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SPOTTED HYAENA SPOTTED ON ISLAND: THE UPPER PLEISTOCENE HYAENAS FROM SAN TEODORO CAVE (SICILY, ITALY) PROVIDE NEW INSIGHTS ON THE PALAEOBIOLOGY, PALAEOECOLOGY, AND SOCIALITY OF *CROCUTA*.

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Abstract. Fossil remains of spotted hyaena, *Crocuta crocuta* (Erxleben, 1777), are commonly found across Eurasian and African Upper Pleistocene sites, especially in cave deposits. While this species had a wide geographic distribution, palaeontological evidence of its presence in Quaternary insular settings in southern Europe is restricted to Sicily, where the most abundant sample of *Crocuta* has been recovered from the Upper Pleistocene site of San Teodoro Cave. Previous research on the site recognised the prominent role of hyaenas as a taphonomic agent, with thousands of coprolites and traces on large mammal remains, but no description of the material from a systematic palaeontology perspective has been published to date. Here, we provide the first comprehensive study of *Crocuta* skeletal remains from the San Teodoro Cave, alongside a comparative analysis of the endocranial anatomy. Biometric and morphological data were compared with those of extant and Upper Pleistocene specimens. Our results reveal that, with respect to roughly coeval samples from mainland Europe, San Teodoro hyaenas were characterised by a slightly reduced body size, indicative of a possible effect of insularity. Furthermore, palaeoneurological analyses demonstrate that the development of the anterior cortex of the brain in the San Teodoro sample is slightly less pronounced compared to extant *C. crocuta*, but consistent with other Pleistocene fossil spotted hyaenas of Eurasia and Africa. This suggests potential differences in the cognitive and behavioural repertoire, encompassing hunting strategies and social complexity, between the Pleistocene and the extant spotted hyaenas.

This study offers new insights into the diversity and distribution of the Middle-Late Pleistocene *Crocuta* of Europe and confirm the crucial role of San Teodoro Cave in understanding Quaternary insular ecosystems.

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Introduction

Since 1858, when Alfred Russel Wallace and Charles Darwin symbolically joined the publication of their preliminary theories on natural selection, islands become strategic locations to explore the diversity and distribution of living and extinct organisms. Investigating the evolution of insular carnivorans is a challenging issue in palaeontology, as their fossil record is scarcer and more fragmented, with some notable exceptions, compared to that of their mainland relatives (Lyras et al. 2010). Some of the best-known species are endemic to the Mediterranean islands, such as the fossil canid *Cynotherium sardous* Studiati, 1857 from the Middle to Upper Pleistocene of Sardinia and Corsica (Malatesta 1970; Abbazzi et al. 2005; Lyras et al. 2006; Lyras & van der Geer 2006; Ciucani et al. 2021), and the fossil otters from Crete (*Lutrogale cretensis* (Symeonides & Sondaar, 1975)), Sardinia (*Sardolutra ichnusae* (Malatesta, 1977), *Megalenhydris barbaricina* Willemsen & Malatesta 1987, *Algarolutra majori* Malatesta & Willemsen 1986), and Sicily (*Lutraeximia trinacriae* (Burgio & Fiore, 1988)), whose fossil record includes some exquisitely preserved skeletons (Willemsen 1992, 2006; Cherin et al. 2016).

Hyaenas are probably among the least represented fossil carnivorans on islands, indeed, the only endemic insular species known so far is the Mele's hunting hyaena, *Chasmaporthetes melei* Rook et al., 2004, from the Pliocene-Pleistocene of Sardinia. This taxon was erected by Rook et al. (2004) and it is known from a single splanchnocranium partially embedded in a sediment matrix. Morphologically comparable to the mainland Pliocene-Pleistocene form of *C. lunensis* (Del Campana, 1914) from Eurasia, the Mele's hunting hyaena possesses relatively smaller teeth (especially in the length of the upper fourth premolar; P^4) and apparently reduced body size, interpreted as an adaptation to the Sardinian insular ecosystem (Rook et al. 2004; Lyras et al. 2010). Most palaeobiological and palaeoecological traits of *C. melei* remain largely unknown or are regarded as similar to those of *C. lunensis* – a cursorial hyaena capable of hunting medium sized prey – but new fossils are needed to evaluate better its morphological and biometric variability as well as the taxonomic integrity of this species.

A few remains of hyaenas, attributed to the giant short-faced *Pachycrocuta brevirostris* (Gervais, 1850), are also reported from the lower Middle Pleistocene of Java, although associated faunas do not reflect substantial isolation from the mainland and measurements of Javanese *P. brevirostris* fall within the variability of continental samples (Dubois 1908; Brongersma 1937; Schütt 1972; Geraads 1979; Lyras et al. 2010; Louys 2014; Volmer et al. 2016). *Pachycrocuta brevirostris* was a lion-sized hyaena with an estimated weight up to 100 kg, commonly known from several Lower to Middle Pleistocene localities of Eurasia (Schütt 1972; Turner & Antón 1996; Qiu et al. 2004; Palombo 2017; Petrucci et al. 2013; Liu et al. 2021, 2025; Iannucci et al. 2021; Nikolskaia et al. 2025).

Mediterranean islands are considered one of the most attractive places for palaeobiogeographical studies as they have yielded remains of a variety of Upper Pleistocene vertebrates. Hyaenas are reported from several localities of Sicily, with the largest sample being that recovered from San Teodoro Cave (Marra et al. 2004). This site was discovered in 1859, while Darwin was publishing his monumental work on the origin of species. The following year, Darwin received a letter from Hugh Falconer describing some elephant and hyaena remains from San Teodoro Cave sent to him by Francesco Anca (Letter 2863, the Darwin Correspondence Project). In this letter, Falconer reported to Darwin that the fossil elephants and hyaenas of Sicily were the same as the present-day African species, thus suggesting that Sicily and Africa had been connected in a recent geological period, a theory later rejected (Vaufrey 1929; Van der Geer et al. 2021). This correspondence shows that the hyaenas of San Teodoro Cave have been part of the scientific debate among the most influential scholars since the cave was discovered. But despite over a century and a half of research, their fossils remain largely unstudied, and their origin still fuels debate among specialists. In recent decades, San Teodoro Cave has been the subject of extensive study (see below). While hyaena remains consisting of thousands of coprolites and numerous cranial and postcranial bones from both juvenile and adult specimens referred to *Crocuta crocuta spelaea* (Goldfuss, 1823), were sporadically referenced in some taphonomic works (e.g., Bonfiglio et al. 2001, 2008; Mangano 2011), a comprehensive and detailed description of this material has never been attempted.

Here, we provide the first formal description of the spotted hyaena remains recovered from San Teodoro Cave. The sample represents the richest collection of *Crocuta crocuta* (Erxleben, 1777) – and more generally of the Hyaenidae – ever reported from an insular context, offering a unique opportunity to deepen our knowledge on the adaptations of this carnivoran to the Late Pleistocene ecosystems of Sicily. In this regard, a key aim of this study is to evaluate the existence and extent of morphological and biometric differences between San Teodoro and continental *Crocuta*, which might reflect the effect of insularity.

The cave hyaena

The best-known of all hyaenas is the extant spotted hyaena, *Crocuta crocuta*. Although today restricted to sub-Saharan Africa, closely related forms once inhabited most of Eurasia. While there is no general consensus in subsuming these forms within *C. crocuta*, or referring to them as different species or subspecies – i.e., *C. spelaea* (Goldfuss, 1823) or *C. crocuta spelaea* in Europe; *C. ultima* (Matsumoto, 1915), *C. crocuta ultima* (Matsumoto, 1915), or even *C. ultima ussurica* Baryshnikov & Vereshchagin, 1996 in Asia – they are broadly known as "cave hyaenas" (Kurtén 1956, 1968; Turner 1984; Werdelin & Solounias 1991; Baryshnikov 1995, 1999, 2014; Diedrich 2008; Sheng et al. 2014; Fourvel et al. 2015; Vinuesa et al. 2016; Sauqué et al. 2017; Iannucci et al. 2021; Lewis & Werdelin 2022; Salari et al. 2025). The cave hyaena was one of the most widespread carnivorans of the Middle and especially Late Pleistocene ecosystems of Eurasia (Iannucci et al. 2021). Its past distribution extended outside Africa, from Portugal at the western margin of Europe (Davis et al. 2007), throughout Ukraine and further east into Asia (Baryshnikov 1999), and in western Europe from Britain in the north (Currant & Jacobi 2011) to the Mediterranean peninsulas in the south (Sauqué et al. 2017; Iannucci et al., 2021). In Italy, fossils of *Crocuta* are documented across the whole peninsula, reaching its south-eastern and south-western continental extremities, and of course even Sicily (Bonfiglio et al. 2001; Mecozzi et al. 2021; Iannucci et al. 2021).

The first mention of fossils that would later become known as the cave hyaena is attributable to Esper (1774), who described and figured a partial cranium and teeth from the Upper Pleistocene Zoolithen Cave in Bavaria (Germany), identified by the author as "non-cave bear remains" (Diedrich 2008, 2011a). Subsequently, Goldfuss (1810) referred to these remains as "Hölen Hyäne" (i.e., cave hyaena), and eventually formally established the new species *Hyaena spelaea* some years later (Goldfuss 1823). The species was then moved to the genus *Crocuta* by Soergel (1937).

Cave hyaenas are commonly referred as such because their remains are often abundantly preserved in Pleistocene cave deposits, but the rationale behind the often-employed formal taxonomic distinction from *C. crocuta* stems from the identification of morphological differences between extant and extinct populations, the latter being larger and possessing different limb proportions than present-day individuals (Kurtén 1956; Sauqué et al. 2017), although recent body mass reconstructions have revealed that some European Pleistocene *C. crocuta* were smaller than the largest-recorded extant *C. crocuta* individuals (Jones 2019). Moreover, behavioural differences have been hypothesized based on both palaeoneurological and taphonomic evidence. These include, for example, a less developed frontal cortex in extinct populations with possible implications for social behaviour (Vinuesa et al. 2016), and an increased tendency to use caves as dens (Lansing et al. 2009).

Over the last couple of decades, several insights on *Crocuta* evolutionary history have been provided from genetic and genomic studies. Rohland et al. (2005) recognised four mitochondrial clades within *Crocuta*, only two of which are still extant. The authors further identified important admixture between African and Eurasian mtDNA sequences, which led them to reject any taxonomic distinction between cave hyaenas and the extant *C. crocuta*. Similar conclusions were reached by Bon et al. (2012) based on the similarity of mtDNA and nuclear genes in coprolites from Coumère Cave, France, to DNA from present-day *C. crocuta*. Conversely, Westbury et al. (2020) assembled and analysed population-level palaeogenomes from the Upper Pleistocene of Eurasia and genomes from modern samples, supporting the monophyly of African and Eurasian clades and identifying a deep divergence between them. Nonetheless, Westbury et al.'s (2020) results also highlighted the occurrence of bidirectional gene flow between the two groups with evidence of an adaptive role of introgression, as well as discrepancies between phylogenetic reconstructions based on nuclear or mitochondrial DNA. Asian and European extinct populations are also well-separated (Hu et al. 2021). Recently, Catalano et al. (2024) provided palaeogenomic data from a single hyaena coprolite from San Teodoro Cave, showing that the Sicilian specimen shares less of an introgression signal with African spotted hyaenas compared to other Eurasian counterparts. Moreover, based on nDNA, the Sicilian genome was described as forming a basal lineage of cave hyaena, suggesting that the genetic structure of European cave hyaenas was more complex than previously documented. In any case, the existence of diverging clades within *Crocuta* allows for the genus' valid separation into different taxa but does not necessary imply that a distinction must be adopted, or indeed at which taxonomic level. Furthermore, despite extant spotted hyaenas belonging to two well-separated genetic clades, these are commonly placed altogether in *C. crocuta*, with no recognised subspecies (Jenks & Werdelin 1998; Rohland et al. 2005; Westbury et al. 2020).

In Europe, the earliest records of *Crocuta* are documented below the Lower-Middle Pleistocene boundary (Matuyama-Brunhes reversal, ca. 0.77 Ma) in the Iberian Peninsula, and slightly after in Italy (Garcia & Arsuaga 2001; Sardella & Petrucci 2012; Walker et al. 2020; Iannucci et al. 2021). Uppermost Lower and lower Middle Pleistocene remains are relatively scanty when compared with the copious Upper Pleistocene findings, although the reasons and timing of this shift in abundance are yet to be clarified (Iannucci et al. 2021). The last occurrence of *Crocuta* was reported during the Late Pleistocene, at around 40 ka in the Urals and central/eastern Europe (Stuart & Lister 2014) with a longer persistence in Mediterranean regions, as in southern Italy at Grotta Paglicci (ca. 30 ka, Stuart & Lister 2014; Jones 2019) and in southern Spain at Las Ventanas Cave (ca. 13 ka, Carrión et al. 2001). Subsequent studies indicated that *Crocuta* was still present in Germany and even China as late as ca. 22 ka (Westbury et al. 2020) and ca. 20 ka (Hu et al. 2021), respectively. A further dated occurrence of *Crocuta* in central Europe is known from Poland at Perspektywiczna Cave, documenting a rather continuous presence of the species during MIS 3, from ca. 50 to 34 ka (Krajcarz et al. 2023). Several hypotheses have been proposed about the causes of the extirpation of *Crocuta* from Europe. *Crocuta* may have been physically intolerant to decreasing temperatures towards the end of MIS 3 (Stuart & Lister 2014; Jones 2019), supported by recent work on modern *Crocuta*, demonstrating that they are less tolerant of cold winters than lions today (Jones et al. 2021). There may have been reduction in prey availability due to overall reduction in prey biomass and/or increased competition from other predators (Stiner 2004; Stuart & Lister 2014, Iannucci et al. 2021). Finally, there may have been increased competition for cave sites with the arrival into Europe of modern humans (Stuart & Lister 2014). Varela et al. (2010) modelled *C. crocuta* distributions during five time intervals (126 ka, 42 ka, 30 ka, 21 ka and the present day) in order to determine whether climate change was the cause of the species' extirpation from Europe. The results indicated that climate was not the sole cause, as there were areas in Europe that were still suitable *Crocuta* habitation at 21 ka. The author instead suggested the prey availability and competition with humans should be investigated. However, at least some of the sites that Varela et al. (2010) included in the 21 ka period yielded *C. crocuta* specimens that were subsequently redated by Stuart & Lister (2014), revealing older dates, thus prompting caution when inferring suitable climatic conditions towards the end of the Late Pleistocene.

During the Late Pleistocene, *Crocuta* strongly contributed to the bone accumulations in caves, which were often used as communal dens, an inference supported by the frequent associated recovery of weaning cubs and adult specimens (Fosse 1997; Fosse et al. 1998; Diedrich & Žák 2006; Turner et al. 2008; Bonfiglio et al. 2008; Mangano 2011; Fourvel 2012; Fourvel et al. 2012; Diedrich 2014; Fourvel et al. 2014; Sauqué et al. 2017). This extensive use of caves over millennia resulted in a great abundance of *Crocuta* remains, which make the European fossil record one of the richest and most intensively explored.

Decades of studies on Middle-Late Pleistocene *Crocuta* have shed light on several palaeobiological traits, including biometric and morphological variability (Baryshnikov 1999; Diedrich 2011b; Lewis & Werdelin 2022), injuries and pathologies (Iurino & Sardella 2015), neuroanatomy (Vinuesa et al. 2016; Petrovič et al. 2018; Flink et al. 2025),

Fig. 1 - Geographical location of San Teodoro Cave (A) (modified from Google Earth) and close-up of the cave entrance (B).

body size (Klein & Scott 1989; Lewis & Werdelin 2022), ontogeny (Jimenez et al. 2019 and literature therein), feeding behaviour (Diedrich 2012; DeSantis et al. 2017; Orbach & Yeshurun 2021; Rivals et al. 2022) and competition with other large carnivorans (Diedrich 2011c; Iannucci et al. 2021). However, our knowledge on insular forms is limited, and as stated above, the only remains of insular *Crocuta* from southern Europe are known from the Upper Pleistocene of Sicily.

Geological and palaeontological framework

San Teodoro Cave is a large karst cavity located at Acquedolci, a small town on the north-eastern coast of Sicily, in the province of Messina (Fig. 1A). The cave opens in the northern cliffs of a Jurassic carbonate succession (San Fratello Massif) at the height of 145 m a.s.l. and is composed of a single large chamber, about 60 m long, 20 m wide and up to 20 m high. The entrance of the cave, which is of triangular shape, is about 12 m wide and 5 m high at present (Fig. 1B).

Currently, the floor of the cave ascends about 15 m from the entrance to the end of the cave along its major axis. The central part of the floor is a detrital fan which slopes down laterally toward the eastern and western walls of the cave.

The San Teodoro Cave deposits were discovered in 1859, and several excavations (although not stratigraphically controlled) were conducted up to the mid-twentieth century. The cave is known mainly for its important Upper Palaeolithic human burials and artefacts, referred to the Late Epigravettian, although an older deposit containing Pleistocene mammal remains has been distinguished underneath the cultural level by all authors (Anca 1860; Vaufrey 1928, 1929; Maviglia 1941, 1942; Graziosi 1943, 1947; Graziosi & Maviglia 1946; Vigliardi 1968, 1989; Fabbri 1993; Martini 1997).

Modern excavations, conducted by one of the authors (LB), started in 1998 and continued until 2006, for a total of eight months and six excavation seasons (1998, 2002–2006). Two trenches have been excavated, named as the "α" trench close to the entrance and the "β" trench inside the cave (Bonfiglio et al. 2008). Only the older deposit (named as "unit B" in Bonfiglio et al. 2001) was investigated, as the Upper Palaeolithic one had been almost totally removed by previous excavations. Recent reworked sediments having different thicknesses overlie the unit B deposit (Bonfiglio et al. 2008).

The large mammal assemblage from unit B is composed of 4.864 fossil bone remains and 10.086 hyaena coprolites. The following large mammal taxa have been identified: *Palaeoloxodon mnaidriensis* (= *P.* n. sp. Herridge 2010), *Equus hydruntinus* Regalia, 1907, *Bos primigenius siciliae* Pohlig, 1893, *Bison priscus siciliae* Roccati, 1904, *Cervus elaphus siciliae* Pohlig, 1893, *Sus scrofa* Linnaeus, 1758, *Crocuta crocuta spelaea, Canis lupus* Linnaeus, 1758, and *Vulpes vulpes* (Linnaeus, 1758). Evidence of contemporary human occupation, such as stone artefacts or cut marks on bone surfaces, are lacking and hyaenas are the only agent responsible for bone accumulation (Mangano 2011). The unit B deposit has been also retrieved from several test-pits excavated at different points of the cave floor, testifying that the whole cave area, having a total surface of about 1.000 m^2, was inhabited by hyaenas; for this reason, San Teodoro Cave is the largest Pleistocene hyaena den so far known in an insular environment (Bonfiglio et al. 2001, 2008; Mangano & Bonfiglio 2005; Mangano et al. 2005).

The stratigraphy of the β trench is complex, compared to the α trench, showing at least three fossiliferous levels – 'B-I', 'B-II' and 'B-III' – and their faunal characteristics suggest different depositional phases, probably of short duration. The 'B-I' and 'B-II' levels are the richest in terms of faunal remains. A preliminary ^{230}Th/^{234}U dating of a speleothem within a fossiliferous level from the β trench, at the top of B-III, yielded an age of 32±4 ka (Bonfiglio et al. 2008). A radiocarbon date of 23–21 cal ka B.P. on bone collagen of an *Equus hydruntinus* specimen from San Teodoro Cave is reported by Antonioli et al. (2016). Biochronologically, the Pleistocene mammalian fauna of Sicily is subdivided into several Faunal Complexes (FC), San Teodoro being the most important site for the definition of the San Teodoro-Pianetti FC, considered to date between ca. 70 and 20 ka (Masini et al. 2008; Antonioli et al. 2016). The large mammalian fauna of this FC is roughly similar to that of the preceding FC, the *Palaeoloxodon mnaidriensis* FC, but it differs from it for the absences of the cave lion *Panthera spelaea* (Goldfuss, 1810) and the small hippopotamus *Hippopotamus pentlandi* Von Meyer, 1832, and for the presence of *Equus hydruntinus* (Masini et al. 2008; Antonioli et al. 2016). Antonioli et al. (2016) reasoned that the earliest dated presence of *E. hydruntinus* in Sicily (i.e., that from San Teodoro) coincided with their reconstructed timing of the land-bridge connection occurred between Sicily and the Italian mainland, which lasted for at least 500 years between 21.5 and 20 cal ka BP. The absence of material of *E. hydruntinus* from B-III would also corroborate with the view that the dispersal of this species in Sicily occurred during this period. On the other hand, B-III yielded just a few fossil remains, and several species are consequently not recorded (Mangano 2011). Most notably, hyaenas are not documented by direct skeletal evidence from B-III, despite the taphonomic consequences of their presence being evident (Mangano 2011). Moreover, Antonioli et al. (2016) did not exclude an earlier dispersal of *Equus hydruntinus* in Sicily, consistently with the estimated beginning of the San Teodoro-Pianetti FC (ca. 70 ka). Indeed, this would coincide with a period of low sea level during MIS 4, and *E. hydruntinus* was widely present in southern Italy at least since the Late Pleistocene (e.g., Mecozzi et al. 2021). The fauna of San Teodoro includes several endemic elements that were already present in the previous *Palaeoloxodon mnaidriensis* FC, while a fully continental character is only reached after the San Teodoro-Pianetti FC, in the Castello FC (Masini et al. 2008; Antonioli et al. 2016; Strani et al. 2025).

Finally, a radiocarbon date on Upper Palaeolithic human bone collagen from San Teodoro Cave gave an age of 15.232 – 14.226 cal ka (Mannino et al. 2011). However, recent radiocarbon dating of charcoal fragments from the same site indicates an older age of 16.500 cal ka BP (Forgia et al. 2025).

According to Vaufrey (1929) and to Burgio et al. (2002), remains of fossil hyaenas have been found in Sicily in the following sites: Arena, Costiera, San Ciro Cave, Maccagnone Cave, Carburangeli Cave, Cape Zafferano, Amorosa Cave, Puntali Cave, Cannita Cave, Monreale Acqua dei Corsari, Zà Minica Cave, Cala dei Genovesi and Caletta Cofanol in western Sicily; San Teodoro Cave, Cape Molinari and Skuzaria in eastern Sicily; moreover, remains of hyaenas have been found in fissure filling deposits of southeastern Sicily (Ragusa) (Fabiani 1927). Unfortunately, many of these remains have been lost, although some are stored in the Gemmellaro Museum (Palermo), including some hyaena remains from San Teodoro Cave (Burgio & Di Patti 1990; Burgio et al. 2002).

Material and methods

The fossil materials from San Teodoro studied in this paper were discovered during the excavations conducted by one of the authors (LB) in 1998 and from 2002 to 2006. The collection counts 106 hyaena remains listed in Supplementary information, represented by 27 postcranial and 79 craniodental remains housed in the repository of the Wildlife Museum, University of Messina. All specimens from San Teodoro Cave are marked with the abbreviation PL (Pleistocene) followed by the catalogue number.

The fossil record of *Crocuta* reveals a huge biometric variability in time and space (e.g., Lewis & Werdelin, 2022). Therefore, to evaluate the potential effect of insularity in the San Teodoro sample, it is necessary to compare it to roughly coeval (i.e., MIS 3) samples from mainland Europe, in order to minimise other sources of variation that might act as confounding factors. To build a comparative dataset satisfying this criterion, we collected measurements on hyaena specimens housed in several institutions (see abbreviations below) from selected continental MIS 3 samples, chosen for the abundance of available remains and as representatives of different areas of Europe. The selected localities are Teufelslucken (Austria), Goyet (Belgium), and Kents Cavern (England). We also considered an extant sample, originating from the area of Balbal, in Tanzania. Raw data and further details are in Supplementary information.

Measurements were taken with digital callipers to the nearest 0.01 mm, following Von den Driesch (1976). Teeth are abbreviated to their initial letter, with superscript and subscript referring to upper and lower teeth, respectively, and a "D" precedes deciduous teeth (e.g., P_2 = lower second premolar; DP^2 = upper second deciduous premolar).

San Teodoro yielded the most abundant sample of hyaenas from an insular setting. However, few anatomical elements are represented by enough specimens to reliably test the biometric differences between them and the MIS 3 continental samples of *Crocuta*. Adopting a threshold of at least 5 observations of the length (L) and width (W) of dental elements, we performed statistical analyses on P^3 L, P_2 L, P_3 L, P_3 W, and P_4 W. First, Shapiro-Wilk tests were used to check whether the data were normally distributed. Depending on the results of these tests, either ANOVA (in the case of normal distribution) or Mann Whitney tests (non-normal distribution) were performed to assess the significance of the observed differences between each pair of groups for each variable. These analyses, as well as boxplots used to visualise data, were produced with the software PAST (Hammer et al. 2001). Boxplots quartiles were constructed using the "interpolation" method provided by the software, following which non-integer ranks are treated using a linear interpolation between the two nearest ranks. Whiskers are drawn above and below the box, and individual observations are plotted.

The cranial remains from San Teodoro Cave (n 13, specimens) were scanned using a Ge Revolution Act 16/32 scanner at Clinica Veterinaria Camagna (Reggio Calabria) with slice thickness of 0.55 mm and interslice space of 0.27 mm. The two neurocrania (MPD13 and MPD15) of Late Pleistocene *C. crocuta* from Melpignano (southern Italy) and skulls of extant *C. crocuta* (n 2, MC 337 and MC 377), *Hyaena hyaena* (Linnaeus, 1758) (n 2, MC 174 and MC 217) from the osteological collection of Museo Civico di Zoologia of Rome, were scanned using a Philips Brilliance CT 64-channel scanner at M.G. Vannini Hospital (Rome). The slice thickness is 0.55 mm and interslice space is 0.27 mm. CT images of extant *C. crocuta* (n 3, UCMVZ 184551, USNM 164506 and USNM 181527) and those of extant *Parahyaena brunnea* (Thunberg, 1820) (n 1, FMNH 34584) were downloaded from MorphoSource database (www.morphosource.org). Raw and literature data are available in Supplementary information.

Brain endocasts were subdivided into the four regions, based on sulcal patterns indicated in the literature (Arsznov et al. 2011; Sakai et al. 2011; Swanson et al. 2012; Vinuesa et al. 2015, 2016; Flink et al. 2025): I) olfactory bulbs; II) anterior cerebrum, located between the olfactory bulbs and the junction of the cruciate sulcus and sagittal plane; III) posterior cerebrum, extending caudally from the cruciate sulcus to the cerebellum (specifically the tentorium); IV) cerebellum plus brain stem, extending from the most anterior border of the tentorium to the foramen magnum. Cranial nerves were not included for volume analysis. The ratio of the volume of each region to the total volume of the brain cavity (consisting of the olfactory bulbs, the cerebrum, and cerebellum plus brainstem) was computed for comparative analysis. 3D models of the paranasal sinuses were generated for morphological analysis. Biometric comparison was not possible due to the partial preservation of the sinuses.

CT image processing and the acquisition of measures were performed using Mimics 21.0, while the image editing and 3D renderings were made with ZBrush 4R6.

Results

Description

Crania

Cranial remains (Fig. 2) include three almost complete braincases referable to one juvenile (PL2928) and two adults (PL4802, PL4818), three isolated fragments of parietals (PL2021, PL2165, PL4540), and a couple of temporals (PL2139, PL3174) of cubs. The three neurocrania are broken at the postorbital constriction, lack the zygomatic arches, and are characterised by a different size and colouration.

The specimen PL4802 (Fig. 2A) is the largest and best-preserved braincase of the samples studied. Its surface is smooth, free of sediment, and brownish in colour. In lateral and dorsal views, the sagittal crest appears well-developed with a curved profile, which is particularly rounded at the junction with the occipital crest. In caudal view, the braincase is triangular in shape, both mastoid processes are broken, the occipital condyles are wide and well-preserved with an almost circular foramen magnum. Both tympanic bullae are broken and separated by a wide basioccipital, which is characterised by the presence of a thin and sharp crest in the middle.

The specimen PL4818 (Fig. 2B) is nearly identical to the previous braincase, except for its slightly smaller size, its light colouring, and the presence of an encrusting patina, which covers the right side of the braincase. The resemblance with PL4802 is so high that even the missing portions are the same and the bones appear similarly broken (e.g., the zygomatic arches, the mastoid processes, the tympanic bullae).

The specimen PL2928 (Fig. 2C) is the smallest and most damaged neurocranium of the sample. The bone tissue is dark, with a whitish-grey veil of calcareous concretion covering the parietals and part of the ventral area of the neurocranium. The sagittal crest is not marked and part of its caudal portion is missing. The right temporal bone, almost all the occipital, and the ventral surface of the specimen are also missing. There are several bite-marks along the broken edges of the bones, some of which are particularly noticeable, as those on the right and left parietals. The incomplete welding of the cranial sutures, the reduced size of the specimen, and its globular shape suggest the individual is of young age.

The specimens PL2021, PL2165, and PL4540 (Fig. 2D-F) consist of very small parietals of globular shape without the sagittal crest (hence belonging to cubs). The dorsal surface of the specimens is smooth and crossed by thin fracture lines, while on the ventral side, marked imprints of the brain convolutions are readily recognisable. The edge of the sagittal suture is stout in PL2165 and PL4540 but quite curved in PL2021. PL2165 and PL4540 could belong to the same individual.

Paranasal sinuses

Since the neurocrania PL4802, PL4818, and PL2928 are all broken at the postorbital constriction, only the parietal portion of the paranasal sinuses is preserved (Fig. 3). The sinuses are well developed and extend towards the posterior margin of the brain in PL4802 and PL4818, whereas in the juvenile specimen PL2928, they occupy only the anterior portion of the parietals. In the latter specimen, the sinuses are also less developed in height, as the cranium is rounded and lacks a marked sagittal crest, while the width is equal to that of the two adult specimens. In all the San Teodoro samples, the paranasal sinuses have a triangular cross-section and are relatively symmetrical in dorsal view, consisting of a series of interconnected chambers of irregular shape and variable size.

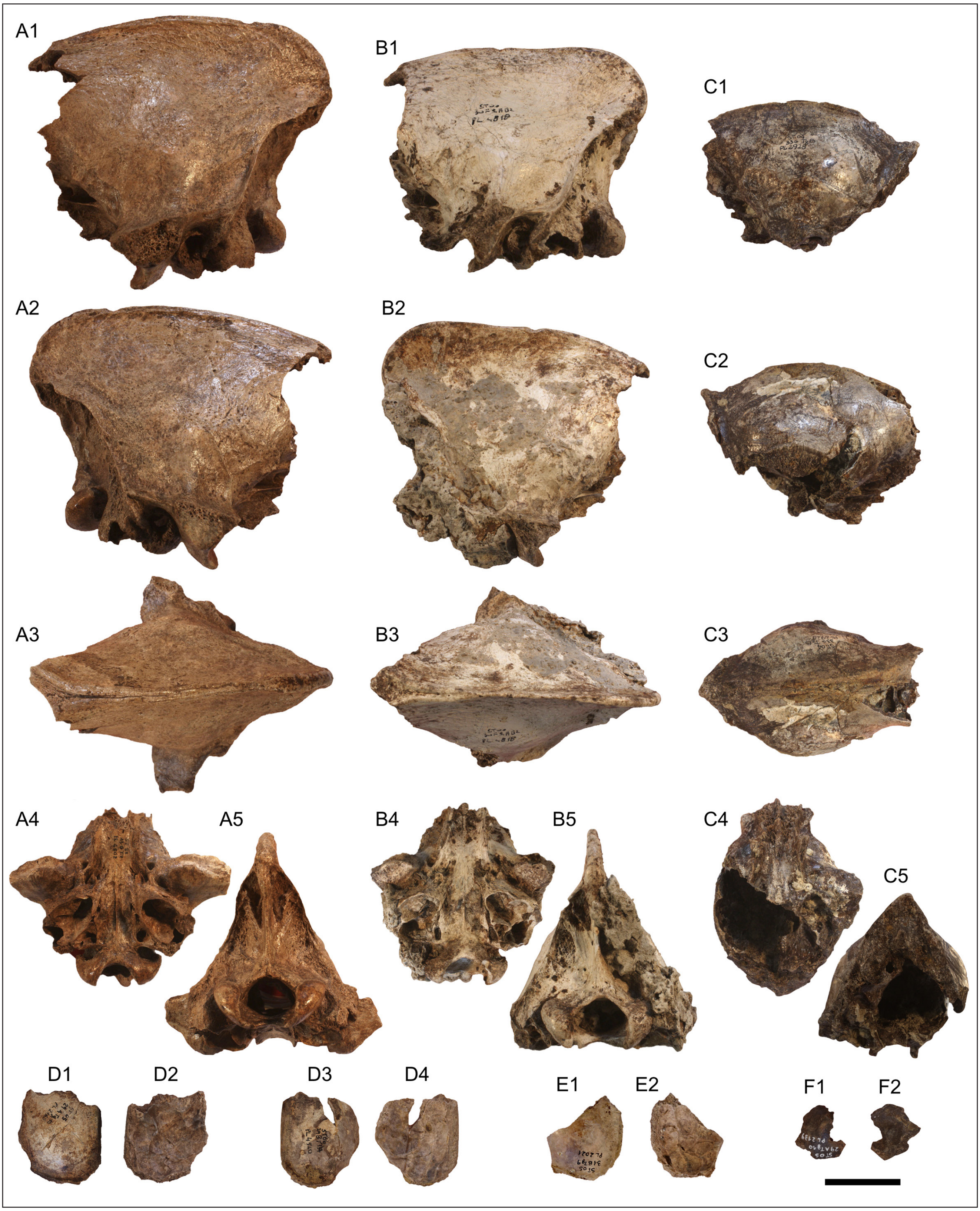

Fig. 2 - Cranial remains of *Crocuta crocuta* from San Teodoro Cave. Neurocrania PL4802 (A), PL4818 (B) and PL2928 (C); parietals PL2165 (D), PL4540 (E) and PL2021 (F). Specimens in left lateral (1), right lateral (2), dorsal (3), ventral (4) and occipital (5) views. Scale bar equal to 50 mm.

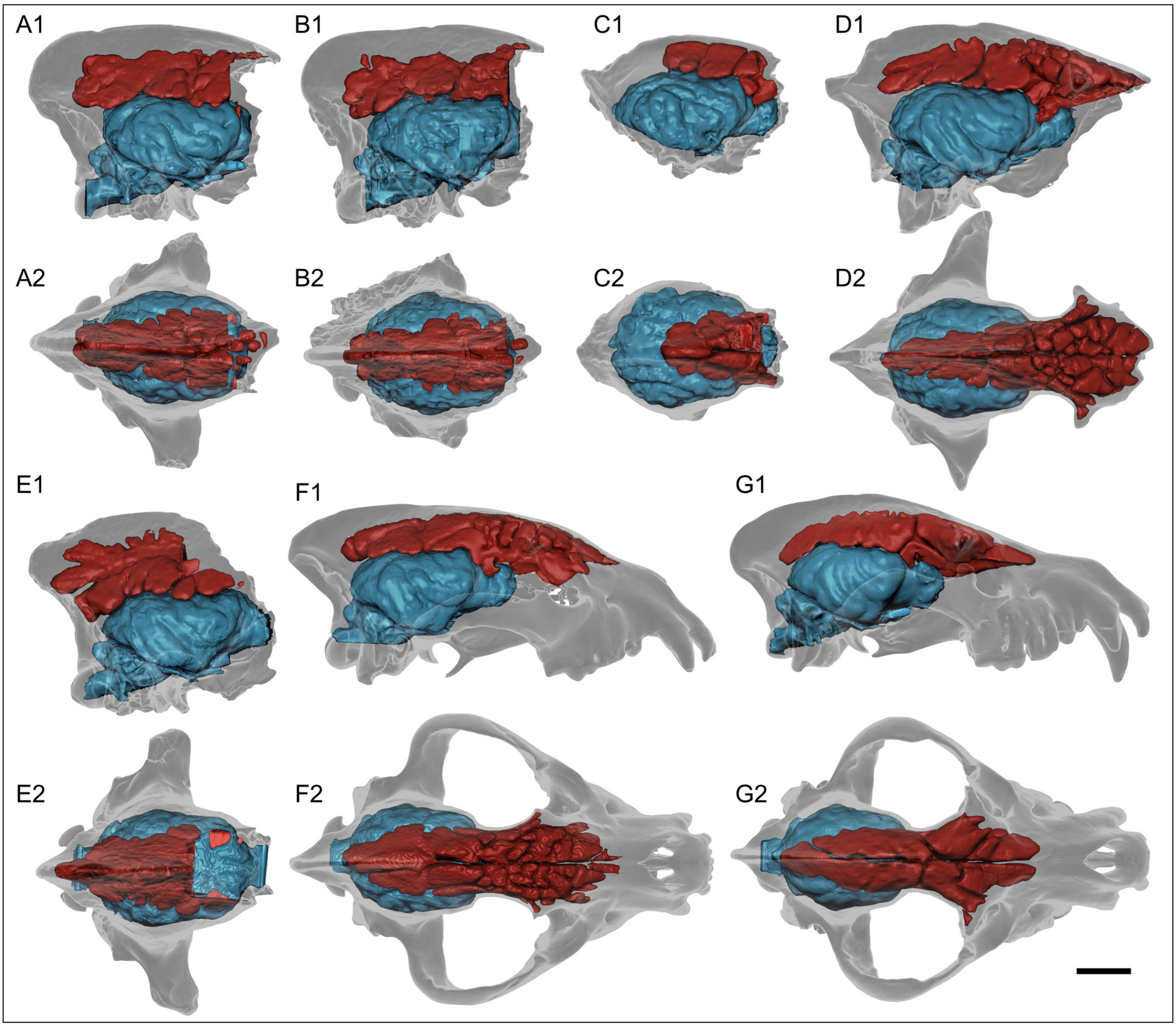

Fig. 3 - CT-based comparison of crania, brain endocasts and frontal sinuses. Late Pleistocene *Crocuta crocuta* from San Teodoro Cave: PL4802 (A), PL4818 (B) and PL2928 (C); Late Pleistocene *C. crocuta* from Melpignano: MPD13 (D) and MPD15 (E); extant *C. crocuta*: MC 377 (F), extant *Hyaena hyaena*: MC 174 (G) and extant *Parahyaena brunnea*: FMNH 34584 (H). Crania in right lateral (1) and dorsal (2) views. Frontal sinuses are marked in red, the brain in light blue. Scale bar equal to 30 mm.

Brains

The brain endocasts (Figs. 3-4) obtained from PL4802 and PL4818 consist of an almost complete and well-preserved cerebrum, a well-developed cerebellum and a portion of brain stem, but both specimens lack olfactory bulbs. In contrast, in PL2928, the brain has well-preserved olfactory bulbs while the cerebellum and the brain stem are missing. The olfactory bulbs of PL2928 are projected slightly downwards, forming a large spongy pad of irregular surface supported by two robust olfactory peduncles. In dorsal and lateral views, the cerebra of the three specimens are globose and all the main sulci and gyri are easily recognisable (for the complete list of the brain convolutions, see Fig. 4). The juvenile specimen PL2928 differs from the two adults by a slight dorsoventral compression of the cerebrum and a shorter coronal sulcus. On the brain endocast of PL4802, a short portion of a Y-shaped blood vessel is recognizable in correspondence of the posterior margin of the longitudinal fissure. Both adult specimens show a well-developed cerebellum with prominent vermis. The latter is broad in the specimen PL4802 and quite narrow in PL4818.

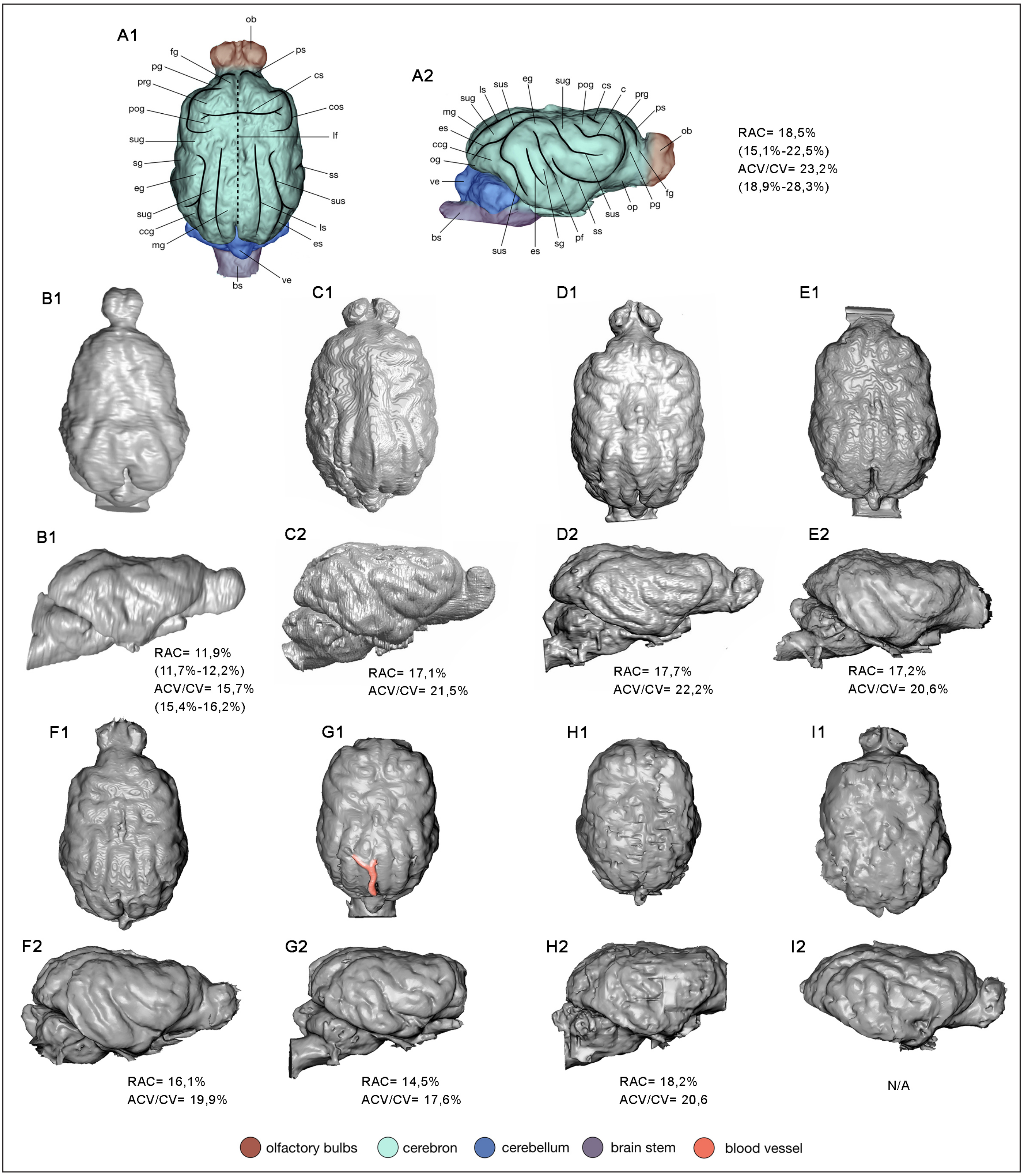

Fig. 4 - Comparison of brain endocasts. Extant *Crocuta crocuta*: MC 377 (A), Early Pleistocene *Pliocrocuta perrieri* IPS36759 from Villarroya (Spain) (B); Middle Pleistocene *Crocuta* from Megenta (Ethiopia): M-ODR-1/1 (C); Late Pleistocene *C. ultima* from Lingxiandong (China): LXD007 (D); Late Pleistocene *C. crocuta* from Melpignano: MPD13 (E) and MPD15 (F); Late Pleistocene *C. crocuta* from San Teodoro Cave: PL4802 (G), PL4818 (H) and PL2928 (I). Abbreviations: ccg, caudal composite gyrus; cos, coronal sulcus; cs, cruciate sulcus; eg, ectosylvian gyrus; es, ectomarginal sulcus; fg, frontal gyrus; is, intraorbital sulcus; ls, lateral sulcus; lf, longitudinal fissure; mg, marginal gyrus; ms, marginal sulcus; ob, olfactory bulb; pf, pseudosylvian fissure; pg, precruciate gyrus; pog, postcruciate gyrus; preg, precruciate gyrus; prg, prorean gyrus; prs, prorean sulcus; ps, presylvian sulcus; sg, sylvian gyrus; ss, sylvian sulcus; sug, suprasylvian gyrus; sus, suprasylvian sulcus; ve, vermis. Brains in dorsal (1) and right lateral (2) views. B modified from Vinuesa et al. (2015); C and D, modified from Flink et al. (2025) with C2 and D2 mirrored. The provided percentages indicate two specific volumetric ratios: the RAC is calculated as the ratio of the anterior cerebrum volume to the total endocranial volume, and the ACV/CV ratio is calculated as the ratio of the anterior cerebrum volume to the cerebrum volume. The reported values for *P. perrieri* and *C. crocuta* represent the mean of 3 and 9 specimens, respectively. N/A = not applicable. All the images are normalised.

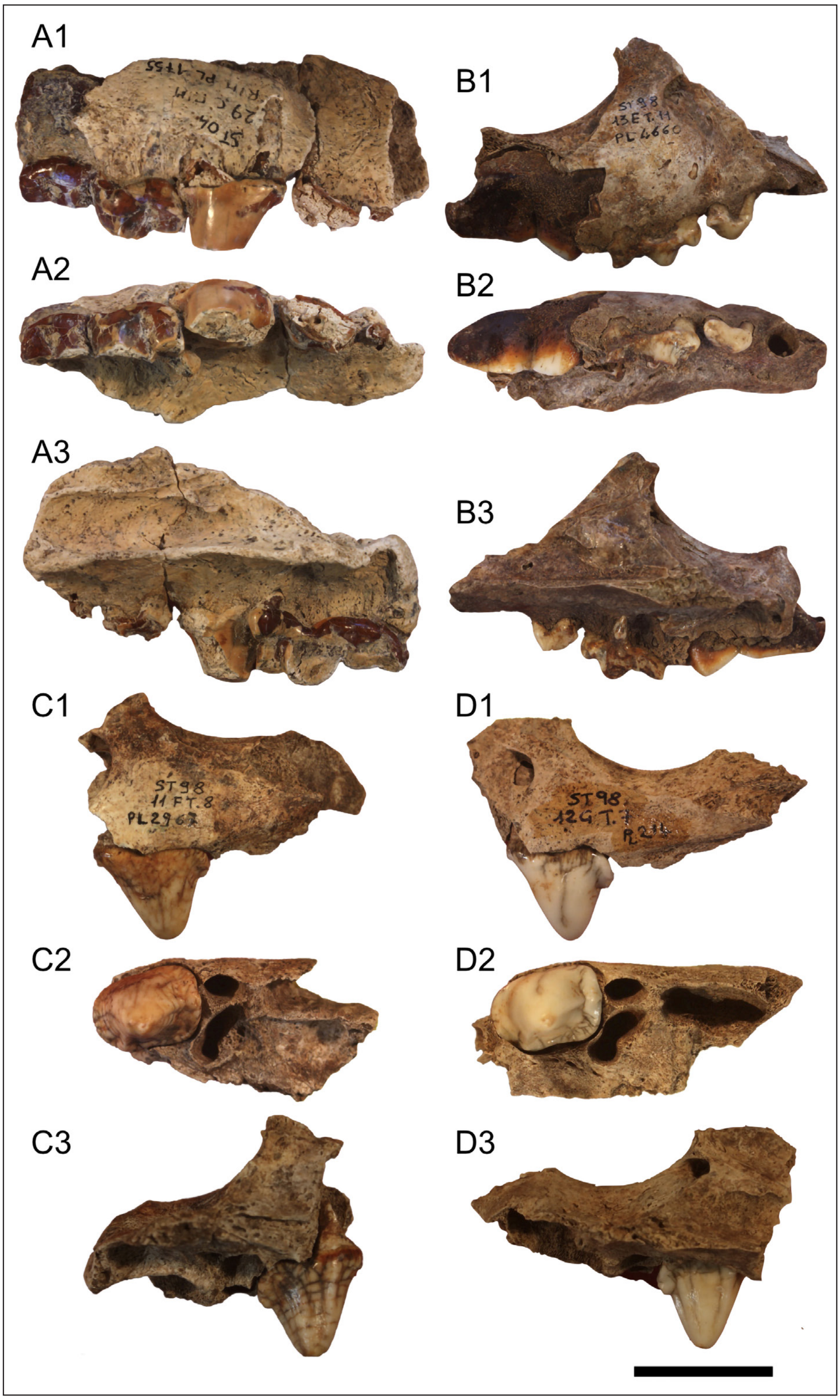

Fig. 5 - Maxillary remains of *Crocuta crocuta* from San Teodoro Cave. PL1755 (A), PL4660 (B), PL2967 (C) and PL214 (D). Maxillae in buccal (1), occlusal (2) and lingual (3) views. Scale bar equal to 30 mm.

Maxillae and upper teeth

The sample consists of 18 remains (Fig. 5) represented by isolated teeth and fragmented maxillaries bearing one or more teeth, except PL3553 which has no teeth. Based on deciduous and permanent teeth, and the degree of tooth wear, 7 cubs, 2 juveniles and 8 adults are recognisable. The most complete specimen of a cub consists of a right maxilla (PL4660) with slightly worn DP^2, DP^3, and erupting P^4. P^1 is missing and only the alveolus, of circular shape, is preserved. Along the bucco-caudal margin, the maxilla is broken, exposing a large portion of P^4. CT images show the presence of additional teeth inside the maxilla, namely the germs of

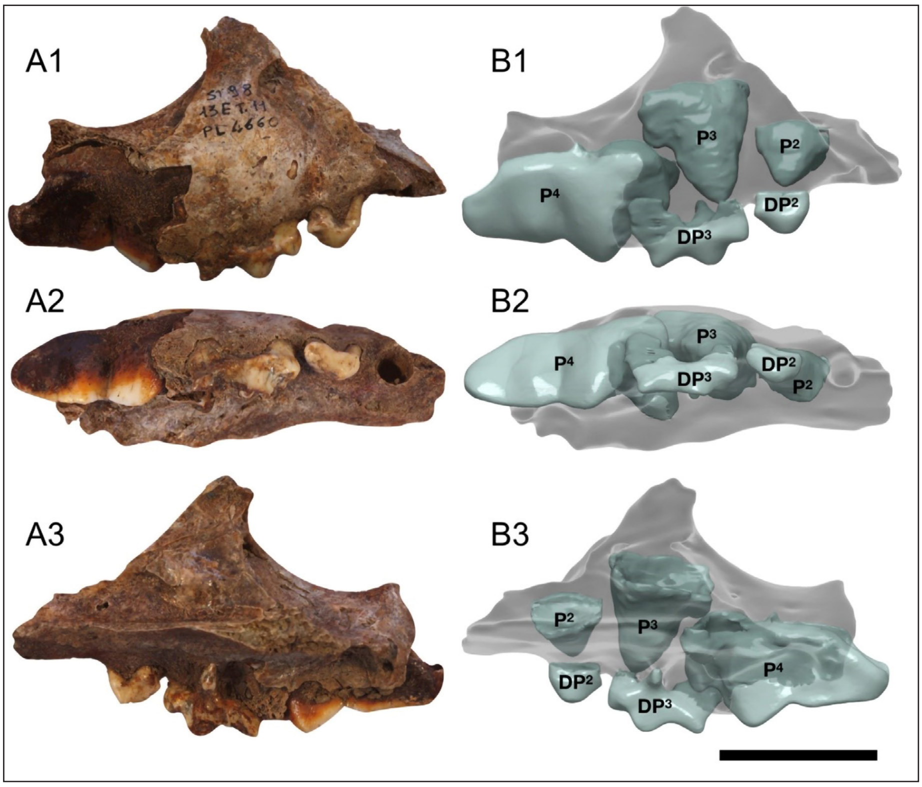

Fig. 6 - Tooth replacement in a juvenile *Crocuta crocuta* from San Teodoro Cave. Photographic (A) and CT-based (B) images of the maxilla PL4660 in buccal (1), occlusal (2) and lingual (3) views. Abbreviations: DP^2, deciduous second premolar; DP^3, deciduous third premolar; P^2, permanent second premolar: P^3, permanent third premolar; P^4, permanent fourth premolar. Scale bar equal to 30 mm.

P^2 and P^3, placed beneath DP^2 and DP^3, respectively (Fig. 6). Except for PL4660, only isolated deciduous teeth testify to the presence of cubs. Both juvenile left maxillae (PL2967 and PL214) are slender and similarly damaged, preserving a fully erupted and unworn P^3, the P^4 alveoli, and the infraorbital foramen. The maxillae of adult individuals are four (PL1755, PL485, PL486, PL3054) all in a poor state of preservation. PL1755 is a right fragment with P^1, P^2, P^3, and P^4. P^3 and P^4 are heavily worn, while P^1 and P^2 are broken, preserving only the basal portion of the crowns. Anteriorly to P^1, the canine alveolus is exposed. The specimen PL485 is a maxillary right fragment with P^3 and P^4 showing an even worse state of preservation compared to PL2967, as the entire lingual portion is embedded in a concretion that reaches up to cover the P^4 cusps. In buccal view, P^3 is exposed from the sediment and shows an advanced degree of wear. The specimen PL486, with P^2, P^3, and P^4, and the specimen PL3054, with P^2 and P^3, are two left fragmentary maxillae almost completely embedded in a hard sedimentary matrix with only small portions of the teeth exposed. In PL486, only P^2 is clearly visible and appears strongly worn, while in PL3054, the teeth are partially visible in buccal view, showing moderate wear.

With respect to the permanent teeth, P^2 has a robust main cusp, with the mesial and distal accessory cusps smaller but well-developed. P^3 lacks accessory cusps and is characterised by a large and stout protocone, surrounded by a cingulum. P^4 has a prominent protocone placed at the level of the parastyle. The protocone is stout and the metacone is the same height of the metastyle. The germs of P^2, P^3, and P^4 have no roots. Regarding the deciduous upper teeth, DP^2 has two roots and shows a simplified crown morphology characterised by a large main cusp and a smaller but well-defined distal cusp. DP^3 has 3 roots and the crown consists of a well-developed paracone, a prominent metacone, and a barely outlined protocone.

Mandibles and lower teeth

The sample consists of 13 left and 10 right fragmented hemimandibles with teeth, and 30 isolated teeth, belonging to 10 cubs, 14 juveniles, and 29 adults, in different preservation conditions (Figs. 7-8). The only complete specimen is a left hemimandible belonging to an elderly individual (PL4819), whose corpus preserves P_2, P_3, P_4, and M_1, all heavily worn. The ramus has an almost complete and well-preserved coronoid process, while the articular and angular apophyses are quite worn. In buccal view, the ramus shows a deep and subtriangular masseteric fossa that extends from the protoconid of M_1 to the angular process of the condyle.

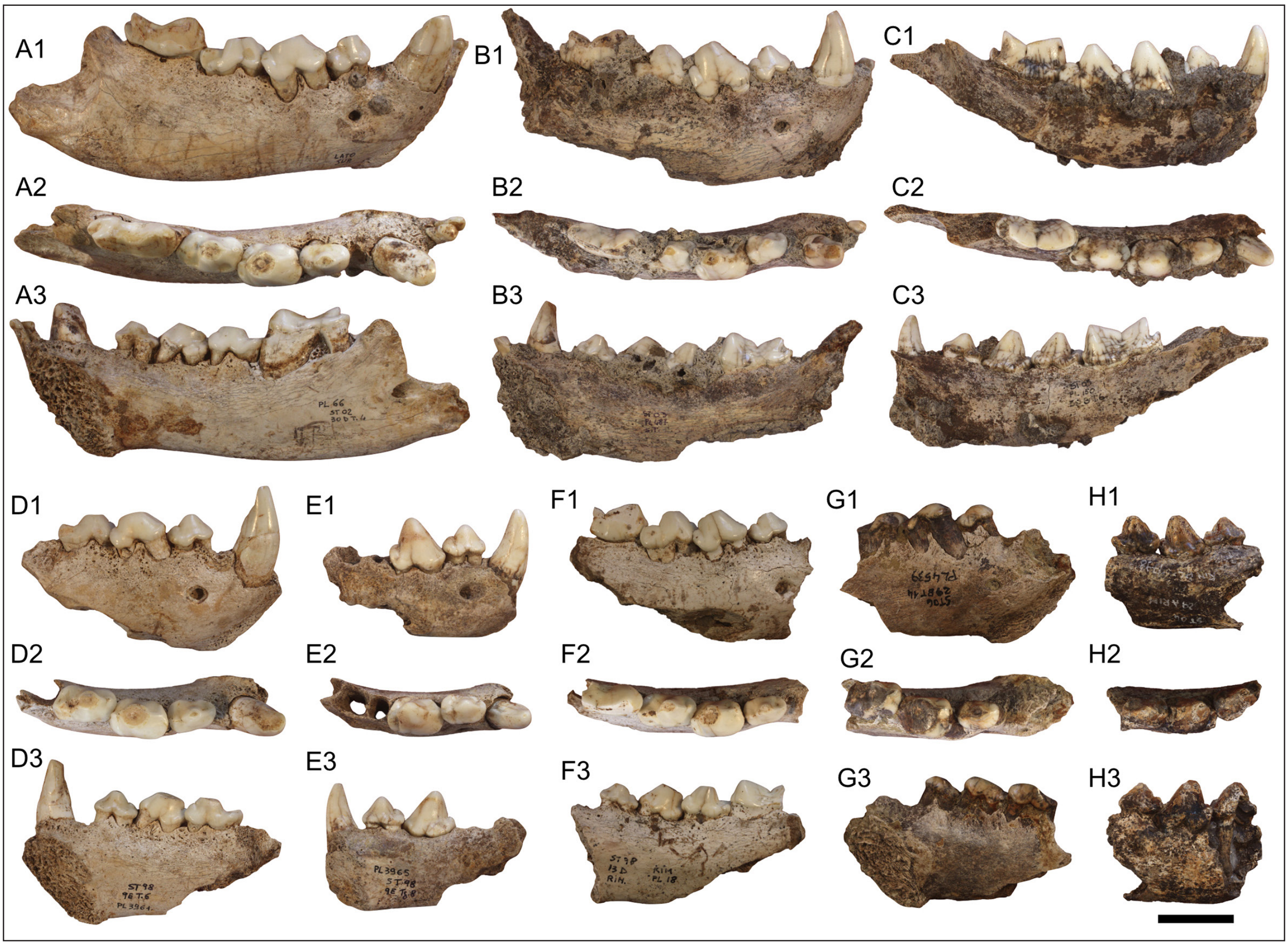

Fig. 7 - Right mandibles of *Crocuta crocuta* from San Teodoro Cave. PL66 (A), PL487 (B), PL150 (C), PL3961 (D), PL3965 (E), PL18 (F), PL4539 (G) and PL1798 (H). Mandibles in buccal (1), occlusal (2) and lingual (3) views. Scale bar equal to 30 mm.

In those specimens where the corpus is preserved, in lateral view, its basal edge is strongly convex at the level of M_1. The hemimandibles are mesio-lingually curved. In all the samples, in buccal view, a single mental foramen is placed at the level of P_2 except in PL17, where a second foramen is placed at the level of the canine. The specimen PL758 is the only hemimandible belonging to a cub, consisting of a proximal fragment of the ramus with unworn DP_3 and DP_4. The mesial root and part of the crown of DP_3 are missing, DP_4 is complete. In ventral view, the ramus is broken exposing the alveoli of the permanent teeth (P_4 and M_1), which are missing. In lateral view, the specimen has a short and well-preserved coronoid process, whereas both the articular and angular apophyses are missing. Compared to adults, the juvenile specimens (PL3470, PL2429, PL150, PL3965, and PL1798) possess a slender mandibular corpus and unworn teeth.

Permanent teeth are well represented. I_1 has a very simple crown, without accessory cusps and with rounded margins. I_2 is similar to I_1, but the crown is more elongated, while I_3 is drop-shaped and has a small distal cusp. C_1 is robust, slightly curved, and separated from P_2 by a short diastema, the size of which varies between individuals. P_2 displays a well-developed protoconid, surrounded mesially by a broad cingulum. The accessory cusp is prominent and separated from the main cusp by a transverse groove. P_3 is characterised by a well-developed and distally tilted protoconid, with a marked cingulum on the mesial and distal edges, and a small distal accessory cusp. P_4 also shows a robust and distally tilted protoconid. Two accessory cusps are recognisable, of which the distal is more developed than the mesial. M_1 has a large paraconid and a less developed protoconid, a broad cingulum on the lingual side, and a short tal-

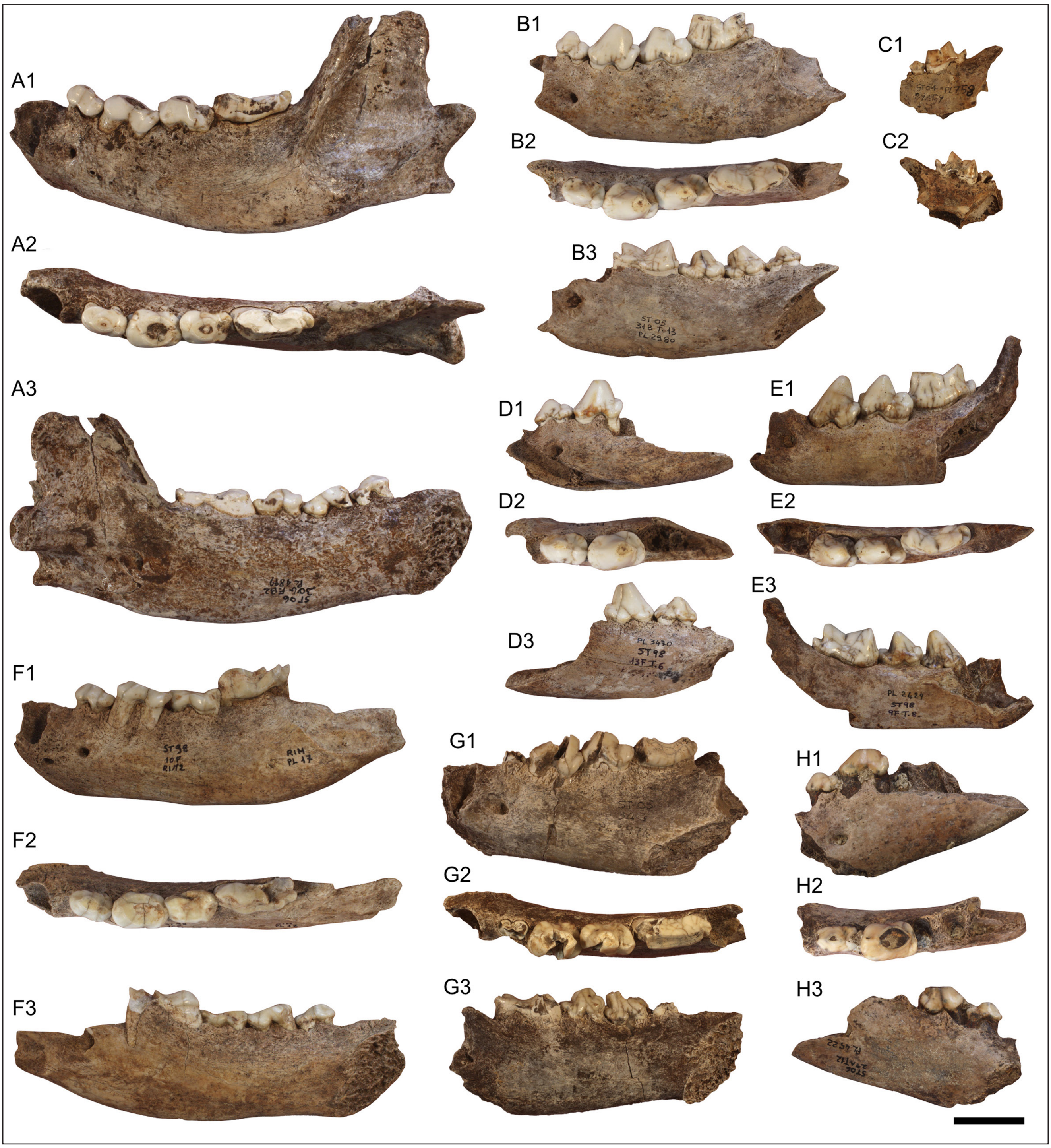

Fig. 8 - Left mandibles of *Crocuta crocuta* from San Teodoro Cave. PL4819 (A), PL2980 (B), PL758 (C), PL3470 (D), PL2424 (E), PL17 (F), PL2974 (G) and PL4522 (H). Mandibles in buccal (1), occlusal (2) and lingual (3) views. Scale bar equal to 30 mm.

onid. Only the specimen PL4819 displays a small metaconid. DP_3 has one main and two smaller cusps, one mesial and one distal DP_4 has two roots, the crown has well-developed paraconid and protoconid, with the protoconid higher than the paraconid, a small talonid and a prominent and stout distal cusp.

Postcranial bones

The sample (Fig. 9) consists of 2 vertebrae (axis), 2 scapulae, 2 humeri, 6 radii, 4 ulnae, 1 hip bone, 2 tibiae, 5 femora, 1 scapholunate, 1 calcaneus, and 2 metapodials, most of the bones are referable to adult individuals, apart from a radius and a tibia. Colour and preservation conditions vary considerably within the sample and only the vertebrae, the calcaneus, and the scapholunate are complete. All the postcranial bones show no evidence of abrasion or weathering, the surface of the bones is compact, and some bitemarks are detectible on long bones.

Vertebra. (Fig. 9A-B) The sample consists of 2 well-preserved and almost complete axes (PL1783, PL3969) with PL1783 larger than PL3969. In the latter specimen, the upper portion of the spinous process is partially missing, the resulting fracture line is irregular and horizontally oriented, while in PL1783 the caudal portion of the corpus is broken. Both specimens have straight and prominent odontoid processes. The superior and inferior articular facets are sub-oval-shaped and smooth. The vertebral foramen is wide with a sub-triangular section, the transverse foramina are oval in shape and bordered by a transverse process that appears stout in PL1783 and markedly thinner in PL3969. Neither vertebrae display evidence of bite marks.

Scapula. (Fig. 9C) The right scapula (PL4150) consists of a small fragment of the articular portion. The glenoid cavity is oval in shape with a pronounced coracoid process, both the anterior and posterior blades are missing while the spine and acromion are strongly worn. The left scapula (PL1904) is a small distal fragment lacking the articular portion.

Humerus. (Fig. 9D) The distal epiphysis of the right humerus (PL3173) is broken above the olecranon fossa, but the articular portion is well preserved. The trochlea is wide, with smooth and compact bone. The olecranon is well developed with a semi-circular supratrochlear foramen. The second humerus (PL2450) is represented only by a small and poorly diagnostic fragment of left diaphysis.

Ulna. (Fig. 9E) The sample consists of 2 mid-proximal left epiphyses (PL439, PL2), 1 proximal right epiphysis (PL4321), and 1 left diaphysis (PL2677). In PL439, PL2, and PL4321 the olecranon process is missing and the coronoid process is well-developed, showing a marked triangular depression below the semilunar notch. PL2 and PL2677 are poorly diagnostic fragments of left ulnae with visible bite marks. PL4321 is a small proximal portion of a right ulna preserving the semilunar notch, with evidence of bite marks.

Radius. (Fig. 9F) The sample consists of 2 mid-proximal right epiphyses (PL2859, PL4804), 1 distal right epiphysis (PL4286), 2 mid-proximal left epiphyses (PL4183, PL4091), and 1 large splinter of a right diaphysis (PL4081). The head of the radii has an oval outline, the radial tuberosity is poorly marked and is placed on the proximolateral portion of the diaphysis. The latter is slightly curved, has a semi-circular cross section, and is antero-posteriorly flattened. PL4804 belongs to a young specimen and shows clear bite marks on both edges of the bone.

Scapholunate. (Fig. 9G) The right scapholunate (PL3053) is flat, complete, and well preserved. Only few small abrasions are visible on the distal surface, exposing the spongy bone tissue.

Hip bone. (Fig. 9H) The right pelvic girdle (PL2949) of an adult specimen is relatively complete, although several portions are missing, and consists of ilium, ischium, and pubis. The ilium is the most damaged bone, both corpus and ramus are deeply fractured with some missing fragments, the wing of the ilium is not preserved. The acetabulum is wide, deep, and circular in shape. The ischium and pubis are also fractured, but on the whole, they retain their integrity and large oval-shaped obturator foramen. The pubic symphysis has an elongated and straight margin, and the ischium tuberosity is partially preserved. Bite marks are visible on the edges of the bones.

Femur. (Fig. 9I) The sample is represented by 1 partially complete right femur (PL295), 2 left diaphyses (PL4817, PL2988), and 2 fragments of diaphysis, right (PL4079) and left (PL4095). Of the femora, PL295 is the best preserved and most diagnostic specimen, although the distal epiphysis is missing and on the proximal epiphysis the greater trochanter is partially damaged. The head is spherical in shape and is connected to the diaphysis by a strong and short neck. The diaphysis is robust, slightly curved with a circular cross-section, which becomes oval at the epiphyses. PL4817, PL2988, PL4079, and PL4095 are robust diaphyses, referable to adult individuals but of little diagnostic value. Bite marks are present throughout the sample.

Tibia. (Fig. 9J) The sample consists of a robust and well-preserved left tibia (PL2613), lacking only the proximal epiphysis. The proximal portion of the bone has a triangular cross-section, which is retained throughout the diaphysis except for the distal portion, where it becomes nearly oval. The tibial crest is wide, while the distal epiphysis is partially damaged, with a laterally projecting, rounded malleolus.

Fig. 9 - Selected sample of postcranial bones of *Crocuta crocuta* from San Teodoro Cave. Axis PL1783 in left lateral (A1) and dorsal (A2) views; axis PL3969 in left lateral (B1) and dorsal (B2) views; right proximal scapula PL4150 in dorsal (C1), cranial (C2) and ventral (C3) views; right distal humerus PL3173 in cranial (D1), left lateral (D2) and caudal (D3) views; left proximal ulna PL439 in left lateral (E1), cranial (E2) and right lateral (E3) views; left proximal radius PL4091 in left lateral (F1), cranial (F2) and right lateral (F3) views; right scapholunate PL3053 in dorsal (G1) and ventral (G2) views; right pelvic girdle PL2949 in dorsal (H1) and right lateral (H2) views; right femur PL295 in cranial (I1), right lateral (I2) and caudal (I3) views; left tibia PL2613 in left lateral (J1), cranial (J2) and right lateral (J3) views; right calcaneus PL4310 in cranial (K1) and caudal (K2) views. Scale bar equal to 50 mm.

Calcaneus. (Fig. 9K) The right calcaneus (PL4310) is complete and quite well-preserved, only the articular surface with the cuboid shows minor damage. The calcaneal tuberosity is robust and elongated, with a marked postero-dorsal process. The body is compact, the talar facets are oval-shaped and smooth. The sustentaculum tali is medially projected.

Metatarsal. The mid-distal left metatarsal III (PL4067) is robust, the diaphysis is straight with a semi-circular cross-section.

Morphological comparisons

From a morphological perspective, the cranial and postcranial sample from San Teodoro, including adults and juveniles, fall perfectly within the variability of *C. crocuta*, taking into account both fossil and extant spotted hyaenas. The similarity of the crania is also confirmed by the endocranial anatomy. Indeed, the paranasal sinuses of the San Teodoro sample are indistinguishable from those of Melpignano and other Late Pleistocene and extant *Crocuta* (Fig. 3). Similarities in sinal cavities between the extant and Late Pleistocene spotted hyaenas have already been reported by Dockner (2006). While *P. brunnea* falls within the morphological variability of *Crocuta*, *H. hyaena* exhibits distinct paranasal sinuses characterized by a smoother and less irregular surface (Fig. 3). This character is also evident in *H. hyaena* specimens figured by Dockner (2006).

Brain morphology and convolution patterns display no significant differences between fossil and extant spotted hyaenas, with the San Teodoro sample aligning perfectly with the morphology of extant and Middle-Late Pleistocene *C. crocuta* (Fig. 4). Among the differences, the brain endocasts of the Pliocene-Early Pleistocene *Pliocrocuta perrieri* are more elongated and possess a narrower anterior cortex compared to other hyaenas, as previously noted by Vinuesa et al. (2015). A slight elongation is also observed in *C. ultima*, but in this species, the cortex appears more globose in shape. Flink et al. (2025) also reported differences in brain convolutions between fossil and extant *C. crocuta* (see Flink et al. 2025, for more details). However, the reported differences, concerning the inclination of the rostral portion of the suprasylvian sulcus – specifically, the contrast between the diagonal orientation in the fossil specimens and the vertical orientation in the extant species – are difficult to assess on the San Teodoro sample and in some extant *Crocuta* specimens. Instead, the proreal sulcus is clearly recognisable and appears more marked in the endocasts of fossil *Crocuta*, as already pointed out by Flink et al. (2025). There are differences in convolution patterns of *P. brunnea* and *H. hyaena* with respect to *C. crocuta*. For instance, *C. crocuta* exhibits a more anteriorly positioned cruciate sulcus, longer sylvian and ectosylvian sulci, and a larger suprasylvian gyrus. Additionally, in both fossil and extant spotted hyaenas, the olfactory bulbs project slightly downwards, whereas in *P. brunnea* and *H. hyaena*, they face upwards, reaching the dorsal plane of the telencephalon in lateral view. These distinctions have been previously reported by Vinuesa et al. (2015, 2016). However, the possibility that these differences, including those observed in brain convolutions, may reflect intraspecific variability cannot be entirely excluded. In all examined specimens, the cerebellum exhibits a trilobate structure with a prominent and well-developed vermis.

Biometric comparisons

The mean and ranges of the linear measurements obtained for the San Teodoro sample, together with those of the comparative dataset, are provided in Table 1 (raw data and details in Supplementary information). Shapiro-Wilk tests were carried out to evaluate the adherence of the considered variables to a normal distribution. The latter hypothesis is verified in most cases, the only exceptions (p-value < 0.05) being P_2 L in the sample from Kents Cavern and P_4 W in the sample from Goyet (Supplementary information). Non-parametric Mann-Whitney tests for equality of medians were used for these cases, ANOVA for all the others (Table 2; Supplementary information). The sample of Goyet is excluded when evaluating the significance of differences in P^3 L, as it is represented only by 4 observations. Linear measurements that have been considered in the statistical analysis are visualised through boxplots in Figure 10.

Considering the results of post-hoc Tukey's tests conducted on ANOVA for P^3 L, P_3 L, P_3 W, and P_4 W, San Teodoro is always significantly (p-value < 0.05) smaller than the other fossil samples, except for P_3 L from Kents Cavern. On the other hand, in P_2 L, San Teodoro hyaenas do not significantly differ from the samples of Teufelslucken, Goyet, and Kents Cavern, but all fossil groups are significantly larger than the extant African sample. Differences between MIS 3 continental samples are few and seldom significant (Teufelslucken being somewhat larger than Goyet and Kents Cavern).

Apart from the results observed for P_2 L, in general, San Teodoro hyaenas are smaller but partly

Group	P^3 L	P_2 L	P_3 L	P_3 W	P_4 W	M_1 L	M_1 W
San Teodoro	22.96 (22.25-23.69)	17.03 (16.13-18.14)	21.52 (20.68-22.65)	14.29 (14.11-14.45)	13.32 (12.46-14.36)	30.97 (29.98-31.79)	13.02 (12.62-13.38)
Kents Cavern	24.61 (21.72-28.49)	16.62 (15.32-18.8)	22.42 (20-24.98)	16.49 (14.57-18.9)	14.93 (12.64-17.11)	32.42 (28.65-36.09)	13.87 (11.76-15.18)
Goyet	25.44 (24.73-26.58)	17 (15.81-17.93)	22.89 (22.11-24.28)	16.41 (15.25-17.52)	14.96 (14.27-16.59)	32.12 (30.23-34.79)	13.87 (13.12-14.45)
Teufelslucken	25.5 (22.34-27.04)	16.86 (14.9-19.3)	22.92 (20.63-24.63)	16.73 (14.62-18.18)	15.3 (13.65-16.8)	33.13 (30.04-36.07)	14.17 (12.85-15.5)
Balbal	21.27 (18.89-23.34)	14.46 (12.88-16.49)	19.87 (18.34-22.16)	13.87 (12.69-15.14)	12.04 (11.05-13.23)	26.6 (24.48-28.78)	11.15 (9.91-12.13)

Tab. 1 - Measurements (in mm) of the groups of hyaenas included in the biometric comparison of the dentition. Mean, minimum, and maximum values are provided. Data in Supplementary information.

P^3 L	Kents Cavern	Goyet	Teufelslucken	Balbal
San Teodoro	*	N/A	*	*
p_2 L	Kents Cavern	Goyet	Teufelslucken	Balbal
San Teodoro	ns	ns	ns	*
p_3 L	Kents Cavern	Goyet	Teufelslucken	Balbal
San Teodoro	ns	*	*	*
p_3 W	Kents Cavern	Goyet	Teufelslucken	Balbal
San Teodoro	*	*	*	ns
p_4 W	Kents Cavern	Goyet	Teufelslucken	Balbal
San Teodoro	*	*	*	*

Tab. 2 - Summary of the results of the comparative statistical analysis carried out for the dentition, indicating significant (*) or not significant (ns) differences, with $\alpha = 0.05$. N/A = not applicable (low sample size). Data and detailed results in Supplementary information.

overlap in linear measurements with continental MIS 3 samples, while they are larger than the extant assemblage from Balbal.

In Figure 10, a bivariate comparison between M_1 L and M_1 W is also shown. Although the paucity of observations for San Teodoro (n = 3) precluded performing statistical tests, the biometric comparison of the lower carnassial provides indications similar to those obtained from the rest of the dentition. San Teodoro hyaenas are, on average, smaller than the other fossil samples, but larger than the extant group from Balbal.

The volume of paranasal sinuses (data in Supplementary information), reveal significant overlap between extant and Late Pleistocene *C. crocuta*. The single *P. brunnea* specimen included in this study also falls within the volume range observed in *Crocuta*. In contrast, *H. hyaena* exhibits the smallest paranasal sinus volumes within the sample. San Teodoro specimens display smaller brain sizes compared to *C. ultima*, which possesses the largest brain and olfactory bulbs in the sample (data in Supplementary information). The San Teodoro endocasts exhibit brain sizes comparable to those reported for other Upper Pleistocene spotted hyaenas, sharing with the Melpignano specimens similar volumes and proportions of the olfactory bulbs, anterior cerebrum, posterior cerebrum, and cerebellum plus brainstem.

The brain of the Middle-Upper Pleistocene specimens falls within the size and volume variability of extant *C. crocuta*, with the exception of *C. ultima*. The relative anterior cerebrum volume (RAC) of extant *C. crocuta* encompasses a wide range of values, indicating that this particular portion of the brain is subject to considerable variability. Nonetheless, in extant *C. crocuta*, the RAC is higher on average and absolute values than across the entire sample included in the comparison (Fig. 4) (data in Supplementary information). Fossil specimens from Africa and Eurasia show very similar RAC values, which are lower than the average value observed in the extant *Crocuta*. The Pliocene-Early Pleistocene *P. perrieri* possess the lowest RAC values among the compared species. While *P. brunnea* and

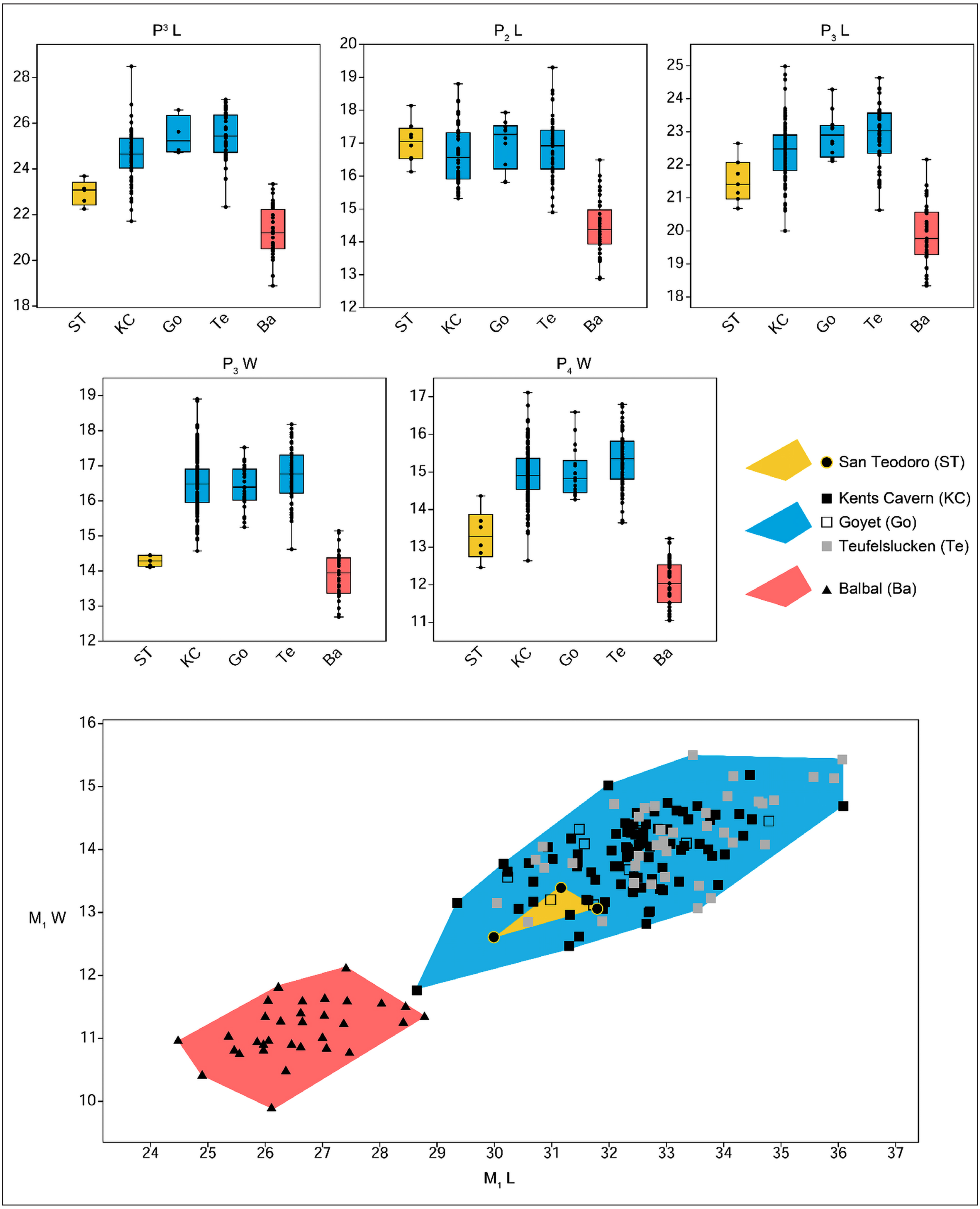

Fig. 10 - Univariate and bivariate comparisons of dental measurements (in mm) of *Crocuta crocuta* from San Teodoro Cave and other fossil (Teufelslucken, Goyet, and Kents Cavern) and recent (Balbal) samples.

H. hyaena exhibit average olfactory bulb volumes comparable to those of fossil and extant *Crocuta*, they display a larger relative volume of the cerebellum plus brainstem.

Discussion

Despite the presence of *Crocuta* in Africa during the Pliocene, around 4 Ma, its earliest evidence in the European fossil record dates back only to around 0.8 Ma, just before the Early-Middle Pleistocene boundary (Iannucci et al. 2021; Lewis & Werdelin 2022). This delayed expansion is considered an important biochronological and palaeoecological event, documenting the spread of an adaptable taxon, capable of coping with the increase in the amplitude of climate oscillations occurring between the late Early and the early Middle Pleistocene, in contrast to the larger and more specialised *Pachycrocuta brevirostris*, which went extinct (Iannucci et al. 2021). Even then, during the latest Early and early Middle Pleistocene, the record of *Crocuta* is, however, quite limited in terms of number of localities and number of specimens. The latter consideration is especially evident, if comparison is made with the hundreds of localities with remains of cave hyaenas known during the Late Pleistocene, some of which represent "massive occurrences" counting thousands of identified specimens (Iannucci et al. 2021; Lewis & Werdelin 2022). The exact timing of this shift in abundance and its potential palaeoecological significance, perhaps indicating some connection with the exploitation of caves (Kurtén 1956), are still unresolved. In any case, the presence of spotted hyaenas in Sicily is emblematic of this moment of great expansion, and the sample of San Teodoro, being abundant and approximately coeval to some extensive continental assemblages, offered us the unique opportunity to investigate the potential existence of differences between Late Pleistocene *Crocuta* inhabiting mainland and peripheral areas.

San Teodoro hyaenas adhere in morphology to other extinct and extant samples of *C. crocuta*. The most salient differences between and San Teodoro and other samples emerge when looking at dental size and proportions. In general, San Teodoro hyaenas are smaller than their counterparts from roughly coeval sites of mainland Europe – which are generally close to one other – but larger than the extant sample. An important exception is P_2 L, which shows no significant difference between San Teodoro and the other samples, apart from Balbal. P_2 is a tooth proportionally reduced in size in *Crocuta* in comparison to other hyaenas, reflecting its minor importance in processing food, compared to the rest of the posterior dentition, especially the role of P_3, a feature that is evolutionary linked to a bone-cracking specialisation (Lewis & Werdelin 2022). The retention of a relatively large P_2 in San Teodoro hyaenas, despite a general smaller size of the rest of the dentition, can be explained considering a period of isolation between Sicilian and continental hyaenas, long enough to cause a reduction in actively selected features, but not enough to cause a reduction in P_2. This tooth, being relatively less important than other teeth, may therefore have retained a size close to that present in the ancestral population colonizing Sicily. *Crocuta* is already present in Sicilian faunas biochronologically included in the *Palaeoloxodon mnaidriensis* FC, which is considered to derive from a colonization event occurred during the late Middle Pleistocene, and in the following Late Pleistocene San Teodoro-Pianetti FC (Masini et al. 2008; Antonioli et al. 2016). An alternative explanation would imply a selective pressure responsible for promoting a lesser degree of bone-cracking behaviour in Sicilian hyaenas, an option that seems unlikely, considering that taphonomic analyses at San Teodoro confirmed the bone-cracking habit especially on bones of medium-sized ungulates, such as *Cervus elaphus siciliae*, *Sus scrofa* and *Equus hydruntinus* (e.g., Mangano 2011). Moreover, taking into account that insular environments are characterised by a low availability of trophic resources, this should favour exploiting carcasses "to the bone", rather than the opposite.

Concerning endocranial anatomy, both the brain and paranasal sinuses of the San Teodoro hyaenas exhibit significant morphological and biometric similarities with extant and Middle-Late Pleistocene *C. crocuta*. Notably, the brain volumes observed in both fossil and present-day specimens fall within the same range of variability, despite the larger body size of Pleistocene spotted hyaenas. The only exception is represented by the Late Pleistocene *C. ultima* from China, which exhibits a larger brain volume than its European and African counterparts, despite sharing remarkable similarities in skeletal morphology and body size. This finding suggests that the brain size in *Crocuta* appears to be relatively unaffected by body size variation. However, as only one specimen of *C. ultima* was available for comparison, a larger sample size is required to establish whether this increase in brain volume is a peculiar feature of Asian populations. If so, the palaeoneurological data could reflect the divergence between Asian and European Pleistocene spotted hyaenas evinced by palaeogenomic studies (Hu et al. 2021).

The relative volume of the anterior cerebrum in San Teodoro specimens falls within the range of variability observed in Middle-Late Pleistocene *Crocuta* and extant *P. brunnea* and *H. hyaena*, even though the latter have generally smaller values. There is some overlap in the relative volume of the anterior cerebrum between extant and fossil *Crocuta*, but the latter are always below the average values of recent individuals (Fig. 8) (data in Supplementary information). The enlargement of this specific brain region appears to be an exclusive feature of the extant African spotted hyaena, the only extant hyaena species exhibiting cooperative hunting and forming large packs. The frontal cortex is known to mediate complex social behaviour in various mammals, including primates (Dunbar & Bever 1998; Dunbar 2003a,b), canids (Radinsky 1969; Iurino et al. 2022; Azzarà et al. 2025), and spotted hyaenas (Holekamp et al. 2007a,b, 2015; Arsznov et al. 2011; Sakai et al. 2011; Vinuesa et al. 2016; Flink et al. 2025). Therefore, a larger frontal cortex may be associated with enhanced social skills, such as the ability to hunt cooperatively in packs or the ability to express a wider repertoire of vocalizations and more complex social interactions among pack members. If this correlation holds true, it is plausible to assume that the spotted hyaenas from Sicily, as well as those from the Middle-Late Pleistocene of Eurasia and Africa, led a more solitary lifestyle, occasionally forming small packs of a few individuals, as documented in the extant *P. brunnea* (Mills 1983) and *H. hyaena* (Califf et al. 2020; Tichon et al. 2020). Based on currently available data, Africa appears to be the area where the increase in anterior cerebrum volume and the subsequent evolution of complex sociality in the genus *Crocuta* occurred. However, we still know very little about the timing of this event. In a recent study on the neuroanatomy of a Middle Pleistocene cranium of *Crocuta* from Megenta (Ethiopia), Flink et al. (2025) reported that the specimen exhibits a relative anterior cerebrum volume exceeding that of other fossil samples from the Upper Pleistocene of Eurasia and aligning with the range observed for the extant *Crocuta*. Based on this, the authors proposed that the evolution of social complexity in *Crocuta* predates the estimated age of 500–350 ka of the Megenta cranium. However, a re-evaluation of the data reported by Flink et al. (2025) (data in Supplementary information) reveals a methodological discrepancy in the calculation of the relative anterior cerebrum volume. Specifically, the authors derived this metric using the ratio of the anterior cerebrum volume (ACV) to the total cerebrum volume (CV). This approach represents a departure from the established protocol of previous studies (e.g., Sakai et al. 2011; Vinuesa et al. 2015, 2016), which defined the relative anterior cerebrum volume (RAC) as the ratio of the ACV to the Total Endocranial Volume (TEV), which includes the olfactory bulbs, the entire cerebrum, the cerebellum, plus brain stem. Consequently, Flink et al. (2025) compared values derived from two distinct and non-equivalent ratios, ACV/CV and RAC (i.e., ACV/TEV). Calculating the RAC of the Megenta specimen reveals that it falls within the range of variability documented for the Eurasian fossil sample, as it does comparing the ACV/CV ratio. Therefore, the neuroanatomical features of the Megenta specimen are congruent with that observed in the Eurasian fossil record.

As aforementioned, although there is some overlap in RAC and ACV/CV between fossil and recent individuals of *Crocuta*, all African and Eurasian Pleistocene specimens fall below the average values reported for the extant spotted hyaena. It is therefore parsimonious to conclude that they did not yet exhibit the great social complexity observed in extant *Crocuta*.

While sociability is the most plausible explanation for the enlargement of the anterior brain in *C. crocuta*, other factors, such as diet or behavioural flexibility, may also play a role (Holekamp et al. 2015). The correlation between frontal cortex volume and diet is based on the observation that living species with a highly developed anterior brain (*C. crocuta*) are mainly active hunters, whereas species with a moderately developed anterior brain (*P. brunnea* and *H. hyaena*) are mainly scavengers, and species with a poorly developed anterior region [*Proteles cristatus* (Sparrman, 1783)] is an insectivore. A large frontal cortex would therefore help spotted hyaenas to deal with new and unpredictable environments and challenging preys, allowing individuals to display a broader behavioural flexibility than other hyaenas. However, since this hypothesis, named the "cognitive buffer" hypothesis (Reader & MacDonald 2003; Richardson & Boyd 2000; Sol 2009a,b; Holekamp et al. 2015), was based exclusively on present-day hyaenas from continental Africa, its applicability in insular settings has never been tested. Considering both taphonomic (Mangano 2011) and palaeoneurological evidence, it is plausible that spotted hyaenas from San Teodoro mainly acted as scavengers and opportunistic hunters, probably operating in small packs (Fig. 11) or even solitarily, resembling in ecology and behaviour the extant brown hyaena. Some populations of the latter species that currently live in environments with scarce trophic resources, such as the Namibian coast, represent an interesting reference, as they actively hunt seals despite being mainly scavengers (Mills 1982, 1990; Wiesel 2006, 2010; García-Nos et al. 2024). Although in contrast with the prevailing assumption that San Teodoro hyaenas exhibited behavioural similarities with extant *C. crocuta*, this alternative hypothesis offers a more reliable explanation, particularly considering the insular context and the co-occurrence of spotted hyaena with a key competitor, the wolf *Canis lupus*. While during the Late Pleistocene Sicily hosted several ungulates, the density of prey populations, as well as their capacity to support two sympatric species of large pack hunter carnivores, is questionable.

The cognitive buffer hypothesis posits that a larger frontal cortex is associated with enhanced cognitive flexibility, which is advantageous in variable environments. Insular habitats are susceptible to rapid and dramatic environmental changes, which may have favoured the development of such cognitive capacities in the San Teodoro hyaenas, despite the lack of direct palaeoneurological evidence. However, we believe that a strict association between frontal cortex development and behavioural and/or ecological flexibility is not supported, as in highly adaptable species with broad geographic distributions, such as *H. hyaena*, *Vulpes vulpes* and *Panthera pardus* (Linnaeus, 1758), the frontal cortex is relatively reduced (Vinuesa et al. 2016; Sakai et al. 2016; Azzarà et al. 2025).

In light of this, palaeoneurological data offer new insights into the neuroanatomy of fossil spotted hyaenas and open new scenarios on their ecology and behaviour, but fail to reveal any evidence of a possible effect of insularity. However, this finding is consistent with the well-documented conservative nature of the brain, which exhibits limited plasticity in response to body size reduction in insular contexts (Van der Geer et al. 2021).

Given the lack of adequate samples (i.e., approximately coeval to San Teodoro and abundant in terms of number of specimens) from continental but peripheral areas of Europe (e.g., Apulia), it is difficult to evaluate to what extent San Teodoro hyaenas are "truly" the result of insularity or just reflect adaptations occurring in a peripheral area. Envisioning a sharp dichotomy between the two possibilities is, in any case, misleading, as peripheral areas like that potentially hosting San Teodoro during part of the Pleistocene – a Mediterranean "peninsula in the Peninsula" – share several characteristics with fully insular environments, most notably a certain degree of isolation and the low availability of trophic resources (Iannucci et al. 2020). We did not rule out a potential contribution of Bergmann's rule, but we considered it an unlikely alternative explanation or of secondary importance for the dimensional shift observed in San Teodoro *Crocuta*. While Roberts (1951) and Klein (1986) found a relationship between *C. crocuta* and Bergmann's Rule today, a study assessing a larger number of morphological features found no clear relationship (Jones 2019). The fauna of San Teodoro includes endemic taxa (indicating the effect of isolation), several studies casted doubt on the generality of Bergmann's rule (e.g., Demment & Van Soest 1985; Dayan et al. 1991; Ashton et al. 2000; Yom-Tov & Geffen 2006; Meiri et al. 2007; McNab 2010; Huston & Wolverton 2011), and several fossil mammals exhibited size fluctuations that often deviate from the rule predictions or call for considering the interplay of many contributing factors (see Iannucci et al. 2020 for discussion). Moreover, palaeogenomic data recently obtained from a hyaena coprolite collected from San Teodoro Cave indicate a low admixture with the African spotted hyaena and a basal phylogenetic position of the Sicilian genome within the Late Pleistocene Eurasian *Crocuta* clade (Catalano et al. 2024), which supports the hypothesis that isolation occurred between Sicilian and continental *Crocuta*. Sicilian cave hyaena could belong to a divergent population that separated from the Eurasian one before the split into the European and Asian lineages and the subsequent bidirectional gene flow occurred among cave and African spotted hyaenas estimated at ~ 475 ka (Westbury et al. 2020). It is plausible this ancestral lineage dispersed across the Italian Peninsula during the Middle Pleistocene, subsequently establishing a presence in Sicily be-

Fig. 11 - The illustration presents the entrance to the San Teodoro Cave, inhabited by a small pack of Late Pleistocene *Crocuta crocuta* with cubs. Artwork by Dawid A. Iurino (no AI).

tween the late Middle Pleistocene and early Late Pleistocene. This arrival coincides with the onset of *Palaeoloxodon mnaidriensis* FC, an interval during which the presence of *Crocuta* is attested (Masini et al. 2008; Antonioli et al. 2016). Spotted hyaenas then experienced a period of isolation from mainland populations until approximately 23 - 20 ka BP (Antonioli et al. 2016), after which they became extinct on the island.

From a taxonomic viewpoint, these results suggest caution should be applied when splitting Pleistocene fossil *Crocuta* into multiple species or subspecies, as chronology and geography are both important dimensions of morphological variations, and their entwined effects are difficult to disentangle. Palaeogenomic studies of fossil spotted hyaenas (Westbury et al. 2020; Catalano et al. 2024) also suggest a broader spectrum of diversity than previously assumed. However, a larger dataset is needed to fully clarify the taxonomic implications of these results. Herein, to prevent further taxonomic confusion, we pragmatically favoured referring San Teodoro and other European samples simply to *C. crocuta*.

The "low level of endemism" displayed by San Teodoro hyaenas is in line with the rest of the faunal and geological evidence. Indeed, the diverse and balanced fauna of San Teodoro includes some endemic taxa, but mainly recognised at a subspecific level, alongside carnivorans other than hyaenas (Bonfiglio et al. 2001, 2008; Mangano 2011).

Conclusions

In this study, the first formal description of the Upper Pleistocene sample of *Crocuta* from the San Teodoro Cave was performed. Osteological analyses show that spotted hyaenas from Sicily have a slightly smaller body size compared to their coeval counterparts from mainland Europe. This finding, coupled with recent palaeogenomic data reported by Catalano et al. (2024), supports the hypothesis of a genetically isolated ancestral *Crocuta* lineage in Sicily. This scenario offers new insights into the diversity and distribution of the Middle and Upper Pleistocene spotted hyaenas of Eurasia and confirms the remarkable scientific and historical value of San Teodoro Cave in understanding Quaternary insular ecosystems.

Furthermore, we agree with Vinuesa et al. (2016) and Lansing et al. (2009) in considering the social and foraging behaviours of extinct *Crocuta* species may have differed from those of extant spotted hyaenas. We think that is a parsimonious approach in inferring the social behaviour of Middle-Late Pleistocene *Crocuta*, considering that their relative anterior cerebrum volume falls below the average of extant spotted hyaenas. Consequently, other extant species, such as *P. brunnea*, may provide more suitable analogues for taphonomic interpretations of Upper Pleistocene spotted hyaenas. However, we must point out that, now that data on a larger number of specimens than previously available are being published, the substantial variability in endocranial volumes within extant *Crocuta* is becoming increasingly apparent, as for the problematics of comparing measurements taken by different operators (Supplementary information). This indicates the need for larger samples and more rigorously developed comparative approaches in investigating palaeoneurology. Pending such efforts, the timing of the occurrence and evolution of complex sociality in *C. crocuta* remains an open question.

Authors' contribution

Dawid A. Iurino: Conceptualization, Resources, Methodology, Data curation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization, Project administration, Supervision. Alessio Iannucci: Conceptualization, Data curation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. Angharad K. Jones: Conceptualization, Data curation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing. Filippo Spadola: Investigation, Writing – review & editing. Gabriella Mangano: Investigation, Writing – review & editing. Nicola Iannelli: Investigation. Danielle C. Schreve: Writing – review & editing, Supervision. Raffaele Sardella: Resources, Writing – review & editing, Supervision. Laura Bonfiglio: Data curation, Writing – review & editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Raw data of dental and endocranial measurements are available as Supplementary Information. CT scan files are available on request.

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