Review

Benthic Foraminifera as Environmental Indicators in Mediterranean Marine Caves: A Review

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Abstract: Marine caves are characterized by wide environmental variability for the interaction between marine and continental processes. Their conditions may be defined as extreme for inhabiting organisms due to the enclosed morphology, lack of light, and scarcity of nutrients. Therefore, it is necessary to identify reliable ecological indicators for describing and assessing environmental conditions in these habitats even more than elsewhere. This review aims to provide the state of art related to the application of benthic foraminifera as proxies in the (paleo)ecological characterization of different habitats of marine caves. Special attention was addressed to a research project focused on Mediterranean marine caves with different characteristics, such as extent, morphology, freshwater influence, salinity, sediment type, oxygenation, and organic matter supply. This review aims to illustrate the reliability of foraminifera as an ecological and paleoecological indicator in these habitats. They respond to various environmental conditions with different assemblages corresponding to a very detailed habitat partitioning. Because marine caves may be considered natural laboratories for environmental variability, the results of these studies may be interpreted in the perspective of the global variability to understand the environmental drivers of future changes in marine systems.

Keywords: benthic foraminifera; marine caves; ecological indicators; paleoecological reconstruction; Mediterranean Sea

1. Introduction

1.1. General Characteristics of Marine Caves

Karst aquifers are among the most significant freshwater supplies for human consumption [1–3], with recent estimates indicating that over 9% of the global population is partly or entirely supplied by karst freshwater [4,5]. As for coastal aquifers, such a resource becomes even more important, being often the only one available to communities living therein [6–9]. Furthermore, the karst aquifers' emergence frequently occurs through submarine freshwater springs. Therefore, study and monitoring become essential to understanding the modality of formation of the cave passages and fully comprehend the hydrogeology of the watersheds feeding the springs [10,11].

Caves observed in coastal areas may be of classical karst origin [12,13] or can be formed through a variety of other processes. In this second case, they are generally attributed to the category of pseudokarst caves since they may involve rocks different than carbonates. For instance, marine caves, produced by the action of sea waves, consist typically of single chambers of limited development, opened to the sea; their later development often occurs through failure mechanisms, with the detachment of further masses of rocks from the cliffs, or through the opening of sinkholes at the surface, along the coast or in nearby areas [14–18], with sinkholes often providing the inland entrance to the system. Still, regarding cliff retreats, weathering processes play an important part in their predisposition

to erosion and failure mechanisms [19–24] and the presence of discontinuity systems, also related to the development of tensional release cracks to the continuous action of sea waves.

Karst caves along the coast may originally have formed inland by freshwater dissolution processes, whilst nowadays they are interacting with the present coastal environment. Their current location is inevitably related to the sea level position, but this, in turn, depends on various factors, such as tectonic uplift or isostasy, or eustatic sea-level changes, with the latter of these significantly caused by glacio-eustasy [25]. In terms of speleogenesis, in the vadose (unsaturated) zone, a cave development is much different from what happens in the phreatic (saturated) zone [26,27]. If we go below the groundwater table into the phreatic zone, the present phreatic coastal caves can be classified as littoral, anchialine, or submarine [28]. Further distinctions can be made based on sedimentary and microfossils characters, as proposed by van Hengstum and Scott [29], but based only on environmental conditions, without considering any genetic issues [30].

The majority of coastal karst caves are in warm latitudes in relatively young carbonates [31,32]. This means that the rocks are typically no older than the Miocene, and are today exposed because of tectonic causes or due to past higher glacio-eustatic conditions; such recent rock masses have a significant porosity (greater than 30%), with void connection creating high permeability, since they have had no time to become compact carbonate rocks through diagenetic processes. In contrast to the older and mature rocks (telogenetic), they were defined by Choquette and Pray [31] as eogenetic. These porosity and permeability characteristics allow for the mixing of water to occur through the whole rock mass, and not be limited to the main discontinuity systems.

The world's highest number of marine caves is formed through the flank margin cave model [33,34]. This requires mixing freshwater with sea water and the effects of sea-level changes produced by glacio-eustatic or local causes, typically affecting eogenetic carbonates. A freshwater lens in coastal environments is produced by the difference in density between freshwater and sea water [35,36]: the first floats on the latter, with a physics explained by the well-known Ghyben-Herzberg model. The boundary separating the two is a halocline or a transition zone where gradual brackish water separates the two bodies. The lens's thickness decreases toward the coast, and, consequently, the flow velocity increases [37,38]. This is exactly the sector where carbonate dissolution is the strongest, as an effect of the thin lens and the abundant organic material entering the system through vadose flow at the top and bottom of the lens itself. Decay of the organic material enhances dissolution, which is further favored by superimposition over a short vertical distance of the mixing water zone along the coast. As a whole, this allows for the development of flank margin caves [34,39] through a single formation event, without additional phreatic overprinting.

The morphological features presented by flank margin caves at the Bahamas have become the morpho-type for identifying caves of similar origin in other parts of the world: they have been used as indicators of both past sea-level position and tectonic stability by Carew and Mylroie [40], and represent the best example for the simple carbonate island model [33].

In flank margin caves, flow is non-turbulent since water goes in and out of the caves as diffuse or laminar flow, thus resulting in an absence of high-velocity structures and turbulent flow wall sculptures, including scallops, as well as of sediments [41,42]. Generally, these caves have no entrance for humans, and access is only later on allowed due to cliff retreat and erosional processes.

Sea level changes cause a direct variation in the position of the freshwater lens. Such a variation has a stronger effect at the coast, where it is thinner. In terms of cave genesis, new caves can be formed over the older ones, thus producing a more complex, multi-stage network of karst voids. New vadose and phreatic conditions may develop in a function of the entity of the sea-level change. Cave elevations are related to prior sea-level highstands because caves often develop at the halocline or at the mixing zone between freshwater and salt water, in which oscillations occur in synchrony with the sea level in the coastal zone [39,42]. In the case of eogenetic carbonates, flank margin caves can be formed

immediately after rock deposition, as syndepositional caves [43,44]. According to other authors, speleogenesis in coastal eogenetic limestones can be strongly controlled also by the distribution of carbon dioxide, with significant input by organic components [45,46]. Flank margin caves can also be found in telogenetic carbonates, linked to the presence of joints and fractures [47,48], marking the level of past sea-level highstands, which are nowadays also far from the coastline [49–51].

For what is stated above, eogenetic caves are, by far, the most common in coastal karst environments. However, this paper focuses on selected telogenetic carbonates of Sardinia and Murcia (Spain), where specific research on benthic foraminifera was performed. The unique environment of anchialine habitats, deriving from a mixed salinity water body for which preservation is contained by a rock mass [32], is common in coastal karsts, which are widespread in the Mediterranean, especially on the northern side (Figure 1). Neverthe-less, it has to be mentioned that the highest distribution of known caves in the northern Mediterranean certainly also reflects a greater number of researches in this sector with respect to the southern coasts of the Mediterranean Basin. In such an environment, karst ecohydrology integrates landscape features with groundwater hydrology and freshwater biology [52]. Studying the organisms present in coastal caves [53–55] represents a unique opportunity to highlight species' wide variety and distribution [56–58] in the function of the most significant environmental parameters characterizing these transition areas between land and waters of different chemistry. Among these parameters, light attenuation is one of the most relevant [58,59]. Many studies in the cave environment concerning sponges, anthozoans, polychaetes, bryozoans, decapods, bivalves, and fishes [60] were carried out with little attention paid to benthic foraminifera (BF). Despite the few studies considering this group, 106 species have been recognized in Mediterranean marine caves [60]. This review aims to analyze the available scientific literature on BF from marine caves to verify their effectiveness as paleoecological and ecological indicators.

Figure 1. Distribution of known marine caves (green dots) in the Mediterranean Sea. (**A**) Isca cave (Tyrrhenian coast); (**B**) Bue Marino and Bel Torrente caves (Gulf of Orosei); (**C**) CT12 (Murcia region) (modified from [60]).

1.2. Benthic Foraminifera as Ecological and Paleoecological Indicators

Foraminifera are both planktic and benthic single-celled eukaryotic organisms (pro-tists) with about 40,000 fossil and 10,000 living species on the whole [61,62]. About 4000 species of living benthic foraminifera (BF), mostly with a mineralized shell, have been described in ecological studies [63]. They inhabit a wide range of aquatic envi-

ronments, from the transitional to the deep-sea [64,65], and are generally abundant in sediments, where they typically constitute well-diversified assemblages. In addition, they also live in environments that may be considered extreme because of the wide variability of one or more parameters (salinity, temperature, pH, dissolved oxygen, nutrients, light, and contaminants) and may rapidly re-colonize the bottom sediment after disturbance events [64,65]. They are also susceptible to environmental changes because diversified assemblages offer a broad spectrum of potential responses. Their short life-cycle (a few months for most taxa) allows for the assemblages' total renewal, quickly adapting to the changing environment [66,67]. For this, surface sediment samples may contain many generations of dead specimens, corresponding to the average conditions, deprived of seasonal effects [68,69]. There are many techniques to distinguish living from dead foraminifera. The most used of these are based on vital functions of the foraminiferal cell and the staining of cytoplasm by biological solution [70,71].

Ecological indicators provide comprehensive and quantitative information of the state of ecosystems because they are linked through a causal relationship with the origin of environmental stress. They may be recognized at different hierarchic levels, from a single specimen to a whole community, ecosystem, or landscape. To be easily and reliably applied, ecological indicators should be based on sensitive, diverse, worldwide widespread, and abundant organisms. Benthic foraminifera are excellent environmental indicators because they have all of these characteristics. Moreover, their mineralized tests preserved in the sediments help recognize the changes of conditions through past times by studying subfossil assemblages from sediment cores and identifying the in-situ reference conditions [72–74]. Based on all these characteristics, in recent decades, BF have increasingly been used as a reliable proxy for the environmental characterization and monitoring of marine habitats and the assessment of the ecological status [75]. They are also suitable for marine caves characterized by physical gradients (light, oxygen, salinity, etc.), a decreasing pattern of nutrients supply, and decrease in species richness and biomass of benthic organisms [76].

2. Reconstructing Paleoenvironments in the Present and Past Marine Caves

The high potential preservation of foraminiferal tests allows for the recovery of fossil or subfossil assemblages bearing reliable and detailed environmental information, despite the possible taphonomic processes which might have modified the original ones [74]. Furthermore, in caves that are currently or in the past located close to the sea-level, foraminiferal assemblages record the long-term environmental changes linked to past climate and sea-level variations, tectonics, and extreme events, such as tsunamis and typhoons [77–85].

Corbridge cave (Berry Head, southwest England), formed in Devonian limestone during the Pleistocene and currently located between 5 and 10 m a.s.l., showed a bottom extensively covered by laminated mud. It was interpreted as a deposit of marine origin due to marine microfauna, such as ostracods, sponge spicules, echinoid spines, and other echinoderm skeletal elements. The most abundant foraminiferal fauna, constituted by shallow-water taxa like *Ammonia beccarii* and *Lobatula lobatula*, was found in the samples with the highest percentages of fine sand (up to 23%). They were interpreted as displaced from a beach or the nearshore marine environment during storm events, providing evidence of the proximity of sea-level. Thanks to dating, these marine sediments were attributed to the marine isotopic stages (MIS) 7 and 5e, allowing for recognizing a paleo sea-level higher than the present one (+7.2 and +5.8 m, respectively) during these warm periods [77].

The most ancient foraminifera typical of cave environments were found in the Late Pleistocene Rumena Cave (Sicily, Italy), currently located 100 m a.s.l. Two encrusting species, *Cornuspiramia* cfr. *adherens* and *Planogypsina acervalis* were associated with Scleractinian corals (Dendrophylliidae and Caryophylliidae), bryozoans, and serpulids. On the whole, the paleoecological significance of this community indicated a cave below the sea-level in the dark to semi-dark zone, which remained close to the sea level, and repeatedly

flowed as a consequence of the interplay of vertical tectonic movements and the climatically driven sea-level fluctuations during the Late Quaternary period [78].

A cave on the northern coast of Sicily, currently located at 52 m a.s.l., contained a semi-dark cave association dominated by the dendrophylliid coral *Astroides calycularis*. *Miniacina miniacea*, a very large (up to 20 mm) sessile foraminifer that may contribute up to 1% of the surface of the total biotic cover [60] was a component of this association which was interpreted as a warm community of Tyrrhenian age [79].

In a coastal cave in Aceh (Indonesia), sediments containing shallow-water benthic species (*Ammonia* spp., *Elphidium* spp.), mixed with planktonic ones (*Globigerina* sp.) of up to 14%, transported by high energy events, were associated with tsunamis. Based on these results and radiocarbon dating, the authors recognized tsunamis events from 7400 yrs. BP to 2004 CE. Interpreting, on the whole, the stratigraphic sequence, they deduced that the recurrence time of tsunamis in the Indian Ocean is comprised between 450 and 2000 years and that long-dormant periods may follow the largest tsunamis, such as that of 2004 [80]. Like tsunamis, typhoons left a peculiar foraminiferal record in a coastal cave of the Salcedo coast (Philippines). The assemblages were constituted mainly by intertidal taxa (*Amphistegina radiata*, *Baculogypsina sphaerulata*, and *Calcarina* spp.) and abraded subtidal taxa (*Peneroplis planatus*). These results showed the potential of coastal caves to host well-preserved archives of paleo storm deposits [81]. The hypothesis of tsunami deposits has also been advanced for sediments of a small Bermudian cave located at 21 m a.s.l. They contained a fossil foraminifera assemblage mainly constituted by brackish-water taxa (*Polysaccammina ipohalina* and *Pseudothurammina limnetis*). However, by comparison with assemblages from modern anchialine caves, it was finally deduced that they derived from a sea-level high stand at 21 m a.s.l. during MIS 11 [82].

The spatial and temporal changes of foraminiferal assemblages in cave environments allowed the reconstruction of environmental changes due to several factors. The distribution of larger BF was studied in dated sediment cores and surface sediments from the Daidokutsu Cave (Okinawa, Japan) using these symbiont-bearing organisms as proxies for light conditions. They reconstructed a decreasing trend that occurred about 5000 years ago. BP was attributable to the narrowing of the entrance for the progressive infilling of the cave [83].

Some studies recognized the spatial and temporal environmental changes related to sea-level variation in the Green Bay Cave (Bermuda). The facies analysis on 12 radiocarbon-dated sediment cores allowed for identification of the succession of distinct depositional environments with peculiar faunal content. Changes in BF assemblages marked the progressive flooding of caves, which occurred during the Holocene transgression, by identifying biofacies with different hydrogeological characteristics [84]. Other well-studied karst systems are in the Yucatan peninsula (Mexico), where surface sediment samples, collected along a transect in the Aktun Ha cave, were analyzed for dead BF (thanatocoenosis). Isotope ratios (δ^{13}C and δ^{18}O) from foraminifera shells were determined to reconstruct salinity variations during shell secretion. The results showed an abrupt transition from a freshwater assemblage, dominated by thecamoebians with rare *Jadammina macrescens* and *Ammonia tepida*, to a marine assemblage with *Bolivina* spp. and *Elphidium* sp. This faunal change was attributed to the flooding of the cave by marine waters during the Holocene sea-level rise [85]. A more recent study on the Aerolito Cave (Yucatan) analyzed the effects of changing terrestrial and marine contributions (water and organic matter) over time on the benthic foraminiferal assemblages from several sediment cores distributed along a gradient from terrestrial to marine conditions. The reduction of infaunal taxa and the increase of epifaunal clinging ones was interpreted as a response to the decrease in the organic matter supply due to the reduction of the mangrove areal extent in the last millennium. This result indicates that landscape changes can impact ecosystem functioning within adjacent subterranean habitats [86].

3. Characterizing Present Environments in Marine Caves

3.1. General Overview on Recent Benthic Foraminifera from Worldwide Marine Caves

Up to now, recent foraminifera in marine caves have been only occasionally studied. Most of these studies are concentrated on the Yucatan and Bermuda cave systems, where foraminiferal assemblages from surface sediment have been described since the early 2000s.

Surface sediment samples from the cenotes of the Yucatan peninsula, characterized by very low salinity (1.5–4.5 psu), revealed four low-diversity assemblages constituted by BF and thecamoebians corresponding to environments with different salinity values. Along the salinity gradient, the brackish-water agglutinated *Jadammina macrescens* was first recorded, associated with freshwater thecamoebians, while, at the highest salinity, *Ammonia tepida* and *Elphidium* sp. were found. The transition from a thecamoebian-dominated to a foraminiferan-dominated assemblage occurred at a salinity of approximately 3.5 psu [87].

A first paper, aimed at illustrating modern foraminiferal species from Bermuda, reported a list of foraminifera from caves, including typical taxa of marginal marine environments, shelf and deep-sea, such as *Ammodiscus tenuis*, *Rosalina* spp., and *Cibicides refulgens*, respectively [88]. Successively, BF from surface sediment samples of the Green Bay cave system were analyzed to investigate foraminiferal ecology concerning habitat variability. Based on foraminiferal data, the authors recognized two environments, the terrestrially-dominated (anchialine) and the marine-dominated, and were each divided into distinct habitats consistent with the local hydrogeology and sedimentology. Typical marsh species were found in the first environment, corresponding to the brackish meteoric lens, while marine taxa (*Rosalina* and *Bolivina*) were present in the second one, below the halocline. In the marine environment *Quinqueloculina* spp. dominated the assemblage at the entrance, while, depending on more or less effective water circulation, *Spirillina vivipara* or *Spirophthalmidium emaciatum* were the most abundant species [29]. Other Bermudian caves (Deep Blue and Cow Cave) were studied to recognize the response of shallow-water benthic foraminifera to water level variability from tidal forcing and the source of organic carbon. The intertidal assemblage, with the brackish-water *Trochammina inflata*, was primarily controlled by tidal exposure. The subtidal-terrestrial and subtidal-marine assemblages were more conditioned by the sediment texture and organic carbon amount and source. The first one was dominated by the infaunal *Bolivina variabilis* and *Melonis barleeanus*, while in the second one, the epifaunal *S. emaciatum* and *Sigmoilina tenuis*, prevailed. These last species were considered to be emerging indicators of subtidal habitats flooded by an oxygenated saline groundwater mass of coastal karst aquifers in tropical and subtropical settings [89]. Finally, another paper considered several Bermudian caves, including those of the earlier studies, to analyze the response of BF to tidal exposure and sediment parameters (sediment grain size, bulk organic matter, total organic carbon, C/N, and δ^{13}C). The results confirmed the earlier findings, better characterizing the foraminiferal assemblages in relation to the organic matter source, recognized as one of the main factors influencing foraminiferal distribution [90].

3.2. The Mediterranean Caves

Caves may be found in many geological settings, produced by different processes, as stated in § 1.1; however, the most common are these are formed by karst phenomena on carbonate rocks. Many sectors with coastal carbonate cliffs characterize the Mediterranean coast, and because of this, the region is rich in marine caves, mostly documented so far on the northern side (Figure 1) [91]. They have been extensively and mainly studied by geologists and speleologists [2,6,7], but also by biologists [92,93], mainly because these environments host rich sessile macrobenthic fauna on their walls and ceilings [60].

Benthic foraminifera from Mediterranean marine caves have been occasionally reported since the 1980s, mostly in studies focused on hard-bottom macrobenthic communities. Due to the sampling methods, aimed at detecting macrobenthic organisms with real or photographic samples, the only foraminiferal species commonly recognized was M. miniacea. It has been found in several Mediterranean marine caves, both in the eastern

and western Mediterranean, often at the entrance, but also in the semi-dark and dark zones [94–97]. It was also recognized, together with macrobenthic taxa, as constituting the fouling encrusting statues and marble fragments recovered from the Grotta Azzurra (Capri, Italy) [98] and as part of bioconstructions [99]. In few cases, other foraminiferal taxa were described as contributors to bioconstruction. An in-situ experiment focused on the development of sessile fauna in a marine cave of the Ionian Sea recorded the presence of benthic foraminifera, identified at a family (Nubeculariidae) or superfamily level (Rotaliacea), among bioconstructors [100]. More recently, another species, *Cornuspiramia adherens*, was reported as encrusting nodular bryozoan concretions in two marine caves of the Aegean Sea [101].

An early paper specifically focused on the study of foraminiferal assemblages considered the biocoenosis from the walls and bio- and thanatocoenosis from the bottom sediment of the Isca cave (Tyrrhenian Sea, Italy). Results of the quantitative analysis showed the dominance of *M. miniacea* (87%) in the biocoenosis of the cave walls. At the same time, the other five species were rare, among which the typically infaunal, deep-water species *Melonis barleeanus* was recognized. Furthermore, only the agglutinated *Rhizammina* sp. was found living in the sediment, despite a diversified dead assemblage with dominant *M. miniacea* and abundant Miliolida (*Quinqueloculina* spp. and *Adelosina* spp.). Considering that nearly all of the species found in the thanatocoenosis may live by clinging to hard substrates, and considering the low number of samples in relation with the foraminiferal density on the walls, the author concluded that all species found were dead in the sediment, except for *Rhizammina* and *Textularia*, which were derived from the walls [102].

3.2.1. Studies Carried out in the Gulf of Orosei (Italy)

Since 2014, a research project aimed at investigating the potential use of BF as an ecological indicator in Mediterranean marine caves has been carried out thanks to the synergic cooperation between cave divers of Global Underwater Explorers (GUE) and researchers of ISPRA (Institute for Environmental Protection and Research). The study was of particular importance because there was no previous record of living assemblages in sediments from marine caves of temperate seas.

The research project started in the Gulf of Orosei (Sardinia, Italy), a coastal karst area that extends for more than 37 km with cliffs directly on the sea. Mesozoic dolostone and limestone, affected by extensive karst phenomena, overlie a Paleozoic Variscan basement composed of granites and phyllites. Karst landforms, such as dolines and dry canyons called "codula" which are active only during heavy rainfall, characterize the landscape.

Many caves, formed by the wave action on joints and structurally weaker areas, are located along the coast extending for many kilometers in correspondence with the freshwater outlets of the karst systems (Figure 2) [103].

In two of these caves, Bel Torrente (BT) and Bue Marino (BM), after a survey of the cave, 15 sampling stations (Figure 3) were positioned in 2014–2015 from the entrance to the inner section along a line at 30 m distance and monitored once every year in the period 2014–2016. In particular, BM was first studied for the North Branch, extending the sampling towards the inner sector in the 2016 campaign; Middle Branch was also included in the study in the same year. Sediment samples have been collected and analyzed at each station for grain size and benthic foraminifera, while a multiparameter probe has measured water parameters.

The BT cave has a total development of 8.6 km even if it is still being explored [104]; it is constituted in the first sector by a main conduit, wide from 5 to 20 m, which develops close to the sea-level for the first 600 m (Figure 3) reaching a 50 m depth in the inner one. It drains waters from the karst canyon of Codula Sisine and has a widely variable flow rate, ranging from 100 to 1000 L s^{-1} during overflow periods and 10 L s^{-1} during dry conditions. After heavy rains, the tunnel is entirely flooded by freshwater with flow of up to 2 m s^{-1}, while during dry periods, marine water is overlain by freshwater forming a mixing zone, known as halocline [105,106].
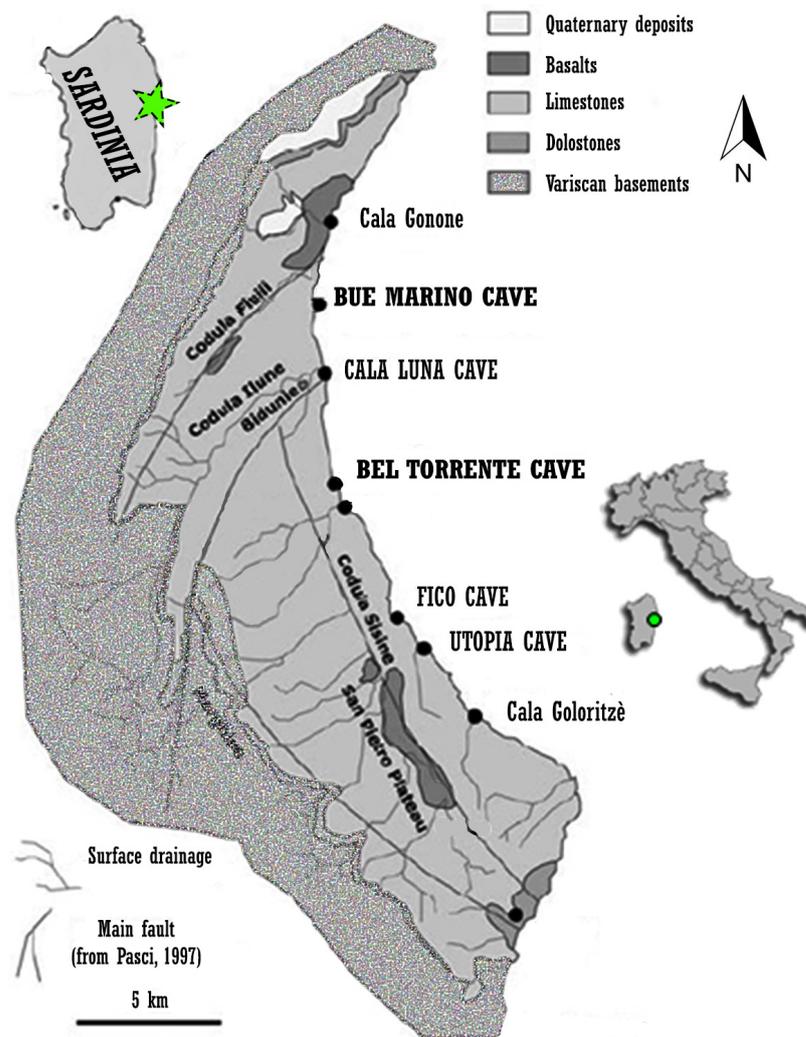
Figure 2. Geological scheme of the Gulf of Orosei with the location of the marine caves (modified from [103]).

The BM cave is an extensive cave system constituted by three branches, the North, Middle, and South Branch, which develops for over 70 km (Figure 3). The North Branch is characterized by a large conduit that drains water from the Codula Fuili recharge area with a base flow of 40 L s^{-1} and discharges large volumes of freshwater (>1 m^3 s^{-1}) during periods of flooding. When the base flow is prevalent, sea water penetrates for 1500 m into the branch. The Middle Branch is the least impressive in dimension and is probably linked to smaller sinks in the Codula Ilune riverbed. Finally, the South Branch has the largest conduit and a very low base flow (a few liters per second), even though it carries large volumes of freshwater originating in the Codula Ilune canyon during heavy rainfall [105,107,108].

In both caves, mainly sandy sediments were recorded, with some gravelly sands or sandy gravels. Sediment was mainly constituted by coarse, or very coarse, mineral grains, quartz, plagioclases, k-feldspars, biotite, volcanic lithic fragments, or rare schists, while the organic fraction was scarce. Pelitic sediment enriched in vegetal debris was recognized only in the BM cave, in station 6, located at the confluence of the North and Middle branches. Sediment composition testifies that the Variscan basement, outcropping some kilometers from the coast, acts as a main sedimentary source (Figure 2). In the BM cave, the peculiar sediment texture recognized at station 6 and the high organic content indicate a supply from the Middle Branch [105,106].
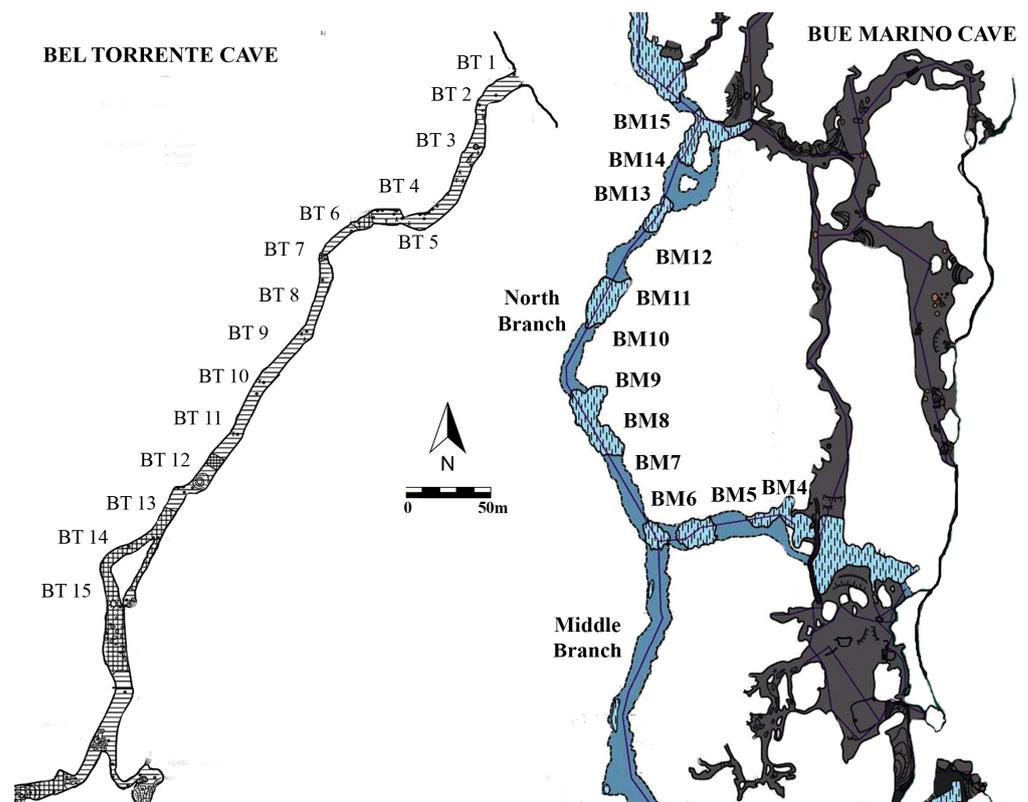
Figure 3. Sampling map of Bel Torrente (BT) from and Bue Marino (BM) caves, Sardinia, Italy [103].

The sampling carried out in 15 stations in each cave in summer 2014 revealed BF's presence in both caves, although with an absolute abundance at most of few specimens per gram of dry sediment in most samples; however, the main taxa were found both as dead and living (rose Bengal stained) in the sediment. While in the BM cave, BF were found in all 15 stations, in the BT cave they were recovered up to station 11 (Figure 3). The succession of three foraminiferal assemblages, corresponding to three different ecozones, was recognized in both caves (Table 1), although to a different extent [105,106] and references therein:

- A marine ecozone, located immediately close to the entrance, was exclusively characterized by taxa with carbonate test (porcelaneous or hyaline). Typical shallow-water symbiont-bearing species, such as *Peneroplis pertusus*, *P. planatus*, and *Elphidium crispum*, prevailed in the assemblage and were exclusive to this ecozone. Because these species are common in the shallow-water assemblages of the Sardinian coast, this assemblage indicates environmental conditions very similar to those that are normally marine.

- The entrance ecozone started within the first 90 m, in correspondence of BT4 and BM4. Hyaline taxa generally prevailed, but the agglutinated ones were also rather abundant. The dominant species, the hyaline *Gavelinopsis praegeri* and *Rosalina bradyi*, are epifaunal taxa that may be attached to phytal substrates or mineral grains. The first one is possibly living in a wide bathymetric range of the continental shelf. The hyaline infaunal *B. variabilis* accompanied them, and the agglutinated *Reophax dentaliniformis* was also abundant. It is an infaunal species common in the Baltic Sea and Norwegian fjords, recognized as a successful opportunistic species in re-colonizing disturbed habitats.

- The transitional ecozone started at 120 and 300 m from the entrance in correspondence of BT6 and BM11, respectively. The innermost foraminiferal assemblage characterized it, mainly constituted by agglutinated taxa. *Eggerelloides advenus*, *Lepidodeuterammina ochracea*, and *R. dentaliniformis* were the most common species. *Eggerelloides advenus* is an infaunal species typical of high latitude basins which tolerates low-salinity conditions, and is considered to be a stress-tolerant opportunistic species. *Lepidodeuter-*

ammina ochracea is an epifaunal clinging species that is typical of cold waters and adapted to live on the coarse sand of high-energy cold waters. Station BM6, although included in this ecozone due to the prevalence of *E. advenus*, showed peculiar features in terms of the low species diversity and high dominance of the main species. In this case, *E. advenus* showed an opportunistic behavior due to the abundant vegetal debris present in the sediment. This species is known to be opportunistic, being able to benefit from the abundant refractory organic material.

Table 1. Mediterranean caves with the main features of foraminiferal ecozones.

	Bel Torrente	Bue Marino	CT12
General features			
Cave origin and characters	karst; Anchialine cave, with development strongly favored by hyperkarst processes (freshwater-saltwater mixing)	karst; Anchialine cave, with development strongly favored by hyperkarst processes (freshwater-saltwater mixing); three main branches	hypogenic origin; submarine cave
Sediments	coarse grain size, terrigenous, terrestrial origin	coarse grain size, terrigenous, terrestrial origin; abundant vegetal debris in the Middle Branch	fine grain size, authigenic micrite, bioclasts
Foraminiferal ecozones			
Marine ecozone	low-mild absolute abundance, high diversity; *P. pertusus*, *E. crispum*, *L. lobatula*, *G. praegeri*	low absolute abundance, mild diversity; *P. pertusus*, *G. praegeri*, *E. crispum*, *L. lobatula*	high absolute abundance, mild diversity; *M. subrotunda*, *L. lobatula*, *G. praegeri*
Entrance Ecozone	low absolute abundance, mild diversity; prevalence of calcareous taxa (*G. praegeri*, *Bolivina* spp., *Quinqueloculina* spp.) over the agglutinated (*R. dentaliniformis*)	low-mild absolute abundance, mild-high diversity; prevalence of calcareous taxa (*G. praegeri* and *R. bradyi*) over the agglutinated (*R. dentaliniformis*)	high absolute abundance, low-mild diversity; *P. corrugata* and *S. vivipara* with similar percentages, *T. inornata*. Increase of epifaunal clinging/attached taxa
Transitional ecozone	low absolute abundance, low-mild diversity; prevalence of agglutinated taxa (*E. advenus*, *R. dentaliniformis*, *C. jeffreysii*) over the calcareous ones (*G. praegeri*, *R. brady*, *A. inflata*)	low absolute abundance, mild diversity; prevalence of agglutinated taxa (*E. advenus*, *L. ochracea*, *R. dentaliniformis*, *C. jeffreysii*) over the calcareous ones (*G. praegeri*, *R. brady*)	high absolute abundance, low-mild diversity; dominant *P. corrugata*. Further increase of epifaunal clinging/attached taxa
Confluence ecozone	not present	high absolute abundance, low-mild diversity; dominant opportunistic agglutinated taxa (*N. polymorphinoides* in spring, *E. advenus* in summer)	not present
Beginning of the barren zone	at about 330 m from the entrance	at about 450 m from the entrance	barren zone not present within the 120 m length of the cave
Driving environmental factors of foraminiferal zonation	salinity and pH gradient, environmental instability due to seasonal freshwater flows	salinity and pH gradient, environmental instability due to seasonal freshwater flows; organic matter in the Middle Branch	sediment grain size, organic matter

Identifying the same ecozones in the two caves testifies that BF are suitable proxies of habitat partitioning in cave environments. Except for the marine ecozone, caves are inhabited by peculiar assemblages which are well-distinct from those of marine shallow-water of the same area. In particular, abundant agglutinated taxa are uncommon in

shallow-water foraminiferal assemblages of the Mediterranean Sea. Overall, the succession of ecozones was not attributed to a single parameter but a comprehensive environmental gradient determining increasing stress due to the decrease of marine influence. Based on the ecological meaning of foraminiferal assemblages, the environmental stress was attributed to high seasonal variability and high water energy. According to different cave morphology, the prevalence of agglutinated taxa starting from 100–300 m from the entrance was probably due to an adaptation to highly variable conditions regarding carbonate availability, which was strongly influenced by the decrease in salinity and pH, and mostly conditioned hyaline and porcelaneous taxa. Moreover, because the agglutinated taxa are not present in typical shallow-water assemblages of the Sardinian coast [109–112], a very effective dispersal as propagules (juvenile specimens, <32 μm, in a cryptic stage) may be supposed for these taxa ([105,106] and references therein).

The results of the 2015 sampling campaign, carried out during spring time, after the end of the rainy season, provided additional information on the seasonal variability of environmental conditions in the two caves, especially when compared with the results of summer 2014 [103]. In the BT cave, living and dead foraminifera were extremely scarce, with 35 living specimens in the 15 stations. This great depletion of foraminifera may not have resulted from prohibitive water parameters (T, Sal, pH, and DO) at the sampling time because they were in an ideal range for the life of BF. The disappearance of living and dead foraminifera let us suppose that they were mostly displaced and/or destroyed by strong freshwater flows during the rainy season, which caused the surface sediment layer to be removed. The few living specimens represented the beginning of the re-colonization, but no ecological zonation was possible. The reduction of foraminiferal abundance was less evident in the BM cave, demonstrating that the intensity of water flow during the winter was lower than in the BT cave. The ecozones identified in the summer of 2014 were also recognized in the next spring, with the same faunal characteristics but to a different extent, due to the development of a new ecozone in three stations (BT4-BT6) with abundant vegetal debris near the intersection of the North and Middle branches (Table 1). The confluence ecozone was characterized by a foraminiferal assemblage with high absolute abundance (FN: 1853–6267) and mild diversity (α index: 10.9–13.7), dominated by *Nouria polymorphinoides*, a very fragile agglutinated species, in association with *G. praegeri* and *Bolivina* spp. It is a shallow-infaunal taxon that does not tolerate oxygen depletion. Such a foraminiferal assemblage corresponded to sediment with a higher pelitic fraction and waters with higher salinity, temperature, pH, and dissolved oxygen. The assemblage structure in the confluence ecozone is the same as that which was recognized in BM6 in the previous summer, although the dominant species was *E. advenus*. It has been supposed that *N. polymorphinoides* is an early colonizer of the confluence ecozone during spring, benefiting from the abundant fresh organic matter supplied by the Middle Branch, when there is still high oxygen levels. In summer, the influence of the Middle Branch on the Northern one is reduced to station BM6, and *N. polymorphinoides* is substituted by *E. advenus*, which tolerates the low-oxygen conditions and uses refractory organic matter. The faunal shift from the hyaline-dominated assemblage of the entrance ecozone to the agglutinated assemblage of the transitional ecozone was attributed to the negative salinity and pH gradients. Small changes in pH (0.1 unit) and salinity could have consequences on benthic foraminiferal assemblages in terms of survival rate, reproduction, calcification, and resistance to shell dissolution ([103] and references therein).

The summer 2016 sampling was only focused on the BM cave where, based on earlier studies, foraminifera showed a wider distribution and recorded diversified environments attributable to different contributions. For this, the new sampling also included four stations of the Middle Branch, while sampling in the North Branch was expanded to the innermost sector (Figure 4) [113].
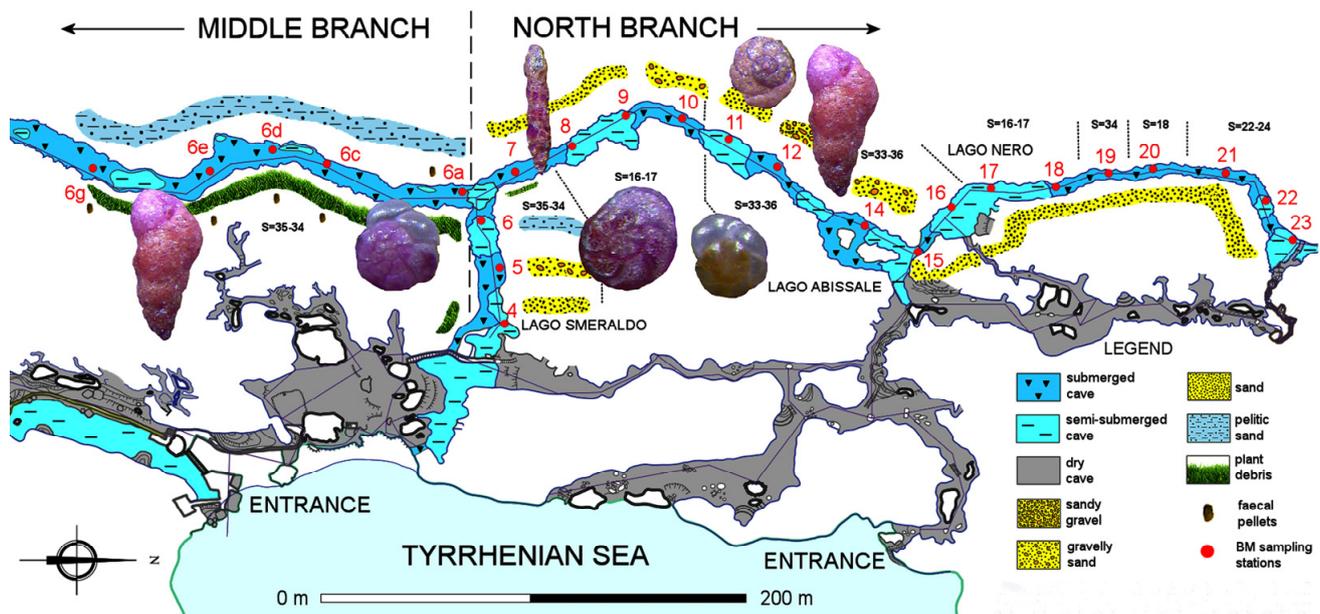
Figure 4. Different biotic and abiotic characteristics of the North and Middle Branches of the Bue Marino Cave. Sediment classification according to modified Shepard and specific constituents (plant debris, fecal pellets) of the cave sediments. Also salinity (S) is reported. The main species of the North and Middle Branches are illustrated. North Branch: *Gavelinopsis praegeri*, *Rosalina bradyi*, *Eggerelloides advenus* (up to 23%), *Reophax dentaliniformis*, and *Lepidodeuterammina ochracea*. Middle branch: *Eggerelloides advenus* (up to 84%) and *Ammonia tepida* (modified from [113]).

Based on the foraminiferal and grain size data and water parameter values, two main environments were identified. A well-oxygenated, less saline environment with coarse bottom sediment, correlated with a mixed calcareous-agglutinated assemblage (*G. praegeri*, *Rosalina* spp., *E. advenus*, and *Reophax dentaliniformis*) with high species diversity and low foraminiferal density, was recognized for the North Branch. In contrast, the Middle Branch revealed a scarcely oxygenated, more saline environment with fine bottom sediment enriched in vegetal debris; this was related to a prevalently agglutinated assemblage characterized by low species diversity and high foraminiferal density, with a high dominance of *E. advenus* (up to 83.6%) associated to *A. tepida*. These two environments corresponded to the entrance and confluence ecozones of the previous studies, respectively. Therefore, they were interpreted as the result of water masses with different salinity, sediment, and organic matter contributions from the karst system in the two branches.

3.2.2. Studies Carried out in the Murcia Region (Spain)

Another Mediterranean area for the study of BF from marine caves was the coast of the Murcia region, close to Cabo Tiñoso (south-eastern Spain). From a geological viewpoint, this area is characterized by two overlapping tectonic complexes of the Betic Cordillera. The older one, consisting of mica-schist, quartzite, gneiss, and marble, constitutes the Paleozoic basement; the other is primarily composed of Mesozoic limestones and dolostones forming imposing cliffs along the coast. In addition, due to extensive karst phenomena, numerous caves of various dimensions and settings have developed, significantly controlled by tectonics ([114] and references therein).

The CT12 cave is of hypogenic origin [115,116], with two marine entrances positioned at water depths of 12 m and 23 m, converging in a unique conduit after a few meters (Figure 5). The cave then develops in a narrow conduit, with a large chamber at the end, for the total development of about 120 m. Sediment samples were collected at seven stations starting from the convergence point of the two entrances and ending close to the wall of the final chamber. Samples were analyzed for grain size and BF. In addition, the brachiopod

thanatocoenosis was also considered. This was the first study that compared the BF and brachiopods' response to the changing environment inside a marine cave. Sediment in the cave was mainly fine (clayey or sandy silt) with some coarser components locally. The fine fraction was constituted by authigenic micrite, while the coarser fraction consisted of bioclasts from organisms living on both the walls and the cave ceiling.
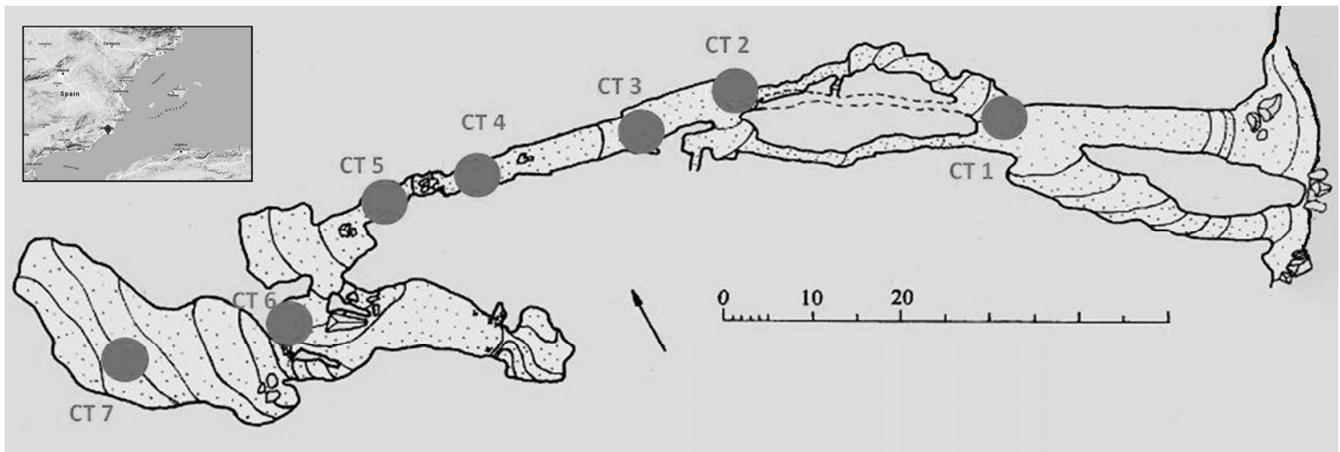

Figure 5. Location and sampling map of CT12 cave, Murcia region, Spain [114].

BF were abundant in the cave (some thousand specimens per gram of dry sediment), without a distinct pattern through the cave. On the whole, species diversity was high, with 100 identified species, and showed a pattern inversely correlated to the distance from the entrance. The statistical analysis recognized three foraminiferal assemblages corresponding to three ecozones. In the sample collected close to the entrance, *G. praegeri*, *Miliolinella subrotunda*, and *Cibicidoides lobatulus* prevailed (Figure 6, Table 1). The four samples collected along the conduit showed similar percentages of the two dominant species, *Patellina corrugata* and *S. vivipara*, at 15–23%, while *Tubinella inornata* was significantly lower (6–18%). In the two samples collected in the final chamber, *P. corrugata* became the dominant species, while *S. vivipara* and *T. inornata* were less abundant. The first two species live clinging to hard substrates, such as rocks, large mineral grains, bioclasts, or wood fragments, while the last one lives attached to hard substrates by an organic cement at the base of the proloculus ([114] and references therein). *Spirophthalmidium emaciatum*, indicative of oxic oligotrophic marine waters in Bermudian caves, was common in the CT12 cave.

Overall, the relative abundance of epifaunal clinging-attached foraminifera increased from the outer to the inner cave, representing an increasing degree of separation from marine conditions. Because the foraminiferal ecozones well corresponded to the cave morphology over small distances, the results of this study demonstrated the high sensitivity of these organisms to small-scale changes of cave habitat. Furthermore, the increase of epifaunal clinging-attached foraminifera corresponded to the increase of typical brachiopods of the cave environment [117].

Considering both BF and brachiopods, it was deduced that, despite the different lifestyles of these two groups, the strict correlation of environmental factors (i.e., light, nutrients, sediment texture, water parameters) changing along the cave determined an environmental gradient, which caused an increase in environmental stress that had similar effects on the different taxonomic groups.
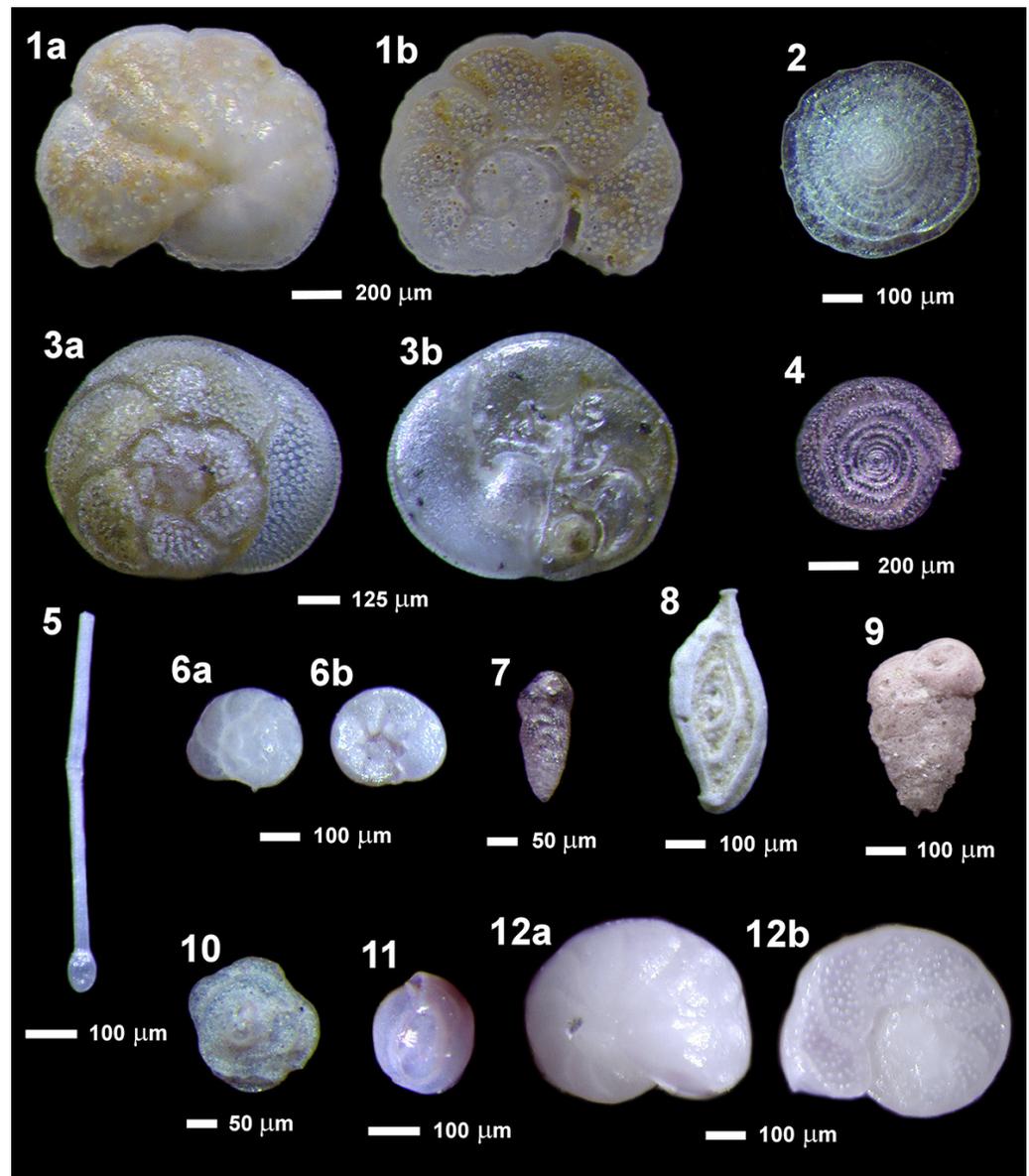
Figure 6. Commonly occurring Benthic Foraminifera in the CT12 cave: (**1**) *Cibicidoides lobatulus*, ventral view (a), dorsal view (b); (**2**) *Patellina corrugata*, dorsal view; (**3**) *Rosalina bradyi*, dorsal view (a), ventral view (b); (**4**) *Spirillina vivipara*; (**5**) *Tubinella inornata*, lateral view; (**6**) *Gavelinopsis praegeri*, dorsal view (a), ventral view (b); (**7**) *Bolivina variabilis*, lateral view; (**8**) *Spirophthalmidium emaciatum*, lateral view; (**9**) *Textularia bocki*, lateral view; (**10**) *Sejunctella* sp., dorsal view; (**11**) *Miliolinella subrotunda*, lateral view; (**12**) *Cibicides refulgens*, ventral view (a), dorsal view (b) [114].

4. Lessons Learned from Foraminiferal Studies in Marine Caves

Considering, on the whole, the studies concerning BF from marine caves, their reliability as paleoenvironmental and environmental proxies, already known for other better-studied environments, is confirmed. This character is particularly important because marine caves are deeply influenced by the changing interaction between marine and terrestrial domains and preserve a record of environmental changes.

The study of fossil foraminifera in caves currently above sea level helps to reconstruct relative sea-level changes due to the interaction between eustasy and local tectonics during the Quaternary. Moreover, by analyzing fossil or subfossil foraminiferal assemblages in sediment cores, the recurrence of extreme events, such as tsunamis and exceptional storms, may be recognized. Furthermore, changes in light conditions may be reconstructed through

the variable abundance of symbiont-bearing larger BF. Additionally, changes through time in the nutrient supply attributable to a change of the terrestrial landscape may be recognized from the ecological meaning of different assemblages.

In the reported studies on recent foraminifera of a soft bottom, the assemblages allowed us to recognize a succession of ecozones in wide cave systems and small marine caves, demonstrating excellent tools for habitat partitioning in marine caves. Common features of these ecozones were foraminiferal assemblages becoming less diverse and increasingly different from the typical marine ones, and moving away from the cave entrance. Furthermore, the faunal change was different according to different factors acting as environmental drivers; in caves affected by continental (freshwater, sediment, and organic matter) supply, such as Bel Torrente and Bue Marino, but also the Bermudian ones, the faunal shift from calcareous to agglutinated assemblage was interpreted as the response to a comprehensive environmental gradient of decreasing salinity and pH, but also environmental instability due to seasonal freshwater flows [103,105,106,113] (Table 1). Overall, this gradient determined that increasing environmental stress more favorable to the stress-tolerant agglutinated taxa, particularly *E. advenus* [118]. On the other hand, in smaller caves with exclusive marine contributions, such as CT12, the faunal response to increasing enclosed conditions with increasing distance from the entrance was the considerable increase in epifaunal clinging/attached taxa to bioclasts, with the dominance of a single species, while absolute abundance remained high (Table 1). This faunal change was interpreted as the response to increasing nutrient availability associated with the more abundant fine sediment fractions [114].

On the whole, studies considered in this review indicated the high sensitivity of BF to respond to changing conditions along the environmental gradient developing a succession of assemblages corresponding to different ecozones. Their ecological significance provides information on the origin of terrestrial and marine contributions, while their yearly monitoring provides information concerning seasonal and short-term climatic variability. These caves are also natural laboratories for predicting future changes in marine systems. In particular, studying the environmental drivers determining the faunal shift from prevailingly-calcareous (*G. praegeri*, *R. bradyi*) to prevailingly-agglutinated (*E. advenus*, *R. dentaliniformis*) assemblages and the total disappearance of BF at an increasing distance from the cave entrance may provide information on global changes, such as ocean acidification. The possible disappearance of calcareous BF as a response to this phenomenon has many implications due to the importance of these organisms for CO_2 sequestration in the carbon biogeochemical cycle and as contributors of carbonate sediments [64,119]. Further, studying small caves that are entirely flooded by marine waters has scientific value because BF demonstrated the capability of habitat partitioning at a small scale, implying that these environments constitute reservoirs of high diversity despite the small size.

Regarding the distribution of species, it has been pointed out that *M. miniacea* is the most widespread hard-bottom foraminifer in the Mediterranean region. Concerning sediment colonizer taxa, some similarities between the assemblage of the transitional ecozone of the CT12 cave and the Bermudian subtidal marine one, are recognizable for the abundance of *S. vivipara* and *S. emaciatum* (Table 2). Another common species in the caves of Sardinia, Spain, and Bermuda was *B. variabilis*. This faunal similarity probably occurs because subterranean environments offer similar conditions also in regions of different climatic zones. It also means that the dispersal mechanism of BF, occurring through the transport of juvenile specimens (propagules) in a cryptic stage, is effective at a global scale and allows penetration into highly confined environments [120,121].

Table 2. List of the main foraminiferal species mentioned in this study, recorded in marine caves and provenance region.

Species	Isca Cave (Tyrrhenian Coast)	Gulf of Orosei (Sardinia, Italy)	CT12 Murcia Region (Spain)	Other Mediterranean Caves	Yucatan (Mexico)	Bermuda	Other Caves Outside the Mediterranean
Adelosina spp.	X						
Ammodiscus tenuis (Brady, 1881)						X	
Ammonia beccarii (Linnaeus, 1758)							X
Ammonia inflata (Seguenza, 1862)		X					
Ammonia tepida (Cushman, 1926)					X		
Ammonia spp.							X
Amphistegina radiata (Fichtel & Moll, 1798)							X
Baculogipsina sphaerulata (Parker & Jones, 1860)							X
Calcarina spp.							X
Bolivina spp.		X				X	
Bolivina variabilis (Williamson, 1858)		X	X			X	
Cibicides refulgens Montfort, 1808						X	
Cornuspiramia adherens (Le Calvez, 1935)				X			
Cribrostomoides jeffreysii (Williamson, 1858)		X					
Eggerelloides advenus (Cushman, 1922)		X					
Elphidium crispum (Linnaeus, 1758)		X					
Elphidium spp.						X	X
Gavelinopsis praegeri (Heron-Allen & Earland, 1913)		X	X				
Globigerina sp.							X
Jadammina macrescens (Brady, 1870) accepted as *Entzia macrescens* (Brady, 1870)					X		
Lepidodeuterammina ochracea (Williamson, 1858)		X					
Lobatula lobatula (Walker & Jacob, 1798) synonim of *Cibicidoides lobatulus* (Walker & Jacob, 1798)			X				X
Melonis barleeanus (Williamson, 1858) accepted as *Melonis affinis* (Reuss, 1851)	X					X	
Miliolinella subrotunda (Montagu, 1803)			X				
Miniacina miniacea (Pallas, 1766)	X			X			
Nouria polymorphinoides Heron-Allen & Earland, 1914		X					
Patellina corrugata Williamson, 1858			X				
Peneroplis planatus (Fichtel & Moll, 1798)		X					X
Peneroplis pertusus (Forsskål in Niebuhr, 1775)		X					
Planogypsina acervalis (Brady, 1884)				X			
Polysaccammina ipohalina Scott, 1976						X	
Pseudothurammina limnetis (Scott & Medioli, 1980)						X	
Quinqueloculina spp.						X	
Reophax dentaliniformis (Brady, 1881) accepted as *Nodulina dentaliniformis* (Brady, 1881)		X					
Rhizammina sp.	X						
Rosalina bradyi (Cushman, 1915)		X					
Rosalina spp.		X				X	
Sigmoilina tenuis (Cžjžek, 1848) accepted as *Spirosigmoilina tenuis* (Cžjžek, 1848)						X	
Sejunctella sp.			X				
Spirillina vivipara Ehrenberg, 1843			X			X	
Spirophthalmidium emaciatum (Haynes, 1973)			X			X	
Textularia bocky			X				
Textularia spp.	X						
Trochammina inflata (Montagu, 1808)						X	
Tubinella inornata (Brady, 1884)			X				

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