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Caves and Bats: morphological impacts and archaeological implications. The Azé Prehistoric Cave (Saône-et-Loire, France)

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Abstract

The Prehistoric Cave at Azé (France) was divided in two parts by calcite flowstone. This isolated the innermost parts of the cave from the entrance, which remained connected to the surface. Since the closure, bats have not been able to access the cave beyond the flowstone blockage. They have been present only in the cave entrance. The byproducts released by bats had a considerable effect on this entrance part. Gaseous exhalations have changed the composition of the surrounding atmosphere, leading to the development of dome-shaped cupolas and other wall weathering features. Guano deposits built up causing the formation of aerosols and acidic leachates. The resulting corrosion of the limestone has led to the formation of phosphate deposits and biogenic karst. The rate of retreat of the cave walls has been estimated at 5 to 7 mm/ka. Corrosion has also affected archaeological artefacts, as well as any traces left on the walls by humans or animals. Bioglyphs linked to bears as well as anthropic graffiti have completely disappeared from the part of the cave used by bats.

Key words: corrosion, bat, cave wall, bioglyph, graffiti.

In memory of Marcel Jeannet who participated in this study by determining the paleontological remains of bats present in the cave.

1. Introduction

In recent times, research carried out in several caves located in equatorial and tropical areas (Lundberg and McFarlane, 2009, 2012, 2015; Dandurand et al., 2019) and in Europe (Audra et al., 2016; Queffelec et al., 2018) has revealed the impact of bat colonies on cave walls and its implications for the conservation of wall art (Bruxelles et al., 2016). These studies, based on the identification of typical weathering morphologies and on specific deposits, have shown deep changes of underground morphologies and significant retreat of cave walls. The ethology of bats and their waste products (urine, guano, breathing exhalations) cause different types of alteration to the surrounding rock (Audra et al., 2018). Chemical reactions occur between the acidic leachates from these waste products and the calcium carbonate in the surrounding rock. On the ceiling, it mainly consists in dissolution by condensation water. The limestone cement is removed in solution, and the weathered limestone remaining on the surface is eventually disaggregated and falls by gravity (Zupan-Hajna, 2003) and by the successive use of the claws of roosting bats (Merino et al., 2019). This ceiling disaggregation can produce a rain of sand (Delaty et al, 2006). On the walls, two distinct phenomena can be identified: (i) water from condensation trickling down the walls dissolves the limestone; (ii) the leachates from guano deposits, containing phosphoric acid, also reacts with calcium carbonate resulting in the formation of phosphatic minerals, mainly apatite-group minerals, forming dark brown encrustations. In wall niches and fissures on the floor, beneath guano deposits, the action of phosphoric acid dominates. On the floor, sedimentary deposits (David et al., 2018), and speleothems are also affected by biogenic corrosion (Audra et al., 2016). It affects the surrounding rock and adjacent sediments, but also any archaeological artefacts.

Several studies have also shown that bat droppings are the source of specific minerals (Martini and Kavalieris, 1978; Hill and Forti, 1997; Audra et al., 2017, 2019, 2021).

These studies also have confirmed the importance of biogenic corrosion, particularly linked to bats, in the evolution of underground landscapes (Audra et al., 2018). In each case it is a matter of destruction, not only of the underground landscape, but also of archaeological remains, especially cave art (Bruxelles et al., 2016). Among the examples studied in this paper, the prehistoric cave at Azé (Mâconnais region, South Burgundy, France (Fig. 1)) stands out because: (i) it is a well-known cave which has been studied for a long time (Barriquand et al., 2011a, 2011b); (ii) the conditions of its genesis and paleogeographic evolution have been the subject of numerous research projects (Barriquand et al., 2006, 2012, 2015a; Dubois et al., 2014); and (iii) both its entrance area and deeper zones have provided a large collection of high quality paleontological remains, which have helped us better understand the conditions in which these areas evolved (Argant, 1988, 1991, 2004; Barriquand et al., 2004; Argant et al., 2007, 2019). Lastly, (iv) its entry zone has been a site of human occupations from the Lower Paleolithic to the 16th century, providing a number of high-quality remains (Combiere et al., 2000; Floss and Hoyer, 2010; Barriquand et al., 2011b).

The goals of the present study are: (1) to describe the Azé site, (2) to provide an overview of the present bat species and their ethology, and (3) to analyze the biogenic processes impacting the natural environment and archeological artefacts. The use of 3D morphometric analysis allows us (4) to evaluate the rate of evolution, directly associated with these processes and to develop a better understanding of the major processes of weathering linked to bats. And (5) to raise the question of the possible role of bat parasites impacting cave surfaces.

2. Material and methods

2.1. The Azé Prehistoric Cave: a highly suitable site for studying the impacts of bats

The Prehistoric Cave at Azé is located in France, in Lower Bathonian limestones, at an altitude of 268 m. The cave is 500 m long and has a relief of about 30 m. Most of the network has been entirely discovered by digging (only 60 m were accessible in 1963) and each year a few meters are gained. Until 1963, the cave was plugged around 60 m from its entrance by calcite flowstone, which completely

isolated the upstream parts of the cave from the entrance area (Fig. 1). Then programs to carry out research and remove obstructions led to breaching the plug and the discovery of the upstream series (Barriquand et al., 2011a).

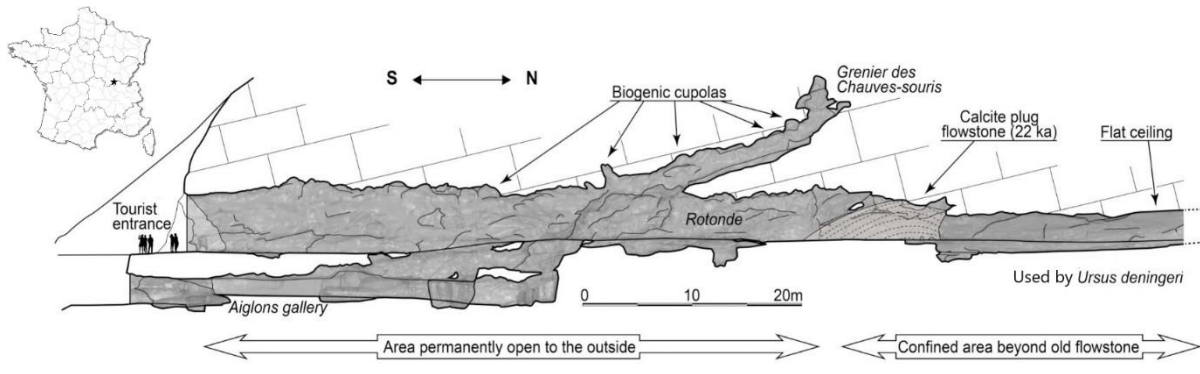


Fig. 1: Location of Azé Caves in France. Longitudinal profile of part of the Azé Prehistoric Cave. To the left, the part which remained open and accessible to bats; in grey, the flowstone obstruction which sealed off upstream parts of the cave; to the right, the part which became inaccessible to bats 22,000 years ago.

Beyond this flowstone, the passage has been almost entirely filled in by fluvial deposits accumulating since the Middle Pleistocene. These deposits formed at least between Marine Isotopic Stages (MIS) 8-9 and 2, that is from 300-350 ka (Barriquand et al., 2011b). A series of twelve uranium/thorium dates the flowstone provided ages between 135 and 22 ka. The age obtained on the ceiling at the top of the flowstone was 22 ka (+ 0.9 / -0.8) (Barriquand et al., 2006). This confirms that since MIS 2, at the minimum, and during all of the Holocene, the inner part of the cave was no longer accessible to bats. However, in all likelihood, the entrance part of the cave always remained open to the surface. There are several locations at the site where there is evidence of more or less continuous human occupations, from the Lower Paleolithic (Combiér et al., 2000; Argant, 2004). Around 350-300 ka, humans used the entrance zone and left numerous artefacts. During the Middle Paleolithic (80-60 ka) and the Gravettian (27-22 ka), groups of humans occupied the Azé site, as revealed by deposits found at the outlet of the Underground River Cave and at the site of the present campground (Combiér and Merle, 1999; Floss, 2000; Floss and Beutelspacher, 2005; Floss et al., 2013). Magdalenians (17-12 ka) also frequented the

cave (Floss and Hoyer, 2010). Later, protohistoric communities caused significant environmental changes inside the cave entrance. During the Final Bronze Age (3 ka), the cave was used for habitation or as a sheepfold. At the end of the Tène period (Late Iron Age) or at the very beginning of the Gallo-Roman period (2.1-1.9 ka BP), several modifications appeared outside the cave. Thereafter all the cave area was used as a place of habitation (Barriquand et al., 2011b). The absence of stratigraphic data from these excavations do not allow us to identify the types of activities that occurred in the cave. Both the site and the cave continued to be used from the Merovingian and Carolingian periods (5th to 10th century) when a wall was built to separate La Rotonde from the entrance. The cave was regularly used until the 16th century, as confirmed by several radiocarbon dates (Barriquand et al., 2011b; Barriquand et al., 2017). During the second half of the 19th century, a park was developed around the cave, which became a popular place for outings.

From a palaeontological point of view, bears were present in the cave, between the Lower Palaeolithic and the end of the Middle Palaeolithic: 140 to 160 ka (Argant, 1988, 1991, 2004; Argant et al., 2007). In all likelihood, they were still present at the end of MIS 4, around 60 ka (Argant et al, 2019). As well as numerous bones, they left claws marks on the cave walls (bioglyphs), visible only beyond the calcite barrier, which closed off the inner part of the cave (Fig. 2).

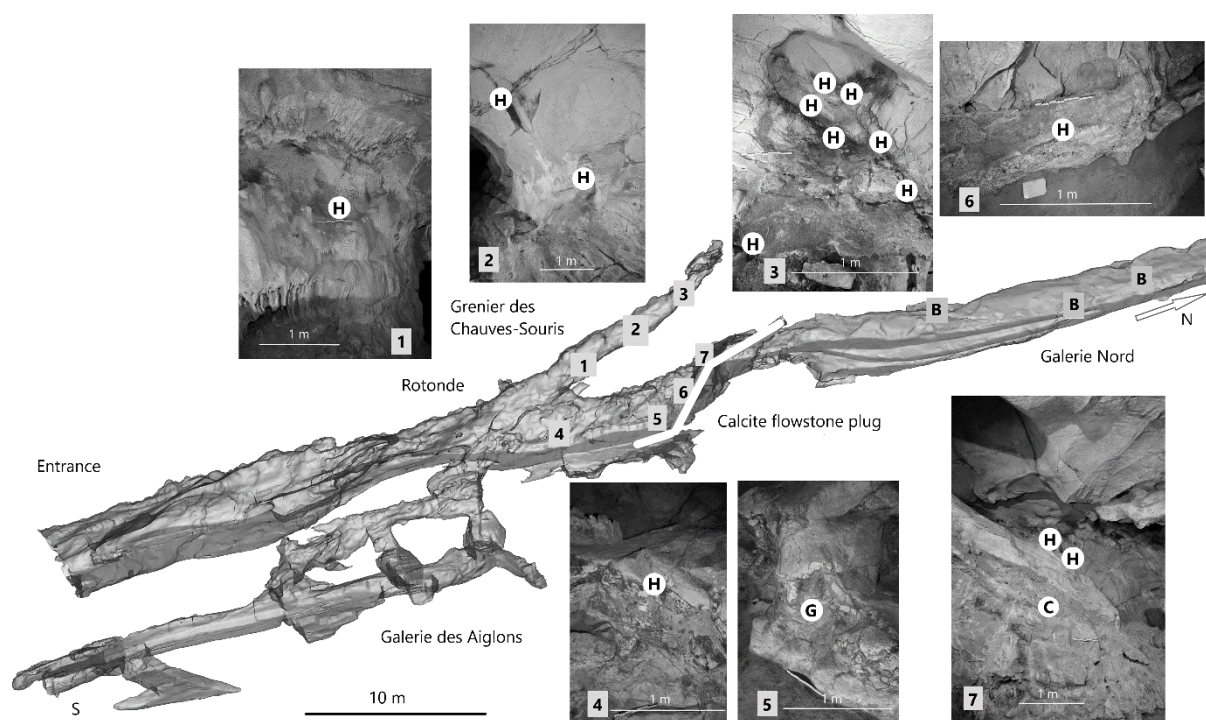


Fig. 2: 3D representation of the Cave (Blanchard et al., 2018). Location of the calcite flowstone obstruction (white line,). Position of samples analysed by XRD, hydroxylapatite (H), gypsum (G), and position of the sample older than the formation of a part of the calcite flowstone (C). Location of bear claw marks (B).

Unlike the walls of the inner cave, those of the cave entrance are perfectly smooth. They do not show signs of frost-shattering, which however has affected the porch of the neighboring Galerie des Aiglons (Fig. 1, 2), and also 200 km to the south in the “La Grotte aux Points”, Ardèche, France, where conspicuous effects of frost-shattering cover 85 m², or 35% of the surfaces (Jaillet and Monney, 2018). Yet, frost-shattering was intense in the Monts du Mâconnais area during the last two glaciations, as shown by the thick deposits covering the slopes of the cuestas (Perthuisot, 1967; Combier, 1969, 1998). To the west of the Azé Prehistoric Cave, such deposits can reach as much as 27 m of thickness, showing at least twelve phases of deposition (Barriquand et al., 2010).

For 300 ka, the Azé cave has been inhabited by humans and animals. However, the traces on the wall are found only beyond the flowstone barrier, as bears claw marks. During the 19th century, people made trips to the caves marking these visits with inscriptions, made by carving or writing with a carbon pencil or soot. Such inscriptions are numerous and quite visible in the majority of caves. The Mâconnais

area is no exception, such as in the neighboring caves, Cailleverdière at Blanot and Furtins at Berzé-la-Ville, which are however less accessible than Azé (Barriquand et al., 2015b). There is no reason why visitors would not have done the same at Azé. Yet today, almost no graffiti can be observed. The almost complete absence of such inscriptions on the walls is evidence of an ongoing rapid destruction of the surfaces and morphology of the passages. We can also assume that these processes were still active in the decades before the cave's tourist development.

The morphology of the cave is clearly different between the part that remained open to the surface and the part that was confined beyond the flowstone plug. In the inner part, the cave has smaller dimensions. Likewise, the 17° dip of the stratigraphy, characteristic of the Mâconnais area, is quite evident on the ceiling, whereas it is not at all visible in the entrance part of the cave that remained open. These first 60 m have therefore undergone a specific morphogenetic evolution, closely influenced by the surface proximity, and this has taken place since the beginning of the Holocene. An evaluation of the evidently profound alteration of the passages, and especially their walls, requires the use of a range of multidisciplinary techniques.

Current research programs are focused on understanding the evolution of the cave system, whether linked to environmental or anthropic changes. The presence of bats over this whole period and the extent of their frequentation have affected the morphologies of the passages and their sediments. The passages have many cupolas whose morphologies seem similar to those described as biogenic in origin and associated with bats (Lundberg and McFarlane, 2015). It therefore seemed important to develop a specific methodology to identify the presence and effects of the bats, including their parasites, on the cave.

2.2. The bats and their parasites in the Azé Prehistoric Cave

In the cave entrance, there are also pupal remains attached to the wall. They are linked to the reproduction of bat parasites. When the pupae of *Nycteribiidae* and *Streblidae* are attached to the

cave wall by the female, they are partially transparent. They gradually become black due to a chemical reaction which may alter the limestone wall.

2.2.1. Bat species in Azé cave

In the Mâconnais region, *Myotis myotis* bats were using the neighboring Vergisson II Cave since MIS 4, ~70 ka (Jeannet, 2018). In Azé Cave, eight species of bats frequented the cave during MIS 3 and 2, between 45-16 ka (Tab. 1). They were still present in the entrance passage at 15,9 ka.

During the 1950s, the cave was the most important bat nursery site in Burgundy (Morel, 1960). Each year, several species were present in “great numbers” (Roué and Sirugue, 2006), as reported in a documentary from 1961 (Nicolas, 1961). Counts carried out between 1952 and 2020 have shown that 11 species were present in the cave during this period (Tab. 1).

Species	Stages MIS 3 and/or 2	15.9 ka (sample OxA12455)	1952-1959	1995-2020	Average mass of an individual (g)	Maternity-hibernation colonies	Maximum number of individuals recorded	Behavior
<i>Rhinolophus hipposideros</i>				17	4-7	1 - 200	1,000	swarms
<i>Rhinolophus ferrumequin</i>			3	20	18-24	20 – 1,000	1,600	dense swarms
<i>Rhinolophus euryale</i>			106		9-14	200-300	5,000	dense swarms
<i>Myotis daubentonii</i>	X	X		7	6-10	140	20,000	compact swarms
<i>Myotis emarginatus</i>				3	6-9	20-500	7,000	swarms
<i>Myotis nattereri</i>				7	7-10	100	8,000	swarms
<i>Myotis myotis</i>	X	X	51	6	20-27	50-1,000	8,000	swarms
<i>Myotis mystacinus</i>	X	X		1	4-7			solitary
<i>Myotis blythii</i>	X	X			19-30	50-500	8,000	swarms
<i>Myotis bechsteinii</i>	X				7-10	10-50	100	solitary
<i>Miniopterus schreibersii</i>	X	X	108		10-14	several thousand	120,000	swarms
<i>Barbastella barbastellus</i>				1	7-10	1200	7,800	swarms
<i>Eptesicus serotinus</i>				1	18-25	10-60	300	solitary
<i>Plecotus austriacus</i>					6-10	5-30		solitary
<i>Plecotus auritus</i>					6-9	5-30	100	solitary

Tab. 1: Species of bats frequenting the Azé Prehistoric Cave during MIS 3 and 2, and the maximum number of individuals by species recently counted in Azé cave (counts made by the Association Culturelle du Site d’Azé, the Comités Départementaux de Spéléologie de Saône-et-Loire, de l’Ain et du Rhône, and the Société d’Histoire Naturelle d’Autun). Ethological and morphological characteristics of these species (Diez et al., 2009; Arthur & Lemaire, 2015).

2.2.2. Ethology of the bats currently present in Azé

Bat ethology and their waste production have caused profound changes in caves. Bats are very faithful to their roost, where they return generation after generation (Casteret, 1936; Entwistle et al., 2000; Furmankiewicz, 2016). Thus, each year at Azé, the same cupola provides shelter for them. Because of man's impact on the area, current bat populations are much smaller than those of previous decades. Some bat species regularly gather in colonies. In Europe, colonies can often reach several thousands of individuals. This is also the case for most species at Azé (Tab. 1). In swarms, the density of individuals can be several hundred, even several thousand, per square meter, e.g. 2,000 / m² for *Miniopterus schreibersii* (Arthur and Lemaire, 2015).

Bats introduce allogenic substances in caves through their wastes, urine and guano. They defecate during flight but also, while hanging in their roost, they can eject their waste laterally (Paladino, 2016) onto the nearby walls. Urine produced during the 12 postprandial hours, is 0.1 and 0.3 g for *Plecotus auritus* and *Myotis daubentoni* individuals, respectively (Webb et al., 1994).

Guano is mainly made up of phosphates, sulfates, potassium, sodium, and calcium. Very soluble ammonia is easily leached away by seepage water (Hill and Forti, 1997), whereas less soluble phosphates gradually become concentrated in the guano pile.

According to the prevailing environmental conditions, the leachates from these phosphate-rich deposits react with the host-rock, the sediments, and the different elements which may be present, to produce phosphatic minerals (Hill and Forti, 1997; Onac and Forti, 2011; Audra et al., 2016, 2019, 2021). Precursor minerals first form (Audra et al, 2019), then evolve towards more stable species, such as hydroxylapatite, one of the most common phosphates.

Mechanical erosion from bats is also responsible of the degradation of cave walls. Bats are using their claws to hang when roosting. The rock is disaggregated, fragments are detached and mixed with the phosphate of the underlying guano deposits (Delaty et al., 2006).

The average body temperature of bats ranges from 36 to 41°C during periods of activity. From a thermodynamic point of view, the body of a bat can be considered similar to that of a human, with a latent heat value of 3.5 kJ.kg⁻¹.°C⁻¹.

Bats' transpiration and breathing release water vapor. The amount of released water contributes to the air moisture (Lundberg and McFarlane, 2015). As any living being, bats expel CO₂. In addition to mouth exhalation, bats also eliminate CO₂ through the patagium (Polturat, 2015). Even though cave CO₂ can have various origins, the breathing of a bat colony can produce a significant additional amount. In semi-confined spaces with low air flow, where CO₂ is not flushed out, the concentration can rise up to 5% (Lundberg and McFarlane, 2009; Audra and Coquin, 2020).

Therefore, through their presence in a cave, bats are responsible for increases in temperature, humidity, and concentrations of CO₂ in the air. Through the combination of these three parameters, a film of water is formed, capable of dissolving the calcium carbonate in the surrounding rock.

2.2.3. Bats parasites

The *Nycteribiidae* and *Streblidae* are exclusive ectoparasites of bats. They are characterised by their morphologies and their specific biology. They have been included in the Pupipara group, because they produce eggs which hatch directly into the nymph stage (Duvallet and Baldacchino, 2017). Although these parasites spend almost all their life cycle on a bat, on which they depend for their nourishment, they must leave their host to lay their eggs on cave walls. When the *Nycteribiidae* and *Streblidae* reproduce, an egg is implanted in the uterus of the female. When the larva has totally developed, the pupa begins to form because it contains sufficient food for the embryo until it hatches. Then parturition takes place. The prepupa is deposited on the cave wall close to roosting bats. Prepupae are expelled from the female's body with an adhesive secretion to enable their attachment to the cave wall. Their shell is initially made up of chitin (Ditmar et al., 2009). The chitin reacts with the calcium carbonate from the limestone to gradually form a hard shell. Studies show that the density of viable pupae can be as high as around 610/m² (Ditmar et al., 2009). A study in Germany shows that the total number of

pupae deposited could therefore be between 1,000 and 2,000 and indicating that only 30 to 57% of pupae are viable (Reckardt and Kerth, 2007).

2.3. Methods

The cupolas were modelled in three dimensions using photogrammetry. Multi-correlation of images of the same object, taken from different angles, was used to generate a meshed topographic model. Photos were taken using a Canon EOS 7D fitted with a 24-120 mm lens. Lighting was provided by halogen floodlights connected to the cave's electrical network, supplemented by battery-powered LEDs. A minimum overlap of 40% was maintained between each picture. 35 cupolas were photographed and measured. The different pictures of each cupola were then assembled using Agisoft PhotoScan© software. Cupolas are described using the following morphometrics: base width (W), length (L), and height (H). At this time, the same technique was used in the Isturitz Cave, Pyrénées-Atlantiques, France (Caillaud, 2017). The results obtained from both caves were compared.

The 3D model was obtained using a FARO Technologies Focus 3D X130 HDR laser scanner (Blanchard et al., 2018). It enables scans over 360° horizontally and 240° vertically. Scenes were assembled using FARO's SCENE software, then the point cloud was meshed using 3DReshaper software to create an integrated model of the cave passage. The average error between two scans was 1 mm, and for the cave as a whole around 20 cm between its two extremities, 350 m apart.

The U/Th dating of the calcite were obtained from a previous study (Barriquand et al., 2006). They are used to constrain the successive changes in the passage being studied.

In order to characterize the impact of bats on the cave sediments, mineralogical samples were taken from old deposits remaining on the cave walls or in small fissures in the Rotonde and in the Grenier des Chauves-souris. Mineral identification was carried out by X-ray diffraction (XRD) using a Rigaku RU-200BH X-ray generator equipped with a rotating anode, an Osmic multilayer optic and a mar345 2D

detector. The wavelength used was that of Cu, $\lambda = 0,15418$ nm, and the power applied was 50 kV and 50 mA. The samples to be analysed were finely ground, the obtained powder was homogenized, then placed in a glass capillary 0.5 mm in diameter. The volume of powder exposed to the X-rays for each measurement was around 0,1 μ l.

The bat population currently present in Azé is limited to a few individuals. Only a few traces of guano remain. The characterization of the latter was therefore based on samples of the same species taken from the neighboring Courtouphle Cave (Ain, France). The analysis of phosphate concentration contained in the guano sample taken from Courtouphle Cave was done after drying the guano for 2 h at 105 °C in a ventilated laboratory oven, then dissolving it with aqua regia (Type NF EN 13346). The total phosphorus was measured using ICP according to NF EN ISO 11885. The pH of the guano was measured after drying for 2 h at 105 °C, then resuspending 50/50 by mass with demineralized water and mixing with a Rayneri mixer.

3. Results

3.1. Guano characterization

In the nearby Courtouphle Cave (Ain, France), where species are similar to those at Azé, the phosphate concentration in guano is 107 g/kg. The enrichment of a guano deposit in phosphate causes a significant reduction in pH, i.e. an increase of acidity ($n = 8$). For Azé, old guano located in the Grenier des Chauves-Souris indicated a pH between 5.0 and 5.3.

3.2. Mineralogical analyses

The fill in the first 200 m of the Prehistoric Cave at Azé was removed at the beginning of the 1960s. There is therefore no ancient guano still in place. Fortunately, small amounts of various deposits remain on the cave walls and in small fissures. A total of 21 samples of these traces and brown encrustations were taken for mineralogical analysis using XRD (Fig. 2). 16 samples contain apatite-

group minerals, probably hydroxylapatite. One sample probably (poor peak) contains gypsum. This sample was taken at a level where the cave floor used to be. 20 samples contained quartz. Terrigenous clasts in the limestone (Deschamps et al., 2015), contribute to the cave sediments after dissolution of the host-rock. Smectite is present only in the clays in the fluvial deposits (Barriquand and Debard, 2010), whereas it has not been found in samples taken from walls in the cave's entrance. Finally, a sample taken from beneath the flowstone plug (Fig. 2(7)) contains a small amount of an apatite-group mineral. At this place, the base of the flowstone was dated by U/Th at $58.9 \text{ ka} \pm 1,4$ (Barriquand et al., 2006).

3.3. Morphological impacts on the walls and speleothems in Azé cave

In the entrance of Azé cave, the ceiling exposed to bats are remarkable because of their overlapping cupolas (Fig. 3).

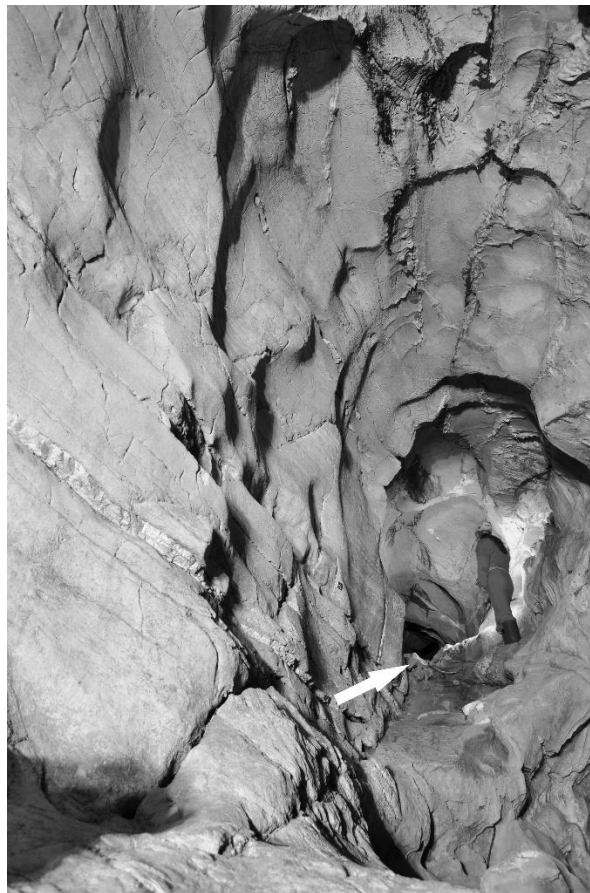


Fig. 3: The entrance to the Grenier des Chauves-Souris viewed from the Rotunda. Note the remarkable array of overlapping cupolas and the corrosion channel (arrow) draining condensation runoff.

They are clearly differentiated from classical ceiling pockets and cupolas (phreatic or vadose) by their complete lack of association with fractures or feedwater routes and they show no evidence of water flowing down the sides or dripping from the ceiling (Lundberg and McFarlane, 2009). Furthermore, their bases are covered in blackish-brown encrustations, confirming their use by bats (Fig. 4). The formation of these cupolas is linked to swarms of bats and to the environmental modifications that they caused (Lundberg and McFarlane, 2009, 2015; Audra et al., 2016). These cupolas cut both the limestone and the calcite, as irregular hollows.

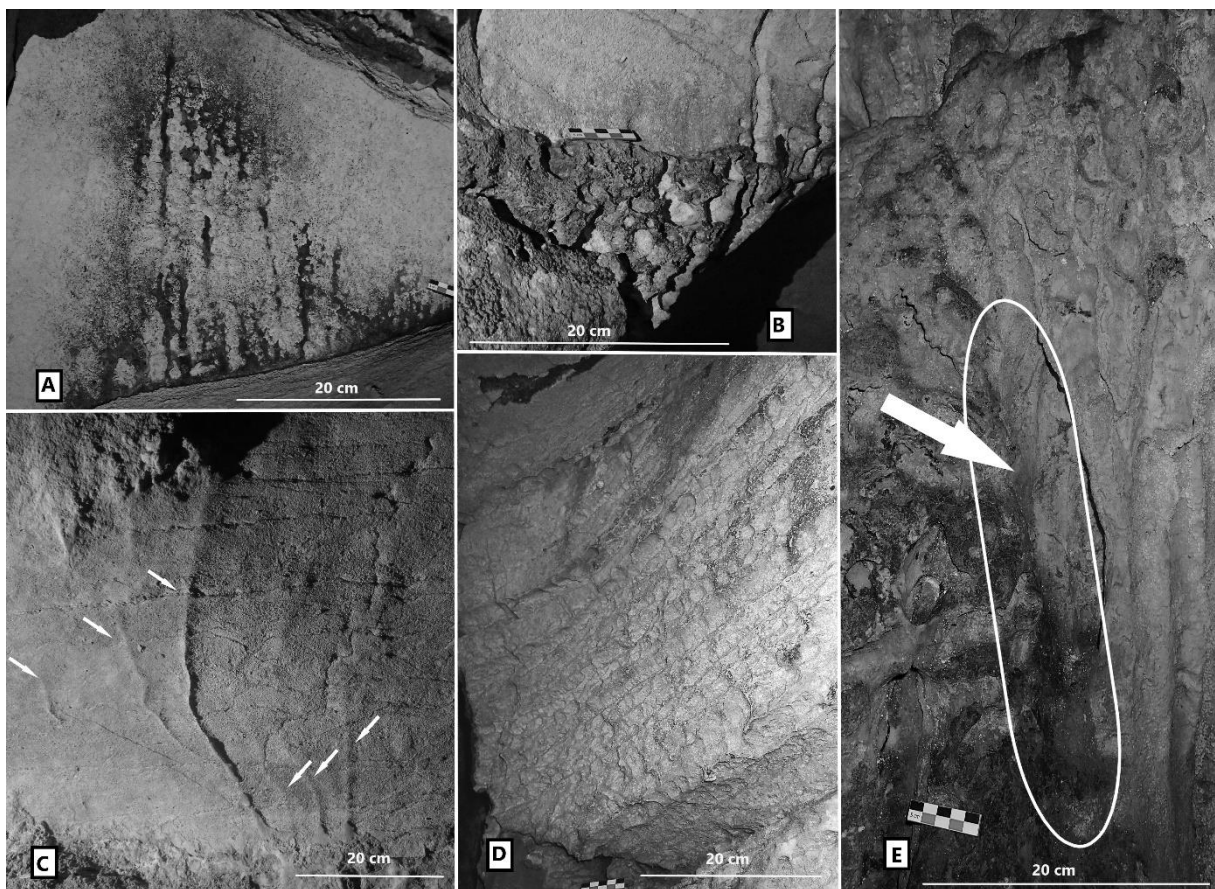


Fig. 4: A: Weathering-linked runoff from a cupola above; B: multicentimetres-thick weathering; C: smooth wall with undulations reflecting differential corrosion and the former presence of calcite curtains; D: small cup-like depressions, once directly exposed to guano; E: cup-like depressions and flow channels on a calcite drapery.

The walls and speleothems on which these cupolas have formed have a smooth and wavy appearance, a characteristic of condensation-corrosion (Audra et al., 2016). There are also gentle undulations on the surface of the walls indicating the former presence of calcite draperies, more resistant than the

host-rock, that have relatively protected the wall from corrosion (Audra et al., 2016). Today the draperies have totally disappeared or remain only as residual pieces (Fig. 4C)

Additionally, some features are developed along the walls through solution and crust deposition. These features are small cup-like depressions or vertical grooves more than 1 cm depth (Fig. 4A, 4B). The cup-like depressions are very numerous on walls and draperies which have been covered by guano deposits. Furrows from running water are also visible on the surface of calcite crusts (Fig. 4D, 4E).

On the floor, sedimentary deposits (David et al., 2018), and speleothems are also affected by biogenic corrosion (Audra et al., 2016). Numerous guano potholes and biogenic holes in the cave floor are visible in the floor of the Rotonde and the Grenier des Chauves-Souris. The latter is remarkable because of the large drainage channel along its long axis connecting to the main Rotonde Passage, which drained crypto-corrosion features along the slope (Fig. 3). This channel has concentrated corrosive leachates from the guano towards the Rotonde. To the north of the Rotonde, the stalagmites located on top of the flowstone plug are also deeply weathered (Fig. 5).



Fig. 5: This stalagmite was still covered by guano in the 1950s. Corrosion has removed a layer more than 3 cm-thick from its surface, demonstrating the intense corrosion of bat guano.

The removal associated with their corrosion is more than 3 cm. Similar corrosion is evident on the flowstone plug where the leachates from the guano have penetrated to a depth of more than 5 cm (Fig. 6).

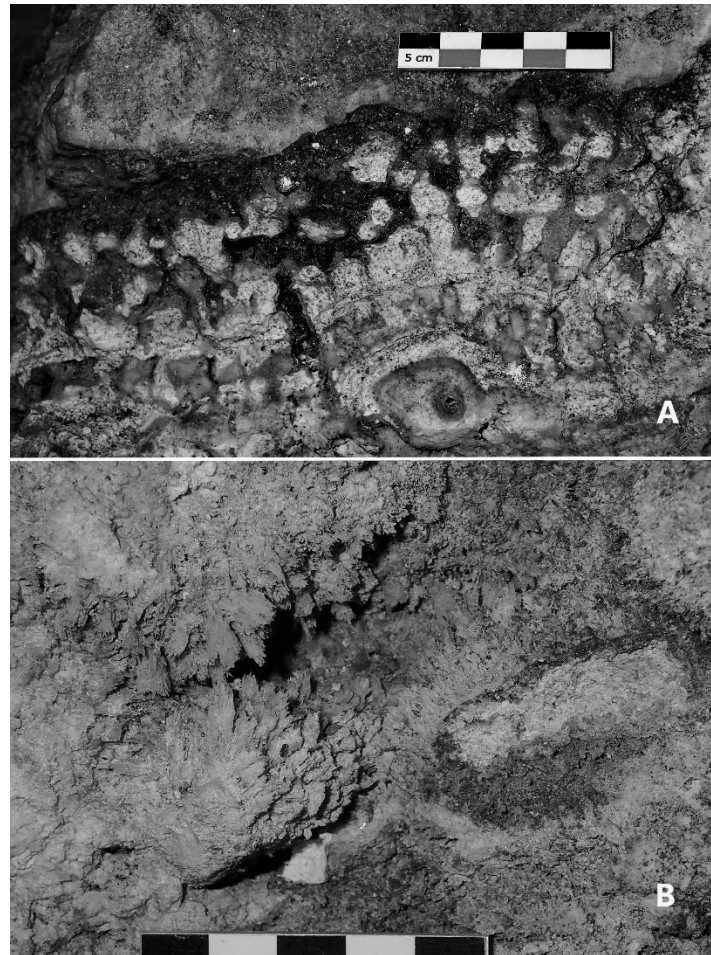


Fig. 6: Weathering of the flowstone plug. A: vertical section of the flowstone revealed when cut through by speleologists; the blackish-brown deposits show the extent of penetration by leachates from guano; B: old calcite weathered by acidic leachates under a guano deposit (black).

3.4. Morphometry of the cupolas

To characterize the cupola morphology, a model obtained by photogrammetry was used to produce views of the cupolas in inverse relief, which makes comparison much easier. Examination of 35 views revealed three different morphologies (Fig. 7):

- hemispherical-cupolas, which are not the most common (n=3) and are often associated with other types of forms or included as part of a larger concavity (Fig. 7A);

- hemi-ovoid cupolas (n=10), which are characterized by their regularity, but are often larger than hemispherical cupolas (Fig. 7B);
- cupolas in the form of a Scottish tam (n=22) are the most common, along with hemi-ovoid cupolas. The angle of curvature of the upper part of the cupola is irregular, continuing to a pointed apex, below which the wall is subvertical, generally overhanging.

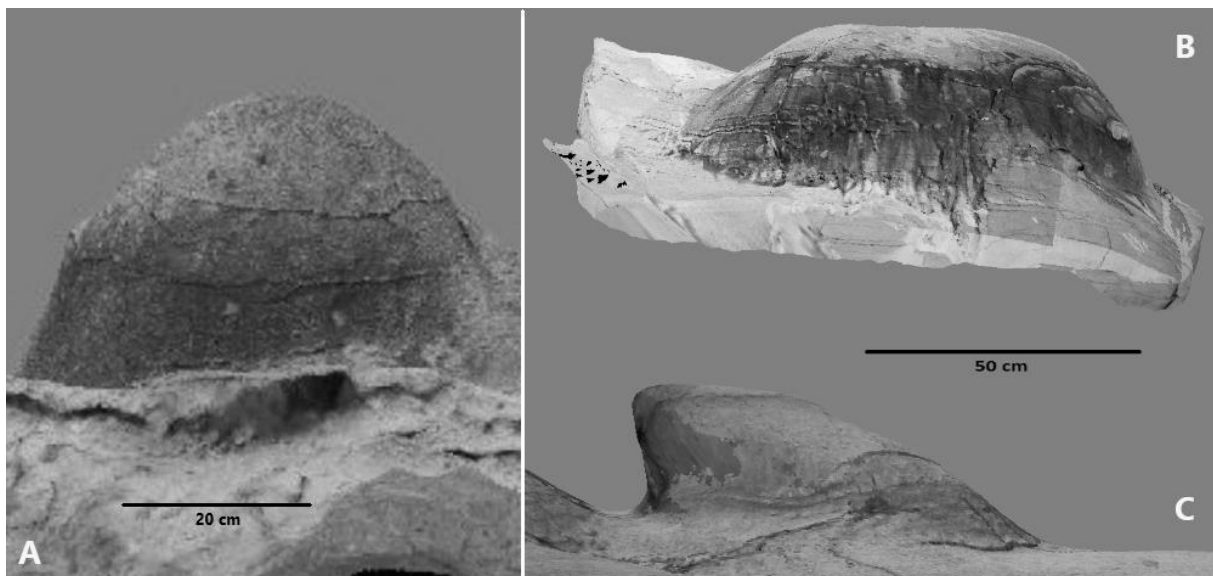


Fig. 7: Inverted 3D views of the cupolas showing the different morphologies linked to biogenic corrosion in the Azé Prehistoric Cave. A: hemispherical cupola; B: hemi-ovoid cupola; C: cupola in the form of a “Scottish tam” (photogrammetry H. Caillaud, 2017).

A statistical analysis of each dimension shows that the distribution of cupolas does not follow a normal law. The elements for comparison of the dimensions will therefore be their minimum, median, and maximum values for both Azé and Isturitz Caves (Tab. 2). The L/W ratio confirms the visual differentiation between hemispherical and hemi-ovoid cupolas, which occur in two groups. When L/W is smaller than 1.1, it corresponds to hemispherical cupolas (n=3). When the L/W is greater than 1.1, the cupolas have a hemi-ovoid or “Scottish tam” form. However, whatever the shape of the dome, L and W seem to be correlated. As L increases, W increases (Fig. 8). Plotting L/W against H shows that both parameters are independent. The same result was obtained in Isturitz Cave (Caillaud, 2017).

	Minimum	Median	Maximum
Length L (cm)	17	70	213
Width W (cm)	16	41	132
Height H (cm)	16	41	196
Length/Width (L/W)	1.00	1.61	2.80

Tab. 2: Geometric characteristics of the biocupolas (n = 35), obtained from morphometric analysis of the 3D scan.

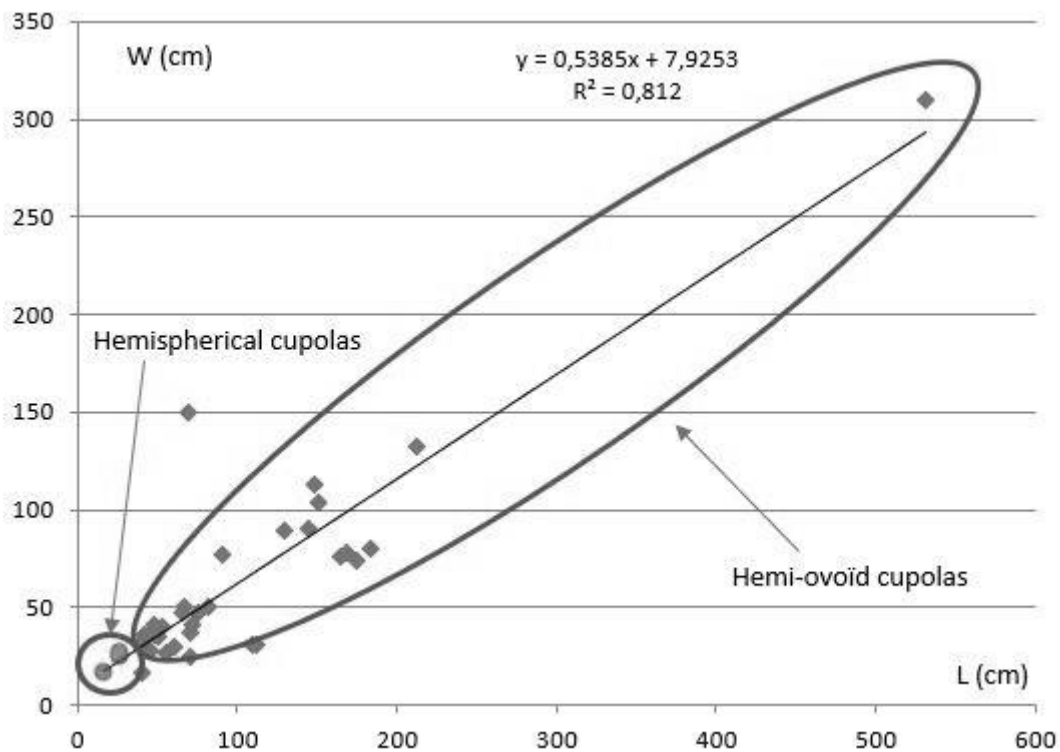


Fig. 8: Correlations between the length (L) of the cupolas and its width (W). The two parameters seem to be correlated. When L increase, W increase. The hemispherical cupolas present the smaller L and W.

Removing the 3 hemispherical cupolas, it is possible to consider the base of the cupola as elliptical and to compare the base surface S ($S = \pi * L * W / 4$) with H. Here, values from both Azé and Isturitz caves were merged (Fig. 9). It appears that the morphometry of the cupolas at Azé and Isturitz is distributed in two groups, for which two distinct mathematical relationships can be established. The coefficients of correlation associated with both models is high, given the precision of the measurements. These two models are independent of the form of the cupola (hemi-ovoid or “Scottish tam”).

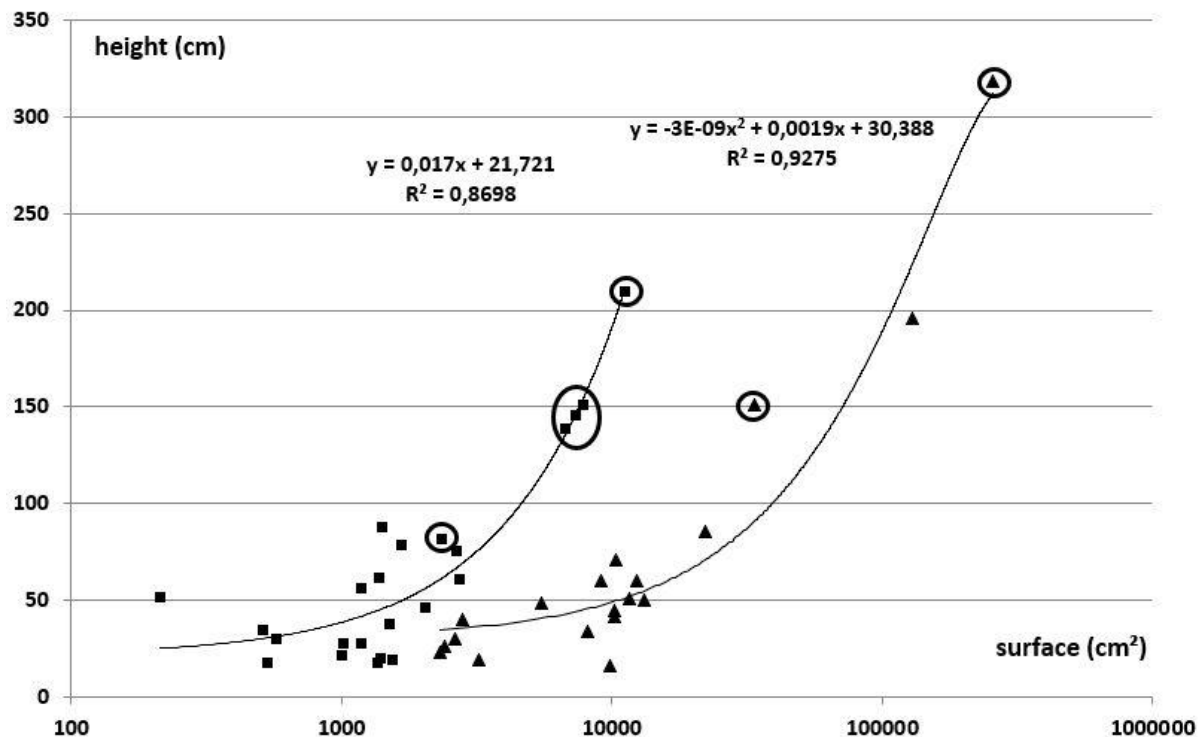


Fig. 9: Correlations between the height (H) of the cupolas and the surface area (S) of their elliptical base for both the Azé Prehistoric Cave and the Isturitz Cave ($n=43$), clearly showing two groups of different cupolas. The models associated with each group are represented by a different mark (group 1: square; group 2: triangle).

From 3D data, it is possible to infer the volume of biocorrosion in the entrance area. At the site of the flowstone barrier and in the protected inner part of the cave, the ceiling is almost flat, and its slope follows the dip of the strata. From north to south, the cave volume dramatically increases, and the morphology of the cave totally changes (Fig. 10, 11). The cross-section of the passage measured in the part accessible to bats is 12.5 m². In the part beyond the blockage it is only 6.1 m². The dip, which is conspicuous on the roof of the inner part, has been totally erased in the entrance part through powerful condensation-corrosion processes. A similar trend has been shown in the entrance of the Bászura Cave, Italy (Audra et al., 2020). In Azé, the ceiling has been modified by the cupolas, in the form of an array of overlapping hollows (Fig. 3). The increase in volume of the passage was mainly upward, becoming less significant laterally with increases in height.

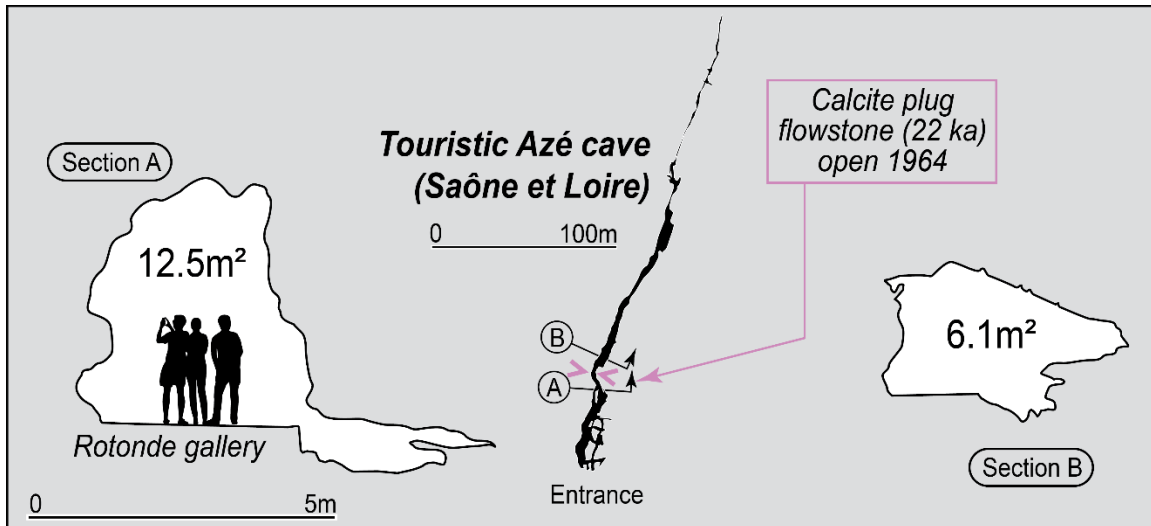


Fig. 10: Cross-sections of the cave. Cross-section A: part of the cave exposed to the presence of bats at La Rotonde. Section B: part of the cave behind the flowstone and not occupied by bats. Surfaces measured for each section: 12.5 m² for the part exposed to bats and 6.1 m² for the part preserve by flowstone.

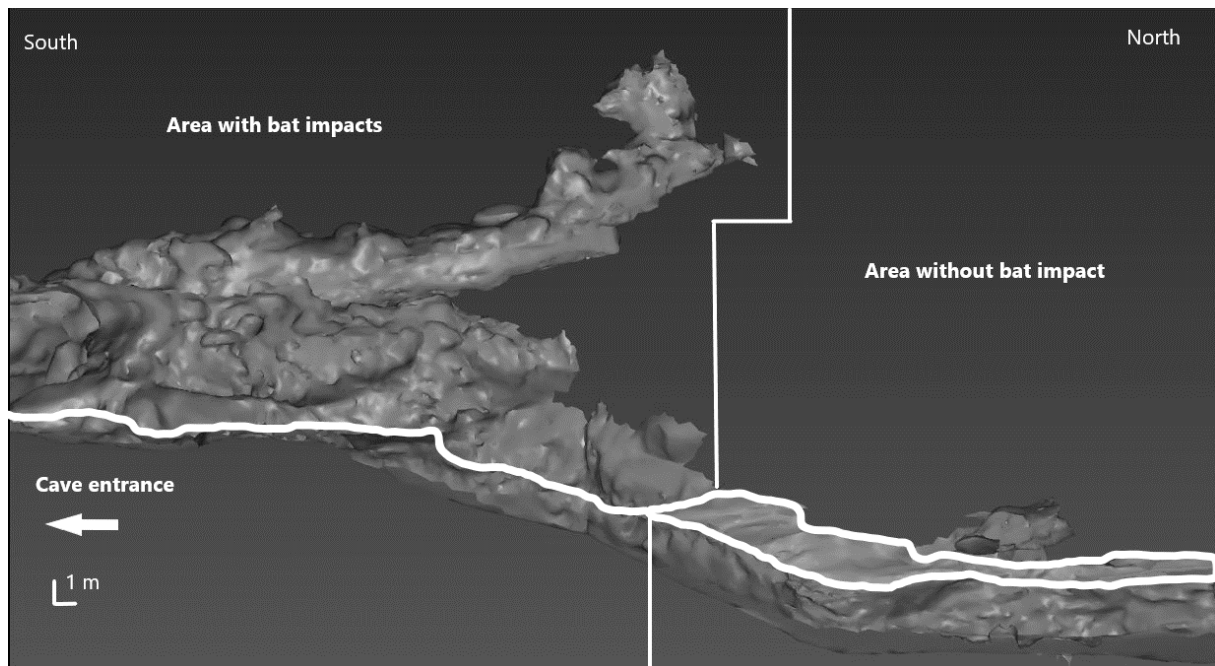


Fig. 11: Morphology of the Prehistoric Cave at Azé on either side of the calcite flowstone barrier (Blanchard et al., 2018). In grey, the limit and surface of the ceiling without evolution linked to the presence of bats.

The highest cupola has a relative height of about 80 cm (Tab. 2). This value is consistent with the increase in volume at the ceiling which is at a minimum.

In the part of the cave near the entrance, biogenic cupolas occur, as a result of the presence of bats. These cupolas have developed on the ceiling following a vertical axis, indiscriminately cutting through the limestone strata which here have a gentle dip, and are independent from the fracture axes (Fig. 12A). In the confined inner part of the cave, cupolas are very rare. They are due to phreatic speleogenesis and follow the discontinuities in the limestone such as fractures (joints), perpendicular to the strata. These cupolas are not vertical and follow the inclination of the fractures (Fig. 12B). In this confined inner part, formation of cupolas linked to condensation-corrosion phenomena can be dismissed. Studies carried out in the cave over the last few years show that since removing the calcite plug, condensation-corrosion now occurs in the area beyond the calcite plug, as was probably the case before this part of the cave was closed. This area clearly shows that the condensation-corrosion features do not lead to cupola formation but lead to the formation of grooves, which are again actively forming, in the limestone beds, and can be more than 10 cm deep. These grooves develop homogeneously over the entire surface of the ceiling, following the dip of the limestone.

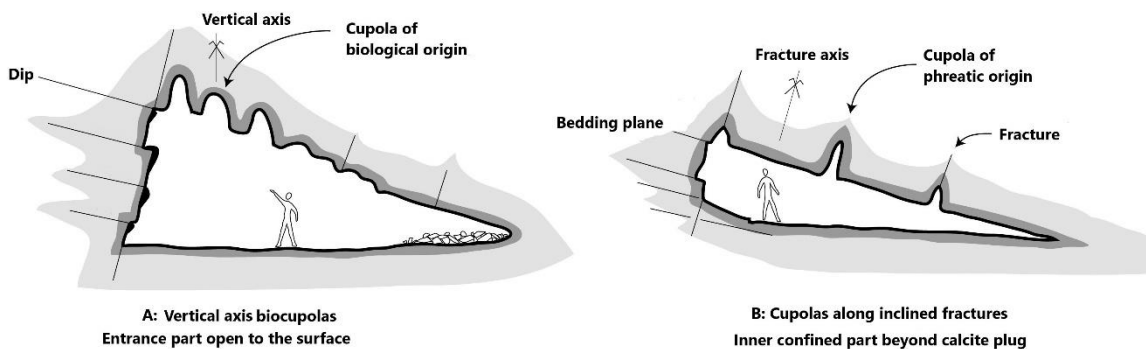


Fig. 12: A: In the entrance of the Azé Prehistoric Cave, biogenic cupolas have developed vertically, independent of the dip of the limestone and the inclined fractures; B: beyond the calcite plug, in the area inaccessible to bats, the rare cupolas have developed perpendicularly to the dip of the limestone, along the inclined axis of fractures.

3.5. Rate of wall retreat

Direct dating of weathered speleothems can give an idea of the rate of wall retreat (Auler and Smart, 2009). The same approach can be applied at Azé (Barriquand et al., 2006). The first measurement was

obtained from the top part of a weathered stalagmite (Fig. 5) dated at $10.3 \text{ ka} \pm 0.4$ (Barriquand et al., 2006). The thickness loss by corrosion of this speleothem is around 3 cm. On a nearby calcite curtain, there is a channel formed by biogenic corrosion with a depth of around 5 cm (Fig. 4e). These data provide a retreat between 3 and 5 mm/ka. It is also possible to estimate the rate using the depth of weathering of the flowstone plug dated at $26.3 \text{ ka} \pm 4.0$ (Fig. 6). It is around 14 cm, which provides a rate of corrosion on the order of about 5 mm/ka. Another way of estimating this velocity is by using the height of the cupolas and by assuming that these cupolas began to form at the earliest known time that bats were present in the cave (57 ka BP). Based on the median height (41 cm), this gives a rate of 7 mm/ka. Since this 57 ka age is the minimal age of bat presence, which could have started earlier, the value of 7 mm/ka can be considered a maximum for the average development of cupolas. The highest one (196 cm), correspond to a maximal retreat rate of 34 mm/ka.

3.6. An indirect and little-known impact: the pupae of *Nycteribiidae* and *Streblidae* bat parasites

After deposition, the pupae become black due to a chemical reaction. During the process of bio-mineralization, chitin gradually hardens with calcium carbonate extracted from the cave wall (Rahman et al., 2019). The carapace resulting from this bio-mineralization is hard and very resistant. This would explain why after hatching, a part of the pupa remains attached to the wall as a black ring (Fig. 13). Non-viable pupae, as well as a part of what remains after hatching, stay attached to the wall for several decades as in the case of those visible at Azé. The surface of the wall thus undergoes permanent alteration.

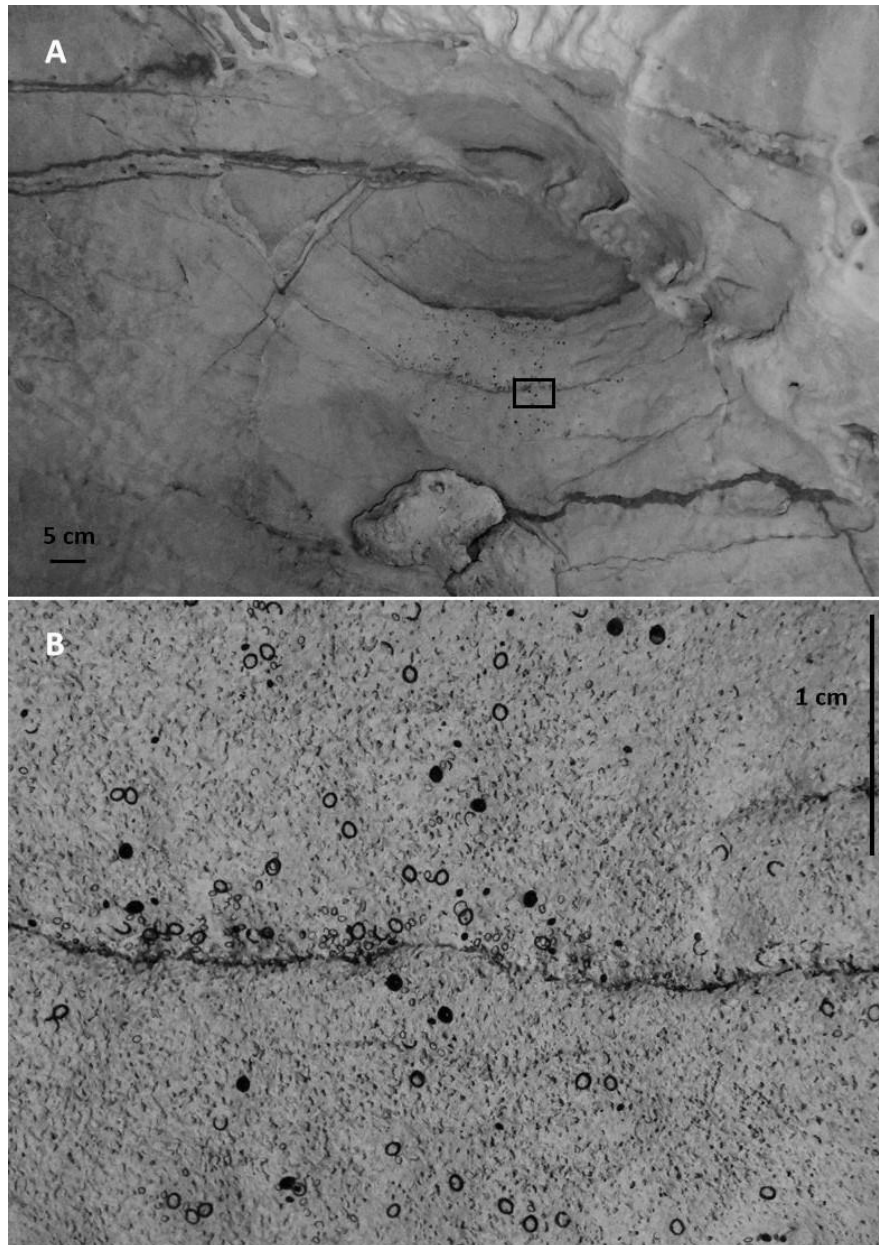


Fig. 13: Pupae attached to the wall of the Rotonde. The pupae are localized within a cupola. Non-viable pupae remain attached and keep their ovoid form. After hatching, a black, oval ring remains on the wall. B = enlargement of box in A.

At Azé, the pupae are around 4.5 mm in diameter. After hatching, the ring which remains on the wall covers a surface of 3.2 mm². Based on this value and the density of pupae, the surface area affected would be 6,340 mm², or 0.6% of the total surface of the area used to deposit pupae. Over time and with the repeated deposition of pupae, one can conclude that the impact of this would not be negligible. It remains to be seen whether the micro-morphological impact envisaged on the cave wall can be assessed more precisely, and if possible, quantified.

4. Discussion

The presence of apatite in the flowstone in Azé Cave shows that bats were present there before the end of MIS 4 (57 ka), and most probably also during MIS 5, which would have been climatically even more favorable for bats. At least 22 ka ago, calcite flowstone isolated the inner part of the cave. It completely blocked any access and prevented the entry of bats. Since, this blockage, the cave walls beyond it have hardly altered, as confirmed by the preservation of bear claw marks on the walls. In contrast, all of the front part of the cave between the entrance and this barrier remained open to the surface and has undergone considerable morphological changes.

Studies of microfauna show that at least 8 species of bats have been present in the cave over a period of several tens of thousands of years. There were still large numbers of bats frequenting the cave in the 1950s. At that time, the cave was considered to be the most important nursery site for bats in Burgundy. Bats are known for their loyalty to the sites they occupy. It is therefore probable that the use of this site by bats for parturition and rearing their young is quite old.

It is known that, during procreation, bats are very active and produce large amounts of excreta. For *Myotis daubentoni*, the species that may have had the largest colonies in Azé Cave (biggest colony known in Europe: 20,000 individuals), this may represent $1.5 \times 20000 = 30,000$ g of urine for 12 h. Their urine is rich in sodium sulphate and urea. Taking into account the environmental conditions and latitude of Azé, the sulfate would mainly produce gypsum deposits, if not lixiviated (Hill and Forti, 1997; Audra et al., 2019), and the urea would be converted to ammonia (McFarlane et al., 1995; James, 2013). Only one sample contained gypsum. It was probably formed on the surface of the floor through evaporation of sulfate solutions near the cave entrance. For the same population and the same period, the quantity of guano can reach $0.033 \times 20,000 = 660$ g/day. Taking into account the reduction of bats for a quarter of the year and the phosphate concentration measured in Courtouphle Cave, a maximum population of 20,000 individuals of this species would produce 6444 kg of phosphate per thousand years. To transform phosphate into hydroxylapatite, would theoretically require 10984 kg of calcium

carbonate. In the cave, the omnipresence of hydroxylapatite on the walls and floors indicates that the impact of guano was widespread. The presence of quartz and the absence of smectite in the samples taken from the walls confirms that quartz came from the weathering of the surrounding rock and not from old fluvial deposits.

Several of the species present at Azé regularly congregate in large swarms, amplifying the impact of these excreta on the cave.

Bat excreta cause the following modifications:

- (i) thermic: the swarms cause a localized increase in temperature of as much as several degrees;
- (ii) climatic: their respiration produces enough water to saturate the ambient air, unless this has already happened naturally;
- (iii) the combination of these two effects causes water to condense and form a film of water on nearby walls;
- (iv) physicochemical: their respiration also releases CO₂;
- (v) chemical: if the swarm is relatively confined in cupolas, part of the CO₂ passes into a solution that become acidic, causing the condensation film to become corrosive to the limestone.

Assuming an average temperature of 38.5°C for a swarm, 12°C for a cave, and the presence of bats in a cave $\frac{3}{4}$ of day (assuming bats spend $\frac{1}{4}$ of their time hunting), it is possible to calculate the daily amount of energy generated by a swarm. For swarms such as those listed above (Tab. 1), the dissipated energy would be between 0.01 and 1.5 kWh, and could even reach 1 to 5 kWh for the largest swarms. Such dissipation of energy is enough to account for a rise in temperature of several degrees in confined spaces, such as in cave cupolas (Lundberg and McFarlane, 2009). The quantity of CO₂ expelled by a *Plecotus auritus* or a *Myotis daubentoni* individual has been estimated at 0.798 g / day (Webb et al., 1994). Part of this CO₂ becomes dissolved in the film of water that often condenses on top of the cupola. Assuming a swarm of 140 individuals of *Myotis daubentoni* (on a surface of 0.3 m²) and bat activity for $\frac{3}{4}$ of a day, they would expel 1.90 mol / day of CO₂. Probably, only a small part of it would

pass into solution. This quantity is determined by Henry's Law and depends on the volume and ventilation of a given cupola. Nevertheless, by way of example, assuming only 1% of the CO₂ is dissolved, the breathing of a swarm of bats results in dissolution of 1.9 g / day of CO₂. For a cupola with a surface of 0.3 m², and assuming that the cave wall is pure CaCO₃, that would lead to a wall retreat of 1 mm/year! This is a huge figure when considering the extended time that bats have occupied caves.

Morphometric analyses show that at Azé, as well as at another cave studied in a similar way (Isturitz), there are 3 distinct types of cupola: hemispherical, ovoid, and as "Scottish tam". This typological analysis is proposed for the first time and can be used as a reference in future international studies on caves. Two different mathematical relationships were found between the base surface of the cupola and its height. We hypothesis that these characteristics might depend on the species of bat frequenting the cupola and/or the size of the swarm. The morphological differences found between the cupolas in the cave's entrance and the few occurrences found in the confined area beyond the flowstone barrier enable an easy distinction to be made between biogenic and phreatic cupolas. The cupolas of phreatic origin follow the fracture axis of the limestone, whereas the cupolas of biogenic origin are vertical.

In 22 ka, the ceilings of the entrance passage of the cave at Azé have greatly evolved and today are modified by cupolas. The section of the passage, which has remained accessible to bats, is now twice as large as the section of the cave closed by the flowstone (12.5 vs 6.1 m²). The retreat of the ceiling is multi-decimetric, and the rate of retreat would be a minimum of around 7 mm/ka, though this would require a continuous occupation, which is probably not the case.

Then:

- the swarms produce large quantities of guano and urine;
- the concentration of phosphate in these excreta leads to the formation of aerosols and leachates (phosphoric acid), which are aggressive toward the surfaces on which they are deposited (floors, walls, speleothems, and archaeological artefacts);

- the chemical reactions between these acidic solutions and their environment leads to mineralization of the guano and the formation of phosphatic minerals.

On the cave floors, these phenomena result in the formation of guano potholes, channels that drained acidic leachates from above (Grenier des Chauves-souris), and cupolas on the ceilings. The formation of hydroxylapatite has been the principal product of mineralogical processes on the cave walls. The rate of floor corrosion has been determined to be around 4 mm/ka.

The phosphate crusts mainly develop at the base of the cupolas. These are associated with corrosion features such as cupolas or vertical grooves. The combination of the effects corrosion products to aerosols and the acidification of the water on the walls leads to differential weathering of speleothems that may be on the wall. The result of this is smooth surfaces as well as wavy walls. All these modifications have a direct impact on the evolution of the walls.

The four values obtained for the retreat rate have the same order of magnitude and are consistent with results obtained in other environmental areas, quite different from Azé (average of 12.5 mm/ka, minimum 3 to 5 mm/ka and maximum 34 mm/ka (Lundberg and McFarlane, 2009, 2012, 2015); 1 mm/ka (Audra et al, 2016)). The rate of weathering from biogenic corrosion at Azé is therefore on the order of 3 to 7 mm/ka. The values obtained for wall retreat by biogenic corrosion confirm fast rates of retreat.

In the Prehistoric Cave, the only known bioglyphs are bear claw marks. These have been found only at several locations beyond the flowstone barrier but none in the part open to the surface and accessible to bats. Biochronological dating of palaeontological deposits discovered beyond the barrier show that bears were present in this part of the cave in the middle of MIS 6, around 140-160 ka (Argant, 1988, 1991). Since this period, there has been very limited retreat of the cave walls upstream of the barrier, since the bear claw marks there are perfectly visible. On the other hand, in the part of the cave that has always remained open to the surface, the retreat is considerable and has probably led to the disappearance of bioglyphs (due to bears) that were once present also in this part of the cave. We mention again the very unusual absence of graffiti. How is it that in a cave so easily accessible to

humans there are no recent or old anthropic traces? Spatial analysis of the position of the art works in the Mas d’Azil Cave, Ariège, France, also shows that these are found only in confined areas not used by bats (Bruxelles et al., 2016). In the Gorges d’Amange Cave, Jura, France, the Aurignacian engravings which have been exposed to phosphates are still visible, but have been deeply weathered (David et al, 2018). In the Chauvet Cave, the art work on the Megaloceros Panel is inscribed into deposits of hydroxylapatite (Ferrier et al., 2012) indicating the occupation of this part of Chauvet cave by bats is older than the artwork. Closure of the cave entrance after the art work was made (Sadier et al., 2012) preserved it from latter biogenic weathering. Lastly, in the Agneux 1 Cave, Saône-et-Loire, France, a microtopographic study was made of the walls on which different engravings were done (Floss et al, 2018). This gives us an idea of the depth of recent engravings (between 0.1 and 0.2 mm) and of engravings attributed to the Upper Paleolithic (between 0.07 and 0.12 mm), also indicating the wall retreat in this cave.

5. Conclusion

The prehistoric cave of Azé has known numerous animal and human occupations over hundreds of thousands of years. Since MIS 4 (57 ka) bats have been present in the cave. The main passage was split in two parts by flowstone plug about 22 ka ago. The inner part of the cave has thus been preserved since that time from bat occupation. This bat population was active until the 1950s in the entrance part of the cave.

The abundance of apatite reflects the impact of their droppings.

The climatic and chemical impacts of these colonies and their waste byproducts was a very significant process for cave development.

- (i) thermic: bat swarms cause a localized increase in temperature of as much as several degrees;
- (ii) climatic: their respiration produces enough water to saturate the ambient air, unless this has already happened naturally;

- (iii) the combination of these two effects causes water to condense and form a film of water on nearby walls;
- (iv) physicochemical: their respiration also releases CO₂;
- (v) chemical.

The combination of these effects at Azé Cave has led to the formation of cupolas on the ceiling, which resulted in an upward expansion of the cave's volume. The presence of the bats led to a doubling of the cave's cross-section. The retreat of the walls and speleothems was about 3 to 7 mm/ka. These alteration phenomena, hitherto totally unknown outside the tropics, are highlighted here in Europe. They are important and must be taken into consideration in many caves frequented by bats now or in the past. Different forms of cupolas linked to the bat occupation, developed in the ceiling. We suggest that these cupolas have a biologic origin, and so are called biocupolas. The walls, which were probably altered by frost-shattering phenomena, are now smooth and have soft shapes.

The impact of these phenomena has a negative effect on traces left by animals or humans, with the total erasure of bioglyphs and graffiti in the entrance area of the cave. Based on the depth of graffiti (initially protected by fillings), measured at Agneux (0.1 mm), and the average wall retreat of 4 mm/ka measured at Azé, it would take only 25 years for graffiti to be erased by biogenic corrosion. Even if the grooves of prehistoric engravings are deeper, only 50 years would be needed for their deletion. Even if deletion were caused by other processes other than bats (corrosion by percolation, exfoliation, frost shattering, etc.), at Azé it is the presence of bats that is mainly responsible for the absence of any wall coating. The legacy of Paleolithic cave art is therefore linked to the absence of bats in the zones where it is found. Wall corrosion is in all likelihood the cause of the disappearance in the entrance of the Azé cave of any traces of frost-shattering, bear claw marks, and even recent graffiti. Biocorrosion is hardly taken into account in studies of the distribution of art work in prehistoric caves around the world. This study shows that it cannot be underestimated and that a review of the caves with art work is necessary in order to determine those that may have been affected by this large-scale phenomenon on the cave walls.

An indirect effect of the presence of bats is presented here for the first time: the impact of the pupae of certain species of bat parasites. The deposition of the pupa is followed by a chemical reaction between the chitin contained in the pupa and calcium carbonate from the host-rock. After hatching, part of the pupa remains attached to the cave wall for a long time. In an extreme case, the area affected could be 0.6% of the surface used to deposit pupae each year, leading to weathering whose scale and characteristics remain to be determined, but which should be significant in the long run.

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