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Pleistocene Caves of Eastern Sicily Coast: Exceptional Archives to Reconstruct the History of the Island's Biota

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Abstract: The distinctive features and fossil content of some caves from eastern Sicily (San Teodoro, Donnavilla, Fulco, Taormina, Tremilia, Spinagallo), altogether spanning from the middle Pleistocene until the beginning of the Holocene, are discussed. Although dating on vertebrate and/or invertebrate remains is available in few instances, coastal notches and marine terraces correlate with the caves, provide further chronological constraint. The San Teodoro and Spinagallo caves are the best known, whereas the Tremilia cave deserves to be better analysed. Most caves, but not the San Teodoro one (including only terrestrial faunas), testify to the transition from submarine coastal environments (documented by biogenic crusts, borings, shelly sediments), to continental conditions (vertebrate remains of the *Paleoloxodon falconeri*, Maccagnone and San Teodoro Faunistic Complexes). The fossil register preserved in these cavities represents a source of information useful to (1) reconstruct the palaeogeography of Sicily and its coastline, largely resulting from the interplay between tectonic and sea-level changes linked to climate fluctuations; and (2) the consequent evolution of the terrestrial biota, including the dominance of insular endemic taxa later replaced by species shared with continental Italy, after the establishment of temporary connection through the Messina Strait.

Keywords: cave habitats; invertebrates; mammals; terraces; palaeobiogeography; Quaternary; Mediterranean basin

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1. Introduction

The coastal area of Eastern Sicily is characterized by wide sectors shaped by Pleistocene to present-day tectonics and concurrent glacio-eustatic sea-level changes [1]. As a result, several raised paleo-shorelines represented by cliffs, abrasion platforms and/or terraced deposits were formed along the coast belt at different heights. These terraces, now located from a few meters to about 600 m a.s.l., include basal marine sediments sometimes topped by continental vertebrate-bearing deposits [2]. Likewise, numerous fossil caves of karstic to a marine origin, today opening along palaeo-cliffs at different altitudes, were carved by tidal notches and *Lithodomus* boreholes and filled by shell-bearing littoral sediments. These morphological and depositional features remain to testify to the history of the caves once they have risen and retreated some distance from the coastline. Caves also often preserve significant fossils of continental vertebrates that lived in or near them during the emersion phases. In this view, they represent archives to reconstruct the history of the nearby coastal land.

The vertebrate fossil content of the Sicily caves is related to three chronologically distinct faunal assemblages. The oldest, located more inland and dated early in the middle

Pleistocene [3], is characterised by the dwarf elephant *Palaeoloxodon falconeri*, endemic micromammals, reptiles and birds. The intermediate one, usually found closer to the present-day coastline and dated from the late middle Pleistocene to early upper Pleistocene [4,5] contains the middle-sized elephant *Palaeoloxodon mnaidriensis*, *Hippopotamus pentlandi*, carnivores, rodents, reptiles, and birds [6]. The youngest, dated to the very late Pleistocene is characterized by a higher species richness and a lower endemicity.

Studies carried out during the last decades concerning the origin of marine terraces and their related palaeo-cliffs have led to equivocal conclusions [7–9]. Consequently, it is difficult to understand the evolution of coastal areas in eastern Sicily. Antonioli et al. [1] distinguish two sectors having different uplift rates. According to these authors, the uplift rate during the Holocene at Cape Peloro has been 0.71 ± 0.11 cm/a while at Taormina it has been 0.87 ± 0.11 cm/a. According to Ref. [10], the uplift rate in the Messina Straits has been 1.3 ± 1.14 cm/a in the last 60 ka. Furthermore, in the Hyblean area the formation of coastal terraces interacted strongly and in a rather complex way with eustasy and tectonics and most marine sediments first deposited at cave openings along paleo-cliffs have been later partly or nearly completely eroded [11]; this mainly happens for caves located close to the sea-level during regression phases. In addition, the "erosion" produced by humans who used the caves and excavated and removed the deposits for different purposes has been often relevant.

Despite these unfavourable interactions, caves, being conservative environments for fossilization, tend to preserve sedimentary deposits and faunal content within them, at least partially.

Therefore, by knowing the age and composition of the cave's fossil content and correlating their altitude and position with respect to the modern coastline, it is possible to obtain precious information on the palaeogeography and Pleistocene outline of the Sicilian coast.

Although Sicilian caves have been extensively studied and documented, until now no global paleogeographic analyses nor comparisons between their faunal contents and palaeoecological meaning has been addressed. In this context, the aim of this paper is to present the current state of knowledge about some Pleistocene caves from different areas of eastern Sicily, making comparisons between them, and raising some critical observations. Particularly, analogies and differences in distinctive features among six well-known fossiliferous caves, located at different heights, near the modern coastline, are discussed. The first step is to correlate the recognised comparable depositional phases inside studied caves in terms of fossil content and time of deposition. As regards the vertebrate deposits, a critical review of faunal biochronology was done, being a reference to investigate paleobiogeography and paleoecology of Quaternary mammals of Sicily. Available data are also used to give a picture of cave vertebrate and invertebrate associations on an island subject to relevant and fast changes in geography and environment, contributing further information to the reconstruction of the most recent Quaternary evolution of Sicily's coastal paleogeography.

2. Geographical and Geochronological Setting

The six caves here examined (i.e., the San Teodoro, Donnavilla, Fulco, Taormina, Tremilia and Spinagallo caves) are located along the coastland of eastern Sicily, very close or at most a few kilometres inland from the modern coastline (Figure 1). A further cave of marine origin from the coastal area Punta Campolato (Augusta) in south-eastern Sicily [12], containing Tyrrhenian deposits with remains of *P. mnaidriensis*, is kept out of this review, because is still under investigation.

For more or less long periods, the history of these caves has been controlled by the sea flooding inside or stationing near the entrance, as testified by the presence of erosional marks, including common bivalve boreholes, marine biotic crusts such as vermetid aggregates, and/or layers bearing marine fossil shells.

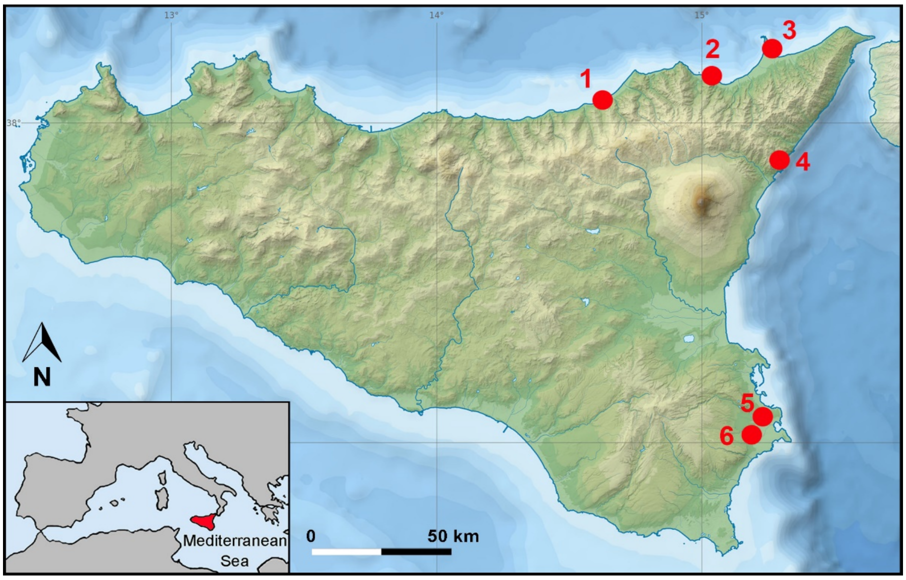

Figure 1. Location of the studied caves. (1): San Teodoro Cave; (2): Donnavilla Cave; (3): Fulco Cave; (4): Taormina Cave; (5): Tremilia Cave; (6): Spinagallo Cave.

All these caves correlate with marine terraces that were forming during the intense uplift affecting eastern Sicily during the Pleistocene. Terraced sediments deposited during sea high-stands correspond to odd numbers in the marine isotopic record (Figure 2).

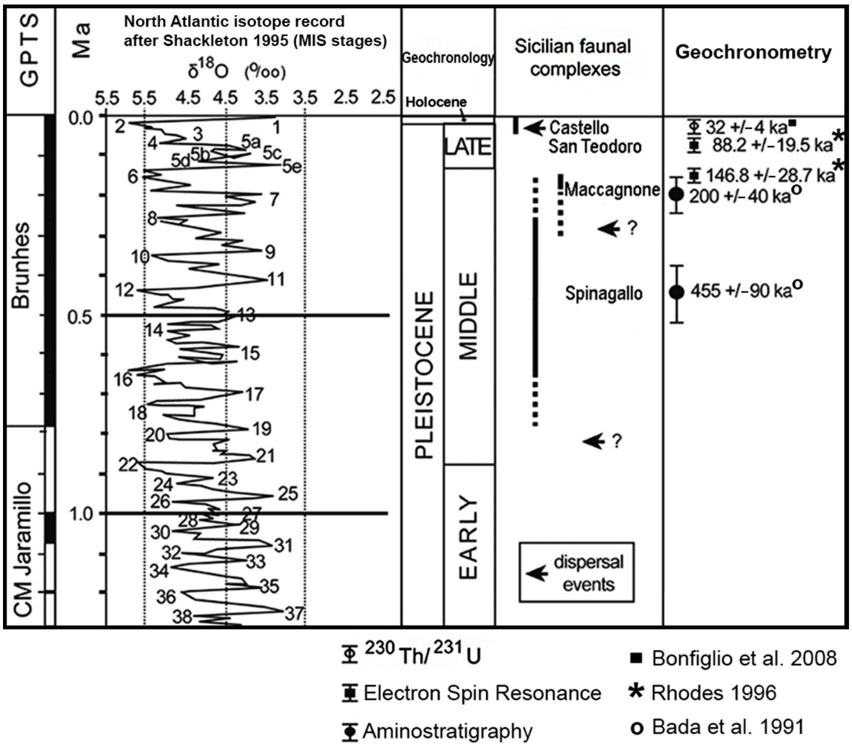

Figure 2. Chronological distribution of Sicilian faunal complexes shown in the frame of marine isotope stages (MIS). CM, Cobb Mountain subchron; GPTS, geo-magnetic polarity time scale. The question marks indicate uncertain times and ways of dispersals. (from Refs [4,5,13,14] modified).

Correlations of cave deposits with the marine isotopic stages can provide an additional independent tool to date fossiliferous deposits. In the strongly uplifted northeastern Sicily, up to six orders of marine terraces may be found from 600 m to 25–30 m a.s.l. [15,16]. Only the widest terrace, located between the altitudes of 150–135 and 60 m a.s.l., has been dated;

this terrace, named "PO" [17]. or "Grand replat" [15] results from multi-cycle marine deposits including two distinct erosional surfaces, named I and II, whose inner edges are respectively at about 130 and 100 m a.s.l. (Figure 3). This distinctive marker horizon forms the basis for regional correlation in northeastern Sicily [6,15,18]. At Capo Peloro, on the west side of the Messina Straits, this terrace is at 110 m a.s.l. and consists of marine sands with the Senegalese Guest gastropod *Thetystrombus latus*; this is the worldwide-known palaeontological evidence for the last interglacial high-stand in the Mediterranean, referred to MIS 5e. Absolute dating, primarily U-series dates on corals directly associated with *T. latus*, provided an independent date of 127 ± 4 ka [19] or 121 ± 7 ka [20].

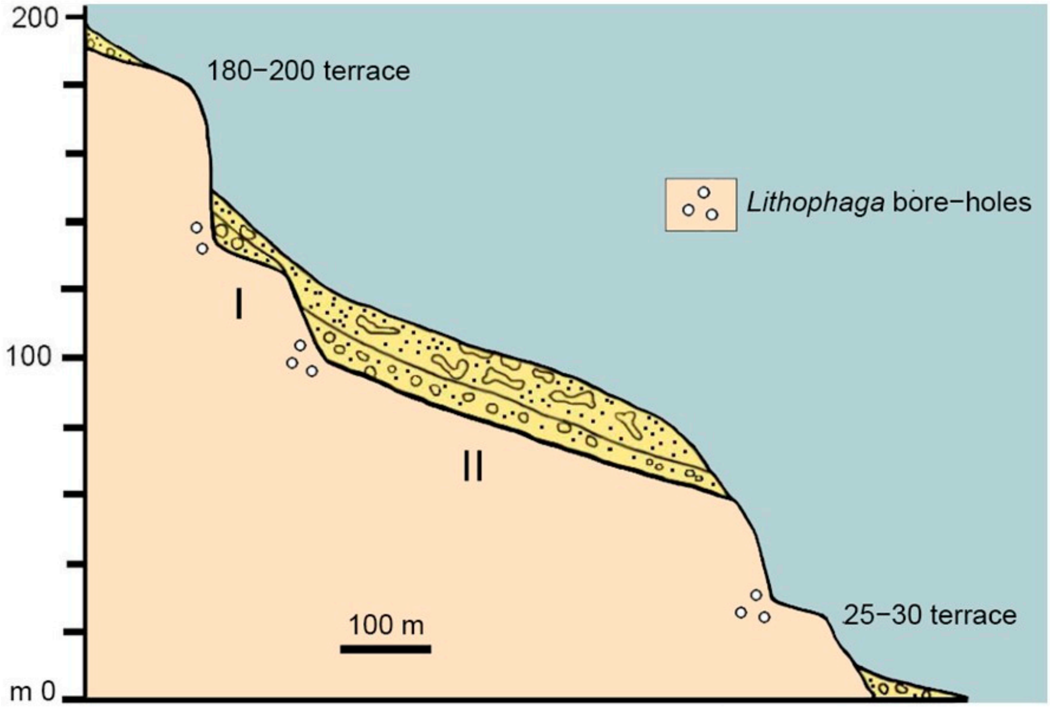

Figure 3. Schematic geological profile of the "PO" polycyclic terrace from northeastern Sicily. I-abrasion platform at 131 m a.s.l; II MIS 5e abrasions platform at 60–90 m. The older terrace located at 200 m and the younger one located at 25–30 m a.s.l. are also shown (from [6], modified).

In the Hyblean Plateau, the highest middle Pleistocene marine terrace is located at 175–200 m a.s.l. [7,21] and Tyrrhenian deposits with *T. latus* occur at 30 m a.s.l. [22]; this contrasts with terraces' elevation in northeastern Sicily, where uplift through the late Pleistocene until today [23,24], happened with a higher rate [1]. [25] refined dating of palaeo-shorelines and estimation of uplift rates for the Hyblean Plateau. These authors showed that palaeocoast elevations in this region increase from the south to the north, but with uplift rates constant through time for each sector.

The evolution and distribution of the Pleistocene caves and terraced deposits with fossil content have been shaped by palaeogeography (Figure 4). The Pleistocene geographic history of Sicily can be broadly summarized as the evolution of a system of emerged islands comprising two main islands besides Malta: a wider northern one elongated E-W, largely corresponding to the already emerged coastal chain, and a decidedly smaller second one located to the SE, formed by the Hyblean Plateau foreland and associated volcanic rocks. The two islands were separated by the Gela-Catania trough, a NE-SW trending relatively wide and locally deep strait, where blue-grey clays deposited from the Zanclean to the Calabrian time. By the late Pleistocene, it was completely filled. Emerged areas increased the extension of connections of these islands and favored the dispersion of continental faunas [26–28]. Furthermore, during the short Pleistocene phases, the Messina Straits, that nowadays represents a barrier to terrestrial faunas, was the site of narrow temporary emerged bridges allowing the passage of some continental mammals including *Homo* as suggested by Ref. [29].

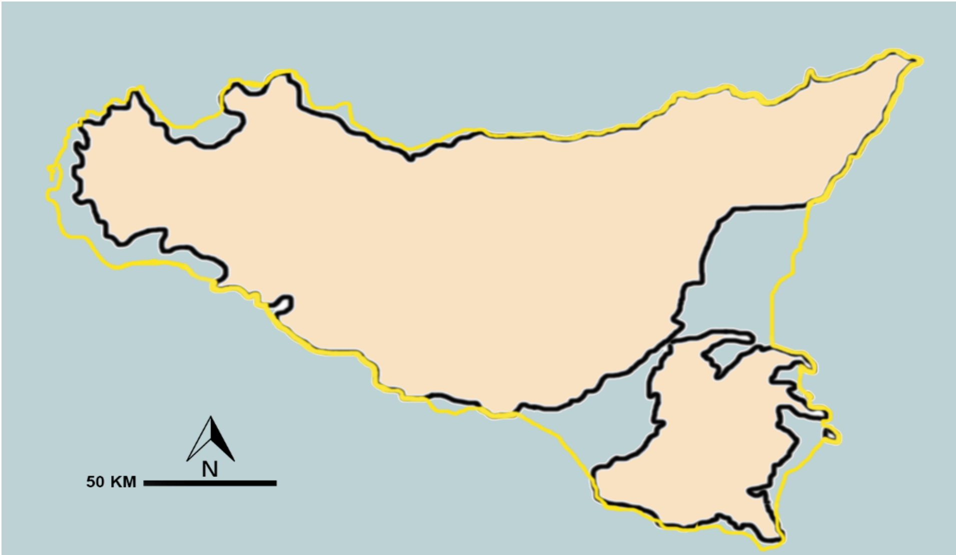

Figure 4. Palaeogeography of Sicily in the middle Pleistocene against present-day coastline (yellow contour). The Hyblean Plateau formed an island separated from the rest of Sicily (from [27], modified).

In Sicily five Faunal Complexes (FCs) of Quaternary vertebrate fauna have been distinguished based on bio-events (extinctions and new arrivals) and evolution of endemic species [6,13,14]. Among these FCs, or continental biochronological units, three have been recognised in the examined caves: the *P. falconeri* FC (early middle Pleistocene, probably MIS 22-11), the Maccagnone (formerly *P. mnaidriensis*) FC (late middle Pleistocene, probably MIS 10-4) and the San Teodoro FC (late Pleistocene, 32,000 ± 4000 yr BP, after ^{230}Th/^{234}U dating on a concretion [30].

3. Description of the Caves

3.1. San Teodoro Cave

The cave opens about two kilometres southeast of the town of Acquedolci (Figure 1) along a cliff, at 140 m a.s.l. (Figure 5). After [31], this karstic cave, formed in Jurassic limestones approximately 8–10 my ago, is over 60 m long, 20 m wide and up to 20 m high covering a total surface of more than 1000 square meters. The cave, discovered and examined since the second half of the 19th century [32–34], preserves an invaluable documentation of now-extinct Pleistocene animals and prehistoric human remains, constituting a landmark for the study of upper Palaeolithic culture in Sicily [35,36].

The cave contains basal sterile sediments (Unit C) overlaid by two fossiliferous Units: the mammal-bearing B Unit and the most recent A Unit including human remains. The C Unit correlates with richly fossiliferous lacustrine deposits cropping out at the base of the subvertical cliff where the cave opens (Figure 6) and reported as the Acquedolci sediments. They deposited on the inner margin of the "PO" recognised from Cape Peloro to Acquedolci along the Tyrrhenian coast. These deposits provided thousands of remains of hippo (*H. pentlandi*) and rare ones of deer (*Cervus elaphus siciliae*), wolf (*Canis lupus*), bear (*Ursus* cf. *arctos*), tortoise (*Testudo* cf. *hermanni*), and only a bone of vulture [6,14,31,37–39]. Excavations in front of the cave entrance recovered a breccia with bone fragments of *H. pentlandi* and rare *Crocuta crocuta spelaea* possibly removed from the highest portion of the lacustrine sediments and redeposited just outside the cave by the penetrating water table of the lake that at least partly flooded the cave [31,39].

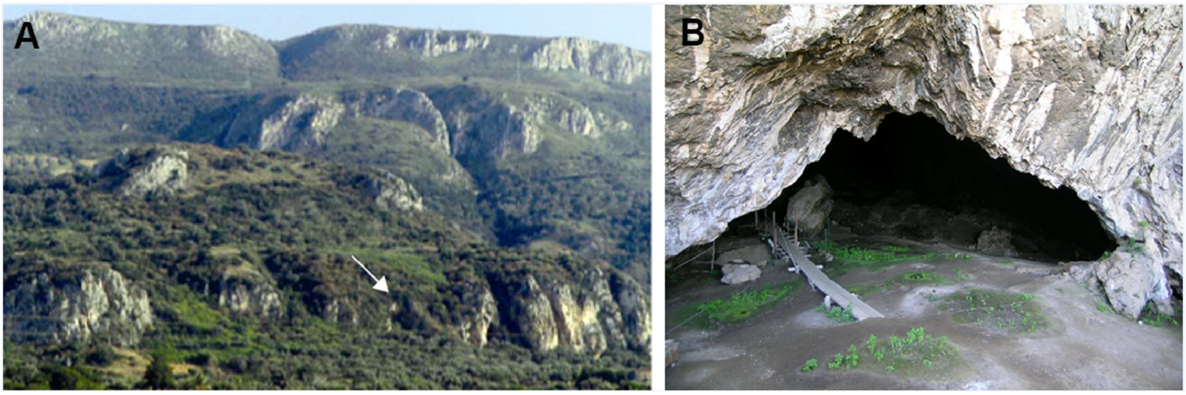

Figure 5. (**A**) the carbonate massif of Pizzo Castellaro where San Teodoro Cave opens (arrowed) with terraces above and below it. (**B**) the entrance of the cave.

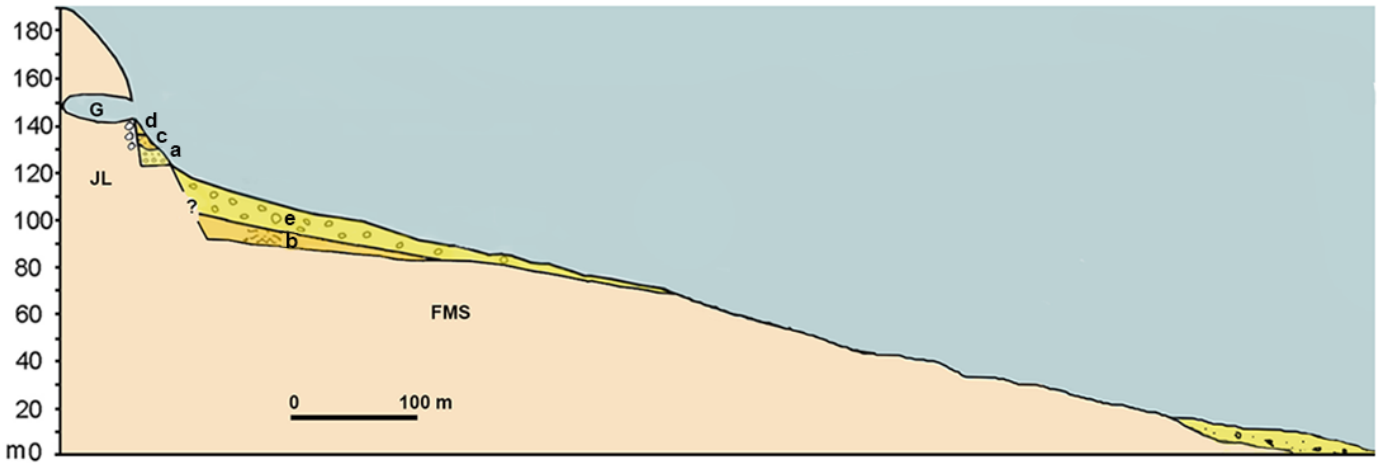

Figure 6. Schematic profile of the Pizzo Castellaro cliff with the San Teodoro Cave (G), the marine abrasion platforms at 130 m and 60–100 m (referred to the MIS 5e), and the terrace at 25–30 m a.s.l. JL: Jurassic limestone; FMS: Monte Soro Flysch. a: beach deposits. b: "PO" fossiliferous deposits referred to the MIS 5e. c: lacustrine silty clays, gravels with bones of *Hippopotamus pentlandi*, and rare deer (*Cervus elaphus siciliae*), wolf (*Canis lupus*), bear (*Ursus* cf. *arctos*), tortoise (*Testudo* cf. *hermanni*), and vulture. d: breccia largely formed by fragments of *H. pentlandi* from the highest portion of the lacustrine deposits flooded inside the cave. e: Sterile deposits overlying the terrace and the platform at 130 m. circles: *Lithophaga* boreholes (from [31,39,40], modified).

Over the years, several trenches excavated in these deposits delivered remains of large mammals of different Pleistocene ages. The two trenches 'α' and 'β' (Figure 7) expose fine sands and gravels [30,39,41–43] including abundant fragmented remains of mammals mostly ascribed to the B Unit, as well as small marine gastropods, presumably penetrated through fractures, from a terrace located at a slightly higher altitude.

The mammal assemblage belongs to the San Teodoro FC and includes an elephant (Figure 8) *Paleoloxodon* sp., previously reported as *P. mnaidriensis* but seemingly representing a new species according to [44], the Sicilian wild ox (*Bos primigenius siciliae*), the Sicilian bison (*Bison priscus siciliae*), the Sicilian deer (*C. elaphus siciliae*) (Figure 9), the wild boar (*Sus scrofa*), the wolf (*C. lupus*), the hyena (*C. crocuta spelaea*), the fox (*Vulpes vulpes*) and the "wild ass" (*Equus hydruntinus*). Small mammals are represented by the Savi vole [*Microtus* (*Terricola*) ex gr. *savii*], the wild mice (*Apodemus* cf. *sylvaticus*), the hedgehog (*Erinaceus* cf. *europaeus*), a shrew (*Crocidura* cf. *sicula*) and bats (*Chiroptera indet.*). A prominent feature of this assemblage is the abundance of bones of *C. crocuta spelaea* as well as its predation traces (crushing, gnawing, chewing and digestion) and coprolites in huge quantity, leading to interpreting the cave as a den where hyenas accumulated their preys [43,45].

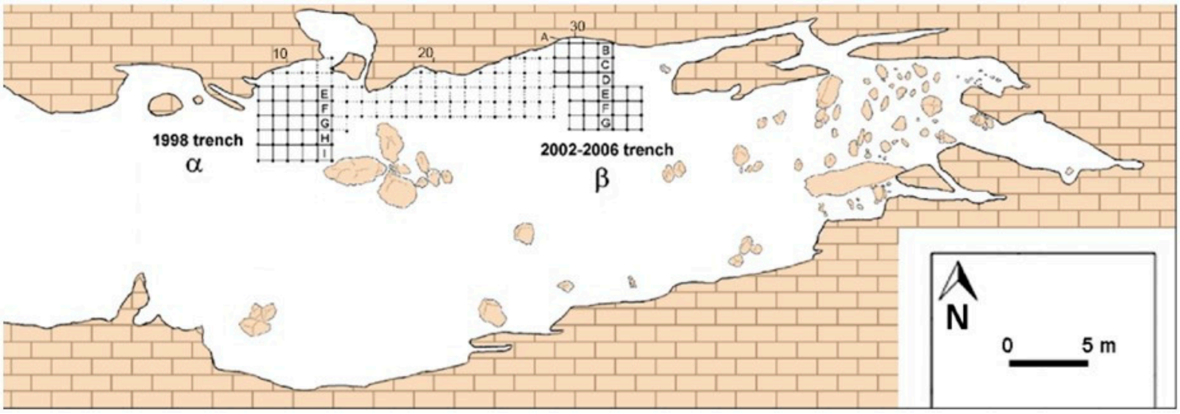

Figure 7. Plan of the San Teodoro Cave. Opening on the west (left side). The location of the α trench (squares E–I/9–13) excavated in 1998 and β trench (squares A–G/29–34) excavated in 2002–2006 is indicated (from [30], modified).

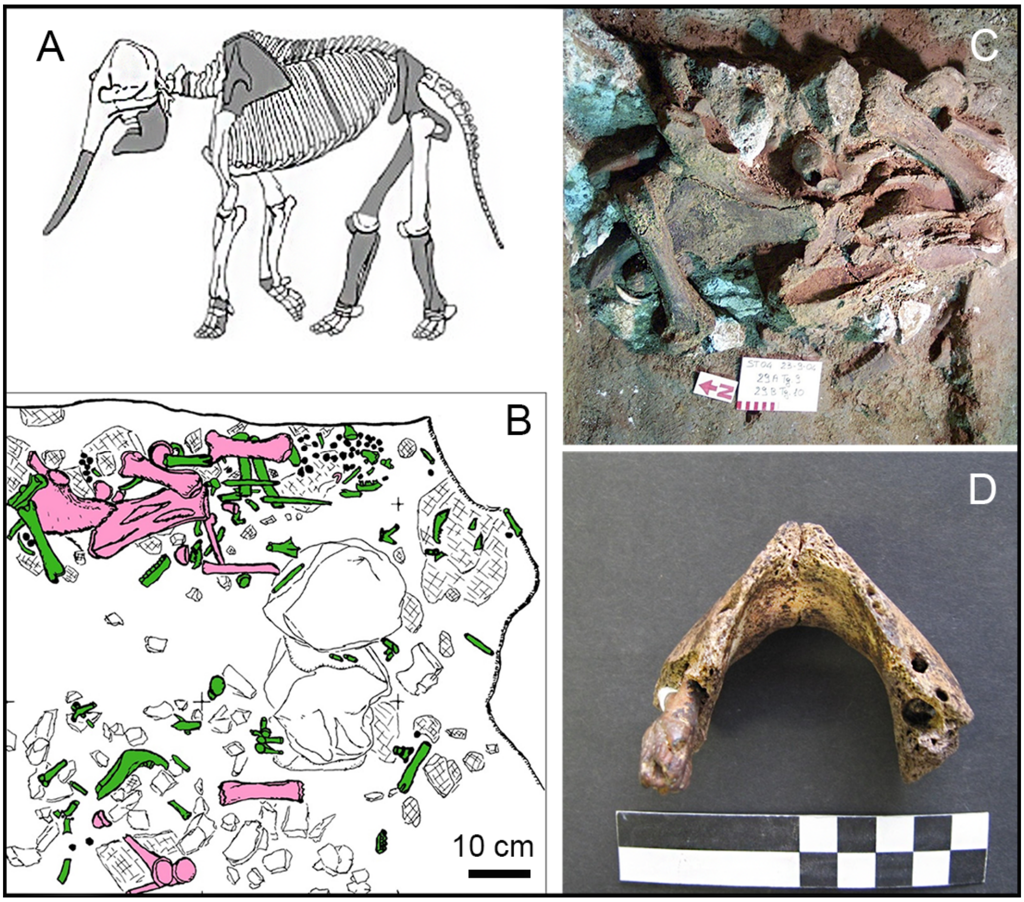

Figure 8. (**A**) Scheme with the position of the bones recovered in the San Teodoro Cave plotted against an elephant skeleton. (**B**) Plan of partially articulated remains of elephant in the β trench (from Ref. [44], modified). (**C**) Detail of the bones on the outcrop. (**D**) A small mandible of a likely *Palaeoloxodon*, probably not born, found below other elephant bones. Pink: elephant bones; green: ox bones.

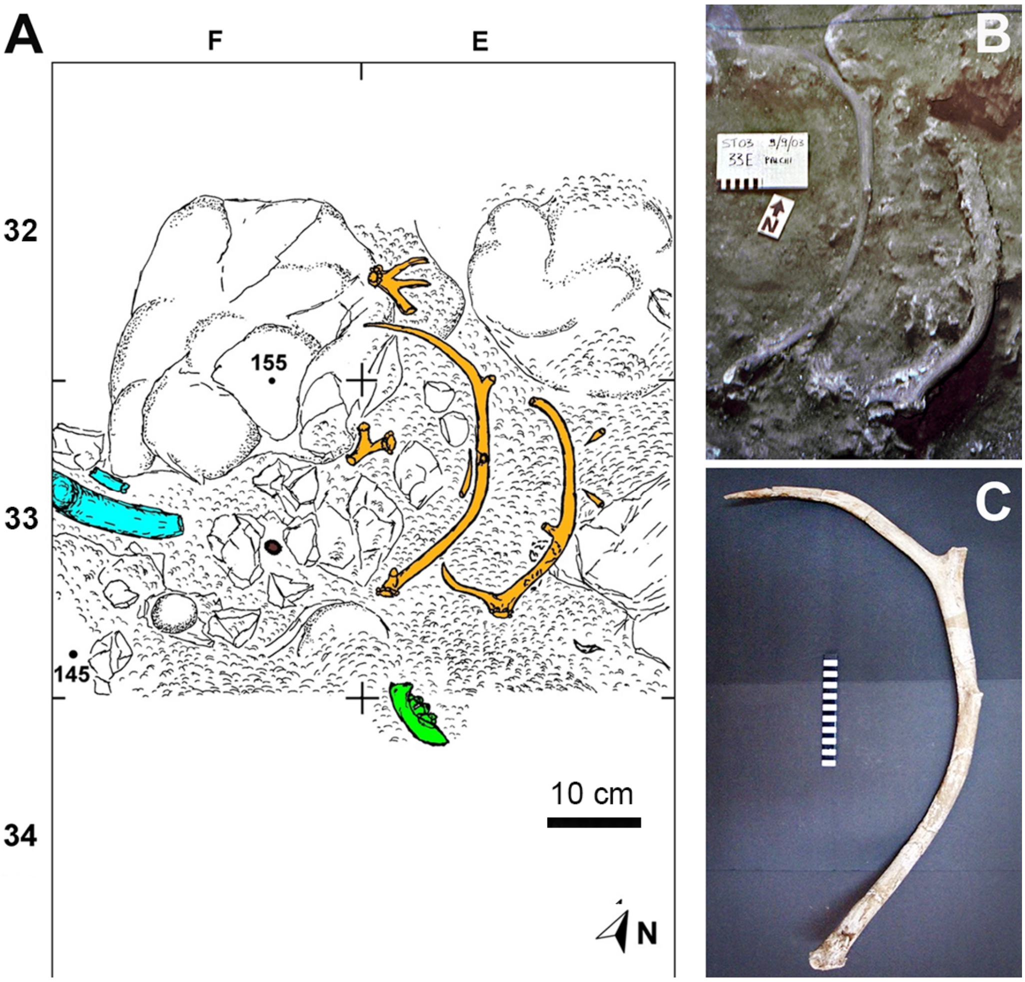

Figure 9. Drawing (**A**) and photo (**B**) with location of the two antlers (orange) of *Cervus elaphus siciliae* in the trench of the San Teodoro Cave before recovering. Light blue: tusks of elephant; green: remains of *Bos*; (**C**) photo of one antler. Scale bar 10 cm. Numbers and letters along the sides of A refer to the excavation grid visible in Figure 7 (from [46], modified).

The uppermost A Unit contains mammal bones interpreted as meal remains of humans associated with stone tools referred to as the late upper Palaeolithic (Epigravettian); it also preserves Neolithic, Bronze and Greek archaeological remains. Sediments also delivered buried remains of *Homo sapiens* including exceptionally complete and articulated skeletons of at least seven humans [35,36,41,47,48]; this makes the San Teodoro Cave the first, and still the only, known Paleolithic burial in Sicily.

Overall, the different faunal associations gathered inside the cave represent three phases of subsequent environmental conditions in the upper Pleistocene that can be placed between 200,000 and 11,000 years ago.

The dating of the deposits inside the San Teodoro Cave provided conflicting results, using different methods and fossil elements: the lacustrine deposits were dated at 200 $\pm$ 40 ky by Ref. [4] using the aminoacids racemization method on dental remains of *H. pentlandi*, but the same authors also dated at 455 $\pm$ 90 ky an elephant tooth from the Anca collection housed at the Gemmellaro Museum of Palermo. A concretion within the clayey layers in the β trench was dated at 32 $\pm$ 4 ka using the ^{230}Th/^{234}U [30] in substantial agreement with the radiocarbon date of 23–21 cal ka BP obtained by Ref. [29] on a metacarpus of *Equus hydruntinus* (Figure 10) collected in the β trench, just above the dated concretion. After these dating, the fossil *Paleoloxodon* sp. from the San Teodoro Cave represents one of the most recent documentation of dwarf elephants in Sicily besides that of Favignana [49].

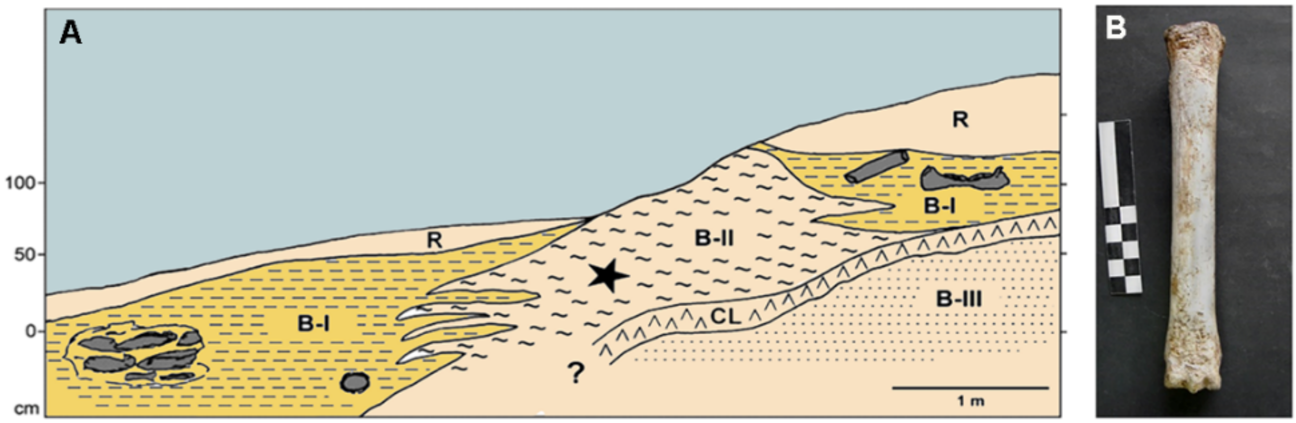

Figure 10. (**A**) NE–SW schematic section of the sedimentary sequence of the B unit deposits cropping out in the β trench. R, recent; B-I, non-concreted B unit; B-II, concreted B unit; B-III; clayey B unit; CL, radiometrically dated concretion with question mark indicating uncertain continuation of the level; grey, partially articulated elephant bones; star, location of the dated *Equus hydruntinus* (from Ref. [30], modified). (**B**) Metapodial of *E. hydruntinus* dated at 23–21 ka.

During the late upper Paleolithic (upper late Glacial), the cave had at least two periods of human occupation. The first one is documented by the burials excavated in the cave and relates to a period when it was still sporadically visited. The second-period documents a more intense occupation, pointed out by the recovery of the industrial production of quartzarenite lithics and rare flints, intensive slaughter of late-glacial boreal fauna and combustion evidence. The 1 and 2σ calibrated age-ranges indicate an age of 15.2–14.7 cal ka BP, which means that the Anthropozoic layer began to form in the late upper Palaeolithic. Ref. [36] proposed an age of about 12,000 years for the Palaeolithic layer, based on ^{14}C AMS dating on a *Bos primigenius siciliae* remain.

The arrival of both humans and other species, such as *E. hidruntinus*, having no swimming skills nor the propensity to venture into water, indicates that a land bridge existed between Sicily and continental Italy during the last glacial maximum, as also demonstrated by further geological evidences in the Straits of Messina area [29].

During the depositional history of the cave, climate and connections of Sicily with the continent changed as indicated by information derived from the mammal fauna as well as invertebrates and pollen. The non-marine molluscan fauna recovered from the two trenches α and β and associated with the basal C Unit is represented by 21 species of subaerial and aquatic prosobranch and pulmonate gastropods and two species of bivalves [42]. The structure of this molluscan assemblage is characterized by the prevalence of dry-open-land taxa and aquatic species typical of slow-running waters points to a cool climate. In the B Unit, the pollen content from *C. crocuta spelaea* coprolites is characterized by the dominance of steppe taxa and associated low percentages of mesophilous woody taxa and suggests pre-late Glacial conditions with the existence of nearby refugia for temperate and Mediterranean vegetation [50]. Upper layers in the β trench, document a decrease of land taxa and a prevalence of freshwater and hydrophilic elements, pointing to a change to more humid conditions. The wide distribution of freshwater taxa in the sediment points to the presence of a permanent spring or slowly running water inside the cave.

3.2. Donnavilla Cave

The Cave, located at Cape Tindari (Figure 1), is hardly accessible because it opens between 75 and 85 m a.s.l. on an overhanging rocky cliff; it is positioned below a 104 m a.s.l. terrace with littoral deposits (Figure 11) and just above an abrasion platform at 90–60 m attributed to the MIS 5e by correlation with the terrace at Rocca Scodonì, ca. 10 km East of Acquedolci [40]. The cave is a triangular shaped fissure, ca. 20 m high and up to

20 m wide (Figure 12), hollowed in Proterozoic and Palaeozoic felsic-Ca-silicate marbles of the Aspromonte unit and oriented following the N-S striking set of local faults.

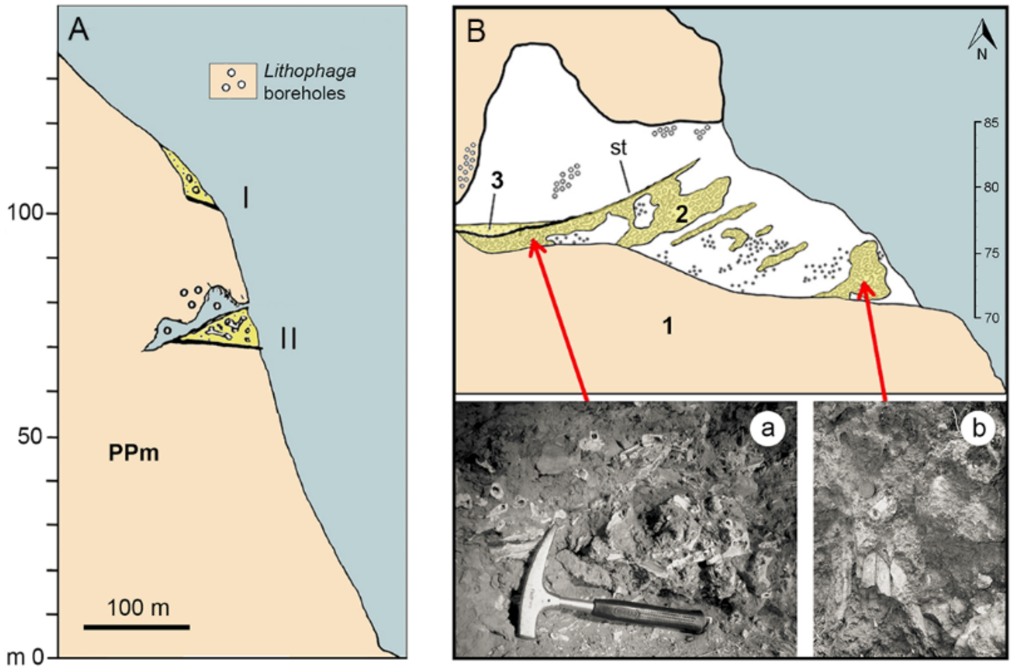

Figure 11. (**A**) Schematic profile of the Tindari steep cliff showing a marine abrasion platform at 104 m (I) and below the MIS5.e abrasion platform and coastline at 90–60 m (II) underlying the mammal-bearing deposit of the Donnavilla Cave. PPm: Proterozoic and Palaeozoic marbles. (**B**) Stratigraphic sequence of the eastern wall of the cave. 1: Substrate; 2: bone breccia with fossil bones in its uppermost sandy-silty brown portion (**a**) and cranial remains of *Hippopotamus pentlandi* (**b**); 3: very fine sands filling a channel and overlying the speleothem; st: dated stalagmite; circles: *Lithophaga* holes (from Ref. [40], modified).

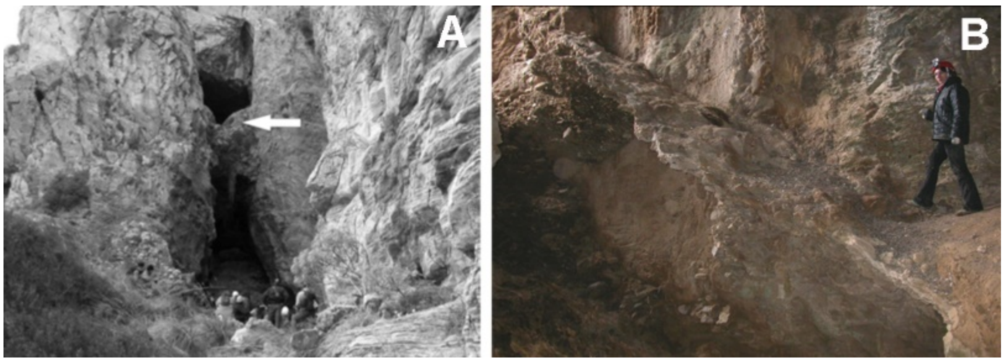

Figure 12. (**A**) The Donnavilla Cave; the hanging speleothem in the upper part of the entrance arrowed. (**B**) The speleothem inside the Cave, overlying a partly eroded bone breccias.

A belt of not abraded densely distributed *Lithophaga* boreholes, pierce both cave walls near the entrance and the cliff outside the cave between 75 and 90 m [46,51]. According to Refs. [52,53] a thick detrital deposit containing irregularly scattered fossil remains of mammals almost sealed the cave. Nowadays, scattered remnants of the bone breccia plaster the bored walls in the outer portion of the cave, while large blocks of the breccia are preserved at the base of the cave's eastern wall and in the innermost sector. The mammal assemblage may be attributed to the Maccagnone FC for the presence of *Dama carburangelensis*, *C. elaphus siciliae*, *H. pentlandi* and *Ursus* cf. *arctos* [53–56]; it was correlated with mammal assemblages from the Tyrrhenian gravels of Rocca Scodonì [40]. In the inner part of the cave, a stalagmite layer cementing scarce remains of the bone breccia is hanging and sloping inward into the cave for about 12 m (Figures 11 and 12).

The portion of the speleothem directly in contact with the fossil remains was dated at 40 ± 4 ka using the ^{230}Th/^{234}U method [46]. The detailed stratigraphic reconstruction, also including: 1. the relationships with the wall portions bored by the *Lithophaga* holes, 2. the comparison with Pleistocene vertebrate-bearing terraces of northeastern Sicily (Acquedolci, Taormina, Scodonì) and 3. the ^{230}Th/^{234}U dating of the speleothem, provided new data and furnished a paleontological contribution to timing tectonics which affected Cape Tindari during the late upper Pleistocene.

3.3. Fulco Cave

The Fulco cave is located on the eastern side of the Capo Milazzo Peninsula (Figure 1). It opens along a road cut on a steep slope, at 51 m a.s.l, within a layer of breccia deposited during the early Pleistocene. Paleozoic metamorphic and Miocene limestone blocks together with rare clasts of isidid-bearing lithified sediments constitute the breccia. Only a section of the cave ceiling is visible along the cut, roughly parallel to the presumed paleo-seashore; it is 10 metres large and up to 2 m high, partially occluded by sediments (Figure 13A) that are prevalently conglomerates of the Tyrrhenian terrace widely cropping out in the Capo Milazzo peninsula between 50 and 85 m [19,57,58]. In the cave, an exceptional invertebrate palaeocommunity encrusts the blocks forming the vault; it consists of very dense colonies of dendrophyllid corals associated with sessile invertebrates [59]. The scleractinian colonies belong to an elongated morphotype of *Astroides calycularis* (Figure 13B) that grew in an upside-down orientation, forming spectacular "hanging gardens" providing the substratum for a rich palaeocommunity including mollusc bivalves (*L. lithophaga*, *Spondylus gaederopus*, *Chama* sp.), serpulids and bryozoans indicating a semi-dark cave habitat in a shallow water setting. The good preservation state of the concretion and the valves of *L. lithophaga* specimens still preserved inside their *Gastrochaenolites* traces (Figure 13C,D), point to a rapid sealing of the cave.

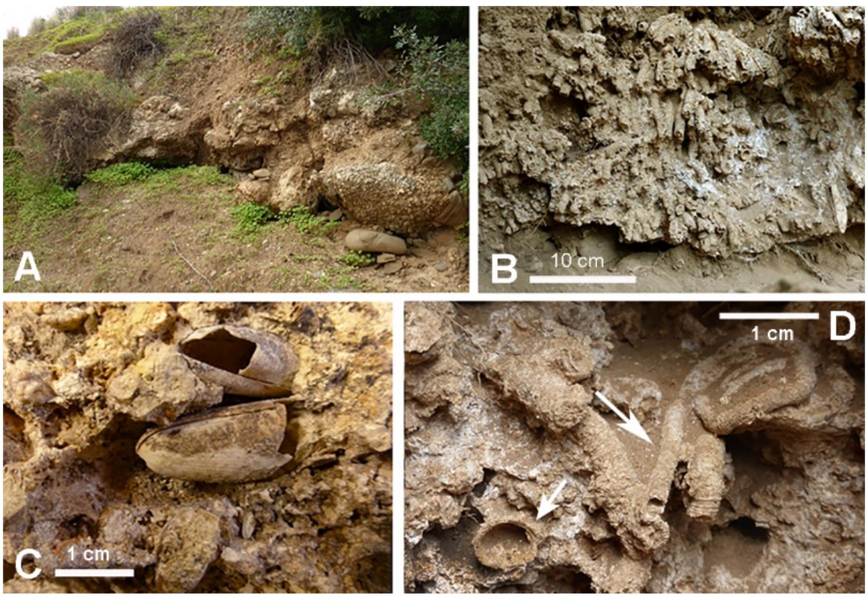

Figure 13. (**A**) Present-day aperture of the Fulco Cave with the Tyrrhenian conglomerates in the foreground. (**B**) Colonies of the scleractinian dendrophylliid *Astroides calycularis* with elongate corallites hanging from the ceiling. (**C**) Specimens of *L. lithophaga* in life position. (**D**) The bivalve *Chama* sp. (short arrow) and the serpulid *Protula* sp. (long arrow) are associated with the corals.

Astroides corallites are exceptionally elongate, possibly as a response to low water motion and/or competition for space and food. The recurrent constrictions occurring on corallite external surfaces point to recurrent periods of slow growth and even growth stasis, possibly related to environmental fluctuations, periodically leading to mortality events.

Taking into consideration the warm climate affinity of *Astroides*, [59] suggested that the colonisation of the cave took place during a warm interglacial period, possibly at the beginning of the Tyrrhenian, when the cave was flooded and fully submerged, during the sea-level rise and highstand, respectively.

3.4. Taormina Cave

This cave is located in the Taormina area (Figures 1 and 14) and opens in Mesozoic carbonate rocks at 131 m of altitude, just above the 90–120 m terraced deposit, corresponding to the abrasion platform II of the "PO", dated to the Tyrrhenian (MIS 5e) based on ESR methods applied to marine shells found at 105 m [1]. The Taormina Cave, subtriangular in cross-section, is 15 m long, 8 m wide and up to 6 m high (Figures 14 and 15). In the inner sector, paleosoils and vertebrate-bearing breccias, including anthropogenic remains of the upper paleolithic, are plastered to the cave walls [60].

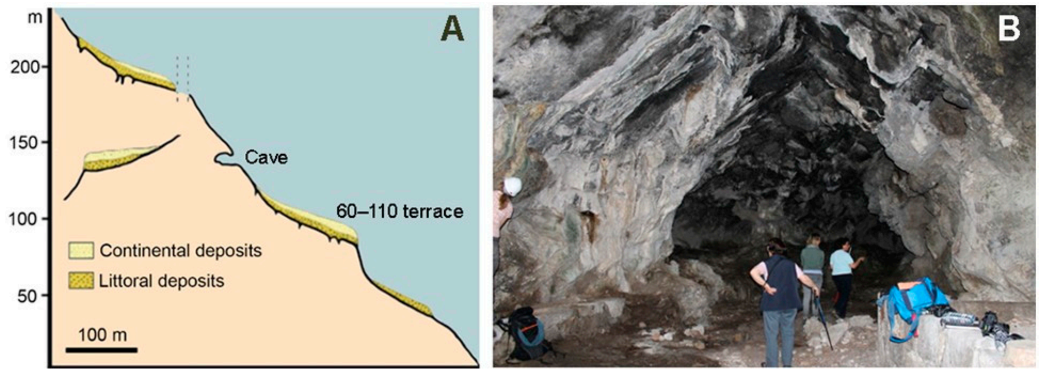

Figure 14. (**A**) Ideal section showing the location of the Taormina Cave in relation to the terraces in the area [60]. (**B**) The Taormina Cave seen from the entrance.

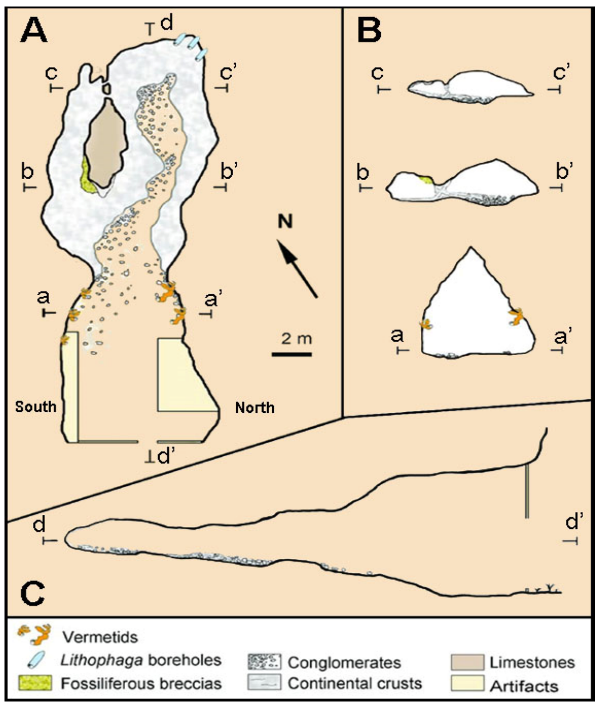

Figure 15. Map of the Taormina Cave. (**A**) Plan view with the indication of transversal (a-a′, b-b′ and c-c′) and longitudinal (d-d′) sections, reported in (**B**,**C**), respectively (from Ref. [61], modified).

A marine notch is obvious all along the walls of the cave and a discontinuous organogenic crust made up of vermetids locally occurs above it (Figure 15) [60,61].

Marine colonisation is documented by crusts of vermetid coiled shells that can be traced along the walls for about 7 m from the entrance inward, and for about 2 m in height, leaving uncovered a narrow belt near the floor (Figures 15 and 16B). Crust thickness is difficult to evaluate, but ranges from 1 to at least a few centimetres. The fossil association is monospecific except for the occurrence of very rare spirorbids and a single bryozoan article. Rare *Gastrochaenolites* also occur. Rosso and coauthors [62] identified as *Dendropoma cristatum* the vermetids and [61] demonstrated that this represents the first record of extensive vermetid biocostructions inside a cave. In a restricted area of the wall, these authors recognised a particular morphology of *D. cristatum* shells which include straight elongated distal portions with numerous internal septa, aligned parallel to each other and facing downward from a sub-horizontal step along the wall (Figure 16). The location of the vermetids crust and the particular ecological requirements of this species (presently forming bioconstructions in exposed rocky shores, characterised by high light intensity and water energy) points to a cave which was semi-submerged and widely open to the water energy at the time of its colonisation. The particular *Dendropoma* shell morphology has been interpreted as an adaption to reach penetrating water flow rich in food and oxygen, an adaptation also seen in further organisms thriving in cave habitats (e.g., *Astroides* in the Fulco cave).

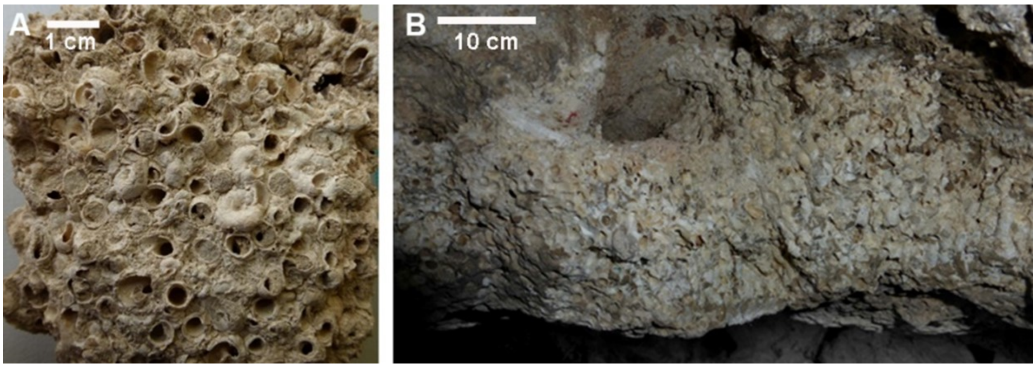

Figure 16. *Dendropoma* encrustations along the wall of the cave. (**A**) Detail of a *Dendropoma* crust with coiled shells. (**B**) Thick crust from the northern wall of the cave, with downfacing specimens having tubular shells slightly undulated and subparallel to each other.

The Taormina Cave preserves a surprising marine invertebrate fossil community that freezes a time of its geological history when it was partly submerged and widely open to the sea. The relevant width of the cave entrance and its exposure along the palaeocoast could have allowed the co-occurrence, at least near the cave opening, of high light intensity and water energy, enough to ensure suitable conditions for the settlement, growth and maintenance of *D. cristatum* populations. This species, presently forming "reef" habitats at sea level in exposed rocky shores, is first reported from cave environments not with isolated specimens but as a builder able to form extensive crusts of densely packed superimposed specimens.

Results of dating attempts of the *Dendropoma* shells (about 72 ka) and of a continental calcite crust (about 78 ka) obtained with the U-Th dating method, were not consistent with the stratigraphic position of the cave indicating that its marine colonization happened during a sea-level high stand older than MIS 5.

3.5. Tremilia Cave

The cave is located west of Siracusa, ca. 3 km inland from the modern Ionian coast (Figure 1). It opens in Miocene limestones on a palaeo-cliff located 86 m a.s.l. on the left side of the Anapo valley. Remains of anthropogenic structures occur close to the entrance (Figures 17 and 18), possibly dating to the mid-20th century [11].

Figure 17. (**A**) Entrance of the Tremilia Cave. (**B**) Sector of the cave at the entrance better preserving the shell-rich deposit.

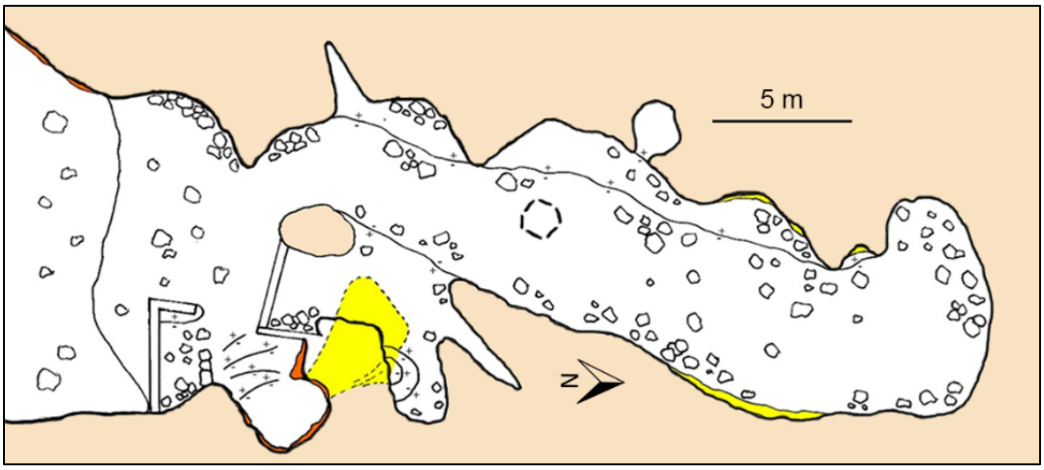

Figure 18. Plan view of the cave. Bold dashed line: hole in the ceiling; solid line: areas situated at lower levels; yellow: shell-rich deposits, sometimes with uncertain limits (light dashed line); orange: vertebrate breccias visible on the walls. Cave relief was performed on 27 September 2021 by two of us (ARe and GMi).

The cave floor is covered by discontinuous shelly rich deposits up to 50 cm thick, better visible in a sector lateral to the entrance where they constitute a large pocket (Figure 19A). These deposits are also locally exposed in the internal sector of the cave, at the base of the walls on either side and almost exclusively consist of a "lumachella" with closely packed and chaotically arranged valves of *Glycymeris* to which very rare remains of few other molluscs and fragments of the coral *Cladocora* add (Figure 19B).

Bivalve shells are abraded and frequently broken, cemented by calcite concretions; this shelly deposit is overlain by unmappable thin layer of marine fossiliferous pebbles containing dominant rissoid, cerithiid and littorinid gastropods, which are in turn overlain by a thick continental breccia containing extremely fragmented usually unidentifiable bone remains. This mammal-bearing deposit has been attributed to the Maccagnone FC and dated to the MIS 5e by [11]. During a recent survey, the continental breccia near the entrance delivered a very small tooth of elephant possibly belonging to *P. falconeri*. Owing to the stratigraphic relationship, we hypothesize for the *Glycymeris*-bearing level an age slightly older if not corresponding to that of the continental breccia, suggested by the mammal assemblages. The finding of *P. falconeri* together with remains of the Maccagnone FC is intriguing, possibly pointing to the occurrence of the *P. falconeri* FC inside the cave; this could suggest an old age for the Maccagnone FC in this cave of ca. 300 ka; however, dating should be verified, and studies are underway both on layers bearing marine molluscs and the overlying continental breccia.

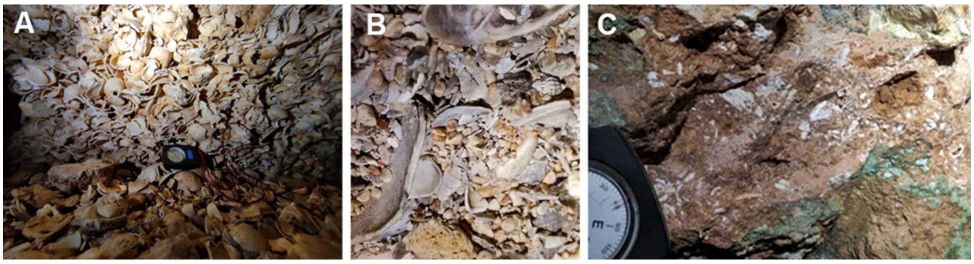

Figure 19. (**A**) Fossiliferous deposit made by *Glycymeris* shells. (**B**) detail showing bivalve shells and other mollusc remains (rissoid gastropods). (**C**) Bone-bearing red breccia.

3.6. Spinagallo Cave and Hyblean Plateau Fissure Fills

The cave is located near the Cassibile village, south-east of Siracusa, 8–9 km from the coastline (Figure 1); it opens on a long palaeo-cliff made by Miocene limestone at an altitude between 120 and 130 m a.s.l. The cliff represented the southern edge of a large palaeo-gulf reached during the transgressive phases of the middle Pleistocene.

The Spinagallo cave is the richest and most important *P. falconeri* locality and the type locality for the *P. falconeri* FC, which is characterised by an unbalanced, highly endemic fossil mammal assemblage. The first fossils were found in the late 1950s. Paleontological excavations, initiated by Professor Bruno Accordi, returned over 2000 remains of dwarf elephants (*P. falconeri*). The Sicilian dwarf elephant, with its height of only 90 centimetres, is one of the most iconic paleontological peculiar species of the Mediterranean islands.

P. falconeri was originally described from Malta (Busk 1868) and has been identified at other sites in Malta and Sicily (e.g., Luparello Cave and the Alcamo travertines), but Spinagallo Cave has the largest volume, and best quality, fossil material (Figure 20). Despite this rich fossil record, there is a lack of robust geochronological evidence for *P. falconeri*, although we constrain its presence on Sicily and Malta to the middle Pleistocene, given a first appearance date of its probable ancestor, *Palaeoloxodon antiquus*, in Europe at 780 ka [63].

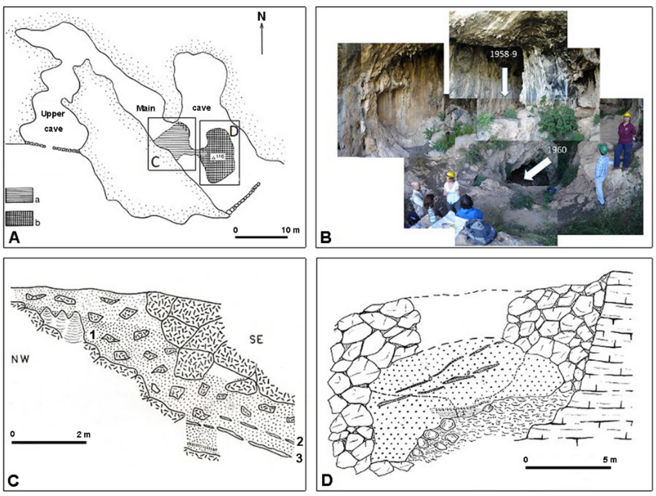

Figure 20. (**A**) Plan of Spinagallo Cave from [64], showing (a) 1958 and (b) 1960 excavation areas. (**B**) Photomontage of the Spinagallo Cave during 2010 field season, showing the excavation areas. (**C**) Section of the area excavated in the 1958 field season, from Ref. [65], showing: 1. the location of 'the front half' of a *P. falconeri* and 2-3: two stalagmitic sheets. (**D**) Section of Spinagallo Cave from Ref. [66] showing the extent of 1958/9 (top) and 1960 excavations, and the presence of two stalagmitic layers. Remnants of these stalagmitic sheets can still be observed on the walls of the lower chamber today.

The date 550 ka based on amino acid racemization (AAR) of a *P. falconeri* tooth from Spinagallo Cave [67] has been considered unreliable. The age of *P. falconeri* has been recently constrained by one of us (VH) using a multi-method dating approach (Uranium series, Optically Stimulated Luminescence and Electron Spin Resonance) on sediments and speleothems with good stratigraphical context and on previously excavated fossil material now stored in museum collections.

Spinagallo Cave can be correlated with palaeoshorelines (Figure 21), and thus regional geology and stratigraphy provide additional chronological constraint. The cave originally formed by karst processes taking advantage of a NW-SE trending fault line [27]. *Lithophaga* holes and probable vermetid crusts on the cave walls, as well as a basal beach deposit (='marine panchina'), provide evidence for a marine incursion generally considered to have occurred in the early middle Pleistocene [68]. A 103−110 m marine terrace near the cave (current height 120 m a.s.l.) has been dated to 525 ka by [25] and provides a minimum age for this marine incursion. The transition from shallow-water marine sands to continental sediments, and then a sandy 'red earth' rich in *P. falconeri* and *Leithia melitensis* fossils can be observed in cave sediments of the lower chamber, reflecting the progressive uplift of the cave from below sea level to its current height [1]. Ambrosetti [64] further referenced the presence of *P. mnaidriensis* and *H. pentlandi* in brecciated deposits in the upper chamber of the cave, indicating a later depositional event correlated with the Maccagnone FC.

The Ragusa platform from early to middle Pleistocene underwent gradual uplifting along mainly NE-SW trending faults. The transitional areas located between the Ragusa platform and the Comiso plain, both in the southern sector of the Hyblean plateau, were affected by fault systems that displace the substratum with progressive sinking below the Plio-Pleistocene circalittoral deposits [69–71]. On the eastern and western edges of the Hyblean Plateau fossil remains belonging to the *P. falconeri* FC and the Maccagnone FC are found in continental sediments correlated with marine deposits [27,38,51,68]. In contrast, on the Ragusa platform, which emerged during the Miocene, fissure-filling deposits not correlated with coastal lines are also known [72–77]. The fissure filling deposits contain faunal assemblages belonging both to the *P. falconeri* and Maccagnone FCs.

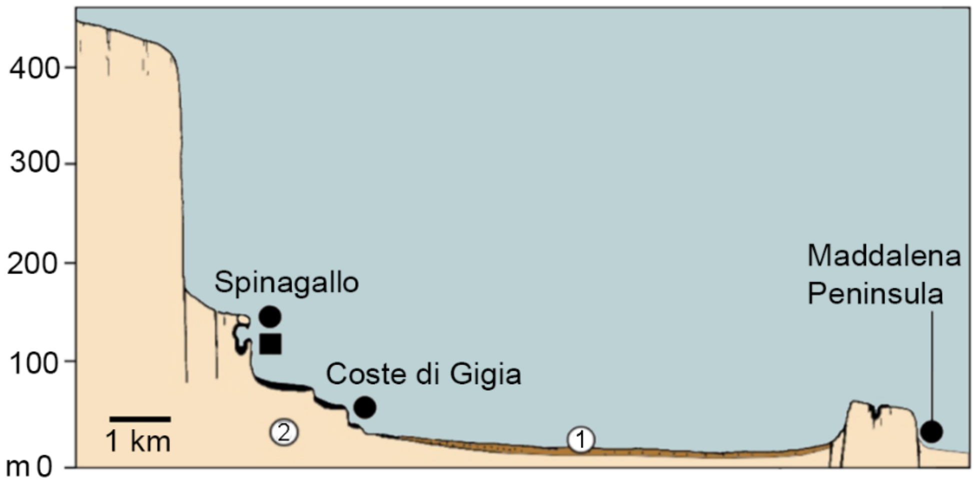

Figure 21. Schematic profile of the eastern edge of the Hyblean Plateau; ① = abrasion platform and calcarenites, ② = substrate, including lower Pleistocene marine deposits. Black squares: older faunal assemblages (*E. falconeri* FC). Black circles: younger faunal assemblages (Maccagnone FC). Note the higher position of the Spinagallo Cave, where both faunal assemblages occur.

Karstic cavities delivered faunal remains during road works at Contrada Cimillà [78], Coste di Gigia [38,64,68] and Contrada Pianetti [68]. In all these cases taphonomic evidence indicates that cavities acted as traps for remains deposited on the surface surrounding the cavities. Taphonomic notes by Ref. [65] may indicate that also Spinagallo Cave has been working as a trap for animals living on the terrace overlying the cave, during the middle (*P. falconeri*) and late Pleistocene (*P. mnaidriensis*, *H. pentlandi*).

4. Discussion

4.1. Palaeoenvironmental Meaning

The Tremilia and Spinagallo caves document a marine phase (with shallow-water invertebrates and their traces) followed by a continental one, through a progressive emersion produced mostly by regional uplift and testified by the continental fossil remains of the *P. falconeri* FC and/or the Maccagnone FC (Table 1).

The San Teodoro Cave, on the other hand, lacks any basal marine deposit and only testifies to a continental phase, indicated by basal sterile sediments overlain by sediments containing vertebrate remains belonging to the San Teodoro FC followed by tardiglacial (Epigravettian) associations.

The Donnavilla Cave shows continental deposits belonging to the Maccagnone FC, but it was subsequently re-flooded possibly during the Tyrrhenian, as indicated by a large belt of *Lithophaga* boreholes, correlated with a coeval paleocoastline.

The Fulco Cave only shows shallow water marine encrusting palaeocommunities but continental deposits are missing; it records a relatively recent (Tyrrhenian, 125 ka) marine flooding, and documents the passage from a submerged paleoenvironment to a beach coast following the interplay of local lifting and sea-level changes.

Due to the presence of marine associations including vermetid crusts and *Lithophaga* holes, the Taormina cave records a high rate uplift producing the rapid emersion of this sector of north-eastern Sicily, and in turn, is older than the underlying Tyrrhenian terrace MIS 5e which represents a subsequent high stand phase [1].

After the Tyrrhenian high stand, all the investigated caves definitively emerged as the result of a combined sea-level lowering and the local tectonic, even if caves raised differentially according to different trends and uplift rates between the northern and southern sectors [1].

Table 1. Summary of the main distinctive features of the examined caves.

Caves	Elevation a.s.l. (m)	Middle Pleistocene					Tyrrhenian		Holocene	Age (ka)	Faunistic Features
		Marine Phase		Continental Phase			Marine Phase		Continental Phase		
		Deposits/ Encrustations	*Lithophaga* Borings	*P. falconeri* FC	*Maccagnone* FC	*San Teodoro* FC	Encrustations	*Lithophaga* Borings	Deposits		
San Teodoro	140									200–11	Hominids, hyenas, *Equus hydruntinus*
Donnavilla	73–85									200–40	*Lithophaga* belt
Fulco	51									125	Hanging corals with elongated corallites
Taormina	131									older than 125–upper paleolithic	Vermetids with downward facing tubes
Tremilia	86									300–200	*Glycymeris* bed
Spinagallo	120–130									?550–200	*Paleoloxodon falconeri*

4.2. Documented Time Spans

Caves of the Hyblean sector document an older time interval in the middle Pleistocene but do not extend to the late Pleistocene whereas the caves from the NE Sicily sector mostly acted during the Tyrrhenian, though sometimes including older and/or younger time intervals.

The Spinagallo Cave opens at a high altitude and contains the most ancient fossil assemblages referable to the *P. falconeri* FC. The Tremilia Cave probably follows being slightly younger, owing to the occurrence of the Maccagnone FC but also of a possible *P. falconeri* tooth presumably pointing to the transition between these two FCs; this is also compatible with the high altitude at which it opens, up to 85 m. The Donnavilla and San Teodoro caves, all document the Tyrrhenian age, with the first originating slightly earlier as it also contains older deposits of the Maccagnone FC. Therefore, in the context of the general uplift and emersion processes leading to the formation of the present-day Sicily island from a previous archipelago, the examined caves record the palaeogeographic history and its consequences on the evolution of the terrestrial biota largely affected by the different connectivity grade produced by the islands' relative location and the amplitude of seaways in between. Evolution can be better reconstructed due to the cave's partial chronological overlap.

4.3. Distinctive Features of the Caves

Despite a somewhat comparable history and a partial chronological overlap between some caves, each cave has distinctive features (Table 1), some relevant to reconstructing the palaeobiogeography and the evolution of the local biota.

The Spinagallo and the San Teodoro Caves include particular faunistic associations, which served for the definition of the *P. falconeri* and San Teodoro Faunal Complexes, respectively.

The San Teodoro cave hosts an impressive quantity of hyena remains as well as evidence of the activity of these animals. The cave also includes the oldest and one of the oldest records for donkeys and the hominids, respectively, as well as one of the most recent records for the dwarf elephants in Sicily, with the exception of the Egadi specimen [49]. Identified fossils also allowed hypothesise paleogeographic connections between Sicily and the mainland Italy during the last Pleniglacial (see Ref. [29]).

The Fulco Cave with its invertebrate dark cave palaeocommunity preserved in life position is unique in hosting hanging corals with exceptionally elongate corallites representing a special morphological adaptation for dwelling in a submarine cave. A somewhat comparable adaptation, possibly functional for intercepting food-bearing currents, was exploited by vermetids growing in the Taormina cave with side-by-side downward-facing elongate distal parts; this particular morphology and the location of these animals within a submarine cave has been so far unreported from elsewhere both in present-day and past habitats.

On the other hand, large belts of fossil *Lithophaga* boreholes (*Gastrochaenolites*) seem to be a common feature, shared by several caves and testify to sea-level stand before the final emersion. *Lithophaga* and its traces can be associated with other diverse faunas (such as in the Fulco Cave) or can sometimes be one of the few or even the only evidence of a cave submersion, such as in the Donnavilla and the Taormina caves.

The Tremilia Cave contains a coquina bed that is unusual inside a cave; it consists of *Glycymeris* shells that accumulated in a relatively ancient time, presumably at about 300 ka.

4.4. Palaeoecological Inferences

The organogenic crusts and the bivalve boreholes were produced by sessile organisms that colonised the rocky walls and therefore, lived in situ within the caves. All recorded species (*Dendropoma cristatum* from the Taormina Cave, *Astroides calycularis* from the Fulco cave, *Litophaga litophaga* from the Taormina, Fulco and Donnavilla caves) testify to shallow depths, from the sea level to a few meters depth. The invertebrate associations found in the sediments deposited inside the caves originate from shallow-water bottoms probably located immediately outside their entrances. In particular, the *Glycymeris* shells from the Tremilia Cave accumulated from bivalve populations typical of upper infralittoral environments characterised by high hydrodynamic energy that were possibly spread in the Floridia palaeo-gulf during Pleistocene temperate phases.

In contrast to marine associations, the continental ones only rarely lived, at least partly, inside the caves. Bones belong to mobile and highly mobile animals that thrived in the immediate vicinity, on the planes in front of the caves or even on top of the hills where the caves were curved. The Spinagallo Cave presumably formed a trap where mammals fell down from the above, while in the cave of San Teodoro some of the mammal bone floated inside from a nearby lacustrine basin (basal levels, Unit B) or derived from animals that inhabited the interior of the cave (upper levels, Unit A). The vertebrate palaeocommunities, mainly constituted by elephants and hippos, allowed us to hypothesise a warm climate and the occurrence of water pools in the areas.

Author Contributions: L.B., R.S. and A.R. (Antonietta Rosso) designed the study and wrote the first draft; V.H., A.R. (Agatino Reitano), G.I., G.M. (Gabriella Mangano) and G.M. (Gianmarco Minnitiand) provided data of some caves. All authors contributed to writing the final version of the text and agreed to the published version. All authors have read and agreed to the published version of the manuscript.

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