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Anatomy of biologically mediated opal speleothems in the World's largest sandstone cave: Cueva Charles Brewer, Chimantá Plateau, Venezuela

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Abstract

Siliceous speleothems can be formed in sandstone caves. Recently, opal "biospeleothems" have been found in the World's largest cave in Precambrian sandstones on the Chimantá Tepui in Venezuela. The speleothems, although reminiscent of normal stalactites and stalagmites from limestone caves, are in fact large microbialites. More than a dozen forms were distinguished, but they share a common structure and origin. They consist of two main types: 1. fine-laminated columnar stromatolite formed by silicified filamentous microbes (either heterotrophic filamentous bacteria or cyanobacteria) and 2. a porous peloidal stromatolite formed by *Nostoc*-type cyanobacteria. The first type usually forms the central part and the second type, the outer part, of speleothems. Fungal hyphae, metazoan and plant remains also subordinately contribute to speleothem construction. The speleothems occur out of the reach of flowing water; the main source of silica is the condensed cave moisture which is the main dissolution–reprecipitation agent. Speleothems which originated by encrustation of spider threads are unique.

Keywords: Tepuis; Sandstone caves; Siliceous speleothems; Microbialites; Stromatolites

1. Introduction

Speleothems are very common in limestone caves, because dissolution and reprecipitation rates of calcite and aragonite are relatively high. Caves formed in silicate rocks, such as sandstones, quartzites, volcanics (e.g., lava tunnels) or even granites are characterized by siliceous speleothems (Urbani, 1976, 1996; Webb and Finlayson, 1984; Wray, 1999; Léveillé et al., 2000; Willems et al., 2002; Forti et al., 2003), in which the dominant mineral is opal (Hill and Forti, 1986). Siliceous sinters precipitated from hot springs (Jones et al., 2001a; Konhauser et al., 2001; Konhauser et al., 2003) are very similar. In cold water, opaline silica has a solubility on the order of 100–200 ppm and quartz silica even lower, less than 10 ppm (Hill and Forti, 1986). Unlike in most of the carbonate speleothems, microbial mediation is common in the precipitation of siliceous speleothems; it is also common in the hot-spring siliceous sinters, but with different biotas being involved, dominated mainly by autotrophic cyanobacteria. In the fossil record, siliceous microbialites occur mainly in the Precambrian and are the main witness of early eucaryotic life since the Archean. Comparison of the microbial communities in the Archean and hot-spring siliceous sinters has been a subject of several studies (e.g., Konhauser et al., 2003). Examination of siliceous speleothems provides a complementary actualistic approach to siliceous stromatolites that originated in non-photic environments.

Siliceous speleothems are commonly small forms (Webb and Finlayson, 1984), rarely exceeding 2 cm in size. Recently, the World's largest sandstone cave, Cueva Charles Brewer, was discovered in Chimantá Tepui, Venezuela (Šmída et al., 2005).

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Within the cave, unusual large examples of previously undescribed speleothems have been found. They represent the largest known cryptic stromatolites and the largest siliceous stromatolites originating in non-aquatic environments. This paper is the first report of their anatomy and composition and it contains inferences concerning their origin.

2. Geological setting — characteristics of the Cueva Charles Brewer and its speleothems

The World's largest sandstone cave Cueva Charles Brewer, was discovered by us (Ch.B.-C.) in 2004 on the Chimantá Plateau (tepui) in south-eastern Venezuela (Fig. 1). The plateau is one of more than 100 tepuis that occur in the area. The tepuis are table mountains of Precambrian quartzites and sandstones of the Guayana Shield, rimmed by steep cliff walls. The tepuis are habitats for a great variety of endemic flora and fauna. During exploration of this isolated environment, karst structures with numerous subterranean systems were discovered.

Cueva Charles Brewer parallels the top of the mountain, 150 to 200 m below the surface. The known length of the cave is 4482 m. In the size of its galleries and its total volume, it exceeds any other known quartzite cave (Fig. 2). The cave appears to be part of a major drainage system for an extensive area of the tepui surface. During the dry season, the water flow of the river inside the cave was estimated to be 200–300 l/s; but during torrential rains, it reaches many cubic meters per second. The cave galleries are typically 40 m wide, but can be much larger. The largest chamber found in the cave, Gran Galería Karen y Fanny, is 40 m in height, more than 355 m in length, and 70 m wide: a volume of about 400,000 m^3.

Opal speleothems were found on many places within the cave but mostly out of reach of flowing water. They have various shapes and forms; more than a dozen types were distinguished by speleologists during the initial phases of exploration. Inorganically precipitated opal to chalcedony flowstone crusts are beyond the scope of this paper, which is mainly focused on dropstone-like speleothems. Mushroom-like speleothems over 10 cm high, with white stems and dark brown caps were named "dolls" (Spanish: muñecos — Fig. 3A, B). Other forms, "black corals" (Spanish: corales negros — Fig. 3) and "guácimos" (Fig. 3D), have more bizarre, branching shape. They resemble coraloid speleothems described from other silicate caves (Swartzlow and Keller, 1937). The lower sides of some

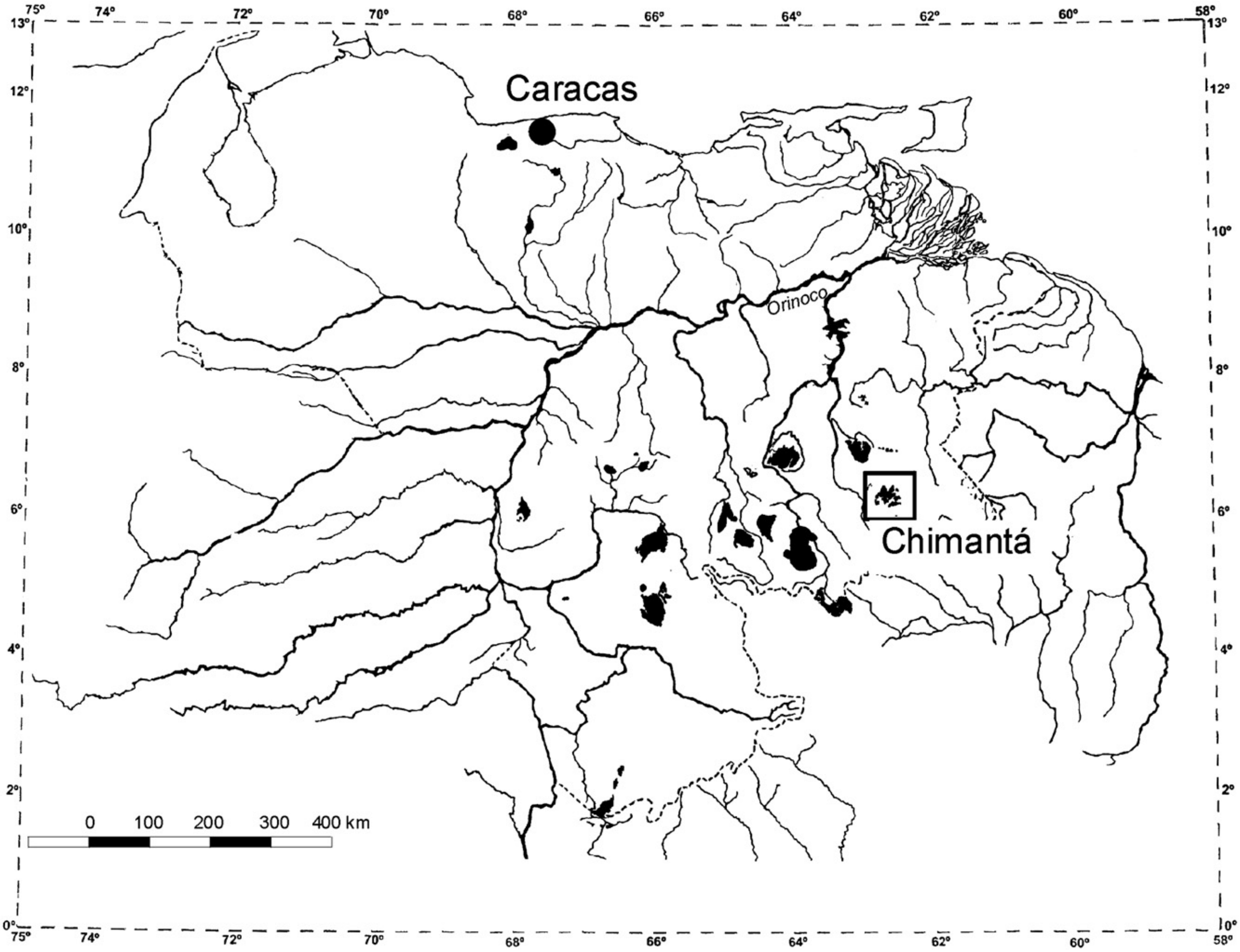

Fig. 1. Position of the Chimantá Tepui.

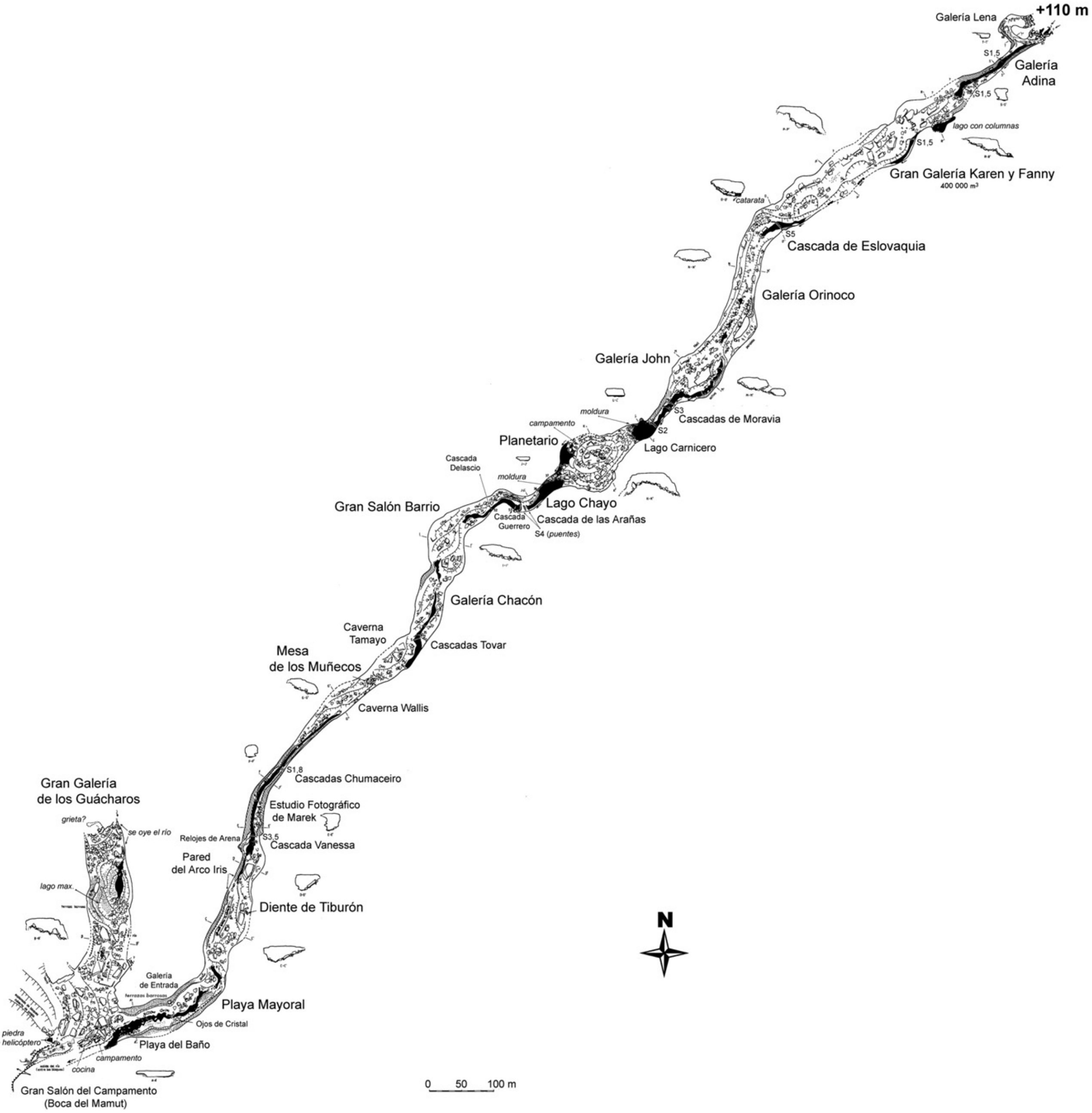

Fig. 2. Plan of Cueva Charles Brewer.

overhanging quartzite beds are lined by ball-shaped speleothems called "champignons" (Fig. 4A, B), by kidney-shaped speleothems (Spanish: riñón — Fig. 4C), and by sponge-like speleothems (Fig. 4D). The most unusual are "cobweb stalactites" (Spanish: telerañas — Fig. 5A–D) that grow under ceilings of some galleries and originate by siliceous encrustation of spider threads. Some of these are bent in the direction of air currents (Fig. 5D). All of these speleothems bear signs of microbial origin.

3. Research methods

A limited number of samples was collected for study to prevent excessive damage to the speleothem decoration of the cave. They were studied in petrographic thin-sections. Material from the "black coral", "guácimo" and "champignon" types was investigated under scanning electron microscope (SEM), utilizing tiny pieces of speleothems that remained after thin-section production. Soft parts of the porous peloidal stromatolite, as well as of the apical parts of speleothems in grow position ("guácimo" and "black coral") were studied in fresh or broken states, whereas the compact laminated opal stromatolites were studied after etching by diluted hydrofluoric acid (etched for 1 day). Etching of the porous stromatolite was unsuccessful because it dissolves rapidly. The samples were gold coated and then observed in JEOL JXA 840 A scanning electron microscope, with an accelerating voltage of 5 kV. Mineralogical composition of the speleothems was determined optically and

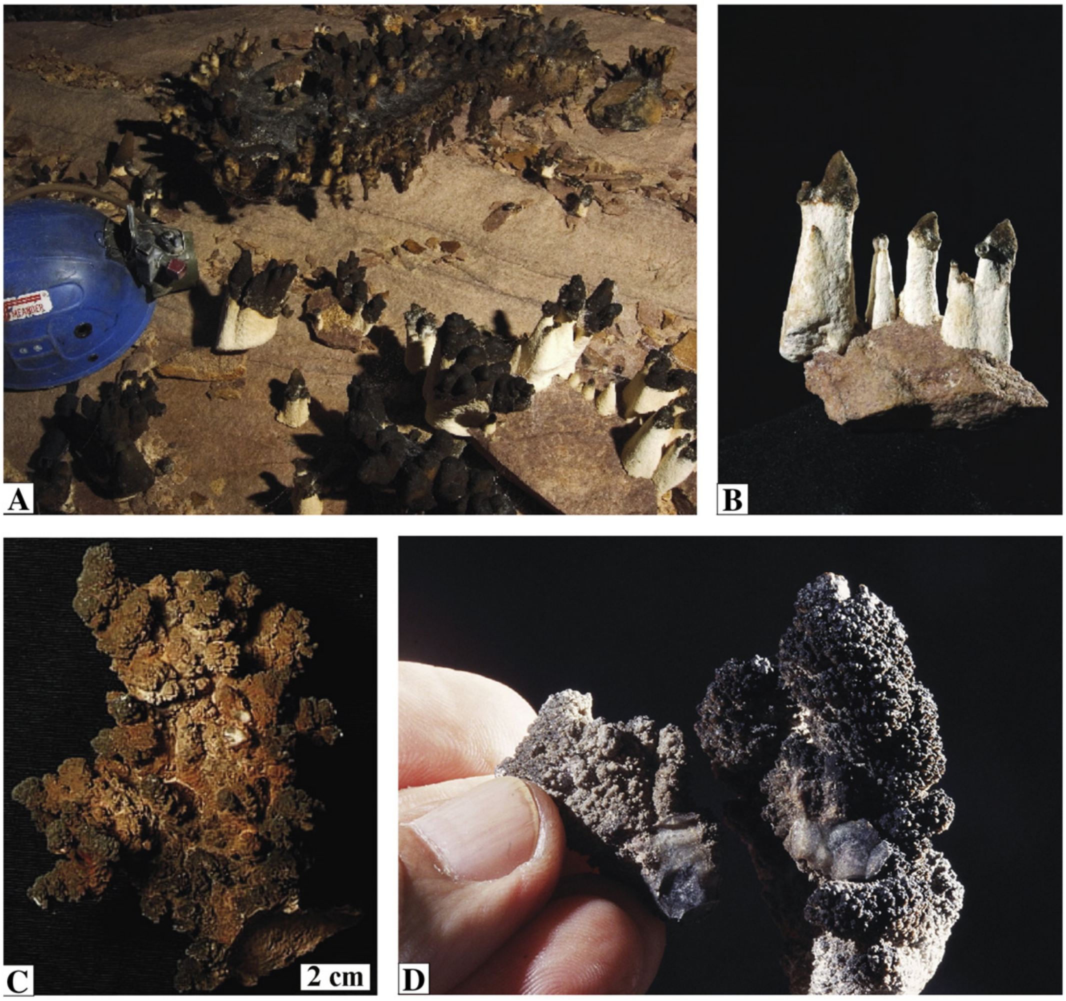

Fig. 3. (A) Fallen block of quartzite (called by speleologists Mesa de los muñecos) overgrown with stalagmitic speleothem forms called dolls. (B) Detailed view of the sample from Mesa de los muñecos. (C) Sample of "black coral". (D) Sample of "guácimo".

by X-ray diffraction analysis (XRD). Analyses were performed with a DRON-3 analyser, using CoKα of the wavelength λ: 1.79021 Å, filter Fe, voltage 30 kV, intensity 15 mA, diaphragms 1;1;0.1, or CuKα of the wavelength 1.54178 Å, filter Ni, voltage 40 kV, intensity 20 mA, diaphragms 1;1;0.5. To ascertain speleothem porosity, as well as the capability of capillary forces to keep the speleothems wet, a staining experiment was carried out, during which the bottom part of a longitudinally cut "doll" was dipped into ink for 1 day.

4. Composition of the speleothems

Despite having numerous shapes and forms, the examined speleothems show remarkably uniform structure which indicates their similar genesis. The speleothems consist of two principal types (Fig. 6): 1. finely laminated columnar stromatolite of non-porous compact opal, 2. highly porous stromatolite formed by soft white porous opal that represents a laminated accumulation of microbial peloids. The term "stromatolite" denotes here microbial deposits with lamination (see Riding, 1999). Some speleothems, e.g., the "cobweb stalactites", consist only of the first type, whereas the porous stromatolite is more developed in "dolls" and "champignons". In the latter two speleothem types, the finely laminated columnar stromatolite forms the inner zone, whereas the porous peloidal stromatolite forms the outer zone. In "black corals" the fine-laminated stromatolite prevails while the porous stromatolite is thin and occurs in some places as interlayers.

Mineralogically, most of the speleothems are formed entirely by opal-A (Fig. 7A). Recrystallization to microquartz was revealed by XRD analysis only in some speleothems, and mostly in the older, inner zones (Fig. 7B). This may indicate that the speleothems are of different ages. Detailed petrographic descriptions of the individual zones are given in the following examples of "cobweb stalactite", "doll", "champignon", "black coral", and "guácimo".

4.1. "Cobweb stalactites" (telerañas)

The sample of the "cobweb stalactite" is formed exclusively of laminated opal columnar stromatolite. Four growth subzones can be distinguished (Fig. 8A): the middle zone (m), central

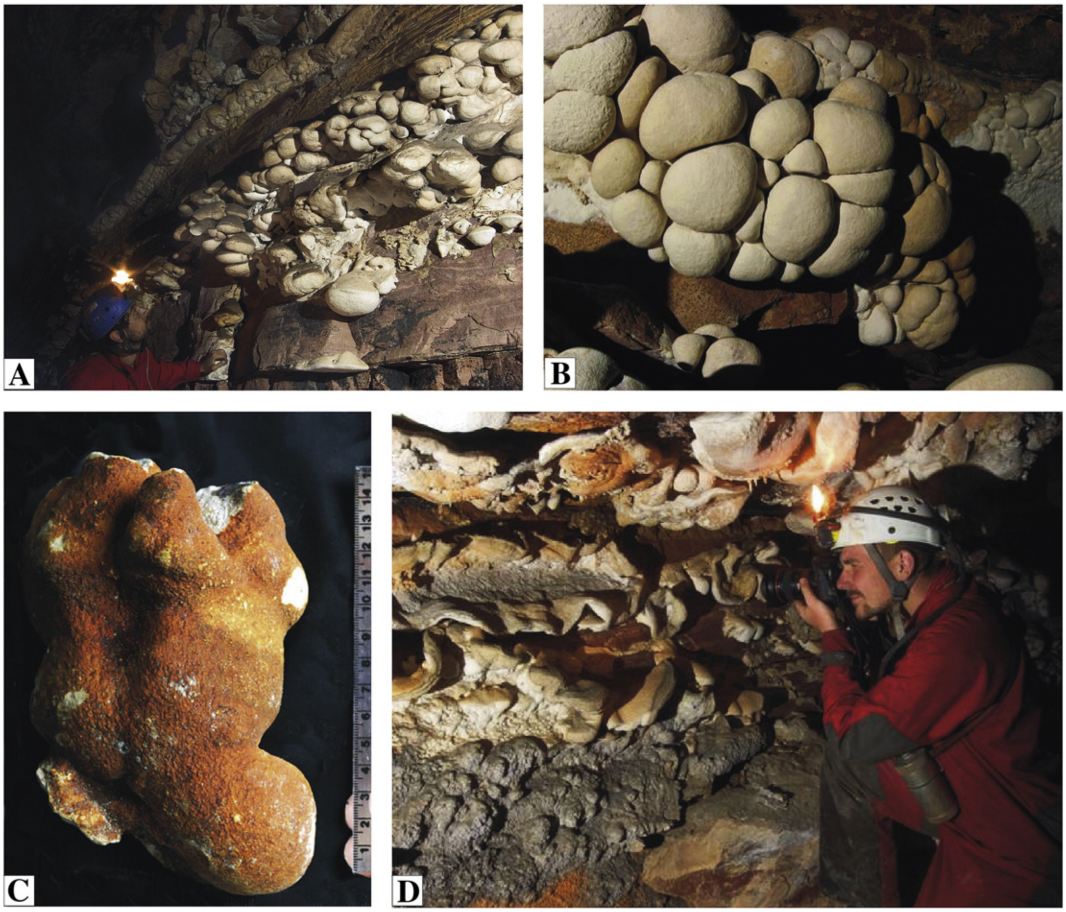

Fig. 4. (A) Ball-shaped speleothems termed "champignons" concentrated under overhanging beds of quartzite. (B) Another example of "champignons". (C) Sample of kidney-shape speleothem (riñón). (D) Speleothems resembling large dish-shaped mushrooms.

zone (c), alveolar zone (a) and outer zone (o). The middle and central zones are discontinuous in 2-D view; possibly due to initial scrolling of the stalactite during growth. The middle zone is formed by brownish (all colours are given as they appear in thin-sections), cloudy to semi-opaque opal, free of distinct lamination. In contrast, the central zone is formed by thin-laminated opal (siliceous stromatolite) which is much clearer and transparent. In the latter two zones, thin spider threads are observed under larger magnifications (Fig. 8B). The inference that they do represent threads, and not tiny fractures, is indicated by the fact that the filaments are very thin and discontinuous, often extending beyond the plane of the thin-section; i.e., they represent linear rather than planar bodies.

The alveolar zone consists of laminated, sometimes cloudy opal, full of alveolar to globular voids (fenestral pores — Fig. 8C). This zone contains numerous quartz sand grains. Spider threads are also found in this zone.

The outer zone consists predominantly of clear (only locally cloudy), finely laminated opal. The lamination is sometimes convex outward from the stalactite, showing the appearance of an inward growing stromatolite (Fig. 8D). As in the previous zones, spider threads are also present. This zone contains considerably fewer fenestral pores and detrital sand grains.

4.2. *"Dolls" (muñecos), "black corals" and "champignons"*

Longitudinal sections through "doll" and "champignon" speleothems indicate that they consist of both principal types, which can be distinguished in thin-sections (Fig. 9A). Branching, fine-laminated columnal stromatolite (s) and porous peloidal stromatolite (m) form most of the speleothem; the "doll" samples have a thin, fine-laminated outer stromatolitic zone (o). Between the stromatolite columns, a central zone can be distinguished in "doll" speleothems, corresponding to the peloidal stromatolite, but with some fenestral pores and numerous trapped detrital quartz sand grains.

The columnar stromatolites are finely laminated, with alternating laminae of clearer and brownish opal (Fig. 9B). In tangential cross-sections, the laminated bodies are alveolar. In some of these stromatolites, a dense meshwork of radial filaments is visible, most likely formed by the stromatolite microbial builders (Fig. 9C). In some places, sphaerical enclosures, probably of organic origin, are trapped in the stromatolite (Fig. 9D).

SEM studies of the apical parts of the "black coral" and "guácimo", which represent the active, living parts of the columnar stromatolite, showed that spiders also contributed to their

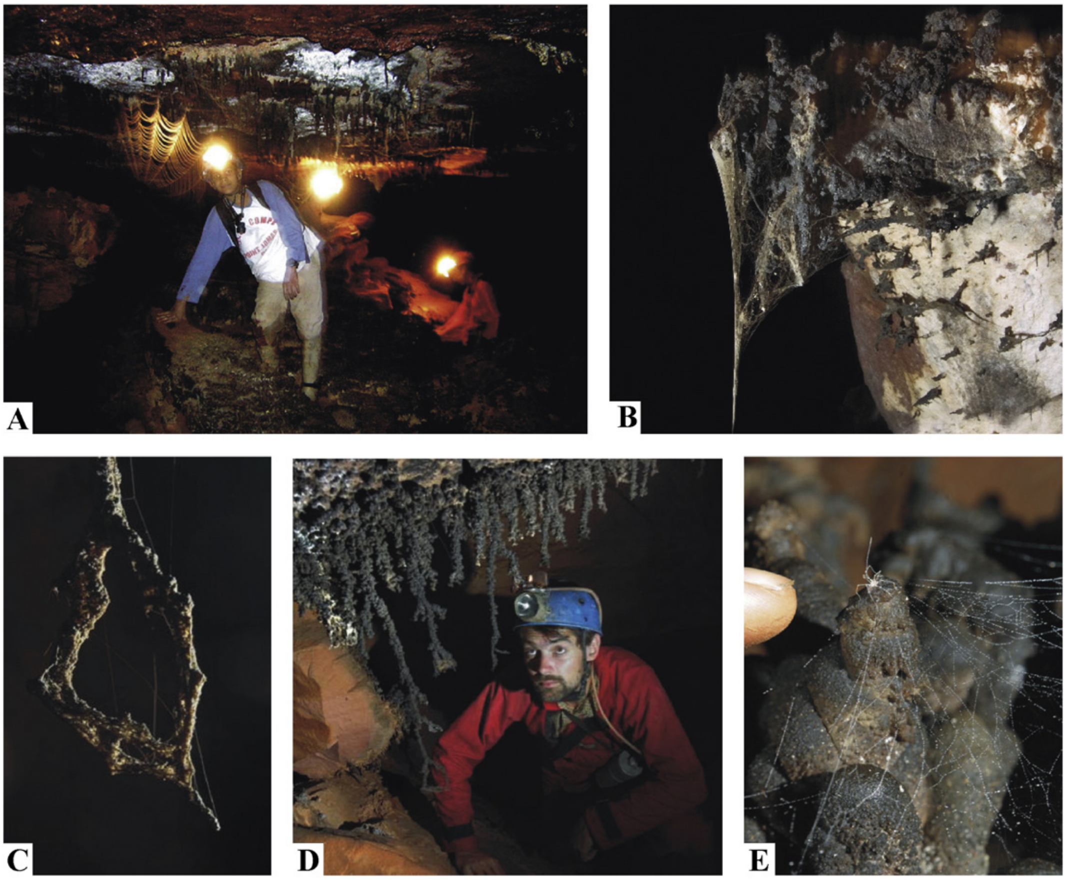

Fig. 5. (A) “Cobweb stalactites” hanging from the ceiling in a gallery with high concentrations of spiders. (B) Cobweb incompletely encrusted by silica. (C) Silica encrustation following the spider threads. The cobwebs serve as the supporting structure for speleothem growth. (D) “Cobweb stalactites” inclined in the direction of air draughts. (E) Spiders also contribute to the construction of stalagmitic forms of speleothems.

origin. On their surfaces, spider threads emerging from opal (Fig. 10A) are clearly visible and readily distinguished from, fungal hyphae for instance (Fig. 10B), which also occur on the speleothem surfaces. The spider threads are much thinner and straight; whereas the fungal hyphae are thicker, curved and branching. In situ field observations in the cave also revealed spider activity, not only on the “cobweb stalactites” but also on stalagmitic forms. The growth plane of these speleothems observed under SEM appears either to be agglutinated from detrital material (Fig. 10C), or to be formed by bizarre alveolar microbial bodies (Fig. 10D), which in closer view resemble small corals (Fig. 10E, F).

Study of etched surfaces of the fine-laminated columnar stromatolite showed that it consists mainly of thin concentric laminae (Fig. 11A) that may also be of abiogenic origin, precipitated directly from water. Backscattered electron images showed no microlamination, which sometimes occurs in hot-spring siliceous sinters and this is interpreted as being due to changes in water composition (Jones and Renaut, 2004). Most of the lamination is related to microbial growth, as shown by densely packed, parallel tubular casts of filamentous microbes (Fig. 11B, C) which are also indicated in thin-section studies. The tubes are 50–80 μm long, straight, non-branching, with circular cross-sections, measuring 5–10 μm in width. They are simple; but small remnants of septa are visible on their inner surfaces (Fig. 11D). The spaces between the septa are regular, measuring approximately 2.5 μm. They most likely represent the same microbes that form the surface alveolar bodies (see above). Locally, irregular (commonly oval), double-layered cross-sections of silicified microbe tubes (or cell casts) occur (Fig. 11E, F). Their diameters are more variable than those of the previous casts, ranging from 10 to 35 μm.

In other places, network-like structures are visible after etching (Fig. 13A). These are probably also related to microbial activity and contribute to formation of the alveolar zone of the columnar stromatolites. Other leafy structures protruding from the opal masses after etching are probably remnants of plant tissues or insect chitin.

The porous peloidal stromatolite consists of ovoid peloids of relatively uniform shape (Fig. 9E, F). They are densely packed and arranged in concentric laminae. Close to the columnar stromatolite they are packed more loosely, and interstitial pores are filled with clear opal. The peloid size ranges from 0.1 to about 0.3 mm. In some places, the peloids with well-defined shapes pass into areas where the peloidal structure is obliterated and the rock attains a mud-crack-like structure in cross-section (Fig. 12A). In some parts of “champignon” samples, larger sphaeroidal bodies can be observed (Fig. 12B). Their size is irregular, varying from 250 to 520 μm. In the central zone of the “doll”, the peloidal structure is also disturbed by fenestral pores

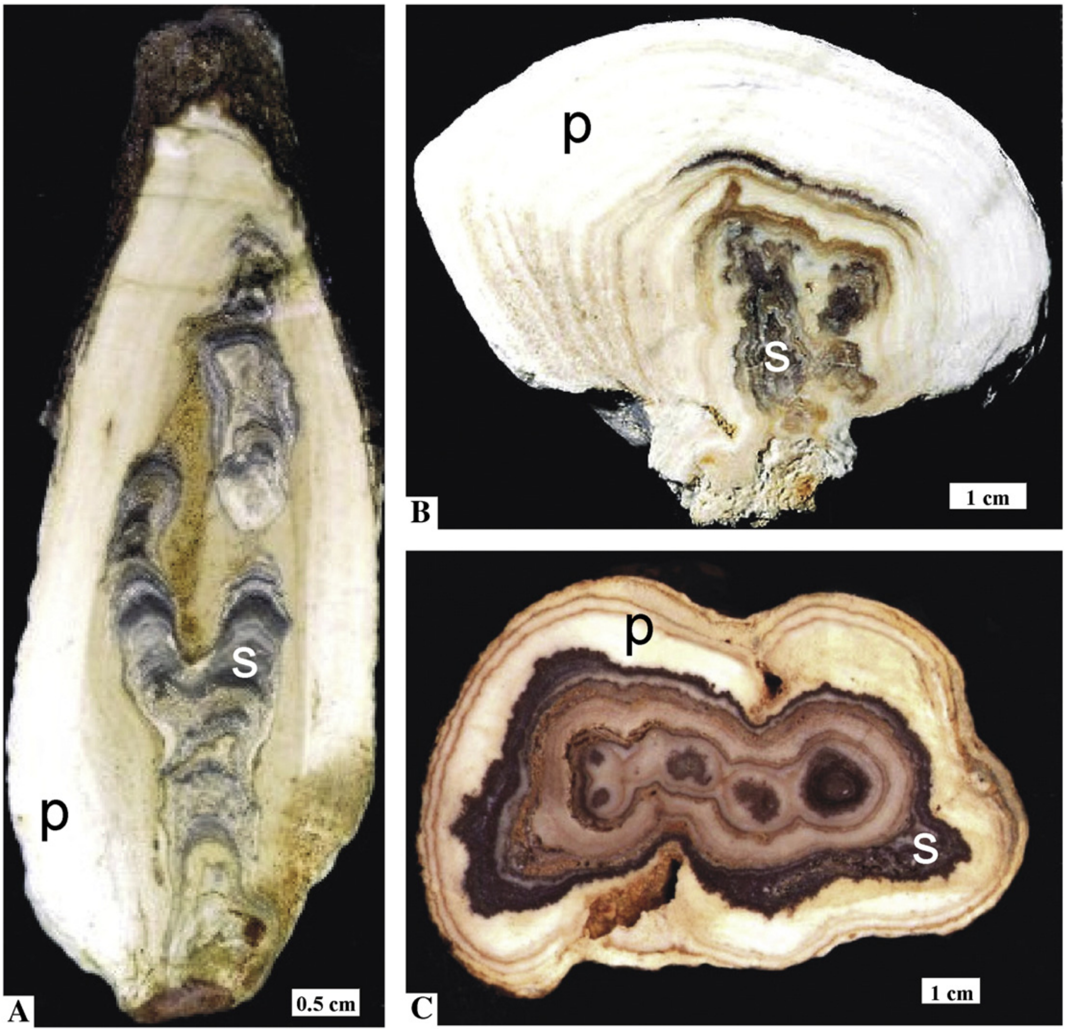

Fig. 6. Slabs of “doll” (A), “champignon” (B) and “kidney” speleothem (C) show two principal zones which form the speleothems — compact dark central stromatolite (s) and an outer, pale peloidal zone (p).

and trapped quartz sand grains. In this zone, some silicified organic remnants, probably of trapped insects, spiders or plants, can be recognized as thin tubes and tube meshworks (Fig. 12F). Unlike the compact opal layers, the peloidal layer was affected only by slight cementation. The peloids are predominantly loosely packed, with open pores between them (Fig. 13B). When cemented, the boundaries between peloids are obliterated, but the porosity remains high. The staining experiment showed that after several hours the ink reached the very apical parts of the speleothem and even the surface became wet. This laboratory observation agreed with field observations in the cave, where the speleothem surfaces were wet and drops of water formed on the tips.

The internal structure of the peloids is mostly obliterated by progressive diagenesis and no microbial remnants are visible. On the surface of peloids from the inner, well lithified parts of the peloidal layer, only tiny irregular spherules are visible and the microbial structure is entirely obliterated (Fig. 13C). The internal structure of only the outer, less silicified zones is visible under large magnifications. These observations show that the peloids, as well as the larger sphaeroidal bodies, are composed of short microbial filaments (Fig. 12C, D). This appearance corresponds most closely to *Nostoc*-type cyanobacteria. The cells in the filaments are generally of uniform size (1.3–1.4 μm in diameter), but some larger cells (1.8–1.9 μm in diameter) also appear (Fig. 12E). These may be interpreted as heterocytes — cells that serve for nitrogen supply and develop mostly in nitrogen-depleted environments. The presence of heterocytes is typical only for the Nostocales order. Under SEM, the cell chains are also visible but their inner structure is not clear due to silica encrustation (Fig. 13D).

5. Discussion

The speleothems studied from Cueva Charles Brewer are predominantly formed by several forms of microbes and partially by metazoans (spiders); they deserve the name “biospeleothems”. Siliceous speleothems are known from numerous silicate caves all over the World (Webb and Finlayson, 1984, Wray, 1999, Léveillé et al., 2000, Gradziński

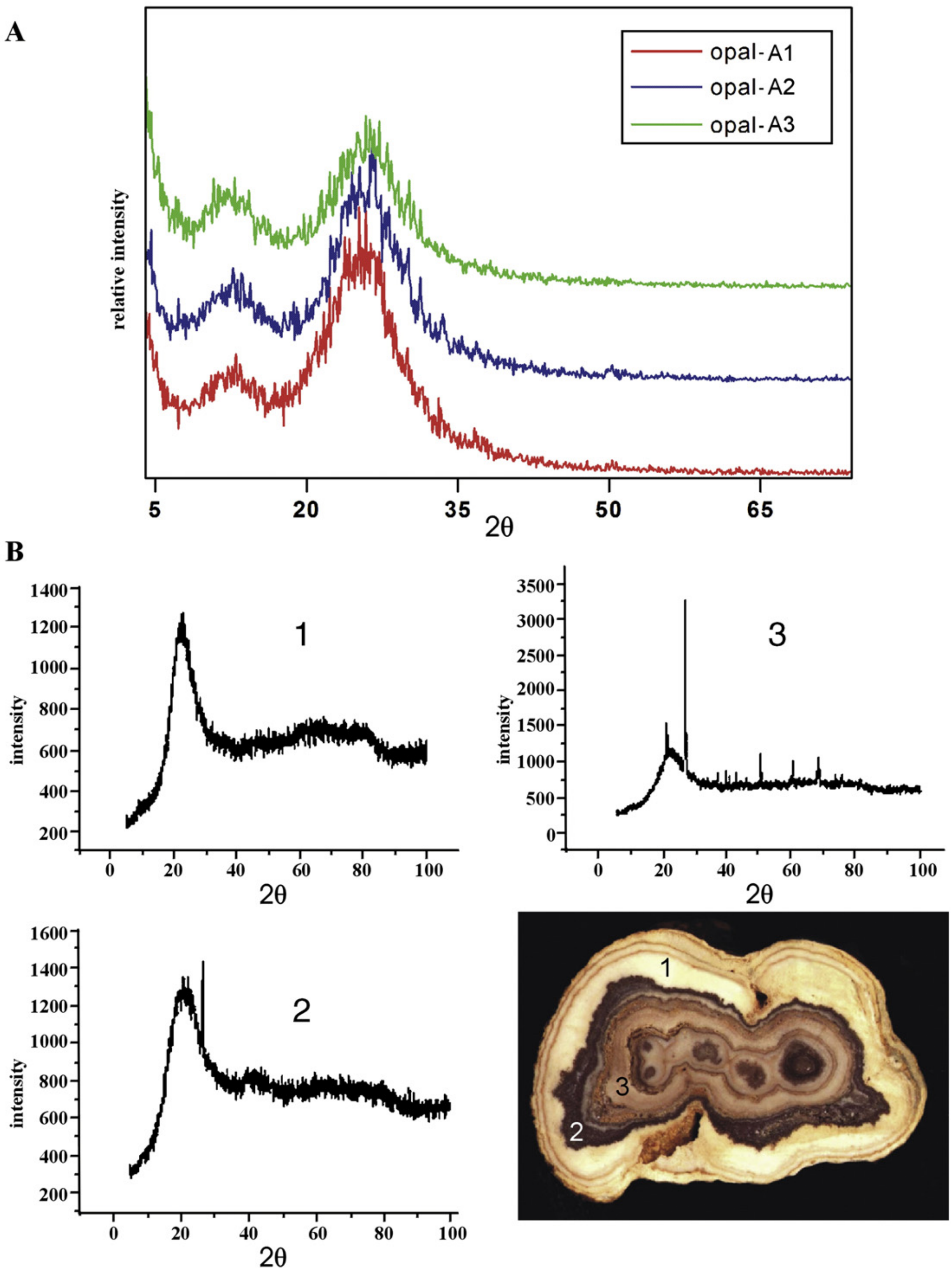

Fig. 7. (A) Representative diffractograms from various zones of “dolls” and “champignons” showing the dominant opal-A mineralogy. (B) Example of XRD analyses of various zones of kidney speleothem show that the pale peloidal zone consists mainly of opal (1), whereas the darker outer layer of the central stromatolite also contains some microquartz (2) and the content of microquartz increases towards the central zone (3).

and Jach, 2001, Willems et al., 2002), and they are also known from other sandstone (quartzite) caves in Venezuela (Urbani, 1976, 1996, Forti, 1994). Siliceous speleothems described previously in the literature represent only small examples, occurring mostly as flowstones only several millimeters thick. Hill and Forti (1986, p. 105) mentioned a 28 cm long opal column from Bilemat Kul lava cave in Korea. The most similar examples to the speleothems studied by us are so called coraloid speleothems (Swartzlow and Keller, 1937). Most of these, however, only reach a maximum length of about 2 cm (Hill and Forti, 1986, p. 104), whereas the speleothems from Cueva Charles Brewer often exceed 10 cm in length. This positive correlation between the cave size and speleothem size may be primarily determined by the total volume of dissolved and

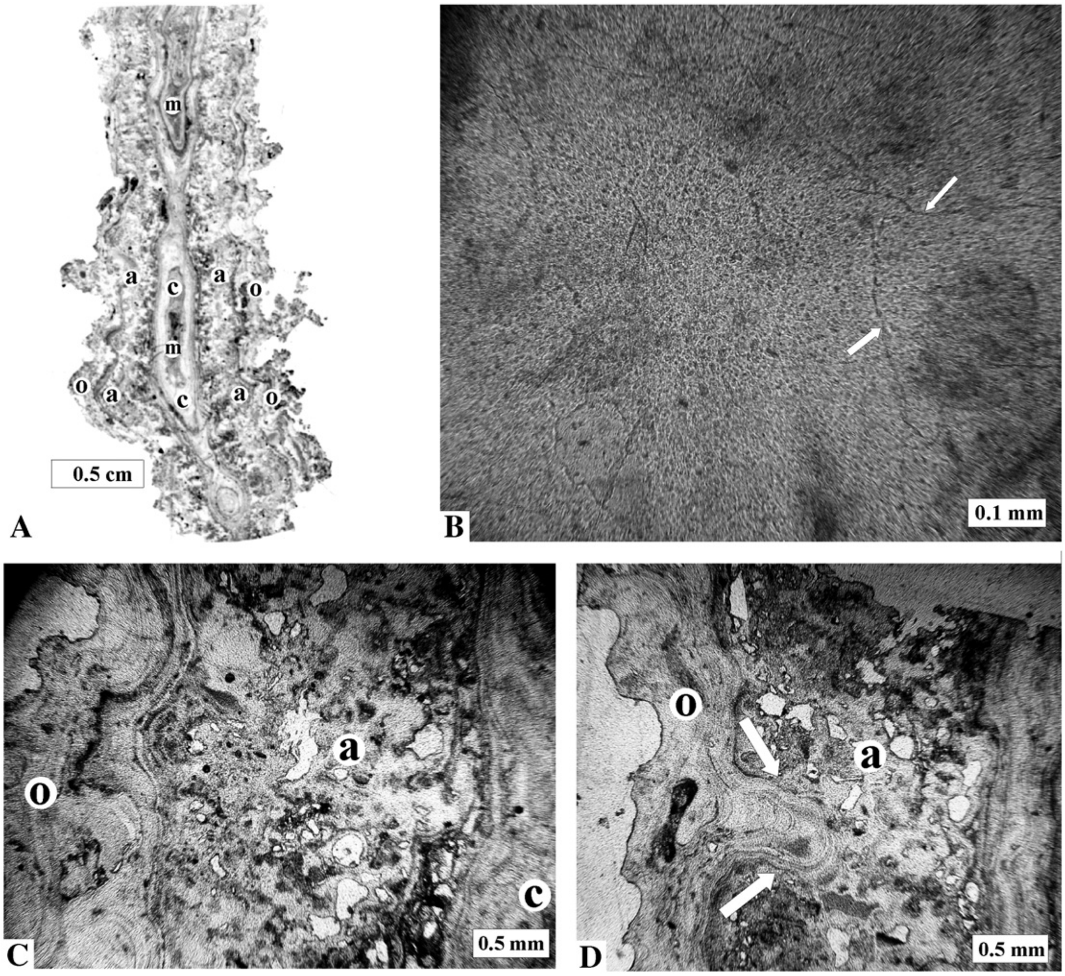

Fig. 8. Thin-section images of "cobweb stalactite". (A) Scanned overview image of a longitudinal thin-section of "cobweb stalactite". The letters indicate zones: middle (m), central (c), alveolar (a) and outer (o). (B) Spider threads (arrowed) preserved in clear opal of the central zone. (C) Alveolar zone (longitudinal cross-section), bordered by central (c) and outer (o) zones. Note bizarre fenestral pores and quartz sand grains trapped in this zone. (D) Convex-out stromatolitic offspur (arrows) projecting inward from the outer zone, implying possible inward growth of the entire stalactite.

reprecipitated SiO_2, but it is also likely that other, as yet unknown, factors influence speleothem size. The speleothems hanging from the ceiling (stalactitic forms) are larger than those growing from below (stalagmitic forms). This is obviously influenced by gravity.

The silica forming speleothems precipitate from four sources of silica solutions. Two primary sources are the subterranean river and seeping water; two secondary sources are derived from them: water spray and condensed moisture on the cave walls. The dissolved silica content in the water flowing on the tepuis is not high (compare Ipiña, 1994). Small subterranean river and seeping waters in the Cueva Charles Brewer are also undersaturated in SiO_2 (Lánczos et al., 2007). All the speleothems were found out of reach of flowing water. However, the evaporation modifies the cave waters significantly and the concentration of the dissolved matters increases in small isolated pools. The evaporation also acts on the speleothems themselves. The dye experiment showed that the peloidal layer is a good conduit for water and that the capillary forces are strong enough to provide moisture to most of the speleothem volume, even when only a little water is available. This moisture not only allows microbial mats to grow but its evaporation from the speleothem surfaces also causes precipitation of SiO_2. A very fine water spray and aerosols that fill the cave create an equally important source of silica. The aerosol droplets are not observable with the naked eye but they were revealed on photographs using a flash light. Evaporation of tiny spray droplets may greatly increase its concentration. Very fine structures of some "cobweb stalactites", with tips inclined towards the air draught imply that their encrustation was not due to seeping water but is more likely due to aerosols (The effect of seeping water would make the cobweb too heavy and consequently the cobweb would hang more vertically from the ceiling.). Finally, hydrogeochemical research showed that moisture condensation on the cave walls is one of the main agents acting in the process of dissolution and reprecipitation of silica. Hydrogeochemical analysis of the small pools made by dripping condensed water showed that despite the low overall concentration of dissolved substances, the concentration of silica is considerably higher than in other measured water sources (Lánczos et al., 2007). In its initial stage, the condensed water is very corrosive as it

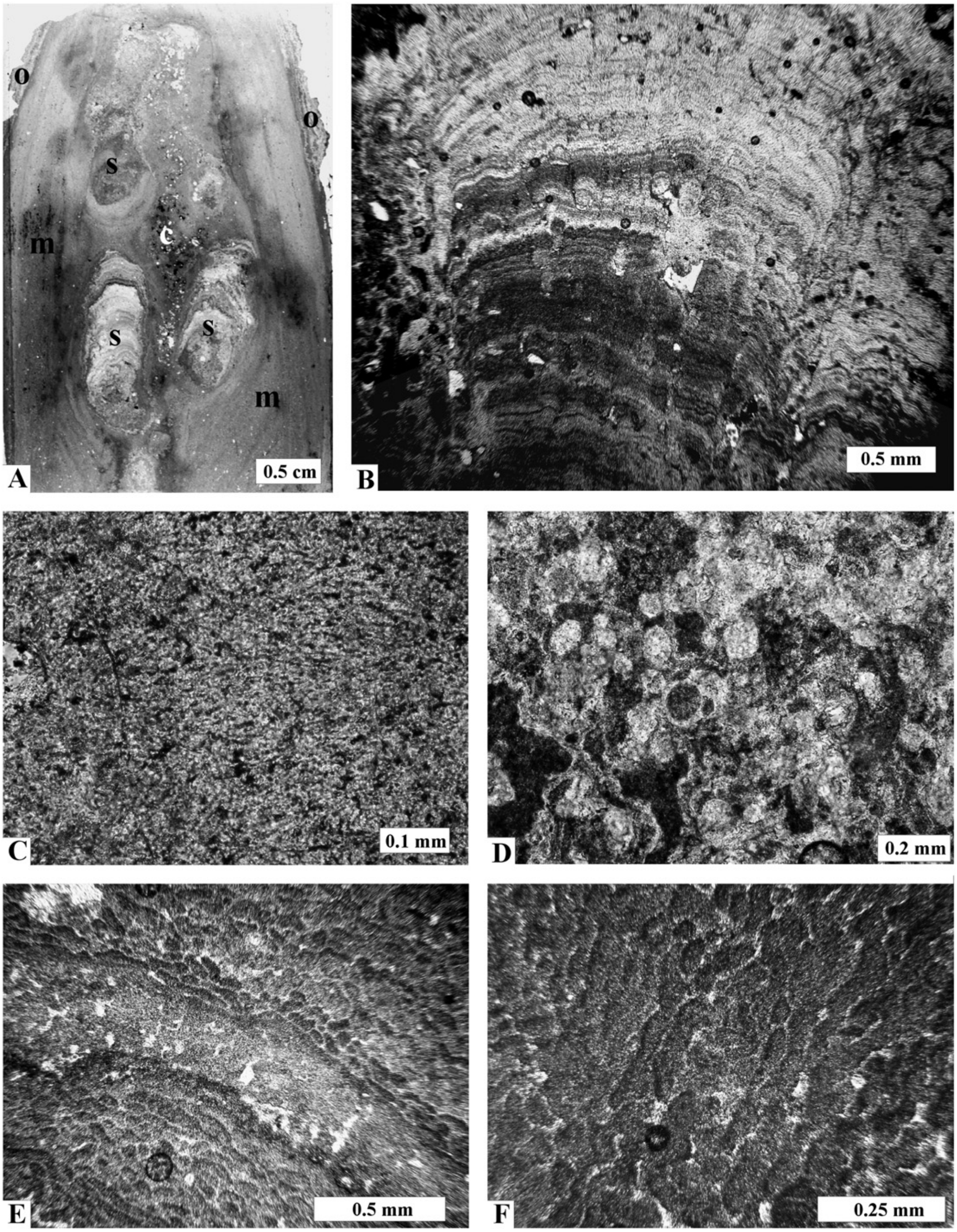

Fig. 9. Thin-section images of the "doll" (see Fig. 8A). (A) Scanned longitudinal thin-section of the "doll". The zones visible in thin-section are: s — columnar stromatolites, m — laminated peloidal microbialites, o — outer stromatolitic zone, c — central peloidal zone with fenestral pores and sand admixture. (B) Longitudinal cross-section of the siliceous columnar stromatolite. (C) Filamentous microbes in the columnar stromatolite visible under larger magnification. (D) Sphaerical enclosures, probably of organic origin, trapped in the stromatolite. (E) Concentric laminae of peloids in the peloidal zone. (F) Detail of the peloids.

condenses on all available surfaces and causes continuous release of the sand grains. Droplets or small streams of this water can transport the sand grains onto speleothem surfaces regardless of whether they represent dropstones or erected forms. This explains the presence of the sand grains in the speleothems, as well as the ubiquity of the speleothems, even under the ceilings in large galleries.

Many researchers have recognized the predominantly microbial origin of siliceous speleothems (e.g. Forti, 1994, Urbani, 1996, Léveillé et al., 2000, Willems et al., 2002), but only a few have provided information on their microbial composition. Biological investigations of microbes in opal speleothems from similar sandstone caves on the Sarisariñama Plateau (Cueva de los Guarachos — Kunicka-Goldfinger, 1982) showed mostly the presence of heterotrophic microorganisms. In cultivated samples the heterotrophic bacteria *Arthrobacter*, *Corynebacterium*, *Bacillus* and *Pseudomonas* occurred together with the nitrogen-fixing bacterium *Azotobacter*, and some

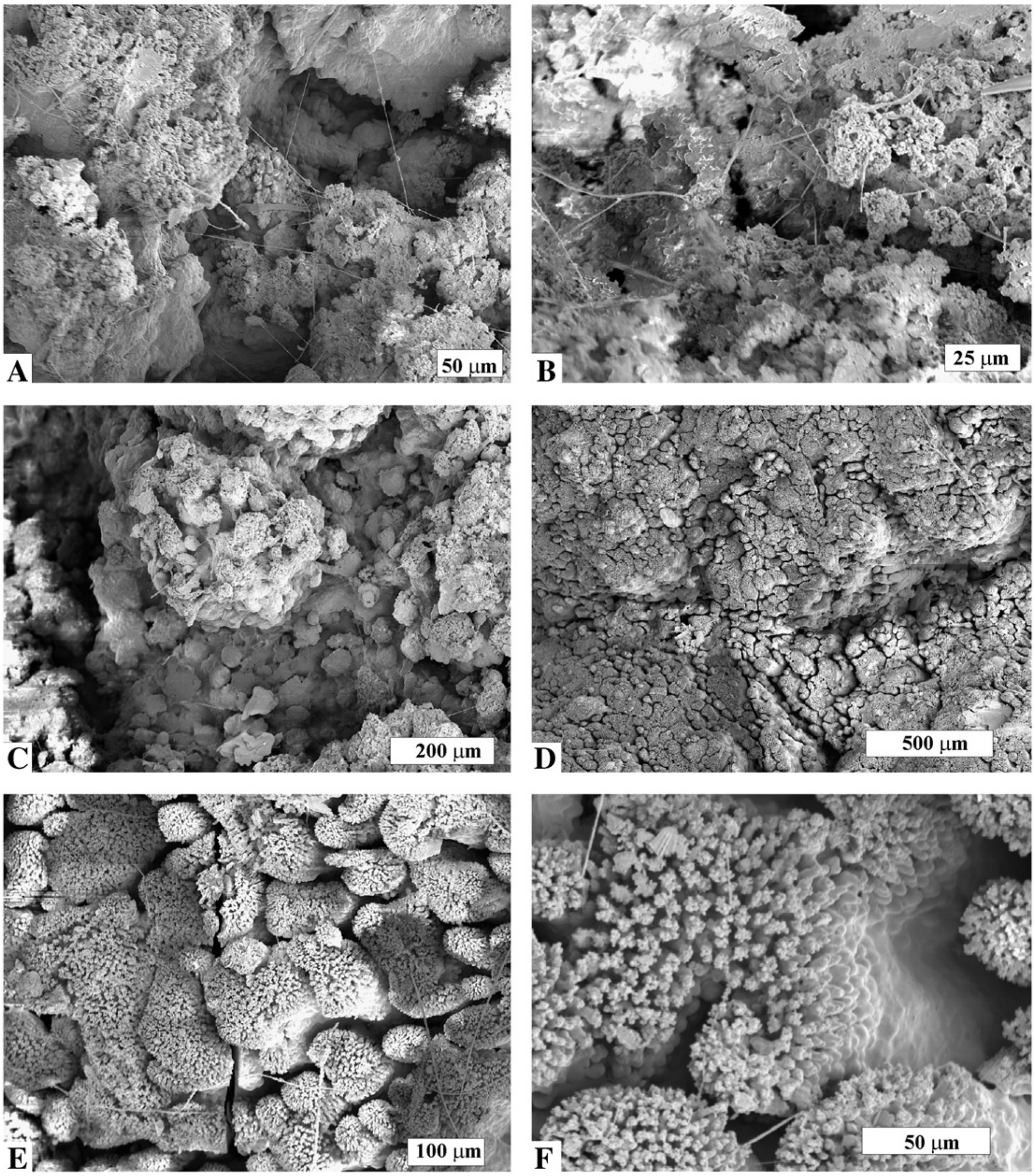

Fig. 10. SEM images of the surface of "black coral". (A) Surface of the growing part of the black coral with spider threads emerging from the opal surface. (B) Branching fungal hyphae on the speleothem surface. These are thicker than the spider threads. (C) Surface of the growing part of the speleothem formed by agglutinated detritic material. (D) Other part of the surface formed by bizarre microbial bodies, likely representing the stromatolite surface with protruding filamentous microbes. (E, F) Enlarged alveolar surface from Fig. 13D, resembling tiny coral bodies. Thin spider threads emerging from the speleothem are visible, too.

cellolytic *Cytophaga* (Kunicka-Goldfinger, 1982). From the autotrophs, nitrifying bacteria and *Thiobacillus ferrooxidans* were found. The trophic mode of life of the microbial flora in Cueva de los Guarachos was adapted to the decay of bat and bird excrement, as well as fruit remnants from their diet.

Phototrophic organisms – diatomaceans – were found to contribute to the formation of similar speleothems in Japan and USA (Kashima et al., 1987; Kashima and Ogawa, 1995). These speleothems, however, occurred close to the entrance, whereas the speleothems examined in this paper came from the deepest parts of the cave.

Much larger opal sinter deposits are known from hot springs and geysers. These also contain abundant microbial assemblages, in which cyanobacteria dominate, i.e., phototrophic organisms (Jones et al., 2001b; Konhauser et al., 2001; Konhauser et al., 2003).

In this study, the character of the filamentous microbes forming the central columnal stromatolite is uncertain but may belong to heterotrophic bacteria, such as sulfide-oxidizing *Beggiatoa* or some nitrifying bacteria. The source of their nutrition may be dissolved organic matter in the water, but could also include plant and animal detritus brought from the surface, as indicated by tissues trapped in the stromatolites. There is also the possibility that the casts belong to cyanobacteria. The simple septate tubes resemble *Phormidium* or other representatives of the order *Oscillatoriales* (Golubic, 1976b, p. 135), and the double-walled (probably sheathed) ones are similar to *Cyanostylon* (see Golubic, 1976a, Pl. I, Fig. 5), or *Entophysalis* (Golubic, 1976b,

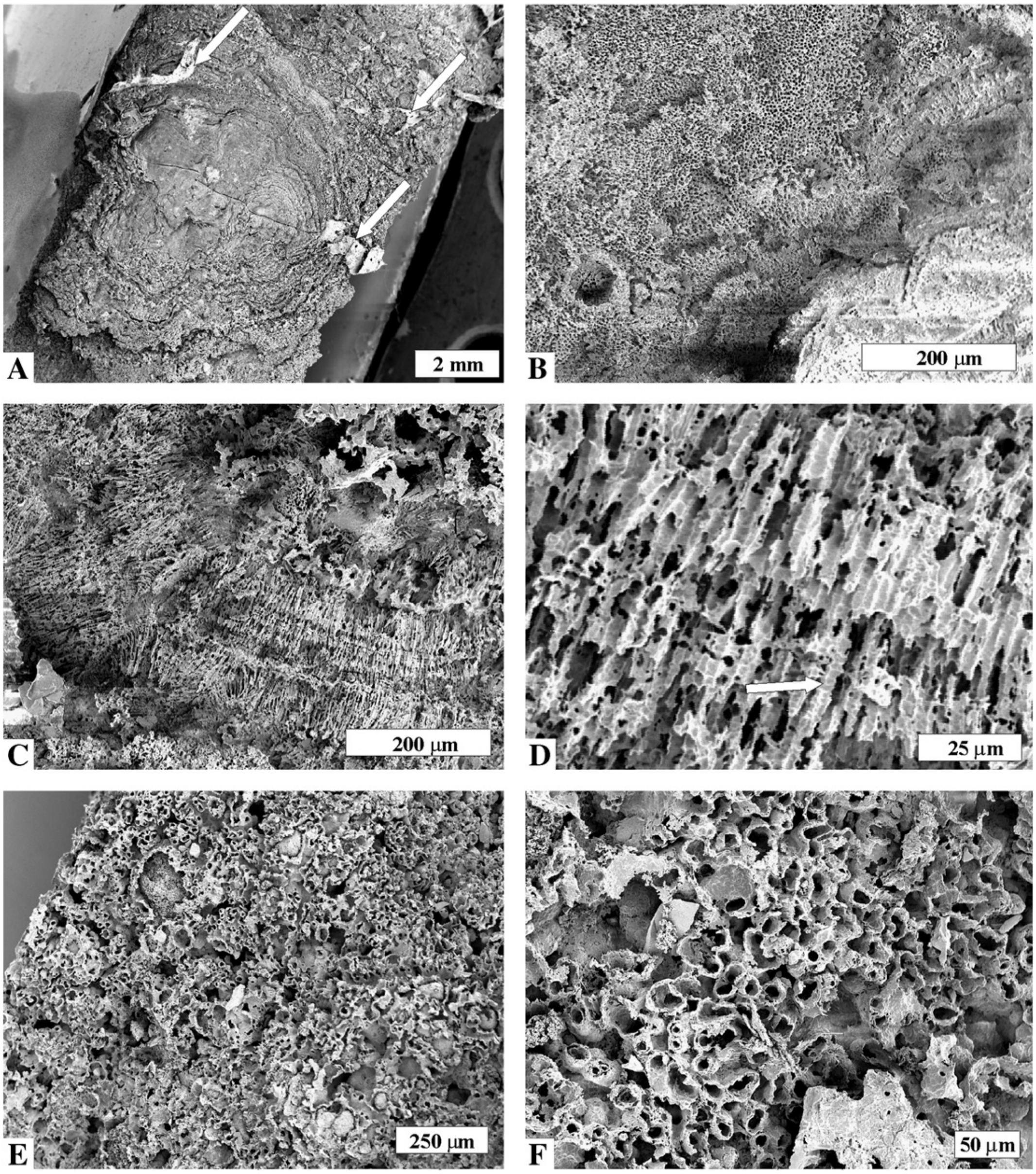

Fig. 11. SEM images of the etched central stromatolite. (A) Transverse cross-section through a branch of the black coral (low magnification) mostly formed by concentric opal laminae. The etched surface reveals leaf-like structures (arrows), resembling artifacts protruding directly from the speleothem. Most probably, they represent organic structures (perhaps remains of plant tissue) trapped in the stromatolite. (B) Pores representing cross-sections of tubular casts after filamentous microbes. (C) Longitudinal cross-sections of the encrusted mat of filamentous microbes. (D) The same under larger magnification. On the inner sides of some tubes there are remains of regular septae (arrow), indicating that the filaments were sectioned. (E) Irregular double-layered cross-sections of tubes likely representing casts after microbes. (F) Detail of previous figure.

p.117) from the order *Chroococcales*. However, exact determination of microbes exclusively on the basis of the silicified remnants and casts is almost impossible (Jones et al., 2001b; Konhauser et al., 2003). For the complete identification of cyanobacteria, about 37 characteristics are needed, e.g., cell morphology, ultrastructure, morphology of colonies or filaments, genetic characteristics (DNA), cultivation conditions and life conditions (Castenholz, 2001). In the material studied, only the morphology of colonies is visible. The morphology of the microbes forming the peloidal zone is more unambiguous; they bear many features indicative of nostocalean cyanobacteria.

The presence of cyanobacteria, which are generally phototrophic organisms, in caves would not be as surprising as it seems to be. Some cyanobacteria do not withstand an excessive light that can damage their cells (Vincent and Roy, 1993; Quesada and Vincent, 1997). Some of them produce protective pigments in extracellular sheaths (e.g. *Lyngbya estuarii* produces pigment scytonemine — Kylin, 1937); others are able to protect themselves against excess light by boring into the substrate, e.g., endolithic boring cyanobacteria *Hormathonema* and *Hyella* (Golubic, 1976a). The genera *Fisherella* and *Calothrix* are even able to change their mode of life to slow heterotrophic in complete darkness (Whitton, 1987).

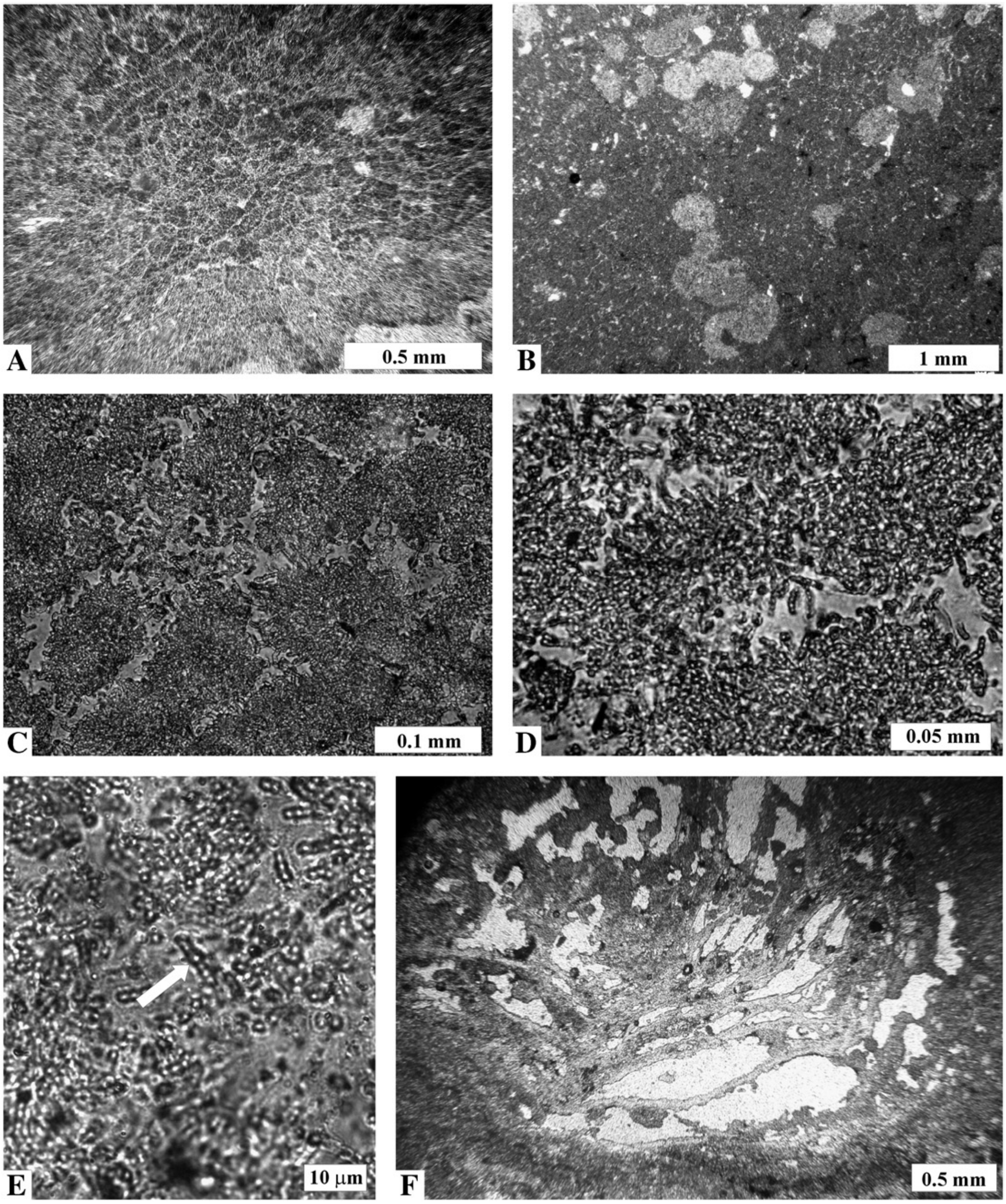

Fig. 12. Thin-section images of the porous peloidal stromatolite. (A) View of part of the peloidal stromatolite, with the structure replaced by mud-crack-like appearance. (B) Sphaeroidal bodies in the "champignon". Together with peloids these mostly resemble sphaerical bodies formed by *Nostoc* colonies. (C) Peloids from the outer, less encrusted part of the "champignon". These are obviously formed by short chains of microbial cells. (D) Enlarged view of peloids from the outer part of the speleothem. (E) Some larger cells (arrow), most likely representing heterocytes — a determining feature of the order Nostocales. (F) Silicified relics of organic structures most likely from insects, spiders or plants, trapped in the central zone.

Finally, the most convincing fact is that some cyanobacteria, e.g. *Geitleria calcarea* and *Scytonema julianum* have been found to live in caves (Friedman, 1955; Bourrelly and Depuy, 1973). *Nostoc* is also easily adaptable to a heterotrophic mode of life, and is a common symbiont (endobiont) in lichens and higher plants. In addition to photosynthesis, its main nutrient source is nitrate fixation (symbiosis of higher plants with *Nostoc* provides them with nitrogen). In our material, only a few heterocytes were found, suggesting that the cyanobacteria grew in a nitrogen-rich environment and were not nutrient stressed, as they did not need to form these nutrient-supply cells. *Nostoc* has also been reported from caves in Israel, growing in various zones, from well illuminated to complete darkness (Vinogradova et al., 1998). The above mentioned three principal microbial morphotypes show that the diversity of microbes participating in speleothems construction is restricted when compared to the diversity of cyanobacteria occurring on the top of the Chimantá Tepui (Ahti, 1992).

Siliceous speleothems which originated from the encrustation of spider threads have never previously been mentioned in the literature. Spiders are ubiquitous in the Cueva Charles Brewer because there are many insect species, either autochthonous or conducted by the river from the surface. The spider threads serve

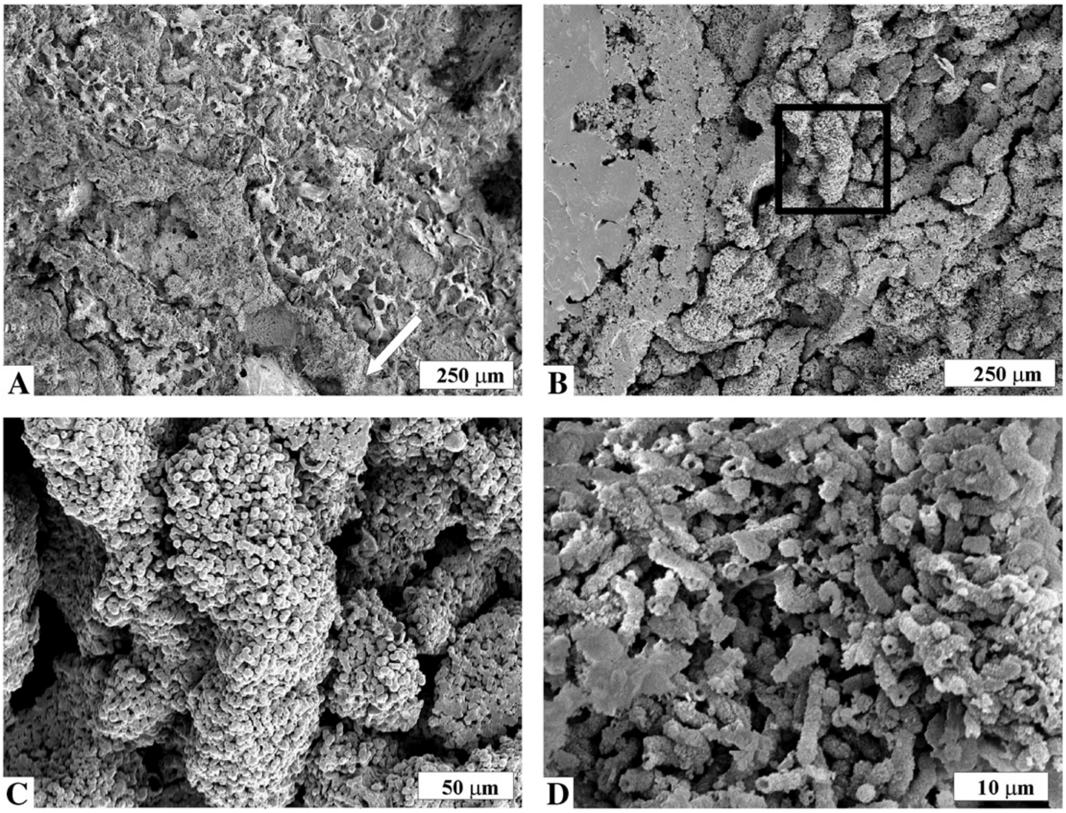

Fig. 13. (A) Irregular network structure that contributes to formation of the alveolar zone of the columnar stromatolite. (B) Freshly broken surface of black coral revealing peloidal layer placed between two cemented layers of compact stromatolite. The peloidal layer is, except in its innermost part (upper left side of the peloidal layer), only slightly affected by cementation. (C) Detail from the previous figure showing enlarged peloid. On its surface, irregular tiny spherules are visible but the microbial structure is completely obliterated by diagenesis. (D) Peloids from the outer, less silicified zones of speleothems showing better preserved microbial structures. Microbes encrusted by silica are visible as meshwork of short curved tubes that show no diagnostic features.

only as supporting structures during the speleothems growth. Their presence was recorded not only on “cobweb stalactites” but also on numerous other speleothems, such as “dolls”, “guácimos” and “black corals”, and this is evident from the SEM photos.

6. Conclusions

Siliceous speleothem samples from the Cueva Charles Brewer are predominantly of microbial origin and can be named biospeleothems. Despite their variable shape, their principal structure and origin are similar. The speleothems consist of laminated stromatolites (mostly forming the central zones) which is compact and well cemented. Its structure is mostly formed by filamentous microbes that may be either heterotrophic bacteria or cyanobacteria that are adapted to a heterotrophic mode of life. In some speleothems, the stromatolite is covered by layers formed by microbial peloids which were most likely created by nostocalean cyanobacteria. The peloidal stromatolite is porous and capillary forces can draw water as high as 10 cm. In this way, the water can reach the top of the speleothem where microbes actively live. Alternatively, a fine aerosol spray that is continuously present in the cave may deliver silica and water to the active growth surface. Hydrogeochemical research showed that the condensed cave moisture is the main silica-bearing agent. Spider threads that occur on most of the speleothems may serve as supporting structures for speleothem growth.

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