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A key site for inferring the timing of dispersal of giant deer in Sardinia, the Su Fossu de Cannas cave, Sadali, Italy

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ABSTRACT

Su Fossu de Cannas (SFC) cave is one of several known cavities in the Sadali plateau in Sardinia, Italy. The evolution of the cave is the result of complex erosional and deposital processes that occurred during the Neogene and Quaternary. A fossiliferous cemented conglomerate, containing various deer remains, now forms the ceiling of a cavity (tunnel). The faunal remains belong to a large cervid, which show some morphological affinity with large deer that have an endemic Sardinian lineage (*Praemegaceros sardous*—*Praemegaceros cazioti*). Palaeoecological data based on some peculiar features and the large size of the SFC deer suggest that it is the most primitive Megacerine found in Sardinia to date, and the first representative of the endemic lineage. The 450 ka U—Th age for the flowstone capping the fossiliferous layer defines: the end of sedimentation in which Sadali deer remains are preserved; and the dispersal from the mainland of the ancestor of the endemic Sardinian Megacerini. Stratigraphic and micromorphological analyses of the cave deposits allow the reconstruction of the timing of the cave's development throughout the Pliocene to the Holocene.

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Introduction

Caves are particularly important to Quaternary paleoenvironmental reconstructions and paleontological analyses, as they may contain deposits that often span multiple millennia (e.g., Sasowsky, 2007; Cuenca-Bescos et al., 2009). Clastic sedimentary fills are typically studied, because they can produce information concerning the evolution of the surrounding territory (e.g., Auler et al., 2004; Bosch and White, 2004; Springer, 2005; White, 2007). Caves also provide stable conditions for the long-term preservation of the skeletal remains of both large and small vertebrates (Nielsen-Marsh, 2000). Vertebrate deposits in caves are sometimes associated with calcium carbonate precipitates (speleothems). These can be dated and provide minimum/maximum ages of the sediment and fossil remains filling a cave (e.g., Burney et al., 2001; Carrión et al., 2003; Auler et al., 2006). Sardinia, which is the second largest island in the central Mediterranean area, is characterized by karst areas that are developed in carbonate rocks of various ages ranging from the Cambrian to the Quaternary and comprise ~9% of the island's area (De Waele, 2009, Fig. 1). Many of these caves provide evidence for past phases of sedimentation and erosion. Remnants of sediment fills and fossil remains are frequently present on the walls and ceilings of the caves, and testify to former sediment infilling episodes followed by one or more phases of sediment removal (De Waele et al., 2005, 2012; Melis et al., 2013). Caves with fossiliferous sediment are mainly located in the Cambrian limestone and Mesozoic dolomitic limestone areas (De Waele et al., 2005; Melis et al., 2013).

Although many of these caves have been studied and explored, geochronological data on the deposits are still scarce (Corbeddu cave, Eisenmann and Van der Geer, 1999; Klein Hofmeijer, 1996; Juntu cave, Benzi et al., 2007 and Grotta dei Fiori, Melis et al., 2013). Accordingly, despite their richness, vertebrate fossil records from Sardinian caves are of little help in decoding the complex chronological framework of the Pleistocene/early Holocene terrestrial fauna of the area (e.g., Palombo, 2009; Palombo and Rozzi, 2014 and references therein). In particular, little is known about the actual timing of arrival in Sardinia of the ancestor of the endemic deer *Praemegaceros cazioti*, the remains and tracks of which are found in

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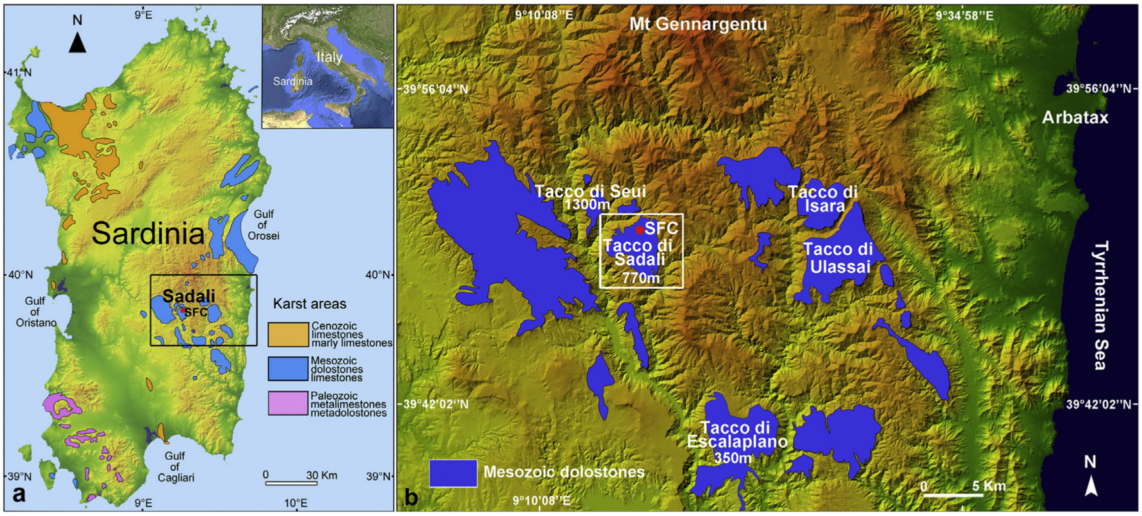

Figure 1. Location of the study area: a) Schematic map of karst areas of Sardinia; b) Location map of the limestone plateaus ("Tacchi") in central-eastern Sardinia. The box shows the location of the geomorphological map of the Sadali plateau in Fig. 2a.

aeolian deposits (e.g., Palombo, 2006, 2009; Fanelli et al., 2007 and references therein).

Various remains of a large deer were discovered during a speleological survey in an eroded conglomerate that nowadays constitutes the ceiling of a narrow tunnel in the Su Fossu de Cannas (SFC) cave, which opens in the Sadali limestone plateau in Barbagia of Seulo, central-eastern Sardinia. The large size of the SFC deer suggests that it may be the most primitive Megacerine hitherto found in Sardinia and the first representative of the endemic lineage (Palombo et al., 2003; Palombo and Melis, 2005; van der Made and Palombo, 2006; Palombo, 2009).

Sardinia has experienced a long history of alternating phases of complete isolation and mainland connections since its separation from the Iberian Peninsula since about 30 Ma. The island was also part of an archipelago of the Tusco-Sardinian palaeobioprovince during the Late Miocene, and then became a complete isolate insular district by the end of the Messinian.

Sardinia experienced several episodes of colonization by European mammals from the Pliocene to the Late Quaternary. These gave rise to successive endemic faunas. The biodiversity progressively decreased from the impoverished, but balanced, Pliocene/earliest Pleistocene fauna (*Nesogoral* Faunal Complex, FC) to the Late Pleistocene–early Holocene version (*Microtus* (*Tyrrhenicola*) FC) (Palombo, 2009; Palombo and Rozzi, 2014 and references therein). The latter is disharmonic, strongly impoverished, and highly unbalanced compared to the fauna inhabiting similar continental ecosystems. This meets the expectations of an insular system that remained completely isolated due to quite severe barriers for long time intervals. The fauna is characterized by the appearance of more evolved species within a number of endemic, small mammal lineages, the diachronous disappearance of the large mammals recorded in the previous Faunal sub-Complex (FsC), and the discrete appearance of alien small and large mammals. Some large mammals (i.e., the ancestors of the *Cynotherium* and *Praemegaceros* lineages) may have reached the Corso-Sardinian massif and arrived on the island by way of a sweepstake overseas dispersal during the late Early Pleistocene. At that time the increased amplitude of sea-level fluctuations in the glacial cycle linked to the so-called Mid-Pleistocene Revolution (e.g. Maslin and Ridgwell, 2005) possibly led to the temporary emergence of limited areas of the platform. This reduced the width of the sea-arms that separated the Corso-Sardinian massif from the mainland (Palombo, 1985). This proposition is fairly consistent with the phylogenetic relationships proposed for both of the endemic lineages, suggesting that the wild canid and giant deer on Sardinia (independent of other authors' contrasting opinions about its putative ancestor) stemmed from the late Early Pleistocene continental stock (Croitor et al., 2006; van der Made and Palombo, 2006; Madurell-Malapeira et al., 2015). Nonetheless, the actual time of this dispersal is unknown, due to the lack of consistent geochronological constraints for a number of local faunal assemblages. This makes it challenging to test any hypothesis on the timing and dynamics of the evolutionary process undergone by endemic lineages.

This is particularly the case when it comes to comparing the evolutionary patterns of insular Quaternary deer from Mediterranean islands. During the Middle–Late Pleistocene and early Holocene, endemic deer, descended from different mainland ancestors (Megacerini, *Cervus*, *Dama*), were a common component of a number of insular Mediterranean fauna (Eastern Mediterranean: Crete, Kassos, Karpathos, Amorgos and Tilos; Western Mediterranean: Sardinia and Corsica, Capri, Pianosa, Sicily and Malta). Each species on each island has it own evolutionary history, and it is therefore difficult to identify a dominant factor in insular deer evolution. The endemic deer from Sardinia and Crete, for instance, although generally regarded as stemming from closely related ancestors (i.e., the Megacerini tribe), underwent different evolutionary processes. The sympatric speciation and radiation process of Cretan deer led to the presence of several species that differed in size and ecological behavior (e.g., De Vos, 2000). Meanwhile, in Sardinia, endemic deer probably underwent a progressive reduction in size from the large, slender deer recorded at the SFC cave to the smallest and stouter deer (unknown age), the *Praemegaceros sardus* from Santa Lucia (450 ± 20 ka; Motoji Ikeya, fide van der Made, 1999 and the *P. cazioti* from Medusa-Dragonara [LGM, Palombo et al., in press], Corbeddu [Tardiglacial, Palombo et al., in press] and Juntu cave [~7.0 ka, Benzi et al., 2007] [see, e.g., van der Made and Palombo, 2006 for a fuller discussion]).

Crucial for testing the hypothesis concerning the time of dispersal of the ancestor of the Sardinian *Praemegaceros* lineage, and providing clues to enable a better understanding to be achieved of the time and patterns of evolution of the Corso-Sardinian Pleistocene is to provide a firm chronological constraint for the largest specimens, i.e., *Praemegaceros* from the SFC cave, which is

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believed to belong the oldest species within the Corso-Sardinian anagenetic lineage.

This paper aims to outline the reconstruction of the evolution of the SFC cave and provide some constraints to the chronology of the arrival in Sardinia of the ancestor of the endemic Corso-Sardinian Megacerini. These goals are achieved by a stratigraphic analysis of the cave's deposits, and dating flowstones that are either interbedded or cover its sedimentary successions. This may provide significant clues for outlining the main steps in the evolution of the SFC cave, and estimating the period of the dispersal to the island of the ancestor of the endemic Sardinian Megacerini.

Geologic and geomorphic setting

The SFC cave is located south of the Gennargentu Mountains and north of the Sadali plateau (Tacco di Sadali central-eastern Sardinia: Fig. 1a). In this area, horizontally stratified Jurassic carbonate rocks unconformably overlay the Paleozoic basement. This basement complex consists of Cambro-Silurian metasedimentary, metavolcanic, and intrusive rocks (Gennargentu Formation) that were peneplained during the Permian–Triassic. Fluviodeltaic rocks of the Genna Selole Formation that were deposited during the Bathonian stage of the Middle Jurassic document the onset of the Mesozoic transgression (Dieni and Massari, 1985; Costamagna, 2015). The rock (marls, quartz conglomerates and coal seams) is overlaid by a succession of marine dolomitic limestones, which are about 300 m thick, and are characterized in the lower part by well-stratified decimetric to metric thick beds, passing to massive beds at the top of the sequence, where they are locally overlaid by coralline and oolithic limestone that is about 30 m thick (Barca and Costamagna, 2000). The lower dolomitic succession belongs to the Dorgali Formation, while the more calcareous uppermost part consists of rocks of the Tului and Bardia formations (Callovian–Kimmeridgian age; Barca and Costamagna, 2000).

At the end of the Mesozoic, the Jurassic marine rocks emerged and the landscape started evolving with the formation of a number of valleys that are prevalently oriented NNE–SSW (De Waele et al., 2005). During the Cenozoic, the Mesozoic marine succession and the Paleozoic substratum were affected by fluvial erosion enhanced by the epirogenetic movements of the Alpine orogeny. Deep valleys developed along the major tectonic directions (NNW–SSE, NNE–SSW and E–W) and divided the dolomitic limestone plateau into several separated blocks that underwent slightly different evolutionary processes (De Waele et al., 2005).

Some minor plateaus (named “Tacchi”) developed at different topographic levels, from 350 (Tacco di Escalaplano) to 1300 m above sea level (asl) (Tacco di Seui) (Fig. 1b), as result of a multiplicity of uplifting movements that affected the area during the Neogene. Karst processes developed during this period in the limestone Tacchi area, and created a variety of different karstic forms such as sinkholes, dry valleys, dolines, caves, stone forests and karren. The “Tacco di Sadali”, at ~750 m asl, where the SFC cave developed, is delimited by a deep valley, except on the eastern side, which is edged by metamorphic reliefs. The Cenozoic tectonic movements affected the development of the hydrographic network and both the deep and superficial karstic evolution of the Sadali plateau. Rock falls are evident mainly along the scarp, where the Mesozoic substratum outcrops, while landsliding and running water processes are still active on all the plateau slopes (Fig. 2a). The wide paleovalleys present on the plateau surface are probably related to an ancient drainage system that flows from the highest surrounding mountains. The main epigenetic karstic forms are a number of solution/collapse dolines. The presence of flowstone and stalactite relicts on the plateau surface testifies to the existence of ancient cavities brought to light by various intense processes of alteration/erosion of the Mesozoic sandy dolostone bedrock.

Hypogean karstic forms are represented by as many as 35 caves that developed along the main faults (Fig. 2a). These caves are mainly horizontal and are characterized by a number of phases of sedimentary filling and erosion. Vertebrate fossil remains are sometimes present in coarse sediments.

The chronology of the Sadali landscape evolution is still poorly understood, although its development was probably similar to the plateaus located east of Tacco di Sadali. According to De Waele et al. (2012), the presence of two planation surfaces on the plateaus at different altitudes, and the clustering of horizontal cave levels at certain altitudes, results from the interplay of different processes that took place at different times. Three levels of caves, which developed after erosion phases, are evident. The evolution of the first two levels occurred before 2 Ma, while the third took place around 1.6 Ma. The caves were formed during long periods of quiescence under humid conditions. They were also gradually filled with sediments that were later washed out during the incision period that followed.

Methods

Paleoenvironmental reconstructions of the cave are mainly based on the stratigraphic and sedimentological analyses of the sections within the SFC cave.

The sediment within the SFC cave was defined on the basis of observable sedimentological and micromorphological characteristics. Granulometric analyses of the sand (<2 mm), silt and clay fractions were performed using the pipette method (Violante, 2000). The percentage of calcium carbonate was determined with a Dietric-Fruhling Calcimeter following Violante (2000). Undisturbed samples were collected for micromorphological analysis. The thin sections were described according to the guidelines definited by Bullock et al. (1985) and Stoops (2003). The sediment color was described using Munsell (1998) soil color charts.

Speleothems were dated by uranium/thorium methods. Four samples were taken: one in Upper Chamber (UCH), from a stalagmite located near the entrance of the cave (Sadali 3 sample), two from the flowstones Fa (Sadali 2 sample) and Fb (Sadali 4 sample) partially filling the shaft A, and Sadali 1 sample from the flowstone covering and partially incorporating the fossil remains in the ceiling of the tunnel. For U/Th dating, pieces of speleothems ranging from 2 to 7 g were cut using a diamond saw for each U/Th analysis. The pieces were dissolved using nitric acid in a Teflon beaker into which a weighted amounts of mixed spike ^{233}Ue, ^{236}Ue, and ^{229}Th had been placed and evaporated. Samples were dissolved using concentrated HNO_3 and approximately 10 mg of iron carrier was added. U and Th were co-precipitated with $Fe(OH)_3$. The precipitate was washed with water, dried and then dissolved in 6NHCl. The U/Th separation was performed on a 2 ml volume AG1X8 anionic resin. The Th fraction was recovered by elution with 6 N HCl and the U and Fe fraction by H_2O. The U fraction was purified on a 0.2 ml volume U-Teva (Elchrom industry) resin. The Fe was eluted with 3 N HNO_3 and the U fraction with 0.002 N HNO_3. Thorium purification was carried out on a 2 ml AG1X8 resin in 7 N HNO_3 and eluted with 6 N HCl. After drying, a final purification was performed on a 0.2 ml AG1X8 resin in 7 N HNO_3 and eluted with 6 N HCl. U–Th measurements were performed using a VG sector TIMS fitted with an electrostatic filter and a Daly ion counter. The U and Th fractions were deposited on a single zone-refined Re filament between two layers of colloidal graphite. The U and Th isotopes were measured in peak jumping mode on the Daly counter. The overall analytical reproducibility was estimated from replicate measurement of a coral from Timor

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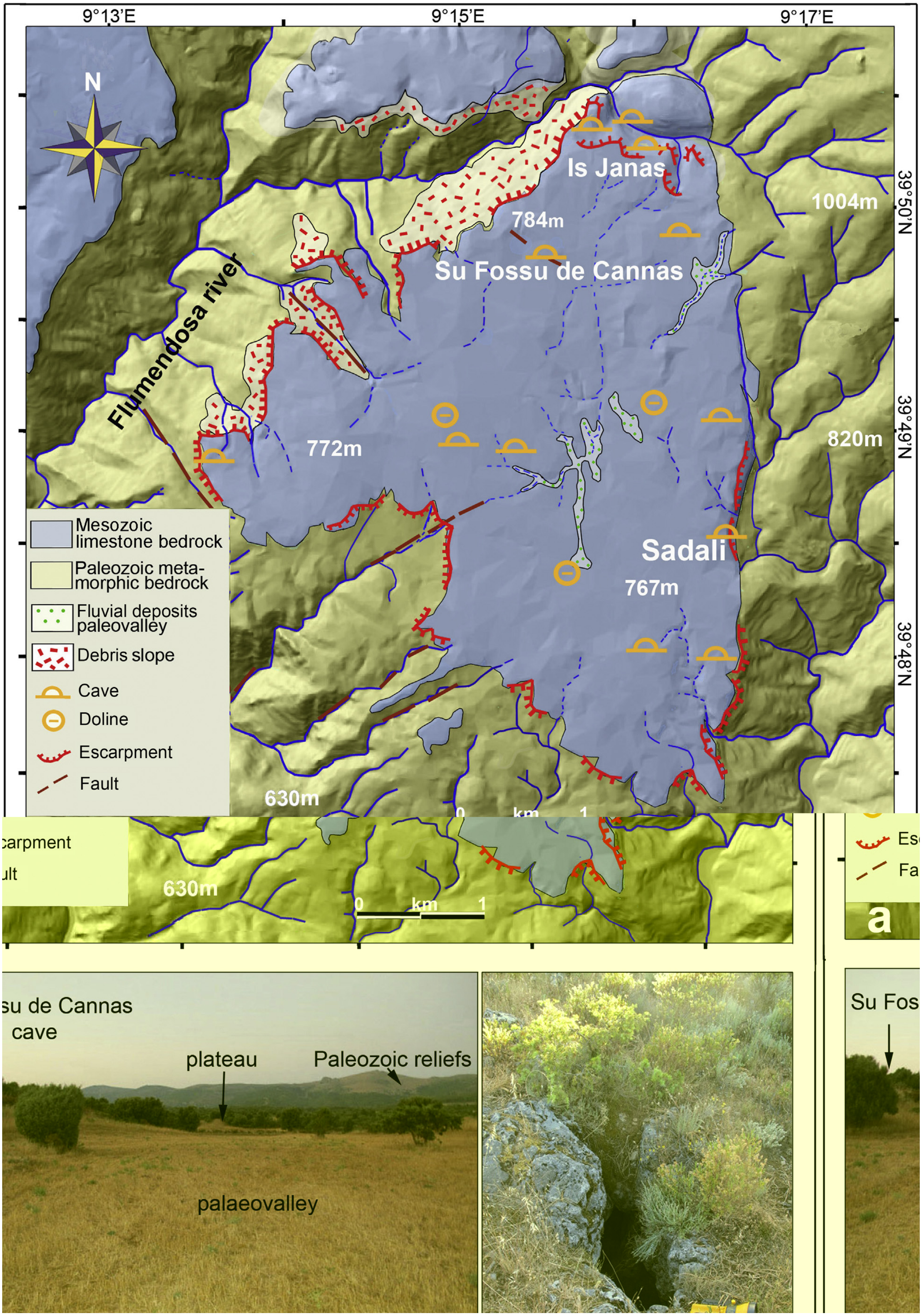

Figure 2. The Sadali plateau: a) geomorphological sketch map of the Sadali plateau; b) panoramic view of the Sadali plateau close to the Su Fossu de Cannas cave; and c) view of the current Su Fossu de Cannas cave entrance.

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Island that dates from the last interglacial age and a Uraninite standard. The precision was generally better than 0.5%.

The Su Fossu de Cannas cave

The SFC cave is situated on the top of a small mound between two paleovalleys (Fig. 2b). At present, the entrance consists of a narrow fissure that opens at 793 m asl (Fig. 2c). A number of remains of flowstones, relicts of stalactites and sinkholes scattered on the land surface near the entrance attest to the presence of ancient caves that were affected by intense karst processes.

Studies carried out on many caves of the Tacchi region (De Waele et al., 2012) suggest that the karsification of the SFC cave started during the Late Miocene–Pliocene. Filling and erosion processes occurred during the Upper Pliocene or Lower Pleistocene age, as supported by ^{26}Al and ^{10}Be burial dating of sediment in four caves located in “Tacco di Isara” and “Tacco di Ulassai”, about 15 km from Sadali, (Fig. 1b; De Waele et al., 2012). Multiple phases of filling and erosion are also evident at Is Janas, a tourist cave situated on the north side of the “Tacco di Sadali”, about 13 m below the SFC cave.

The SFC karst system developed along a NW–SE fault in the dolostone of the Dorgali Formation (Middle–Upper Jurassic) and consists of a narrow subsurface Upper Chamber (UCH) connected, across a shaft (A in Fig. 3), to an underlying horizontal tunnel (Fig. 3).

The ceiling of the tunnel mainly consists of a fossiliferous bone-bed that contains some remains of a large deer (*Praemegaceros* n. sp. aff. *P. sardus*; Palombo et al., 2003; Palombo and Melis, 2005).

By dating the main speleothems, we are able to outline the key steps in the evolution of the SFC cave, analyse the characteristics of the sediment, and provide a terminus for limit before which the deer remains were deposited.

Depositional–erosional dynamics

Upper Chamber (UCH)

The UCH, which is 8 m-long and 1.5 m-wide, is characterized by abundant concretions and flowstones. A thick layer (~1.5 m) of dolomite, showing several fractures completely filled by concretions, separates the UCH from ground level. Seven meters from the entrance, a thick flowstone (Fa), which extends from the cave ceiling to the floor (Fig. 4a), partially obstructs the passage and continues into the shaft (A) located at the end of the UCH. Another flowstone (Fb) is present in this part from the ceiling to shaft A (Fig. 4b).

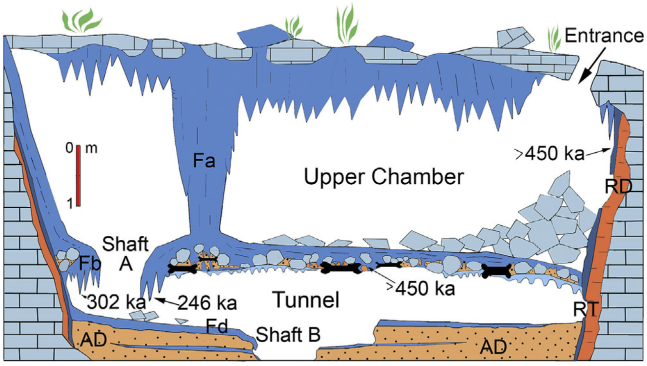

Figure 3. Sketch section of the Su Fossu Cannas cave showing the relationships between the upper chamber, tunnel, sediments, flowstones and dated speleothems. RD and RT: reddish clay sediment; AD: reddish sandy clay deposit; A and B: shafts; Fa, Fb and Fd: flowstones. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

The speleothem layers are the only ones that have a clear paleoenvironmental meaning, denoting prolonged percolation without intervening clastic episodes. Percolation is scarce or absent and speleothems probably formed in climatic conditions that were wetter than today. Loose sediment with poorly sorted clasts of dolostone and speleothems imbedded in a silt and sand matrix cover the floor of the UCH. Near the entrance, the deposit forms a debris cone made of breakdown debris and blocks that migrate into the cave from the land surface. Some of the debris possibly originated from blocks placed by shepherds to close the entrance because no rock fall deposits are present beneath the cave walls.

The remains of un-fossiliferous, reddish (5YR5/6) clay sediment (RD, in Fig. 3) are visible on the walls of small lateral branches of the UCH located near the entrance (Fig. 4c). Speleothems older than 450 ka (U/Th dating, Table 1, Sadali 3) overlay the red sediment. Thin sections of the speleothems show a succession of thin layers of columnar calcite, acicular aragonite and red clay (Fig. 4d), indicating that they were formed in the course of periodic climatic oscillations (cf., e.g., Railsback et al., 1994; Frisia et al., 2002).

Micromorphological analyses of the reddish sediment (RD) reveal the micro-graded bedding of clay and silt affected by crack voids that suggest deposition in quiet or slow-moving floodwater, while the fissures probably formed during a successive dry period (Fig. 4e). The presence of black mottles in the clay layers suggests local wet conditions. The sediment present on the walls is probably due to a deposition phase older than 450 ka, during which period the cave was filled. Similar deposits are present in the Is Janas cave, where they are visible on the ceiling. The sediment includes some fragments of stalactites in a horizontal position, the presence of which can be explained by supposing that the stalactites fell (perhaps due to tectonic movement) on the reddish sediment filing the cave and were subsequently eroded when the present cavity developed. This and the Sadali cave filling processes may have occurred after 2 Ma during a fairly long period of stable, humid climatic conditions (cf. De Waele et al., 2012).

Tunnel

At the base of shaft A, through a lateral entrance (40 cm-wide and 35 cm high; Fig. 5a), it is possible to access a narrow tunnel that developed below the UCH (Fig. 5b). The floor is covered by a flowstone (Fd) that gently slopes towards the inner part of the tunnel. The flowstone Fd possibly originated from the water dropping from the Fa and Fb flowstones and entering the tunnel through shaft A. Along the floor, about 2 m from the entrance, there is another small shaft (B, in Fig. 3) that is more than 60 cm deep, where a reddish sandy clay deposit (AD, in Fig. 3) with about 8 cm-thick interbedded concretion levels covers the speleothems outcropping on the walls.

Micromorphological analyses show that sub-angular quartz and dolomite grains prevail in the reddish (in the web version) sandy clay deposit (AD). There is ferruginous impregnation in the interstitial material, usually in the form of bridges between the grains (Fig. 5c). Sparitic calcite coatings cover the walls of the voids (Fig. 5c). No faunal remains were detected.

Relics of reddish (5YR5/6) clay sediment (RT, in Fig. 3), similar (if not the same) to RD deposit of UCH, are locally present on the walls of the tunnel, and are overlaid by a layer of speleothems. The reddish clay deposit is characterized by graded levels consisting of repetitive fining-upwards sequences of fine sand, silt and clay that are usually less than a few millimeters thick. Individual laminas are well sorted and in general show sharp contacts (Fig. 5d).

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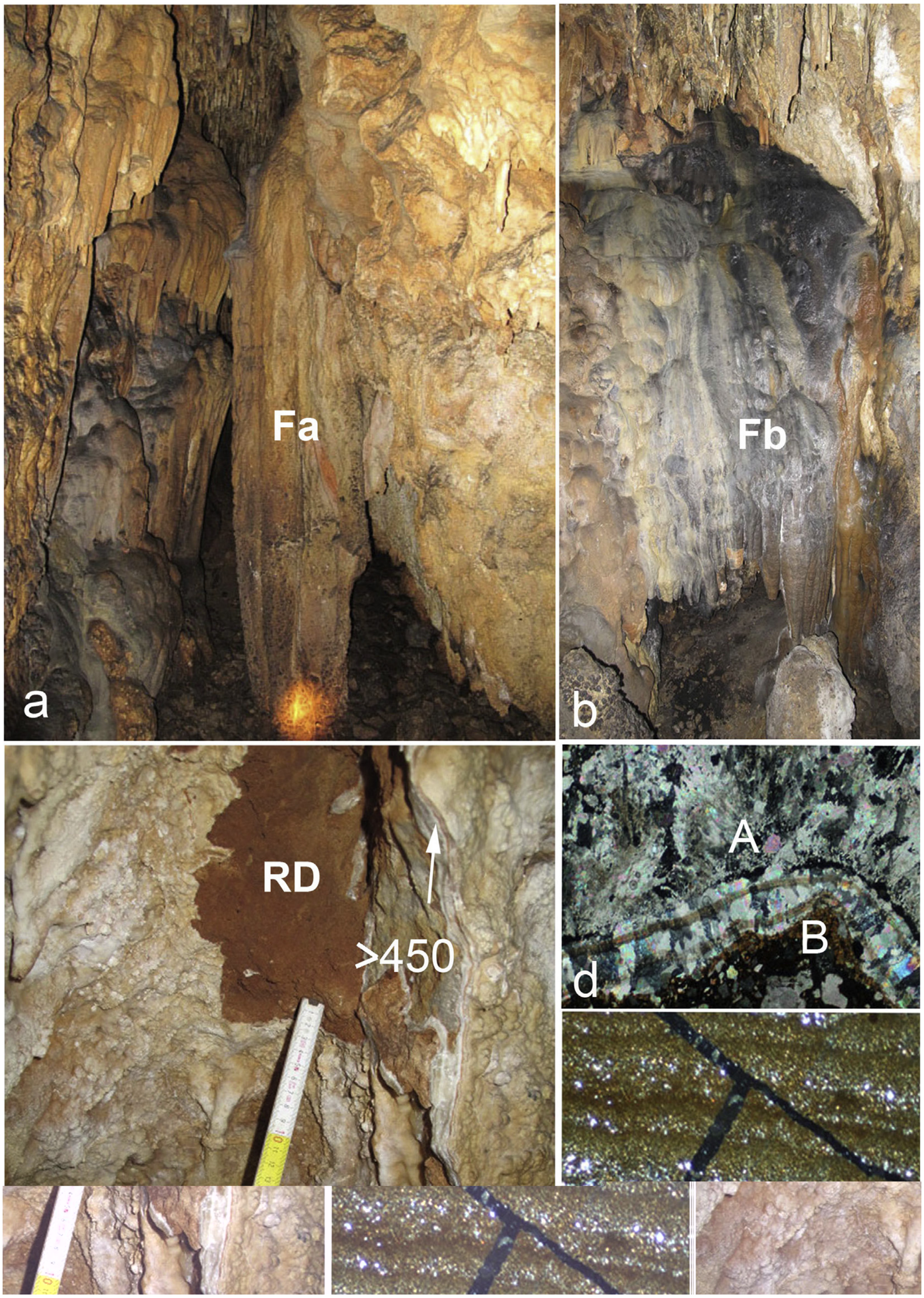

Figure 4. The upper chamber: a) the Fa thick flowstone, which extends from the ceiling to the floor; b) the Fb flowstone present at the end of the upper chamber from the ceiling to Shaft A; c) the reddish un-fossiliferous clay sediment (RD) on the walls of the upper chamber; d) thin section of the speleothem that buried the RD sediment: A: columnar calcite, B: red clay level (XPL, ×10); and e) thin section of reddish sediment (RD) showing the micro-graded bedding of clay and silt affected by crack voids (XPL, ×2.5). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Such repetitive depositional events imply the presence of a static water body affected by pulses of sediment that were washed therein such as during storm events (e.g., Goldberg and Bar-Yosef, 1998; Knapp et al., 2004; Shunk et al., 2006). The rip-up subangular clay clasts (Fig. 5d) present in the sandy laminas suggest individual storm events followed by quiet water conditions that allowed the deposition of fine suspended sediment and the formation of the laminated clays (cf. Knapp et al., 2004).

The internal characteristics of the rip-up clayey red clasts indicate that they originate from the erosion and subsequent

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Table 1
Uranium-series data for four samples (errors are 2σ) from the Su Fossu de Cannas cave: Sadali 1: Flowstone partially incorporating the fossil remains in the ceiling of the tunnel; Sadali 2: Flowstone Fa partially filling shaft A; Sadali 3: Stalagmite near the entrance; and Sadali 4: Flowstone Fb partially filling shaft A.

Samples	^{238}U ± 2σ ppb	^{232}Th ± 2σ ppb	(^{234}U/^{238}U) ± 2σ	(^{230}Th/^{238}U) ± 2σ	^{230}Th age ± 2σ (ka)
Sadali 1	432.269 ± 3.308	72.276 ± 0.739	1.008 ± 0.009	1.015 ± 0.007	>450
Sadali 2	1868.269 ± 12.063	37.024 ± 0.224	1.037 ± 0.007	0.939 ± 0.005	246 ± 9.8
Sadali 3	240.362 ± 2.054	2.273 ± 0.011	1.027 ± 0.011	1.054 ± 0.008	>450
Sadali 4	524.812 ± 2.601	27.540 ± 0.261	1.019 ± 0.009	0.959 ± 0.010	302 ± 2.2

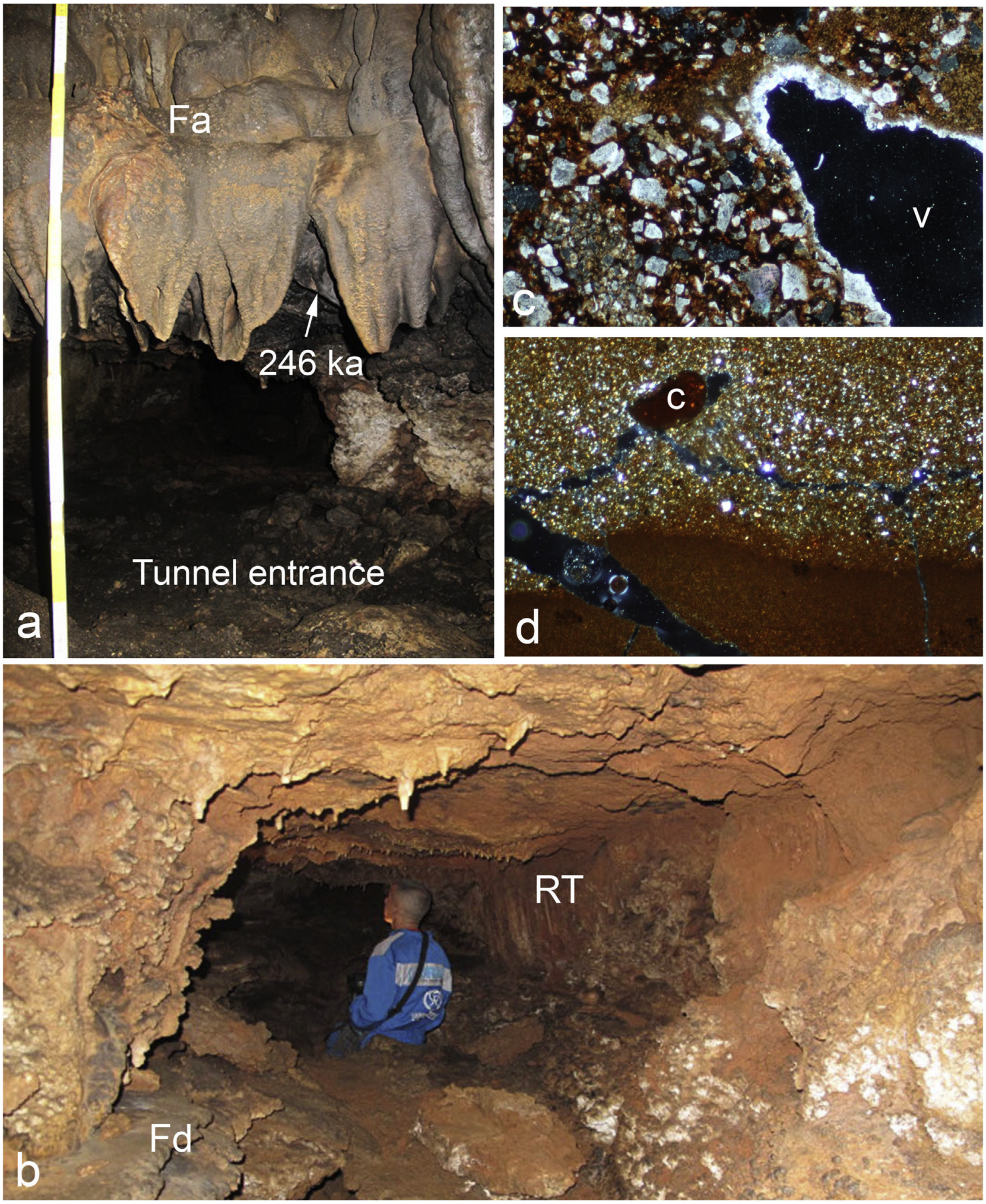

Figure 5. Tunnel features: a) the tunnel entrance in Shaft A below the Fa flowstone; b) view of the narrow tunnel; c) thin section of the AD sediment characterized by ferruginous impregnation between the grains and calcite coating on the void (v) walls (XPL, ×2.5); and d) thin section of the RT sediment: c: clay clast in the graded level (XPL, ×2.5).

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re-deposition of external rubefied soils, which had developed under hot and humid climate conditions. Results obtained from an XRD analysis of the RT deposit show that the clayey fraction contains kaolinite, illite and chlorite. Cave sediment with a detrital origin usually contains more than one clay mineral that derives from surface soils (Foos et al., 2000). Boero and Franchini (1992) found that in xeric sites, illite and kaolinite are the main clay mineral phases in ‘red-earth’ soil. Indeed, in the Mediterranean area, clasts of red-earth soils are common in cave sediments (Goldbergand Bar-Yosef, 1998; Goldberg et al., 2007; Karkanas and Goldberg, 2013). Most authors consider the red-earth to be a polygenetic relict soil formed during the Neogene and/or Quaternary warm and humid periods (e.g., Altay, 1997; Bronger and Bruhn-Lobin, 1997). The sedimentological and micromorphological characteristics of this clayey RT sediment are similar to those of the RD clay deposits present on the walls of UCH. The ceiling of the tunnel is formed by a sandy matrix conglomerate, which is strongly cemented and contains heterometric calcareous pebbles, gravel, and several remains of a large deer (Fig. 6). In thin section, the sandy matrix consists of subangular quartz and calcareous grains immerged in a sparitic carbonate groundmass with ferruginous impregnation.

The upwards fluctuation of the water table is responsible for such ferruginous deposits. The walls of the voids are covered by a secondary sparitic calcite layer. The AD sediment underlying the Fd flowstone in shaft B has similar features. This suggests that when the conglomerate that is now on the ceiling of the tunnel was deposited it overlaid the AD sediment that at that time filled the cave and was successively eroded.

The deposition of the conglomerate layer, probably due to a runoff episode, took place in a period of extremely dry climatic conditions with sparse vegetation (see, e.g., Brain, 1995; Brook et al., 1987). Subsequently, the humid climate with a rich vegetation allowed water to drip into the cave through the fissures and resulted in cementation of the conglomerate, making it more resistant to erosional processes than the underlying AD sandy sediment.

U/Th ages

The results from the four samples are summarized in Table 1 and are reported with a 2σ error. The evolution of ^{230}Th/^{238}U vs ^{234}U/^{238}U in a closed radioactive system is shown in Figure 7. Samples Sadali 1 and Sadali 3 clearly plot in the zone beyond the limit of the method while samples Sadali 2 and Sadali 4 plot between isochron 250 and 300 ka. Only the Sadali 2 and Sadali 4 samples, taken respectively from the Fa and Fb flowstone in Shaft A, yield a calculable age, corresponding to 246 ± 9.8 and 302 ± 22.2 ka, respectively. Sadali 1, from the conglomerate with fossil remains, and Sadali 3, from the stalagmite near the SFC entrance, produced an infinite age, beyond the limit of the method. This suggests that if the radioactive systems remained closed, the samples Sadali 1 and Sadali 3 are older than 450 ka.

Discussion

The general evolution of SFC cave

The sedimentary successions filling the SFC cave analyzed herein probably represent the terminal phases of the evolution of the cave. The analysis of the SFC deposits provides some clues for inferring the late depositional history of the cavity and the age of

Figure 6. The fossiliferous layer on the ceiling of the tunnel containing the remains of the large deer: a) Hemimandible; b) fragmented bones of *Praemegaceros* aff. *P. sardus* partially included in the flowstone older than 450 ka, capping the fossiliferous conglomerate; and c) several deer bones that are present in the flowstone, including a partially uncovered metatarsal, encrusted by a calcite film.

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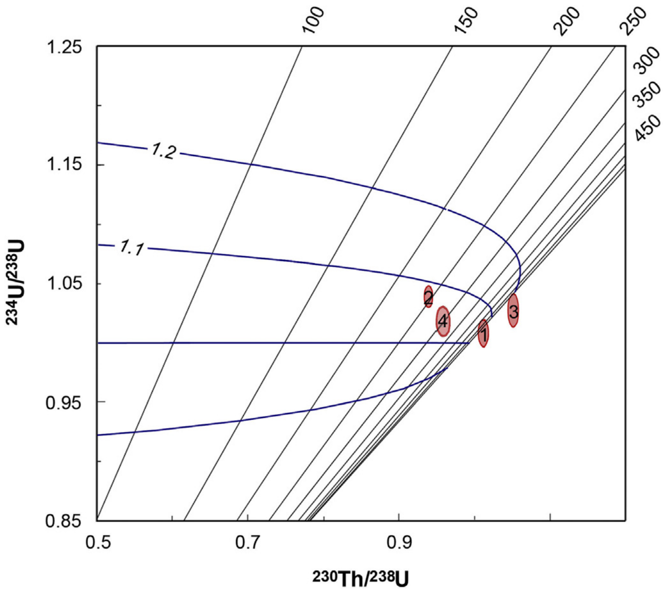

Figure 7. Using Isoplot 3 from Ken Ludwig (USGS): A 2D projection of a 3D Abaca. This illustrates the systematics of the U-series data of Sadali samples 1, 2, 3 and 4. The scatter data point around the isochron line is quite large, illustrating the diagenetic effects on the ^{238}U-series isotopes. The data-point error ellipses are 2σ.

the fossil remains. Available data suggest that the present setting of the SFC cave resulted from two cycles of infilling and erosion processes, and from two important episodes/periods of speleothem deposition, which may have occurred over several hundred thousands of years. This was possibly during most of the Pleistocene, if it did not start earlier.

Four phases of development were likely (Fig. 8):

1) The presence of the reddish sediment on the walls of the upper chamber and the tunnel suggests that the cave was filled during a relatively long period of quiescence after it developed, and probably occurred during the Late Miocene–Pliocene. The characteristics of the reddish clay deposits with pedorelicts indicate sediment transport by the water which dropped into the cave clasts due to the erosion of rubefied soils that developed outside the cave in a period of humid and warm climatic conditions. The humid conditions also led to some water stagnation inside the cave, as supported by the presence of manganese nodules in the sediment. The lack of numerical ages does not allow us to make any firm chronological assessment of this filling phase. However, geological surveys and research performed in the area surrounding the cave enable us to hypothesize that the sedimentation took place in the Pliocene, or at least before 2 Ma (c.f. Marini and Ulzega, 1973; Bianco and De Waele, 1992; Ardau and De Waele, 1999; Bartolo et al., 1999; De Waele et al., 2005).

2) After a long period of stability, water erosion processes probably related to either Plio-Pleistocene tectonic activity (cf. Casula et al., 2001; Cocco, 2013) or climatic conditions (glacial periods, possibly MIS 20 or 22) caused a variation in water levels inside the SFC cave, and consequently the erosion of the previously deposited clay sediment.

   A period of stability followed the erosional episode, as documented by the occurrence of speleothems covering the red sediment remains still blanketing the cave walls. The U/Th dating of the speleothems present in the upper chamber confirms that the erosion took place before 450 ka.

3) Another phase of the sedimentation due to water circulation at low energy is documented by the presence of a sandy deposit in the tunnel that lies above the remains of the reddish clay sediment and previously deposited speleothems. The coarser material that overlies the sandy sediment and characterizes the fossiliferous layer with deer remains indicates that a somewhat extreme event may be linked to climate change and caused an increase in the energy of the water flowing from the outside.

   After these events, a period follows during which the speleothems formed and the cementation of the fossiliferous conglomeratic occurred. The speleothem formation required a combination of wet and hot climatic and favorable local conditions (Pickering et al., 2007). Taking into account the U/Th dating of the carbonate matrix of the conglomerate (>450 ka), the hypothesis that the conglomerate cementation occurred during an interglacial in the Early–Middle Pleistocene (maybe MIS 15) cannot be discounted.

4) During this evolutionary phase, an increase in precipitation and changes of internal drainage caused the erosion of the sandy deposits below the conglomerate and, consequently, the formation of shaft A and the tunnel. A long period of stability followed, during which the Fa and Fb flowstones developed, covering the walls and partially filling Shaft A. The 302 and 246 ka ages obtained for the flowstones suggest that they probably formed during MIS 11 and MIS 9, when a supply of cave drip waters and the wet and hot climatic conditions favored flowstone formation (cf. Richards and Dorale, 2003; Pickering et al., 2007). Meanwhile, Shaft A possibly formed between MIS 15 and MIS 11. The absence of sediment intercalated to the flowstones and the lack of deposits above the fossiliferous conglomerate may be linked to the closure of the cave, with the outside being from MIS 9 to the present.

Implications for inferring the timing of deer dispersal

During the Pleistocene, three endemic deer species, with significant differences in size, have been recorded in Sardinia, i.e., deer from the SFC cave, *P. sardus* and *P. cazioti*.

Accepting that the difference in size results from an anagenetic evolution towards an average smaller size and shortened and stouter metapodials and, in turn, the assumption that "evolution" is an irreversible process (but see Palombo and Rozzi, 2014, as far as Pleistocene Sardinian mammals are concerned), the morphological and dimensional traits of the few bones from the SFC cave available for analysis suggest that the SFC deer may be the largest and least advanced hitherto known in Sardinia (Palombo et al., 2003; Palombo and Melis, 2005; van der Made and Palombo, 2006). Unfortunately, neither small mammals nor any other large mammals have yet been found in the SFC fossiliferous conglomerate. As a result, a possible chronological gap, if any, between the SFC deer and its putative descendent *P. sardus* remains unaddressed.

The remains of *P. sardus*, which is smaller than that from Sadali but larger than its descendant *P. cazioti*, were found together with the endemic vole *M. (Tyrrhenicola) henseli* in the Santa Lucia (Iglesias, south-western Sardinia) and Capo Figari (Forsyth Major collection) local faunal assemblages (LFAs), and in some fissure fillings at Monte Tuttavista (van der Made and Palombo, 2006). ESR ages obtained for deer teeth from Santa Lucia (450 ± 20 ka) and Capo Figari (368 ± 20 ka) (Motoji Ikeya, fide van der Made, 1999), confirm that *P. sardus* was present in Sardinia during most of the early Middle Pleistocene (~540–290 ka). Accordingly, it is rational to suppose that the transition from *P. sardus* to the last representative of the Sardinian *Praemegaceros* lineage, *P. cazioti*, might have

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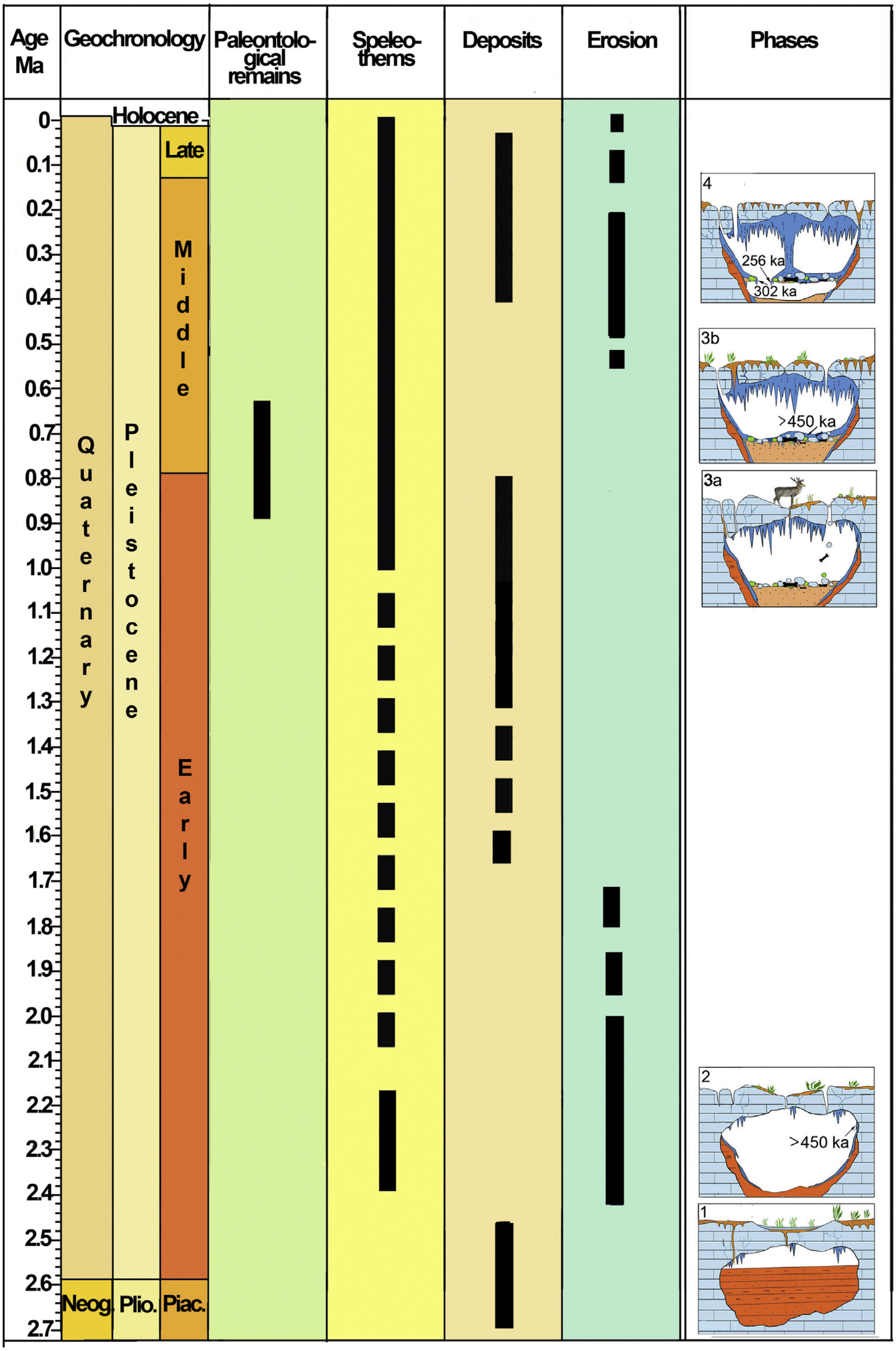

Figure 8. The geochronological synthesis of the development and sedimentary history of the Su Fossu de Cannas cave.

taken place during the late Middle Pleistocene (Palombo and Rozzi, 2014). Consistently, on Corsica the most ancient remains of *P. cazioti* have been recorded at Castiglione (dating back to 0.32 Ma), and in the Coscia cave (0.30 Ma; Croitor et al., 2006 and references therein).

P. cazioti is the most common and the smallest deer species in the fossil record. Remains and tracks of *P. cazioti* are known from a variety of Sardinian deposits that are mostly attributed to the Late Pleistocene, although the species was possibly present from the late Middle Pleistocene to the early Holocene (see e.g. Dehaut, 1911;

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Azzaroli, 1952, 1961; Comaschi Caria, 1955, 1956; Cordy and Ozer, 1973; Caloi and Malatesta, 1974; Caloi et al., 1981; Gliozzi et al., 1984; Klein Hofmeijer, 1997; Antonioli et al., 1998; Ginesu et al., 1998, 2003; Melis et al., 2002; Abbazzi et al., 2004; Benzi et al., 2007; Fanelli et al., 2007). The two species, *P. sardus* and *P. cazioti*, are associated with *M. henseli*, and belong to the Sardinian *Microtus (Tyrrhenicola)* Faunal Complex (FC), in particular to the youngest Dragonara Fauna sub-Complex (FsC: Palombo, 2006, 2009). Data from the fossiliferous stratigraphic succession of Grotta dei Fiori (Carbonia, south-western Sardinia) indicate that *M. henseli* was already present on the island during the early Middle Pleistocene, at ~500 ka (Melis et al., 2013). This is in agreement with the maximum age inferred for *P. sardus*. Available data cannot confirm the coexistence of the SFC deer, which are presumed to be older than *P. sardus*, with voles typical either of the Dragonara, i.e., the larger and more derived *Microtus* (*Tyrrhenicola*) *henseli*, or Orosei 2 FsC and the small and primitive *Microtus* (*Tyrrhenicola*) *sondaari*. Morphological traits of *M. sondaari* suggest that the species probably stemmed from an advanced mainland stock of *Allophaiomys ruffoi*, which dispersed in Sardinia no earlier than 1.3–1.2 Ma (cf. Sala and Masini, 2007 for the chronology of Italian arvicolids).

The uncertainty on the actual chronological range of the three Sardinian species of the endemic Megacerini makes challenging any inferences about the actual time and mechanism of the species replacement, and their evolutionary rates. The latter, indeed, cannot be estimated, because the time of entry of the putative ancestor onto the island is unknown and the appearance of dwarf forms is poorly dated. Following most authors, there is a chance that the ancestor of the Pleistocene Sardinian deer might have entered Sardinia during the marked post-Jaramillo sea level lowering (MIS 24 and 22, roughly between 0.95 and 0.85 Ma), but who the ancestor was still needs to be addressed. The hypothesis that *P. cazioti* belongs to the Megacerini tribe, in particular the so called "*Praemegaceros verticornis* group" as intended by Azzaroli (1979) has been widely accepted (e.g., among others Comaschi Caria, 1955, 1956; Azzaroli, 1961, 1979; Radulesco and Samson, 1967, Caloi and Malatesta, 1974; Kotsakis, 1980, Caloi et al., 1981; Abbazzi et al., 2004; van der Made and Palombo, 2006; Croitor et al., 2006; Vislobokova, 2013), although some authors have expressed a different opinion on its phylogenetic relationship. Deperet (1897), for instance, regarded the Corso-Sardinian species as a late descendent of the genus *Eucladoceros*; Klein Hofmeijer (1996, foot note p. 8) and Sondaar (2000 personal communication to MRP) have suggested that the Sardinian deer would be related to *Dama*; and van der Made (1999) noted that the possibility of a descendence from *Dama*-like deer, a form close to *Eucladoceros tetraceros*, or from *Etruridelphis giulii*, or from *Arvernoceros* should be further investigated although he did not completely discard a possible relationship with Megacerini. The hypothesis that the endemic deer from Sardinia and Corsica stemmed from one of the large deer of the Early–Middle Pleistocene of Europe is supported by some cranial (see Caloi and Malatesta, 1974), dental (e.g., the P4 morphology) and antler features (e.g., the presence of a posterior tine in the fully-grown antlers) that *P. cazioti*, the best known Sardinian species, shares with some continental representatives of the genus *Praemegaceros*.

However, despite many studies specialists still do not agree on the species from which the endemic megacerine lineage originated, i.e., *P. verticornis* or *Praemegaceros solilhacus*. According to Croitor (2006), the number and significance of the morphology traits, i.e., similar antler construction and some details of dental morphology shared by *P. cazioti* and *P. solilhacus* indicate that both species descended from the same ancestor. Croitor (2006) stated that this evidence would be enough to include *P. cazioti* and *P. solilhacus* in the subgenus *Nesoleipoceros*, while *P. verticornis* (as well as in Croitor's opinion *Praemegaceros pliotarantoides*) would belong to the subgenus *Ortogonoceros*, and *Praemegaceros obscurus* and *Praemegaceros dawkinsi* to the nominal subgenus *Praemegaceros*.

Vislobokova (2012, 2013) includes the three species *P. verticornis*, *P. obscurus* and *P. solilhacus* in the new Praemegacerina sub-tribe, and indicates that the last of these was the ancestor of the Corso-Sardinian endemic lineage.

Assuming that the phyletic relationship with the *P. solilhacus* lineage may be correct, a question arises about the time of such an origin. The mainland species was certainly present in Southern Europe from the beginning of the early Middle Pleistocene, although some authors report its presence, or that of closely related taxa, in the post-Olduvai Early Pleistocene. Croitor (2006) argues that both species, the mainland (*P. solilhacus)* and the insular *(P. cazioti)*, would have originated from a species represented by a single, largely incomplete, antler in the late Villafranchian LFA of

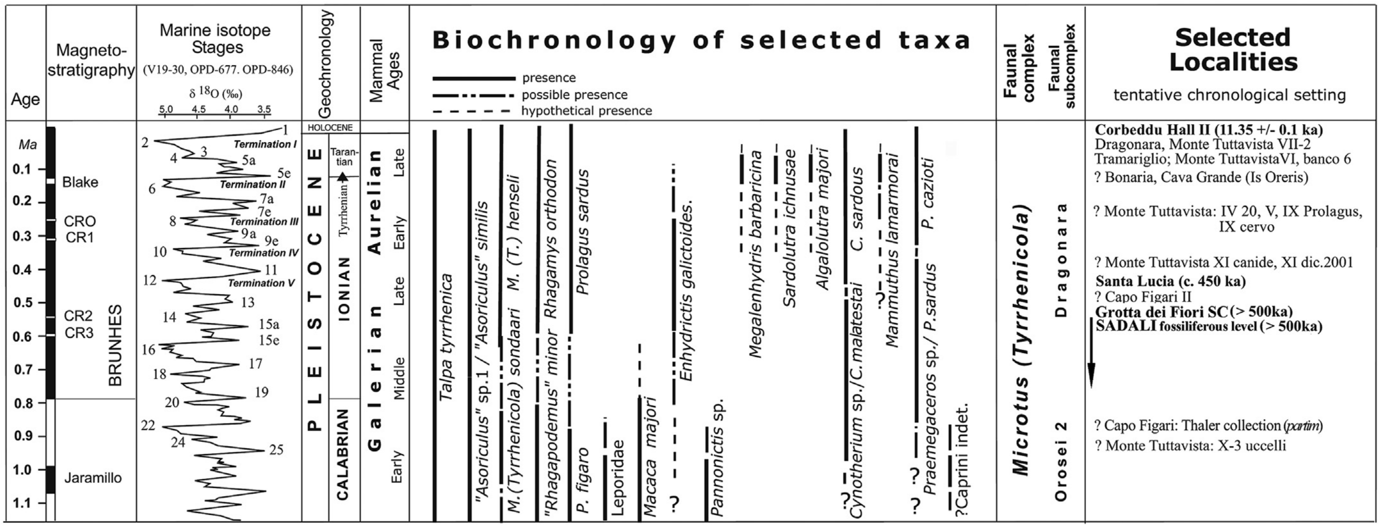

Figure 9. Chronological range chart of the mammalian taxa documented in the Pleistocene to early Holocene Sardinian local faunal assemblages (updated and modified from Palombo, 2009).

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Pietrafitta (Umbria, central Italy), which is a site that has yielded a number of remains of *P. obscurus* (Abbazzi, 2004 and references therein). Few remains of *P.* aff. *P. solilhacus* were reported by Abbazzi and Masini (1997) in the Pirro Nord LFA in Apulia, southern Italy (possibly 1.5–1.4 Ma, see Palombo and Rozzi [2014], for a discussion). Abbazzi (2004), however, considered this identification to be provisional because of the inadequate fossil sample. Other Early Pleistocene findings (e.g., those of Venta Micena, Guadix-Baza Basin, Spain, Menéndez, 1987) have been regarded by some authors as being close to *P. solilhacus*, but the identification divides researchers. Data from the SFC cave provides little contribution when it comes to solving the debate on the phylogenetic relationship of the Sardinia *Praemegaceros* lineage, because of the paucity of the remains retrieved from the hard matrix of the conglomerate, the difficulty of inferring the actual morphology of the mandible and teeth, and the lack of any antler remains.

A more complete morphological and biometric analysis of the SFC deer, assuming that these specimens are older than those from Santa Lucia (as roughly supported by the numerical dating of the flowstone capping the fossiliferous conglomerate) and taking into account the presence of the giant deer in southern Europe during the late Early Pleistocene, is needed to help test the hypothesis that the ancestor of the endemic lineage entered Sardinia during one of the most important post-Jaramillo sea level lowerings (~0.95–0.85 Ma). Moreover, in view of the presence of a phalanx of a young individual (?*Cynotherium* sp.) in the Cava X-3 Uccelli at Monte Tuttavista, where the canid is associated with some species already recorded in the *Nesogoral* Faunal Complex, as well as newcomers such as the archaic vole *Microtus (Tyrrhenicola) sondaari* (Abbazzi et al., 2004; Madurell-Malapeira et al., 2015), the hypothesis that *Praemegaceros* could have already been present in Sardinia LFAs belonging to the Orosei 2 FsC (sensu Palombo, 2006, 2009) cannot be rejected (Fig. 9).

Conclusion

Available data indicate that the evolution of the SFC cave has been greatly influenced by the structural geological setting of the site. The first cavity, with its lateral branches almost totally filled with fine sediment, and the narrow horizontal underground tunnel represent the uppermost portion of an only partially explored cavity. This cavity is aligned and probably developed along a NW–SE fault, but whose extension and depth are still unknown.

The cave's basic origin is linked precisely to karst dissolution processes and clastic filling triggered by a water supply. Variations in climate and the water regime contributed to sedimentation and erosion episodes, both chemically and physically, through a low-energy water flow.

The fossiliferous conglomerate, which was deposited by a high-energy water flow coming from outside, probably represents what remains of the final filling of the cavity. Subsequently, cementation processes and the deposition of a flowstone of unknown thickness protected the conglomerate from the erosion stage during which the cave, or at least the uppermost portion, was partially unfilled.

Overall, evidence from the SFC cave provides a minimum age (>450 ka) for the presence of endemic large deer in Sardinia, but there is only limited chronological information on the time of the anagenetic evolutionary transition from large to smaller deer within the *Praemegaceros* Corso-Sardinian lineage.

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