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New ichnofossil discovery in Mallorcan caves: Linking ancient and modern bat-ectoparasites coprolites

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Abstract: Bat ectoparasitic ichnofossils can be useful to elucidate microbial mediation in mineralization processes of organic material, supplying valuable information on ancient parasitology and palaeoecology, among other topics. Rod-shaped features found in Cova des Pas de Vallgornera (Mallorca, Spain) are described for the first time. They are related to an ancient bat colony inhabiting the cave in the Early Pleistocene. These micro-morphologies are cylindrical in shape with sizes of a few hundred microns in length and less than one hundred microns in diameter. They are composed by a mash of microscopic calcite particles of different sizes and shapes, lying on deposits that contain phosphates and clay minerals. Some of these rod-shaped morphologies are covered in microscopic crystals, whose mineralogy is composed mainly of calcite, associated with dolomite, quartz and clays, These deposits are interpreted as fecal droplets of bat ectoparasites (probably *Nycteribiidae*), that infested an ancient bat colony living in the cave before the collapse blocking of its natural entrances; from 2.4 Ma to present, the cave has remained sealed, preserving these deposits as a new ichnofossil related to invertebrate's coprolites. The observation of similar micro-structures in Cova de sa Guitarreta, another Mallorcan cave currently used as a bat roost, provided an opportunity to study a modern analogue. In this case, the rod-shaped structures consist of organic detritus with lenticular, concave forms (possibly resembling red blood cells) and minute mineral particles. These cylindrical features are therefore hypothesized to represent excreta from bloodsucking bat flies, with present-day deposits observed in Cova de sa Guitarreta and fossilized coprolites identified in Cova des Pas de Vallgornera.

Keywords: Bats, nycteribiidae, ectoparasite, coprolites, ichnotaxobases

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INTRODUCTION

In recent years Cova des Pas de Vallgornera (CPV) and Cova de sa Guitarreta (CSG), both located in the municipality of Llucmajor, Mallorca (Spain) have been the subject of several mineralogical studies and especially those devoted to the morphologies and minerals associated with bat colonies and guano accumulations (Onac et al., 2005; Merino et al., 2019, 2022). Regarding the presence of bats, CPV represents an uncommon case since the cave hosted bat colonies until the collapse of its natural entrances circa 2.4 My ago; since that moment until its discovery in 1968, the cave remained sealed. This occupation was evidenced by the existence of bat claws and bat thumbs marks left by chiropters on walls and ceilings, together with corrosion morphologies related to ancient guano deposits. Moreover, an array of guano-related minerals, mainly phosphates, were also identified (Merino et al., 2019).

On the other hand, CSG, currently maintains a middle-sized breeding bat colony, between 150 and 500 specimens (Balcells, 1968; Alcover & Muntaner, 1986). As in the case of CPV, the cave hosts a wide range of morphological bat-related features and others linked to guano accumulations paired with a remarkable cave mineral association of phosphates (Merino et al., 2022).

These studies led to the discovery of micro-mineral rod-shaped morphologies (cylindrical-shaped) in CPV, presumably related to ancient bat colonies living in Early Pleistocene times. They were first observed while photo-documenting a small cluster of celestine crystals on the SW edge of Galeria del Tragus (**site 780**); years later a massive assembly of these morphologies were also located at the **Jacuzzi site** during the investigation of guano-related minerals.

The crucial point was to discover similar micro-cylinders in CSG while studying the minerals and

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guano-related morphologies associated to the present-day bat colony inhabiting the cave. Firstly, a few tiny-calcified cylinders were observed while photographing insect pupae remains on the cave walls. This caught the attention of the researchers who in turn, visited the cave with the aim of finding comparable recent cylindrical deposits. Due to its diminutive size, it was quite hard to locate them, but finally an aggregate of rod-shaped morphologies, and others scattered on one of the walls of the cave were identified. The focus of this research is to provide description of a new ichnofossil related to bat ectoparasites and its paleoenvironmental and paleoparasitological implications. Here we also discuss the possible processes that led to its fossilization and preservation.

GENERAL GEOGRAPHICAL AND CAVE SETTINGS

Mallorca is the main and central island of the Balearic Archipelago (Fig. 1a), located in the western Mediterranean basin (Fornós et al., 2002). All along the southern and eastern parts of the island, the Migjorn karst region is a coastal platform constituted by Tortonian-Messinian carbonates that includes an extensive and well developed reefal environment (Pomar et al., 1996), with overlying mangrove and oolitic carbonate facies. The two studied caves are developed in the reef calcarenites, being their morphology and genesis conditioned by the lithological variability of the bedrock.

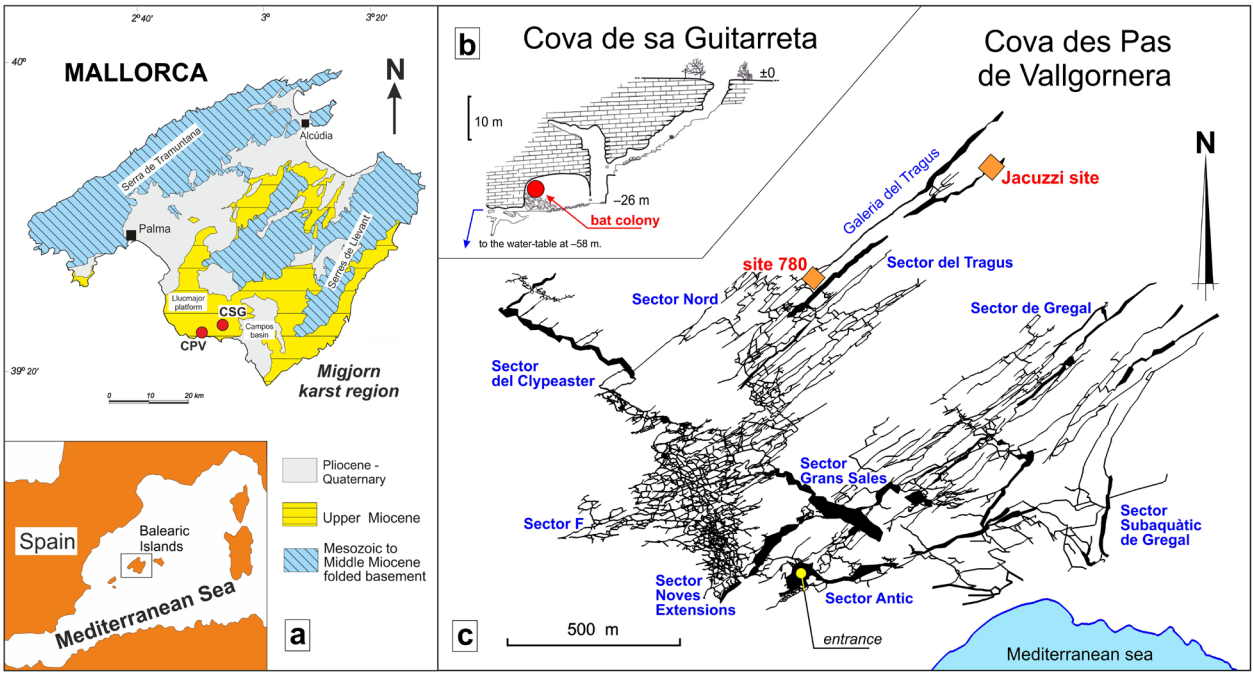

Fig.1. a) Geological sketch of Mallorca Island with the location of investigated caves (CSG: Cova de sa Guitarreta; CPV: Cova des Pas de Vallgornera). Location of the sampled sites. b) Profile of the entrance sector of Cova de sa Guitarreta, according to Bermejo et al. (2021). c) Planimetric survey of Cova des Pas de Vallgornera (source: Federació Balear d'Espeleologia, 2018).

Cova de sa Guitarreta

It is located in the municipality of Llucmajor (Fig. 1a), with its entrance situated at an elevation of 58 m a.s.l. The cave has a modest development not exceeding 300 m and its deeper extensions reach the lukewarm waters (27.1ºC) of the coastal phreatic aquifer (Fig. 1b). The main chamber, located at a depth of -26 m (Fig. 2a), houses the largest bat colony. This chamber is littered by collapse rock blocks partially covered by thick guano deposits from an important bat colony; sampling of minerals linked to these deposits were conducted by Onac et al. (2005) and Merino et al. (2022). Descending through the blocks at the lowest part of the main room, it is possible to reach the phreatic water table (at a depth of -58 m) following a prominent fracture along the western flank of the collapse structure that formed this chamber.

In addition, some authors have argued the possible involvement of hypogene processes in the generation of solutional basal voids, that triggered the collapse processes conducive to the formation of the main chamber. This hypogenic deep karstification would be related to the geothermal anomalies reported in the Llucmajor Platform, where some of the most relevant karst caves of Mallorca occur (Ginés et al., 2017).

Cova des Pas de Vallgornera

The access to this important cave system is located at an urbanized area in the coast of Llucmajor municipality (Fig. 1a), at an elevation of 22 m a.s.l. It is the most extensive cave in Mallorca Island, with a total development currently exceeding 78,000 m (Merino, 2023). The cave has currently only one artificial entrance drilled when excavating a cesspit, but at least five today blocked entrances have been documented which were functional during Plio-Pleistocene (Merino et al., 2019). One of them was located at the northeastern end of Galeria del Tragus, not far away from the sampling sites of this investigation (Fig. 1c).

Several different sectors can be distinguished, which show distinctive characteristics linked to the lithological properties of the rock where the passages are developed within the Tortonian-Messinian carbonates (Ginés et al., 2014). Therefore, in the calcarenites corresponding to the reef front facies, intrincate mazes and big breakdown chambers

are dominant in those sections situated in the seaward part of the cave: Sector Antic, Sector Noves Extensions, Sector F, Sector del Clypeaster and Sector Grans Sales (Fig. 1c). On the other hand, the inward parts of the cave (Sector Tragus, Sector Nord, Sector de Gregal and Sector Subaquàtic de Gregal) are developed in more calcisistitic back-reef facies, where the presence of joint-guided galleries and conduits following mainly a SW-NE trend is a common denominator.

The chronology of the main speleogenetic phases falls back, at least, to mid-Pliocene times, based on the Early Pleistocene vertebrate palaeontological remains recovered from the cave (Bover et al., 2014).

MATERIALS AND METHODS

This investigation is the result of several research projects conducted during a multi-year period aimed at studying the presence of bats, guano associated morphologies and phosphatic mineral associations in CPV and CSG. Due to the reduced size of the investigated morphologies, magnifying lenses helped to locate them, as well as using macro-photography, because they are hardly seen with the naked eye. For photography purposes two cameras were used, a Nikon D-90 equipped with a Sigma 105 mm DG MACRO lens and a small Pentax Option WP in macro mode. Before collecting samples, the first step was to determine by means of macro-photography the best options to select the sampling specific sites. More than 53 photos were taken in each of the caves; therefore, nine samples were collected from CPV while 4 were from CSG.

Mineralogy was determined using a Bruker D8-Advance X-ray diffractometer on randomly oriented powders of the bulk samples. The pressed powder diffraction patterns were recorded from 3º to 65º 2θ in steps of 0.03º, 0.3-s counting time per step, at 25ºC room temperature, and logged to data files for analysis. Semi-quantitative mineral analyses were based on the peak areas obtained using Diffrac EVA ver.7.0 software. Selected samples were observed on a Hitachi S-3400N scanning electron microscope (SEM) equipped with a Bruker energy-dispersive X-ray analysis system (X-Flash Detector 4020).

ROD-SHAPED (COPROLITE) MORPHOLOGY AND SAMPLING SITE CHARACTERISTICS

Cova de sa Guitarreta

The features found in this cave are associated to the bat colony currently using this cavity for breeding purposes. The documented main site is formed by a cluster of about 100 cylinders disseminated within 1 cm^2 (Fig. 2a). They have also been observed at other spots, but as isolated calcified individuals or small groups of them, meaning they are older in age. These rod-shaped forms are micron in size, reaching the longest ones, from 291 µm to 173 µm in length and between 85 µm to 55 µm in diameter. They show cylindrical shape and circular section, color is black or dark brown (Fig. 2b). These cylinders are composed of an organic matrix with some debris and authigenic minerals clearly recognizable mainly on their surface. The mineral composition of these coarse particles is gypsum, phosphate grains, calcite, dolomite, and different related clay and feldspar minerals, with dimensions ranging from 19 µm for angular forms and 2-4 µm for the more rounded ones. This mineral assemblage would be related to the calcitic substratum affected by bat excreta and urine.

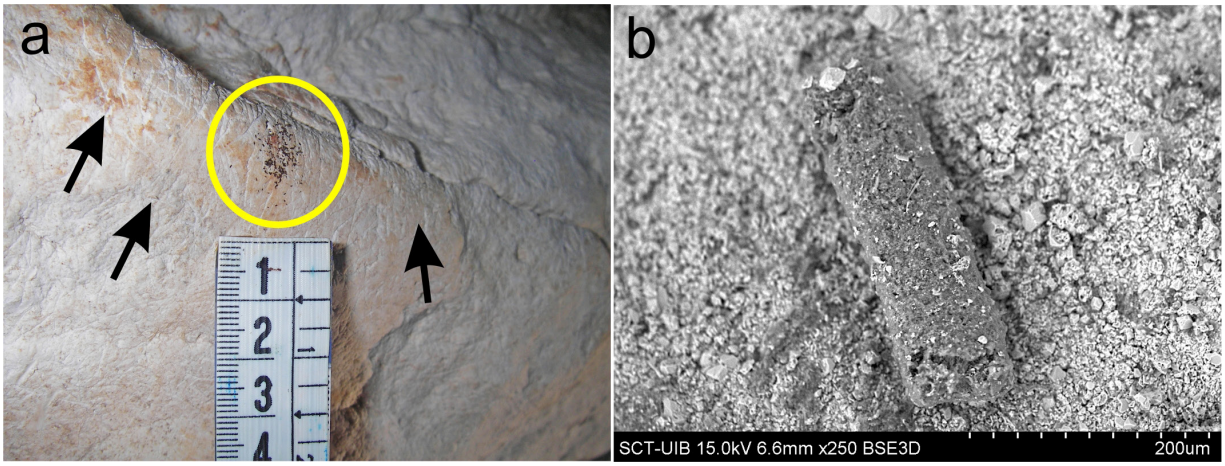

Fig. 2. Cova de sa Guitarreta. a) Agglomeration of current rod-shaped morphologies. This deposit is formed by about 100 cylinders stuck to the wall rock surface (yellow circle) which is stained by bat excreta together with clear bat claws and thumb marks (black arrows). b) Present-day rod-shaped deposit. The jumble organic matrix shows some autochthonous mineral particulates stuck on its surface.

In CSG the rod-shaped forms have been discovered at different locations which in general, show multiple bat scratches and are commonly covered with a thin brownish surface caused by bat projections of urine. The surrounding areas exhibit abundant guano deposits and crypto-corrosion features. The mineral assemblage hosting the rods is formed, mainly, by a mixture of different phosphates covering ceiling, walls and boulders surfaces (Merino et al., 2022). The microscopic images show a cylindrical body composed of organic detritus which include minute mineral particles (Fig. 3a). One sample presents a noteworthy lenticular concave form, resembling contact lenses, as well as fungi that proliferate along its length (Fig. 3b). At one of the spots, in the vicinity of the cylinder-shaped morphologies, an accumulation of several pupae (Fig. 4), possibly belonging to *Nycteribiidae* or *Streblidea* ectoparasites, were detected (Merino et al., 2022).

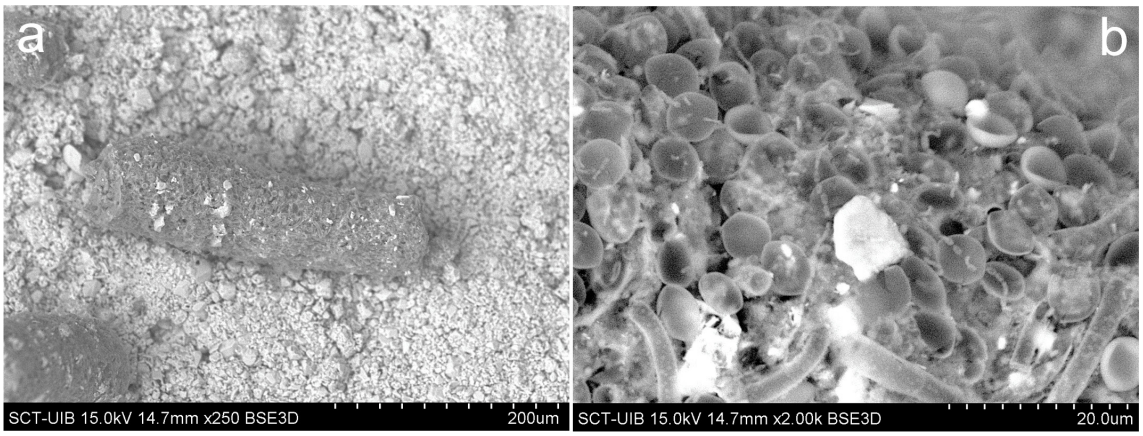

Fig. 3. Cova de sa Guitarreta. a) Rod-shaped morphology exhibiting abundant lentil in shape structures (resembling contact lenses) along with what seems fungal hyphae. b) Enlargement of Figure 3a which evidences the presence of fungal hyphae and lenticular shaped structures, presumably corresponding to intact red blood cells.

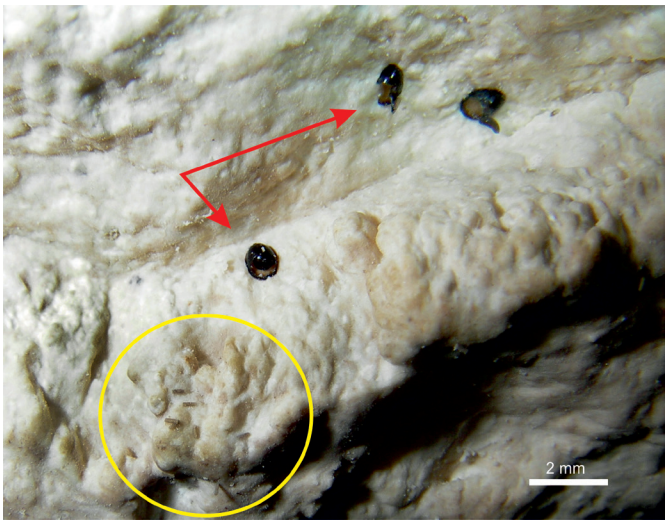

Fig. 4. Cova de sa Guitarreta. Group of pupae in the proximity of calcified rod-shaped morphologies. Light brownish surfaces surround the cylinders and pupae area.

Cova des Pas de Vallgornera

As mentioned previously this cave system does not host bat colonies since its natural entrances were blocked by collapse in the Early Pleistocene (Bover et al., 2014). The main accumulation of rod-shaped features is located at the **Jacuzzi site** covering several flat boulders surfaces (Fig. 5). These morphologies are micron in size, in general ranging from 528 µm to 257 µm in length and between 171 µm to 71 µm in diameter, measures corresponding to the longest and largest forms observed (Fig. 6). They display almost perfect cylindrical shape, their cross section is circular, and color varies from beige to pure white. They are composed by a mash of microscopic particles of calcite of different sizes and shapes, while the rounded forms are about 3 µm in diameter, the larger ones with sharped edges reach about 34 µm (Fig. 7). They often occur scattered on horizontal flat surfaces lying on deposits that contain phosphates.

Fig. 5. Jacuzzi site at Cova des Pas de Vallgornera. The rod-shaped morphologies are abundantly spread over the boulder surfaces intermingled with phosphatic minerals (yellow arrow). The lower half part of the boulders is lined by calcite crystallization and marks the level reached by the accumulation of vadose waters (blue dashed arrow). The wall over the boulders exhibits visible biomechanical erosion caused by bats when trying to cling.

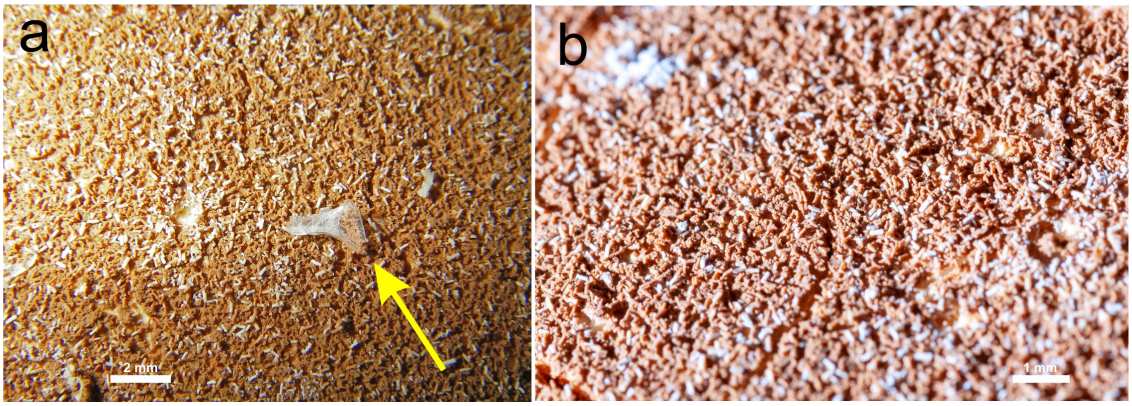

Fig. 6. Jacuzzi site at Cova des Pas de Vallgornera. a) General view of the boulder surface covered in tiny white rod-shaped morphologies; the brownish ones are camouflaged among them. Fluorapatite small crystallizations are spread over the area (yellow arrow). b) Detail of Figure 6a displaying numerous visible rod-shaped morphologies, white and beige in color.

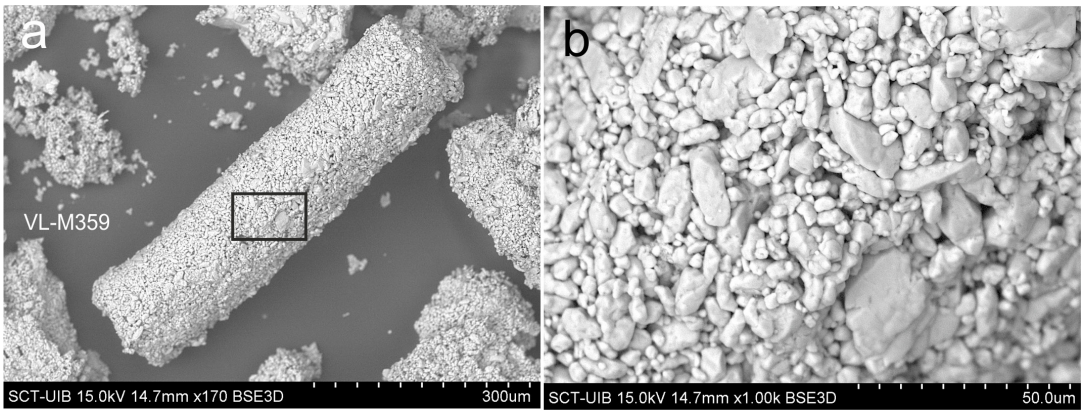

Fig. 7. Cova des Pas de Vallgornera. SEM image of a rod-shaped morphology collected at the Jacuzzi site. a) The microphotography shows almost a perfect cylinder composed by a mash of minuscules particles of calcite of different shapes and dimensions. b) Magnification of the surface of the rod-shaped feature in (a).

A second deposit was discovered hidden among fallen blocks in the SW edge of Galeria del Tragus, namely **site 780** (Fig. 8a). At this location, the rod-shaped morphologies, are beige in color, with dimensions ranging from 818 µm to 457 µm in length, and between 243 µm and 143 in diameter; they are intermingled with shiny celestine crystals. Unlike the samples from the **Jacuzzi site**, they seem composed of a micritic aggregate instead of an agglomeration of minuscule particles (Fig. 8b).

To date, no other convergent cave morphologies or deposits have been found that could explain or be compared to these forms.

These morphologies have been mainly identified in the **Jacuzzi site** (Fig. 1c), a passage that exhibits a rich area containing well-preserved and abundant bat claws and thumb marks caused by biomechanical erosion, morphologies related to guano deposits and an assemblage of guano-related minerals (Merino et al., 2019). Specifically, the major concentration of rod-shaped forms has been discovered on a side location whose walls show clear biomechanical erosion, they are developed as scattered minute tubes on a thin layer of a brownish pasty deposit that contains fluorapatite. The other locality with these morphologies is situated at the SW third of Galeria del Tragus, **site 780** (Fig. 1c), where they are not so abundant, but have been recognized lying on a calcarenite boulder surface coexisting with celestine crystals. Not far, bat remains have been discovered. The SEM images make evident that cylinders at the first locality are formed by an amalgam of micritic calcite (Fig. 7), accompanied by some clay-related minerals, while the second locality, **site 780**, exhibits cylindrical features covered in microscopic crystals, whose mineralogy is composed mainly of calcite, associated with dolomite, quartz and clays (Fig. 8b).

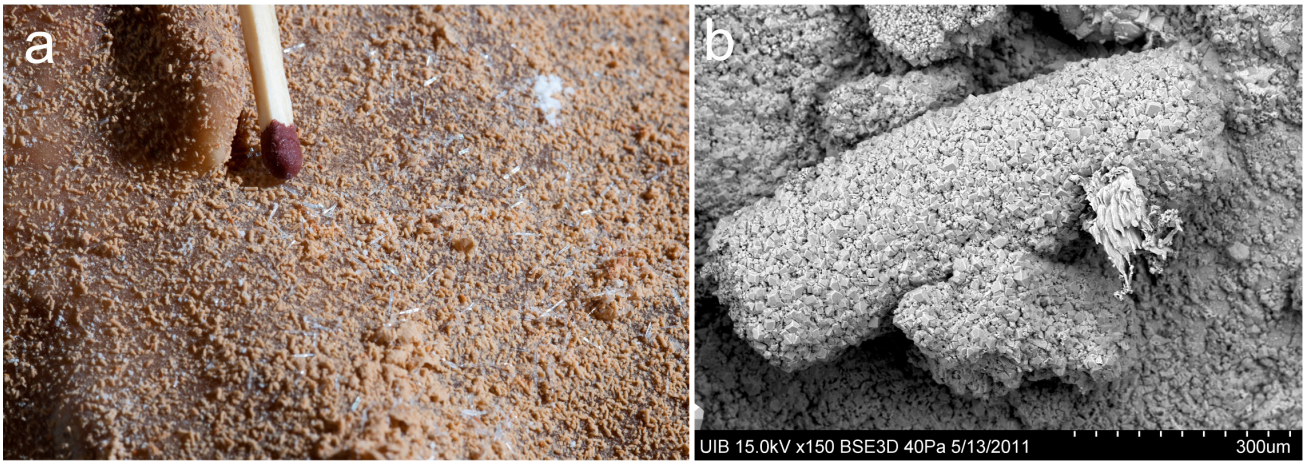

Fig. 8. Site 780, Cova des Pas de Vallgornera. a) Accumulation of beige in colour rod-shaped morphologies. Shiny celestine crystals can be clearly seen among them and on the cylinders (match for scale). b) SEM image showing a rod-shaped morphology covered in what seems microscopic crystallizations.

DISCUSSION

Biology and ecology of *Nycteribiidae*

Bats host numerous ectoparasitic groups, among them bat flies. Their occurrence in Mallorca was already described by Balcells (1968) and Kock and Quetglas (2003), identifying six species belonging to *Nycteribiidae* family; until present no *Streblidae* have been documented.

Nycteribiidae are a peculiar group of hematophagous ectoparasites solely associated with bats (Dick & Patterson, 2006). They are distributed worldwide, but the main diversity is found in the tropics more than in temperate areas. This family of bat flies is highly specialized and adapted to parasitize bat hosts. These small, wingless flies measure between 1.5 and 5.0 mm in length and, with their spider-like appearance, are remarkably agile walkers. Spending most of their life on the bat fur or wing membrane, the females leave their host during reproductive activity to deposit a mature larva on the walls of the roost or in a suitable substrate, not far from bats.

Nevertheless, pupal deposition behaviour seems to be variable; in the case of *Nycterophilie*, would drop their pupae freely, falling off on any surface (Dittmar et al., 2009). Almost immediately, the larva pupates and undergoes a metamorphosis that takes between 16 and 55 days in hatching, depending on temperature and the presence or lack of bats, resulting in an adult nycteribiid (Dick & Patterson, 2006; Lourenço, 2008; Duvallet et al., 2017). During this pupae evolution, the female provides maternal nurturing, therefore visiting frequently the site and spending more time in the surrounding area of the deposition (Balcells, 1961; Estrada-Peña et al., 2006). Nycteribiids reproductive activity substantially fluctuates along the year, notably intensifying during bats pregnancy and nursing season, reducing this activity during winter while hosts hibernate (Lourenço, 2008). In addition, these parasites are subjected to rather constant roost temperatures in caves which would provide a steady and, in many cases, warmer environment which would boost reproduction.

Bats flies feed frequently and start defecating droplets within the first 15 minutes after the ingestion of blood. The excremental dropping exhibit abundant intact red blood cells (Fig. 3b), because these hematophagous insects would digest the cells content without breaking the cells membranes (Fritz, 1983).

Evidence

Based on the evidence collected from the two caves, we can summarize the most important findings.

In the case of CSG the following points must be remarked: 1) Rod-shaped morphologies are composed mainly of organic matter; 2) Morphology, composition, and minute dimensions of rod-shaped morphologies, are questionable directly produced by bats; 3) They have been identified close to pupae (Fig. 4); 4) In general, they are deposited near areas with clear bat scratches (Fig. 2a); 5) Small particulates of minerals belonging to the chemical group of phosphates have been determined blended with the organic matter (Fig. 2b); 6) Ethology and biology of bats and their specific ectoparasites are coherent with our findings. 7) The discovery of large amounts of what seems intact red blood cells in the cylindrical features marks a milestone and could prove the origin of these features (Fig. 3). Therefore, we could envisage that these cylindrical morphologies are present-day excreta from bloodsucking bat flies, probably related to the period when bat flies females leave their host to put the pupae, frequently visiting the site.

In CPV we can summarize the following points: 1) Rod-shaped morphologies are formed mostly by calcium carbonate, with no traces of organic matter; 2) Currently the cave does not harbor any bat colony, neither pupae nor guano accumulations, it was sealed by the collapse of its natural entrances circa 2.4 My ago (Bover et al., 2014; Merino et al., 2019); 3). Since that period, there has been very limited weathering retreat of passage walls, among other passages at the **Jacuzzi site**, which still exhibits abundant and clear bat scratches; 4) The morphology of the cylindrical features are similar to those found in CSG (Fig. 7 and 9);

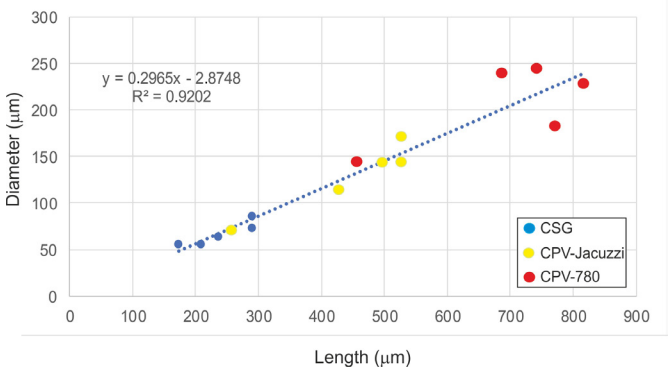

Fig. 9. Measurements of a random selection of rod-shaped morphologies sampled in CSG and CPV.

5) The **Jacuzzi site** is the richest area in CPV exhibiting crypto-corrosion features and an extensive array of guano-associated cave minerals (Merino et al., 2019); 6) Fluorapatite has been identified intermingled with paste-like deposits and rod-shaped morphologies (Fig. 10).

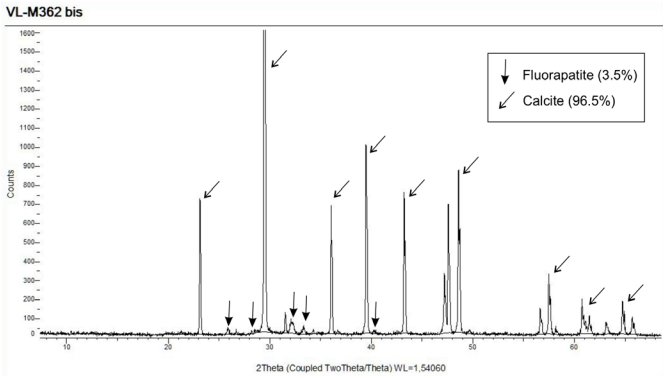

Fig. 10. Cova des Pas de Vallgornera. X-ray spectrum of sampled cylinders, revealing their calcitic nature and the presence of fluorapatite.

The morphometric analysis of the cylindrical features shows some differences in size. One of the reasons for this variability of dimensions could be related to the existence of different bat ectoparasite species. Considering the dimensions of the rod-shaped morphologies found at CPV Jacuzzi as the cornerstone of this study (this location displays the most abundant concentration of cylinders), it can be clearly seen that the largest forms are located at site CPV-780, where they exhibit a crystallized surface which can also be the reason for their larger dimensions. Rod-shaped morphologies from CSG present the smallest size which could be influenced by the reduction in size caused when samples are subjected to the vacuum preparation process before the SEM observation, this compaction would cause a collapse in the sample structure.

Finally, despite of this variety in sizes, the proportion between diameter and length of most of the samples are quite similar in the three sampled locations. Current knowledge of the past biodiversity and species of the order Chiropters in CPV is due to Bover et al. (2014), who identified remains of one middle-sized bat, belonging to *Rhinolophus* aff. *mehelyi* and a second bat species attributed to a small *Pipistrellus*. These discoveries were made at a well-

preserved fossiliferous deposit of vertebrates located at the northernmost passage called Galeria del Tragus (Fig. 1c). The faunal composition, which include among others *Myotragus* aff. *kopperi* (goat), *Hypnomis onicensis* (dormouse), *Neosites* aff. *ponsi* (shrew), suggests that the chronology of the bones deposit should be considered Early Pleistocene. The bat fossil record of the Balearic Islands is scarce and with low diversity and could represent late relicts of a wider distribution in the past (Galán et al., 2024).

Comparing and extrapolating all available data suggest that the rod-shaped morphologies discovered in CPV likely represent fecal deposits from an ancient, sizeable community of hematophagous parasites, specifically *Stribidae* and/or *Nycteriibidae* that infected the bat colony occupying the cave, including the **Jacuzzi** passage. Therefore, the rod-shaped morphologies are fossil features that could be classified as invertebrate coprolites.

Roosting habitats and parasitism

A combination of local environmental factors, features of host's habitat and roosting sites influence relationships between bat flies and their hosts (Patterson et al., 2007). When roosting in more stable and enclosed structures, such as caves, bat species are more likely to be infested and carry heavier parasite loads as well as harboring more species of ectoparasitic flies (Patterson et al., 2007). After larviposition, the larva immediately pupates and undergoes a metamorphosis process which duration will depend, among other factors, on temperature and host presence (Szentiványi et al., 2019).

Previous research (Merino et al., 2019) clearly reflected that the microclimatic conditions that prevailed in CPV while harbouring bat colonies were suitable for breeding and nursery groups, especially, at isolated locations as the **Jacuzzi site**. Temperature and presence of abundant bat breeding females would have promoted high levels of infestation among the colony.

Mean rates of infestation with ectoparasites can affect the 49% of the bat colony (Bendjeddou et al., 2016), whereas the pupal mortality can range from 22.5% up to 62.0% (Fritz, 1983). Finally, bat grooming seems to be the main cause of bloodsucking fly mortality. When these parameters are evaluated and compared to the current abundance of rod-shaped morphologies that have persisted since their deposition at the **Jacuzzi site**, it can be concluded that the bat population and infestation rates must have been exceptionally high.

Potential formation mechanisms in the development of rod-shaped morphologie

The genesis of rod-shaped morphologies is not easy to interpret in CPV since all the consulted bibliography (Hill & Forti, 1997; Ercole et al., 2001; Melim et al., 2001, 2008, 2010; Northup et al., 2000; Self & Hill, 2003; Barton & Northup, 2007; Nader., 2007; Palmer., 2007; Onac & Forti, 2011, among others) does not shed light on any similar form, neither about how this particular cylindric aggregate can be molded. Our analysis and hypothesis are based on onsite observed characteristics, collected data, scanning electron microscopy investigations and mineral composition of the collected samples.

Most of the common chemical deposits that precipitate in caves are composed mainly of crystallized calcium carbonate, besides a wide range of other minerals belonging to all chemical classes. The physico-chemical reaction that leads to these precipitates are controlled by cave temperature, relative humidity, carbon dioxide partial pressure and pH levels; on some occasions, this process is triggered by microorganisms.

The physical microstructure of the rod-shaped morphologies located at the **Jacuzzi site** does not show evidence of crystallizations, conversely, they exhibit a massive and compacted aggregate of micro particulates composed, mostly, of calcium carbonate and a few grains of phosphates. The substrate upon which the cylinders are developed, exhibits the same texture and structural composition to that of the rod-shaped morphologies.

The morphologies discovered at **Site 780**, represents a different case, since the cylinders surface shows a crystallized cover and larger dimensions (Fig. 8b, 9). This site is currently concealed by a massive collapse of boulders detached from the ceiling and walls, which would make very difficult for bats to reach. Moreover, all this section of the Galeria del Tragus shows important and visible fissures affecting all the rock structure. This could indicate that, firstly, the morphology of this section of the passage was different in the past, allowing the former bat colony to roost. Secondly, it seems likely that the microclimatic conditions prevailing on this passage, affected by important air-movements (Merino et al., 2019), were different to those at the **Jacuzzi site**. Finally, the larger dimensions of the rod-shaped morphologies likely resulted from partial recrystallization, suggesting either a prolonged exposure period of the deposits or distinct paleo-microclimatic conditions.

Studies on microbial ecology in the decomposition of organic matter within caves remain under-investigated compared to similar processes in terrestrial and aquatic ecosystems (Ravn et al., 2020). Recent research in microbial activity and its role in the production of soils as a result of organic matter decomposition (Witzgall et al., 2021), may help clarify the possible origins of the rod-shaped morphologies. The referenced authors reveal that fungi primarily decompose organic matter, converting it into microbial biomass, while the growth of fungal hyphae can lead to the translocation of particulates. Furthermore, the particulate organic matter not only fosters microbial activity, but also acts as hotspots for the occlusion and formation of minerals and aggregates. Most importantly, microorganisms play a crucial role in forming and stabilizing soil structures, a process that can be partly attributed to the exudation of compounds like polysaccharides from fungal hyphae. In caves, the concept that microorganisms can somehow promote biomineralization through enzymes synthesized or provide nucleation support for mineral deposits was

already suggested by different authors (Northup et al., 1997; Boston et al., 2001; Ercole et al., 2001; Onac & Forti, 2011).

In the present paper we hypothesize that the physico-chemical environmental conditions along with the microbial processes involved in the genesis of this first-described feature would encompass different phases. Some of these phases occurred after the cave was naturally sealed, providing unique and stable environmental conditions that facilitated the formation and conservation of these morphologies. The envisaged phases are:

1) While the cave remained open, bat flies deposited cylindrical fecal droppings, on a surface covered with limited guano accumulations.

2) Decomposition of organic matters started, causing biochemical transformation, which was influenced by abiotic factors, while maintaining the structure.

3) Fungi and bacteria may act as hotspots of microbial activity, providing nucleation support for aggregates formation. Fungal hyphae could promote the translocation of tiny grains of cave soil, including phosphates, which would be integrated in the rod-shaped morphology.

4) Microbial metabolism released metabolic products that likely act as a glue, binding the tiny particulates together, causing the compaction of these features.

5) Throughout the entire development process and up to the present, the microclimatic conditions in the locations where the rod-shaped morphologies are found have remained stable.

6) Restricted and local environmental and physico-chemical processes could have led to the crystallization of rod-shaped morphologies (**Site 780**).

Ichnotaxonomy

Invertebrate coprolites, as trace fossils, can be classified through a set of significant characteristics that encompasses, shape, size and internal-external structure, etc. (Knaust, 2020). Sub-millimetric coprolites are defined as micro-coprolites when their maximum size is below 5 mm (Vialov, 1974).

The present study does not intend to classify this new trace-fossil hierarchically on each of the different ranks but based on the evidence and current knowledge, adopt an initial approach. Size and abundance of rod-shaped morphologies allow to qualify them as micro-coprolites. Ichnotaxobases compiled from fossilized invertebrate fecal droppings in CPV, along with present-day micro-coprolite remains from CSG (minute size, cylindrical morphology, surface features and homogeneous structure), clearly indicate that the rod-shaped morphologies belong to the ichnofamily *Bactrylliidae* (Knaust, 2020).

CONCLUSIONS

Rod-shaped features are a unique and new ichnofossil described for the first time in Cova des Pas de Vallgornera, indicating the ancient presence of bat ectoparasites. The abundance of these morphologies, found in only two small areas of the cave, suggests that once hosted a large bat colony, that was heavily infested with numerous ectoparasites.

Understanding the drivers behind the dynamics and biochemically mediated diagenesis that led to the formation of these features is intricate and not entirely clear. However, it seems feasible that microorganism activity and microbial metabolism processes may have contributed to the concentration and compaction of matter in stable and unique microclimatic conditions, preserving the original shape of the excrements. Probably, the paleoenvironmental factors involved would include humidity, temperature, CO_2 concentration, and presence of organic matter.

The physical environment at the locations that contain these ichnofossils would have been quite restricted, with limited air movements, without dripping water and absence of capillary seepage, conditions that would have prevailed since the Early Pleistocene till present. The observations made in CSG have supplied a present-day analog on the physical characteristics and ectoparasitic origin of these features.

Detection of these features was challenging due to their reduced size, which allowed them to blend in with the cave deposits. During research project in caves, it is essential to highlight the utility of carrying a small camera with good macro capabilities to photo-document any tiny deposits for later analyses or investigations.

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