the *y*-axis. This led to the formation of pseudo landmarks scaled to the unit centroid size, which became the Procrustes shape coordinates used to explore shape variation through principal component analysis (PCA; Bailey et al., 2016, Bailey et al., 2020; Benazzi, Douka, et al., 2011; Benazzi et al., 2012). Crown outlines were projected into the shape-spaces of our comparative samples consisting of N, EHS, UPHS, and RHS from published (Bailey

TABLE 1 Number of teeth in the Uluzzo C sample and in the comparative samples used for the crown outline analysis.

Specimen	dm_1 [a]	dm^1 [b]	dm_2 [c]
Uluzzo	1	1	2
RHS	103	15	58
UPHS	9	5	16
EHS	4	-	5
N	15	8	23

Abbreviations: dm_1, lower deciduous first molar; dm^1, upper deciduous first molar; dm_2, lower deciduous second molar; EHS, early *Homo sapiens*; N, Neanderthal; RHS, recent *Homo sapiens*; UPHS, Upper Paleolithic *Homo sapiens*.

[a]Compared with published (Bailey et al., 2020) and unpublished sources.

[b]Compared with published (Benazzi, Douka, et al., 2011) and unpublished sources.

[c]Compared with published (Bailey et al., 2016 and Benazzi et al., 2012 updated with Lugli et al., 2022) and unpublished sources.

et al., 2020; Benazzi, Douka, et al., 2011; Bailey et al., 2016 and Benazzi et al., 2012 updated with Lugli et al., 2022) and unpublished sources. The list of the individuals used in the comparative samples is shown in Table 1 and Tables S2–S4. A permutation test (R package Morpho v. 2) was performed using the first three principal components (PCs) ($N = 10.000$) on the comparative samples (excluding Uluzzo C teeth) to identify differences in crown shapes that are potentially significant ($p < 0.05$) between groups. Several Shapiro–Wilk tests were carried out to investigate the normality of the distribution of the Procrustes shape coordinates for each group in the comparative sample, ensuring compliance with the assumption necessary for linear discriminant analysis (LDA). Because the assumption of normality of variance was violated, the "leave-one-out" cross-validation quadratic discriminant analysis (QDA) was performed to investigate the probability of discriminating Neanderthal and *H. sapiens* groups, based on the crown outline and to derive posterior probabilities (P_{post}) of taxonomic attribution of the Uluzzo C deciduous molars to one of these groups. In the QDA analysis EHS was excluded due to its small sample size. For the QDA, we used a different number of PCs for each tooth, selecting the minimum number of combination of variables describing the highest variance within the range of 70%–90% of variation (Bailey et al., 2020; Jolliffe, 2002). The data were processed and analyzed in R v. 4.1.2 (R Development Core Team, 2021).

3 | RESULTS

3.1 | Morphological description

Based on the assessment of the crown morphology (Figure 5; Table 2), we determined that all teeth are deciduous and represent one incisor, two canines, and four deciduous molars. The dental classes assigned to each specimen are as follows: Uluzzo 850-Rdi^2, Uluzzo 851-Rdc^1, Uluzzo 852-Ldc^1, Uluzzo 853-Rdm_1, Uluzzo 854-Rdm^1, Uluzzo 855-Rdm_2, and Uluzzo 856-Ldm_2. Despite their high quality, only the crowns were cast. Therefore, it was not possible to assess age at death beyond the age of crown formation. It appears that most of tooth crowns were completely developed. However, it is important to note that the cervix is not preserved in any of the casts. As a result of this missing information, in at least one case (Uluzzo 850-Rdi^2) the crown could be either complete or at an intermediate stage between crown ¾ and crown complete. The sharp cusp tips suggest that the crowns either were not in functional occlusion or were only in functional occlusion for a short time before the death of the individual.

Uluzzo 850 is an upper right deciduous lateral (second) incisor (Rdi^2). The crown is somewhat asymmetrical, with the mesial edge higher and shorter than the distal edge. The lingual surface exhibits weak shoveling (Grade 2). The mesial marginal ridge is moderately developed while the distal marginal ridge is weak. The crown exhibits strong labial convexity (Grade 4). No tuberculum dentale is present.

Uluzzo 851 is an upper right deciduous canine (Rdc^1). It shows shoveling (Grade 2) and the mesial and distal marginal ridges merge into a moderately developed cingulum. The crown is weakly asymmetrical with a mesial edge slightly shorter than the distal one.

Uluzzo 852 is an upper left deciduous canine (Ldc^1). Like its antimere, the crown is weakly asymmetrical and it shows shoveling (Grade 2). Unlike the Rdc^1, the mesial and distal marginal ridges do not extend to the basal cingulum.

Uluzzo 853 is a lower right deciduous first molar (Rdm_1). The protoconid and metaconid are connected by their essential ridges to form a continuous transverse crest. The well-developed mesial marginal ridge, together with the transverse crest, define a deep and wide anterior fovea. The metaconid is nearly as high as the protoconid, while the two distal cusps are low. The distobuccal cusp (hyponconid) is larger than the distolingual (entonconid) cusp. There is no tuberculum molare. The lingual aspect is straight, while the buccal aspect bulges considerably. The cusps are internally placed, well-developed and appear to be unworn.

Uluzzo 854 is an upper right deciduous first molar (Rdm^1). The mesiobuccal aspect shows a moderate tuberculum molare. The cusps appear internally placed. The protocone is slightly lower than the paracone. There is also an incipient metacone (grade 3 M1). This is indicated by a weak occlusal ridge connecting the distal portion of the paracone to the protocone. No groove or furrow defining a hypocone is present. In occlusal view the crown is trapezoidal, narrower distally than mesially. A weak mesial marginal ridge and an open distal fovea are present.

Uluzzo 855 is a lower right deciduous second molar (Rdm_2). The crown is ovoid in occlusal view and is slightly wider distally than mesially. The five main cusps are well-developed and no accessory cusps (C6 or C7) are present. The cusp tips appear unworn and internally placed. The protoconid and metaconid are joined by a low but continuous middle trigonid crest (MTC; Grade 2). The MTC and mesial marginal ridge circumscribe a wide anterior fovea (Grade 3). No distal trigonid crest is observed. The buccal grooves separating protoconid from entoconid and entoconid from hypoconulid are deep and extend one-third to one-half the crown height.

Uluzzo 856 is a lower left deciduous second molar (Ldm_2). Like its antimere, only five main cusps are present. They are well-developed

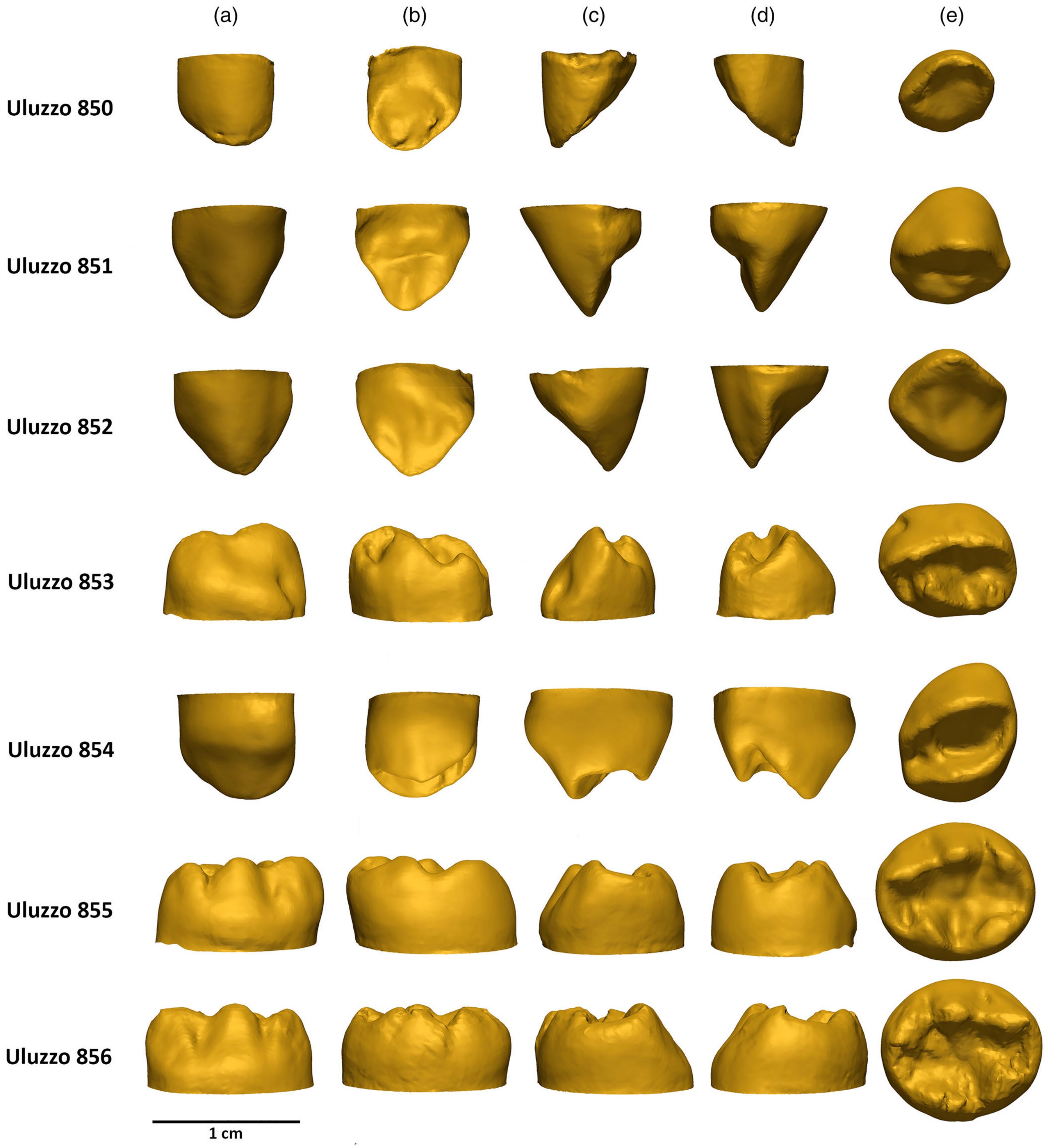


FIGURE 5 Teeth from Uluzzo C in labial/buccal (a), lingual (b), mesial (c), distal (d), and occlusal (e) views. Uluzzo 850-Rdi^2, Uluzzo 851-Rdc^1, Uluzzo 852-Ldc^1, Uluzzo 853-Rdm$_1$, Uluzzo 854-Rdm^1, Uluzzo 855-Rdm$_2$, and Uluzzo 856-Ldm$_2$. Scale bar: 1 cm.

and internally placed. The cusp tips appear to be unworn. The moderately developed mesial marginal ridge and weak MTC (Grade 1) circumscribe a wide anterior fovea (Grade 3). No distal trigonid crest is present. The entoconid may have had a split/doubled dentine horn or this morphology could be the result of an artifact during the making of the cast.

3.2 | Metric comparison

Table 3 presents the MD and BL diameters of the teeth of Uluzzo C and the comparative samples. In general, the dimensions of all teeth from Uluzzo C fall within the N ranges. However, overlap can be seen as some teeth also fall within the EHS (Uluzzo 851, 852, 853, 855,

TABLE 2 Dental morphological traits observed in the teeth of Uluzzo C compared to fossil and recent human groups (Bailey, unpublished data).

Non-metric dental traits	Uluzzo	N % presence (*n*)	EHS % presence (*n*)	UPHS % presence (*n*)	RHS % presence (*n*)
di^2 shovel (grade 2+)	P	100 (7)	-	0 (1)	32 (50)
di^2 convexity (grade 2+)	P	100 (7)	100 (2)	100 (1)	44.2 (52)
dc^1 shovel (grade 2+)	P	100 (5)	-	-	57.6 (66)
dc^1 distal accessory ridge (grade 2+)	A	0 (4)	-	-	1.8 (56)
dm^1 distal trigonid crest (any presence)	P	92.9 (14)	100 (4)	71.4 (7)	68.5 (54)
dm^1 hypocone (grade 4- or 4)	A	66.7 (12)	100 (4)	33.3 (9)	22.3 (121)
dm^1 tuberculum molare (moderate)	P	92.9 (14)	60 (5)	66.7 (9)	63.8 (152)
dm_1 tuberculum molare (moderate)	A	37.5 (8)	25 (4)	16.7 (6)	7.7 (130)
dm_1 transverse crest (continuous)	P	93.3 (15)	50 (6)	0 (11)	1.7 (121)
dm_1 anterior fovea (grade 2+)	P	92.9 (14)	66.7 (3)	41.7 (12)	74 (12)
dm_2 anterior fovea (grade 2+)	P	84.2 (19)	50 (4)	33.3 (12)	34.9 (106)
dm_2 middle trigonid crest (grade 2+)	P	78.9 (19)	50 (6)	8.3 (12)	3.8 (106)

Note: The symbol "-" indicates sample size is 0.
Abbreviations: A, absence; di^2, upper deciduous second incisor; dc^1, upper deciduous canine; dm^1, upper deciduous first molar; dm_1, lower deciduous first molar; dm_2, lower deciduous second molar; EHS, early *Homo sapiens*; N, Neanderthal; *n*, number of individuals in the comparative sample; P, presence; RHS, recent *Homo sapiens*; UPHS, Upper Paleolithic *Homo sapiens*.

and 856), UPHS (Uluzzo 853, 854, 855, and 856), and RHS (Uluzzo 854 and 855) ranges.

3.3 | Geometric morphometrics and statistical analyses

GM and statistical analyzes were performed on the deciduous molars of Uluzzo C (853-Rdm_1, 854-Rdm^1, 855-Rdm_2, and 856-Ldm_2).

Uluzzo 853-Rdm_1 Figure 6 illustrates the results of the shape-space PCA (PC1-PC2) for the dm_1. The first two PCs explain 50.1% of the total variance. The range of variation of RHS is wide and evenly distributed in all four quadrants of the PCA plot, overlapping with UPHS, EHS, and N. However, while the N group primarily clusters along the negative scores of PC1, the RHS group clusters more closely along the positive scores of PC1, which accounts for a rectangular crown outline shape, representing an asymmetrical shape of the crown with a pronounced talonid. Uluzzo 853 falls along negative scores of PC1, in an area covered by both RHS and N, owing to a trapezoidal crown outline shape, which is projected at the level of the protoconid. A permutation test ($N = 10.000$) carried out on the first three PCs (62.1% of the total variance) reveals significant differences between N and RHS ($p = 0.001$), RHS and UPHS ($p = 0.001$), N and UPHS ($p = 0.031$), and between UPHS and EHS ($p = 0.023$; see Table S5). Shapiro–Wilks test shows that RHS ($W = 0.96971$, $p < 0.05$) group is non-normally distributed, while UPHS ($W = 0.9338$, $p > 0.05$), N ($W = 0.91025$, $p > 0.05$), and EHS ($W = 0.99054$, $p > 0.05$) groups are normally distributed; therefore, the QDA was used instead of the LDA. The QDA based on the first six PCs (86.2% of the total variance) distinguishes N, RHS, and UPHS (RHS and UPHS not grouped together, EHS were excluded due to the small sample size) with an accuracy of 74.6%, and Uluzzo 853 is classified as RHS with a probability of nearly 100% (Table 4).

Uluzzo 854-Rdm^1 Figure 7 illustrates the results of the shape-space PCA (PC1-PC2) of the dm^1. The first two PCs explain 69.4% of the total variance. RHS specimens fall mainly on the left side of PC1, with negative scores. PC1 describes a buccolingually elongated shape with convex mesial and distal aspects. N are mainly distributed along the right of PC1 with positive scores, representing a triangular crown shape with a buccally expanded paracone. Uluzzo 854 falls outside the range of variability observed in RHS, UPHS, and N. Nevertheless, it is closer to N with negative scores of PC1 and PC2. PC2 is characterized by a significantly expanded paracone on the mesiobuccal surface, accompanied by a mesiolaterally expanded buccal region and a relatively reduced BL outline. A permutation test ($N = 10.000$) carried out on the first three PCs (81.1% of the total variance) reveals significant differences among all groups (N-RHS, $p = 0.001$, RHS-UPHS, $p = 0.013$, and N-UPHS, $p = 0.001$; see Table S6). Shapiro–Wilks test shows that RHS group ($W = 0.83837$, $p < 0.05$) is non-normally distributed, while UPHS ($W = 0.9898$, $p > 0.05$) and N ($W = 0.95532$, $p > 0.05$) groups are normally distributed; therefore, the QDA was used instead of the LDA. Table 4 shows the results of the QDA based on the first three PCs (81.1% of the total variance). The QDA distinguishes N from RHS and UPHS (RHS and UPHS not grouped together) with an accuracy classification of 67.9%, and Uluzzo 854 is classified as N with a probability of 85.1%.

Uluzzo 855-Rdm_2 and Uluzzo 856-Ldm_2 Figure 8 illustrates the results of the shape-space PCA (PC 1-PC2) of the left and right dm_2s. Uluzzo 855 was mirrored for comparison. The first two PCs explain 53.8% of the total variance. The RHS dm_2s are distributed in

TABLE 3 Mesiodistal (MD) and buccolingual (BL) crown diameters of the Uluzzo dental casts and comparative groups (in millimeter).

	di^2 (850)		dc^1 (851)		dc^1 (852)		dm_1 (853)		dm^1 (854)		dm_2 (855)		dm_2 (856)	
	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL
Uluzzo	6.8	6.08	7.97	8.23	8.07	7.6	9.61	7.94	7.91	9.56	11.19	9.89	11.17	10.31
N	6.43 (5.82–7.04)[a]	5.52 (5.09–5.95)[a]	7.59 (6.97–8.21)[c]	6.86 (6.32–7.4)[c]	7.59 (6.97–8.21)[c]	6.86 (6.32–7.4)[c]	8.83 (8.39–9.27)[a,i]	7.56 (7.09–8.03)[a,f,i]	7.9 (7.39–8.41)[j]	9.0 (8.59–9.41)[j]	10.4 (9.8–11)[j]	9.3 (8.83–9.77)[j]	10.4 (9.8–11)[j]	9.3 (8.83–9.77)[j]
	n = 9/11[a]	*n* = 9/11[a]	-	-	-	-	*n* = 24[a,i]	*n* = 24[a,f,i]	*n* = 14[j]	*n* = 14[j]	*n* = 41[j]	*n* = 31[j]	*n* = 41[j]	*n* = 31[j]
	-	5.7 (5.0–6.3)[b]	7.7 (6.4–8.4)[d]	7.3 (5.5–8.9)[d]	7.7 (6.4–8.4)[d]	7.3 (5.5–8.9)[d]	8.9 (8.3–9.9)[d]	7.6 (6.6–8.7)[b]	8.5 (7.2–11.0)[d]	9.1 (8.8–9.8)[b]	10.55 (10.03–11.07)[a]	9.40 (8.92–9.88)[a]	10.55 (10.03–11.07)[a]	9.40 (8.92–9.88)[a]
	-	*n* = 7[b]	*n* = 9[d]	*n* = 9[d]	*n* = 9[d]	*n* = 9[d]	*n* = 21[d]	*n* = 13[b]	*n* = 17[d]	*n* = 5[b]	*n* = 32[a]	*n* = 32[a]	*n* = 32[a]	*n* = 32[a]
	-	-	-	-	-	-	-	7.6 (7.0–8.1)[d]	-	8.9 (6.8–9.9)[d]	10.71 (10.0–11.75)[k]	9.4 (8.7–10.5)[b]	10.71 (10.0–11.75)[k]	9.4 (8.7–10.5)[b]
	-	-	-	-	-	-	-	*n* = 21[d]	-	*n* = 17[d]	*n* = 10[k]	*n* = 14[b]	*n* = 10[k]	*n* = 14[b]
	-	-	-	-	-	-	-	-	-	-	-	9.41 (8.7–10.2)[k]	-	9.41 (8.7–10.2)[k]
	-	-	-	-	-	-	-	-	-	-	-	*n* = 10[k]	-	*n* = 10[k]
EHS	4.6[a]	4.1[a]	8.28 (7.78–8.78)[c]	7.17 (6.74–7.6)[c]	8.28 (7.78–8.78)[c]	7.17 (6.74–7.6)[c]	9.2 (9.0–9.4)[e]	7.6 (7.1–8.1)[e]	8.4 (8.29–8.51)[j]	8.9 (8.33–9.47)[j]	10.9 (10.32–11.48)[j]	9.5 (8.7–10.3)[j]	10.9 (10.32–11.48)[j]	9.5 (8.7–10.3)[j]
	n = 1[a]	*n* = 1[a]	-	-	-	-	*n* = 6[e]	*n* = 6[e]	*n* = 3[j]	*n* = 3[j]	*n* = 11[j]	*n* = 11[j]	*n* = 11[j]	*n* = 11[j]
	-	-	7.6 (7.0–8.2)[e]	6.3 (5.4–7.2)[e]	7.6 (7.0–8.2)[e]	6.3 (5.4–7.2)[e]	-	-	-	-	11.25[a]	9.55[a]	11.25[a]	9.55[a]
	-	-	*n* = 5[e]	*n* = 5[e]	*n* = 5[e]	*n* = 5[e]	-	-	-	-	*n* = 2[a]	*n* = 2[a]	*n* = 2[a]	*n* = 2[a]
	-	-	-	-	-	-	9.05 (8.1–9.7)[g]	7.38 (6.8–8.5)[g]	-	-	-	-	-	-
	-	-	-	-	-	-	*n* = 11[g]	*n* = 11[g]	-	-	-	-	-	-
UPHS	-	-	6.95 (6.47–7.43)[c]	4.8 (4.2–5.1)[b]	6.95 (6.47–7.43)[c]	4.8 (4.2–5.1)[b]	8.13 (7.38–8.88)[b,h,i]	7.23 (6.47–7.99)[b,f,h,i]	7.2 (6.69–7.71)[j]	8.6 (7.98–9.22)[j]	10.5 (9.95–11.05)[j]	9.4 (9.07–9.73)[j]	10.5 (9.95–11.05)[j]	9.4 (9.07–9.73)[j]
	-	-	-	*n* = 3[b]	-	*n* = 3[b]	*n* = 11[b,h,i]	*n* = 11[b,f,h,i]	*n* = 10[j]	*n* = 8[j]	*n* = 9[j]	*n* = 10[j]	*n* = 9[j]	*n* = 10[j]
	-	-	-	6.23 (5.76–6.7)[c]	-	6.23 (5.76–6.7)[c]	-	7.0 (6.3–8.0)[b]	-	9.4 (9.0–9.8)[b]	-	9.1 (7.8–10.5)[b]	-	9.1 (7.8–10.5)[b]
	-	-	-	-	-	-	-	*n* = 7[b]	-	*n* = 3[b]	-	*n* = 11[b]	-	*n* = 11[b]
	-	-	-	-	-	-	8.5 (7.4–9)[g]	7.1 (6.3–7.8)[g]	-	-	-	-	-	-
	-	-	-	-	-	-	*n* = 16[g]	*n* = 16[g]	-	-	-	-	-	-

(Continues)

TABLE 3 (Continued)

	di^2 (850)		dc^1 (851)		dc^1 (852)		dm_1 (853)		dm^1 (854)		dm_2 (855)		dm_2 (856)	
	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL
RHS	5.17 (4.88–5.46)[a]	4.75 (4.48–5.02)[a]	6.94 (6.47–7.41)[c]	6.1 (5.7–6.5)[c]	6.94 (6.47–7.41)[c]	6.1 (5.7–6.5)[c]	7.91 (7.55–8.27)[a]	6.9 (6.51–7.29)[a]	8.1 (7.53–8.67)[j]	7.7 (7.27–8.13)[j]	10.2 (9.72–10.68)[j]	9.4 (8.8–10)[j]	10.2 (9.72–10.68)[j]	9.4 (8.8–10)[j]
	n = 32[a]	*n* = 32[a]	-	-	-	-	*n* = 18[a]	*n* = 18[a]	*n* = 151[j]	*n* = 151[j]	*n* = 151[j]	*n* = 151[j]	*n* = 151[j]	*n* = 151[j]
	-	4.0[b]	-	-	-	-	-	7.01 (6.44–7.58)[f]	-	8.5[b]	10.03 (9.63–10.43)[a]	8.67 (8.26–9.08)[a]	10.03 (9.63–10.43)[a]	8.67 (8.26–9.08)[a]
	-	-	-	-	-	-	-	*n* = 100[f]	-	-	*n* = 18[a]	*n* = 18[a]	*n* = 18[a]	*n* = 18[a]
	-	-	-	-	-	-	-	7.51 (7.3–7.7)[b]	-	-	-	9.3 (9.0–10.0)[b]	-	9.3 (9.0–10.0)[b]
	-	-	-	-	-	-	-	*n* = 4[b]	-	-	-	*n* = 4[b]	-	*n* = 4[b]

Note: For each comparative sample, the mean is followed by the range in brackets and the number of individuals analyzed. The symbol "-" indicates missing data.

Abbreviations: dc^1, upper deciduous canine; di^2, upper deciduous second incisor; dm_1, lower deciduous first molar; dm^1, upper deciduous first molar; dm_2, lower deciduous second molar; EHS, early *Homo sapiens*; N, Neanderthal; *n*, number of individuals in the comparative sample; RHS, recent *Homo sapiens*; UPHS, Upper Paleolithic *Homo sapiens*.

[a]Bermúdez de Castro et al., 2017.

[b]Bailey & Hublin, 2006.

[c]Romandini et al., 2020.

[d]Becam & Chevalier, 2018.

[e]Hershkovitz et al., 2016.

[f]Arnaud et al., 2016.

[g]Riga et al., 2018.

[h]Frayer, 1978.

[i]Toro-Moyano et al., 2013.

[j]Zanolli et al., 2012.

[k]Benazzi, Fornai, et al., 2011.

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all four quadrants of the PCA plot, overlapping with N and fossil *H. sapiens*, although N mainly cover the negative scores of PC2. Uluzzo 855 and 856 fall along the negative scores of PC2, owing to an expansion of the buccodistal portion of the crown outline. RHS and UPHS groups cluster more closely together with positive scores of PC2, which are associated with a reduction of the buccodistal crown outline shape. A permutation test ($N = 10.000$) carried out on the first three PCs (63.4% of the total variance) reveals significant differences between N and RHS ($p < 0.001$), and between N and UPHS ($p = 0.002$), but not between RHS and UPHS ($p = 0.049$; see Table S7). Shapiro-Wilks test shows that RHS ($W = 0.9088$, $p < 0.05$), UPHS ($W = 0.86707$, $p < 0.05$), and N ($W = 0.88277$, $p < 0.05$) groups are non-normally distributed, while EHS ($W = 0.95341$, $p > 0.05$) group is normally distributed; therefore, the QDA was used instead of the LDA. Table 4 shows the results of the QDA based on the first seven PCs (85.6% of variance). The QDA distinguishes N from *H. sapiens* groups (RHS and UPHS grouped together, EHS were excluded due to the small sample size) with an accuracy of 91.7%, and Uluzzo 855 and Uluzzo 856 are classified as N with a probability of 93.9% and 99.1%, respectively.

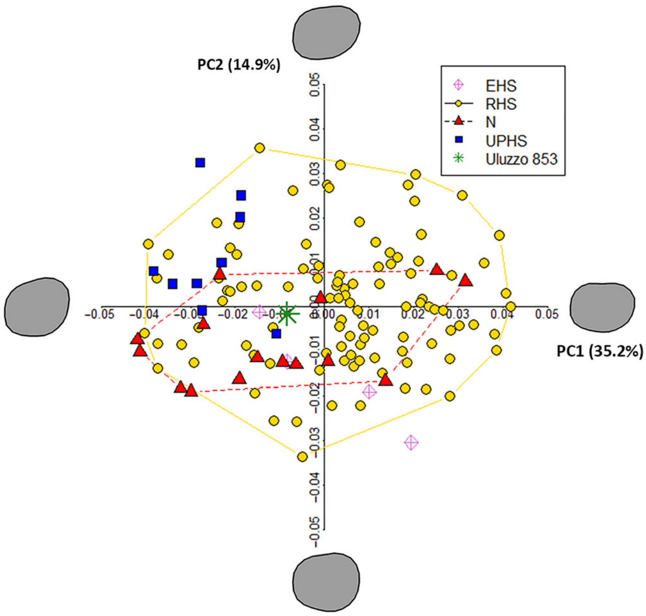

FIGURE 6 Principal component analysis (PCA) plot of dm_1 crown outline. The green symbol represents Uluzzo 853 (mirror imaged) projected in the morpho-space constructed on recent *Homo sapiens* (RHS); Upper Paleolithic *Homo sapiens* (UPHS); early *Homo sapiens* (EHS); and Neanderthals (N). Extreme shapes are shown on the axes of each principal components (PC).

4 | DISCUSSION

In this study, we provide the first systematic examination and description of the only human remains known from Uluzzo C. These remains comprise seven teeth preserved in the form of plaster casts. While not a perfect representation of the original teeth (e.g., they do not preserve microwear, caries, or hypoplasia), the size and morphology are accurate enough to compare them to other fossil and recent human groups. Based on similarities in size and morphology of the antimeres, non-duplication of elements, and stages of crown development, the dental sample most likely belongs to a single infant (suggested by the high and sharp cusp tips) or if the Rdi^2 (Uluzzo 850) was still with the crown in formation, the MNI would be two individuals.

Table 2 provides a summary of crown characters in the Uluzzo teeth and in those of comparative samples of Neanderthals, fossil, and recent *H. sapiens*. It is important to keep in mind that it is the combination of dental traits, rather than individual traits, that distinguishes Neanderthals from *H. sapiens* (Bailey & Hublin, 2013).

The combination of dental characters in the teeth from Uluzzo C is consistent with Neanderthal attribution. On the anterior teeth these characters include marked convexity and moderate shoveling on the

TABLE 4 Specimens % of correct classification and total accuracy.

		RHS + UPHS	RHS	UPHS	N			RHS + UPHS	RHS	UPHS	N
Tooth class	PCs	Correct %	Correct %	Correct %	Correct %	Total accuracy	Uluzzo specimen	P_{post} %	P_{post} %	P_{post} %	P_{post} %
dm_1	PC 1–6	-	79.4	33.4	66.7	74.6	Uluzzo 853[a]	-	~100	<0.001	<0.001
dm^1	PC 1–3	-	73.4	40	75	67.9	Uluzzo 854[b]	-	14.9	<0.001	85.1
dm_2	PC 1–7	93.2	-	-	86.9	91.7	Uluzzo 855[c]	6.1	-	-	93.9
							Uluzzo 856[c]	0.9	-	-	99.1

Abbreviations: dm_1, lower deciduous first molar; dm^1, upper deciduous first molar; dm_2, lower deciduous second molar; N, Neanderthal; PCs, principal components; P_{post}, post-probability; RHS, recent *Homo sapiens*; UPHS, Upper Paleolithic *Homo sapiens*.

[a]Compared with published (Bailey et al., 2020) and unpublished sources.

[b]Compared with published (Benazzi, Douka, et al., 2011) and unpublished sources.

[c]Compared with published (Bailey et al., 2016 and Benazzi et al., 2012 updated with Lugli et al., 2022) and unpublished sources.

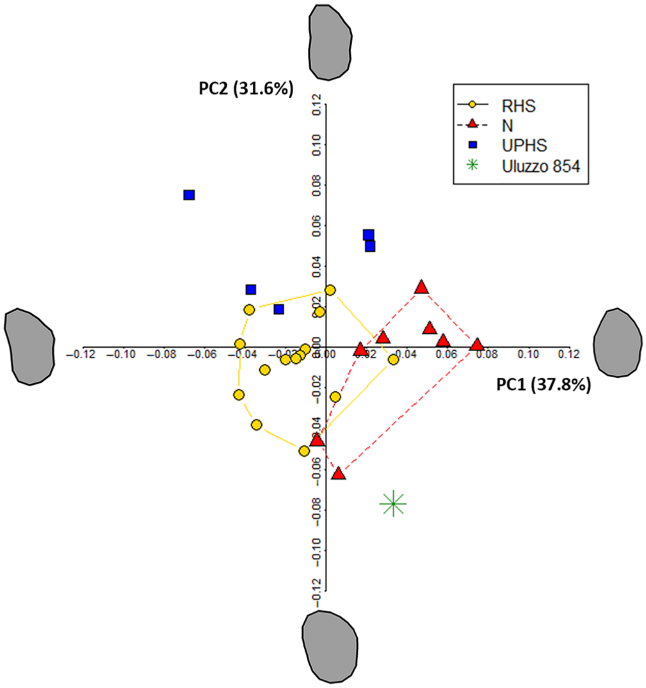

FIGURE 7 Principal component analysis (PCA) plot of dm^1 crown outline. The green symbol represents Uluzzo 854 (mirror imaged) projected in the morpho-space constructed on recent *Homo sapiens* (RHS); Upper Paleolithic *Homo sapiens* (UPHS); and Neanderthals (N). Extreme shapes are shown on the axes of each principal components (PC).

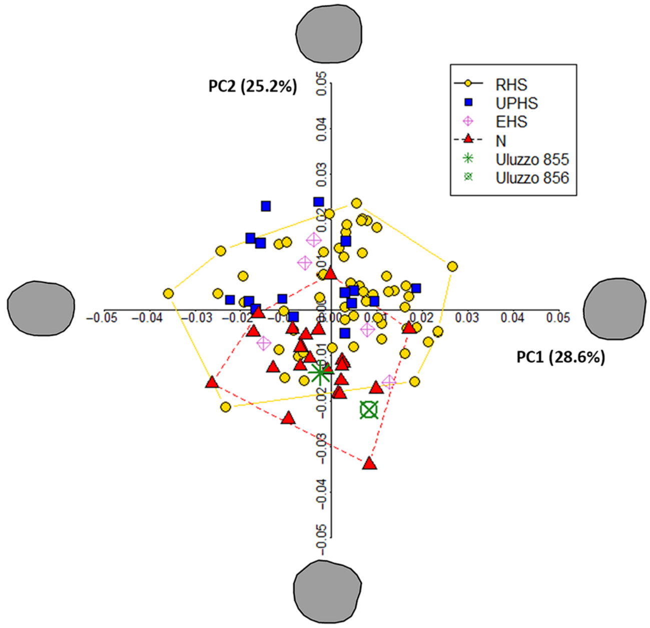

FIGURE 8 Principal component analysis (PCA) plot of dm_2 crown outline. The green symbols represent Uluzzo 855 (mirror imaged) and 856 projected in the morpho-space constructed on recent *Homo sapiens* (RHS); Upper Paleolithic *Homo sapiens* (UPHS); early *Homo sapiens* (EHS); and Neanderthals (N). Extreme shapes are shown on the axes of each principal components (PC).

Rdi^2 (Uluzzo 850) and both dc^1 (Uluzzo 851 and 852), as well as moderate cingulum development on the Ldc^1 (Uluzzo 852). As regards the posterior dentition, the distal trigonid crest that connects the Rdm^1 (Uluzzo 854) paracone and protocone and the tuberculum molare are observed in much higher frequencies in Neanderthals than in *H. sapiens*. On the lower molars, the continuous transverse crest observed on the Rdm_1 (Uluzzo 853) is nearly ubiquitous in Neanderthals and much less frequent in *H. sapiens*. Likewise, the combination of a wide and deep anterior fovea and a MTC observed on the dm_2s (Uluzzo 855 and 856) occur much more frequently in those of Neanderthals than in those of *H. sapiens*. Although we could not quantify cusp placement because of the difficulty in accurately locating cusp tips on the plaster casts, we noted that the cusps of both dm_2s (Uluzzo 855 and 856) and the dm^1 (Uluzzo 854) appear to be internally compressed. Tattersall and Schwartz (1999) observed that Neanderthal dm_2s can be distinguished from those of *H. sapiens* by their internally compressed cusps. Bailey (2004) found that cusps of Neanderthal permanent upper first molars were significantly more internally compressed than were those of *H. sapiens*. We should note that not all non-metric traits of the Uluzzo teeth are Neanderthal-like. The single exception is the absent hypocone on the dm^1 (Uluzzo 854), which is present in a majority of Neanderthals (>60%) but present in only 33% and 22% of Upper Paleolithic and recent *H. sapiens*, respectively (Table 2).

Crown measurements of the Uluzzo teeth (MD and BL diameters; Table 3) are also consistent with Neanderthal attribution, as all MD and BL diameters fall within the Neanderthal range. However, tooth size is not a reliable discriminator between Neanderthals and *H. sapiens* since their ranges overlap significantly (Bailey & Hublin, 2005; Smith, 1982). Therefore, it should not be surprising that, with the exception of the Rdi^2 (Uluzzo 850), the Uluzzo crown dimensions also fall within the variability range of *H. sapiens*.

In contrast, there is much less overlap in the crown outlines of Neanderthals and *H. sapiens*. Our analysis of crown outlines reveals significant differences between Neanderthals and *H. sapiens* in the shapes of molar crowns. The analyses assigned the Rdm^1 (Uluzzo 854) and the lower dm_2s (Uluzzo 855 and 856) to Neanderthals with moderate-to-high accuracy (67.9% and 91.7%, respectively; Table 4). The moderate accuracy of the Rdm^1 assignment is a little surprising, given that previous studies have shown high accuracy discriminating species for the upper deciduous molars compared to lower deciduous molars (Bailey et al., 2020; Benazzi, Douka, et al., 2011; Benazzi et al., 2012). Specifically, the dm^1 has shown 96%–100% accuracy in distinguishing Neanderthals and *H. sapiens* (Benazzi, Douka, et al., 2011). The triangular shape of the Rdm^1 (Uluzzo 854), which results from the lack of hypocone development (see morphology above) is, no doubt, reflected in its moderate accuracy of Neanderthal attribution. A previous study showed that the crown outline of the dm_1 is not particularly reliable for distinguishing the two species (Bailey et al., 2020). This poor discrimination is likely due to the significant variability in the shapes of recent *H. sapiens*, which can sometimes resemble those of

Neanderthals (Bailey et al., 2020). Therefore, it is not surprising that while morphological traits of the Rdm_1 (Uluzzo 853) fall within Neanderthal variability, it is assigned to RHS by the QDA with moderate accuracy (74.6%; Table 4).

5 | CONCLUSION

The data and results obtained from this work contribute significantly to the existing literature on Paleolithic human presence in southern Italy. Despite the limitations inherent in studying dental casts, including the inability to examine the internal morphology of the original teeth, our results suggest the only known human remains from Uluzzo C belong to Neanderthal species, adding to the already intriguing array of discoveries in Uluzzo Bay (Benazzi, Douka, et al., 2011; Benazzi et al., 2012; Fabbri et al., 2016; Moroni et al., 2018). The utilization of a combination of methods, including non-metric dental traits, metrics, and GM, allowed us to provide the analysis of these of human remains, even in the absence of the original teeth. This strategy ultimately maximizes the number of specimens available for examination in paleoanthropological studies.

Our efforts to find authentic dental remains will continue. The recovery of the original specimens would allow us to carry out a comprehensive set of analyses (digital and biomolecular), adding further fundamental information regarding their taxonomic attribution and association with a specific cultural horizon.

AUTHOR CONTRIBUTIONS

Francesca Seghi: Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (lead); validation (equal); visualization (equal); writing – original draft (lead); writing – review and editing (equal). **Rita Sorrentino:** Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); validation (equal); visualization (equal); writing – original draft (equal); writing – review and editing (equal). **Shara E. Bailey:** Data curation (equal); investigation (equal); validation (equal); visualization (equal); writing – original draft (supporting); writing – review and editing (supporting). **Erica Piccirilli:** Validation (supporting); visualization (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Antonino Vazzana:** Data curation (supporting); writing – review and editing (supporting). **Eugenio Bortolini:** Writing – review and editing (supporting). **Owen A. Higgins:** Writing – review and editing (supporting). **Giulia Marciani:** Writing – review and editing (supporting). **Medica A. Orlando:** Resources (supporting); writing – review and editing (supporting). **Enza E. Spinapolice:** Writing – review and editing (supporting). **Adriana Moroni:** Funding acquisition (supporting); investigation (supporting); project administration (supporting); validation (supporting); writing – original draft (equal); writing – review and editing (supporting). **Stefano Benazzi:** Conceptualization (equal); funding acquisition (lead); project administration (lead); resources (lead); supervision (lead); validation (equal); writing – review and editing (supporting).

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Francesca Seghi https://orcid.org/0000-0002-3506-2717
Rita Sorrentino https://orcid.org/0000-0002-6529-7250

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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