

VENEZUELAN TEPUI

THEIR CAVES AND BIOTA



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Cover: Roraima Tepui from the E, with Kukenán and Yuruaní tepuis behind.

Photo: Charles Brewer-Carías

VENEZUELAN TEPUIS THEIR CAVES AND BIOTA

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1. Preface

The world at the top of the tepuis of Venezuela is amazing. Ever since Sir Arthur Conan Doyle wrote “The Lost World”, the enigma of the South American steep and isolated table-mountains have attracted many people. Everyone in our research team dreamt about exploring these “blank spaces on the map”. However, despite this great attraction, scientific literature concerning tepuis has remained rather scarce. We are therefore proud to present this scientific monograph on tepuis, which is considered to be only the second issue of its kind, following the work of Huber (1992). This volume summarizes the main scientific results of expeditions to these tepuis between 2002 and 2011. The major research described in this monograph is dedicated to the great caves discovered in Roraima and Churí tepuis. The geological research was accompanied by biological research on cave and surface fauna, with a special focus on malacofauna, herpetofauna and insects. Although some of the data from this research has been previously published in scientific articles, it did not always obtain the justifiable space to present all gathered documentation and to elucidate all relevant scientific problems from a greater perspective. It is therefore our great pleasure to present this monograph containing detailed information on all research currently performed by our interdisciplinary research team. This is accompanied by a large number of fascinating photographs and several informative maps and diagrams. The greatest benefits to be gained from this combined monograph compared to short scientific publications is that more space is available to discuss currently unresolved problems, to ponder new intriguing questions and to envisage future necessary research. It is our sincere hope that all our readers will appreciate the unique information presented in this manner, and we hope you will really enjoy this monograph and find interesting topics for your research.

2. Cave systems in Churí and Roraima tepuis – geomorphology, speleogenesis and speleothems

2.1. INTRODUCTION – STUDIED AREAS, GEOLOGICAL SETTING AND CLIMATIC CONDITIONS

The main feature of the area of Guyana, encompassing southern Venezuela, northern Brazil and Guyana are its tepuis. These tepuis are table-mountains composed of Precambrian quartzites and sandstones from the Guyana Shield, rimmed by steep cliff walls. More than 100 table-mountains can be found in this area, and the tepuis provide important habitats for a great variety of endemic flora and fauna. Their isolated environments produce interesting and authentic laboratories harbouring different kinds of evolutionary processes. Many organisms show signs of endemism, often tied to one specific tepui where their individual evolution took place. An example of this can be found in Chapter 3 which summarizes the results of zoological research focused on malacofauna and the fauna of reptiles, amphibians, and insects.

Karst structures with large subterranean systems were also discovered during the exploration of these tepuis' isolated environments. The Chapter 2 devoted to this phenomenon describes their speleology and geomorphology, and also elucidates the genesis of these cave systems and the origin of their unique speleothems.

From a geological viewpoint, the caves and surface areas explored herein are situated in the Venezuelan Guyana, in the northern part of South America (southeastern Venezuela – Gran Sabana, Bolívar State, Fig. 1). The Gran Sabana area comprises Archaean rocks of the Guyana Shield which is the northern part of the Amazonian Craton. The Guyana Shield has a Proterozoic sedimentary cover formed by Roraima Supergroup sediments which are mainly clastics derived from the northern Transamazonian Mountains (Fig. 2). Sedimentological studies showed that the depositional environments ranged from alluvial fans to fluvial braided-river deposits together with lacustrine, aeolian, tidal, shallow-marine deposits and some shallow water turbidites (Reis & Yáñez, 2001; Santos et al., 2003). Sandy continental deposits are dominant here. The Roraima Supergroup mainly forms tabular plateaus (tepuis), cuestas and hogbacks which rise steeply above the Paleoproterozoic basement (Fig. 3). The thickness of the group ranges from 200 m to approximately 3000 m, and it consists of the following lithostratigraphic units arranged in stratigraphic order (see Fig. 4); the Arai Formation, Suapi Group, Uaimapué Formation and the Matauí Formation (Reis & Yáñez, 2001). Tepuis developed mainly in the uppermost, Matauí Formation formed by quartzites and sandstones. Their age was determined as 1873 ± 3 Ma (Late Paleoproterozoic), based on

U-Pb analyses of zircons from a green ash-fall tuff of the Uaimapué Formation (Santos et al., 2003). Since most of the previous authors accepted the theory that quartz dissolution require a long time, the recent landscape, including commencement of the cave-forming process, is considered to be inherited from the Mesozoic period (e.g. Cretaceous – see Galán & Lagarde, 1988; Briceño et al., 1991). However, there is currently no supporting data for this estimation. The oldest datings (U-Th) of siliceous speleothems provide only the Pleistocene ages (Lundberg et al., 2010^a).

The speleological research of our team started in 2002 with the discovery of the Ojos de Cristal Cave System, which is currently estimated to be the second longest discovered sandstone cave system in the world as discussed in chapters 2.2. and 2.4. The geological and geochemical data presented in this chapter were collected in expeditions during the 2007 and 2009 dry seasons. The main research targets of these expeditions were the geomorphological forms on the surface of the Chimantá Massif (the partial plateau named Churí Tepui) and Roraima Tepui, as well as the caves in these tepuis which form the two largest sandstone cave systems in the world: the Charles Brewer Cave System (Šmída et al., 2010) and the Ojos de Cristal Cave System (Šmída et al., 2003). Different types of geochemical and geotechnical measurements were performed in the largest cave in the Charles Brewer Cave System – the Cueva Charles Brewer (Fig. 16), as well as in Cueva Cañon Verde, Cueva Colibrí sector and Cueva Juliana. Sampling was also taken from Cueva de los Pémones and Cueva de Gilberto in the Ojos de Cristal Cave System (Fig. 26).

The climate in the wider area of the Gran Sabana is mainly influenced by meteorological conditions in the tropical Atlantic Ocean. The sea surface temperature (SST) meridional gradient over the tropical Atlantic has a profound impact on the climate and weather conditions in the Gran Sabana area, which is located in the eastern part of South America. Several additional parameters may also exert either direct or tele-connected indirect atmospheric influence on climate variability over South America. This influence also extends to high-latitudes (Garraud et al., 2009) by high-latitude forces such as the Antarctic Oscillation (AAO), the North Atlantic Oscillation (NAO) and the El Niño Southern Oscillation (ENSO) phenomena, rooted in the ocean. During the last decade, climatologists have therefore begun to describe the climate of the northern and central part of this continent as monsoon-like (for further information, please see the updated review of the “South American Monsoon System [SAMS]” by Vera et al., 2006).



Fig. 1: Location of the examined tepuis.

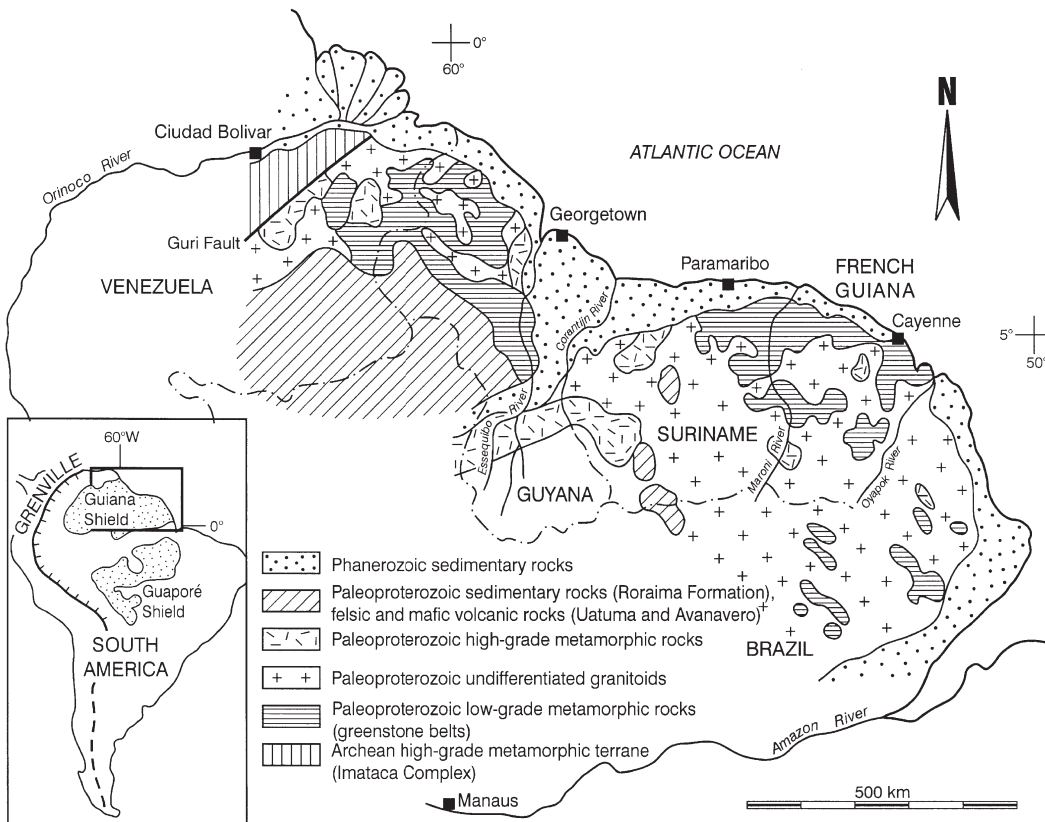


Fig. 2: Geology of the Guyana Shield – from Voicu et al. (2001).

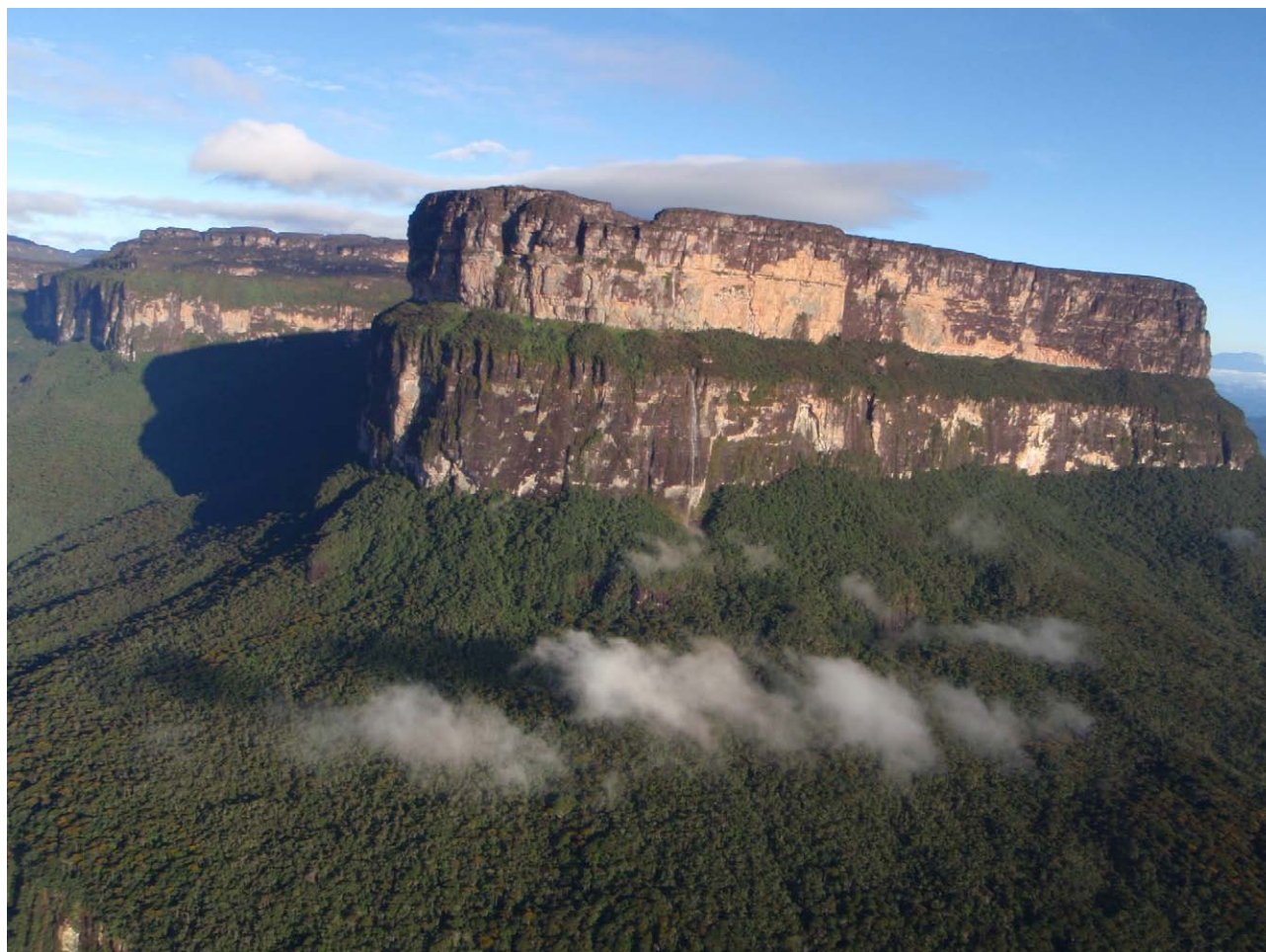


Fig. 3: Example of tepuis – tabular plateaus formed by arenites of the Roraima Supergroup, covering the Guyana Shield. Tirepón Tepui, Chimantá Massif.

The climate of the Gran Sabana region has been classified as tropical, because of its extremely humid headland climate (Galán, 1984). According to climatic data from the Kavanayen meteorological station, the annual precipitation of 2,548 mm is unevenly distributed, with a mean monthly rainfall of 60 mm during the December to March dry season (Hernández, 1994).

Unfortunately, only a few authors have currently presented climatic data measured directly on the mesetas of the tepuis (Steyermark, 1967; Huber, 1976; Colonnello, 1984; Galán, 1992). According to their findings, the Chimantá region is characterized by a tropical climate, with an isothermic regime due to its geographical latitude. However, the climatic conditions on the mesetas of the tepuis are quite different to those in the Gran Sabana surrounds. The main differences consist of lower average temperatures and considerably higher rainfall, resulting in extreme humidity. Although the thermal conditions are quite uniform throughout the year, remarkable oscillations of the temperature may occur on a daily basis. While the medium annual thermal oscillation is only around 2 °C, the medium daily oscillation often exceeds 10 °C (Galán, 1992). The vertical thermal gradient is 0.6 °C (Röhl, 1952). Lower annual medium temperatures were recorded with increasing height: these were 21 °C at 1,000 m a.s.l. and 13.9 °C at 2,200 m a.s.l. (Galán, 1992).

The mean annual rainfall at 2,200 m a.s.l. is approximately 3,351 mm (Galán, 1992). Normally, only the first part of the year from January to March is quite dry (Fig. 5), with the rest of the year characterized by differing amounts of rainfall. The rainy season generally begins in mid April and ends in December, with the highest rainfall recorded from May to September.

Different total annual rainfalls have been recorded dependent on height and region. For example, 2,500 mm was registered at 1,200 m a.s.l. on lowlands in the Kavanayen area, and 3,600 mm on the highest part of the meseta at 2,420 m a.s.l.

A summary of the rainfall distribution and the main wind direction and circulation is depicted in Figure 6. Based on this figure, it is quite obvious that rainfall increases with height, which in turn creates a cloudy level around the higher parts of the walls and mesetas. These conditions consequently induce both the cold and the extremely humid climatic conditions on the mesetas, and also the higher rainfalls around them especially during the rainy season.

Since the retention capacity of the soil and the massif creating the karstic aquifer is rather weak, surface and underground stream discharges become strongly dependent on the actual rainfall. The stream discharge response to rainstorms is therefore usually very rapid. A perfect example of this is the underground

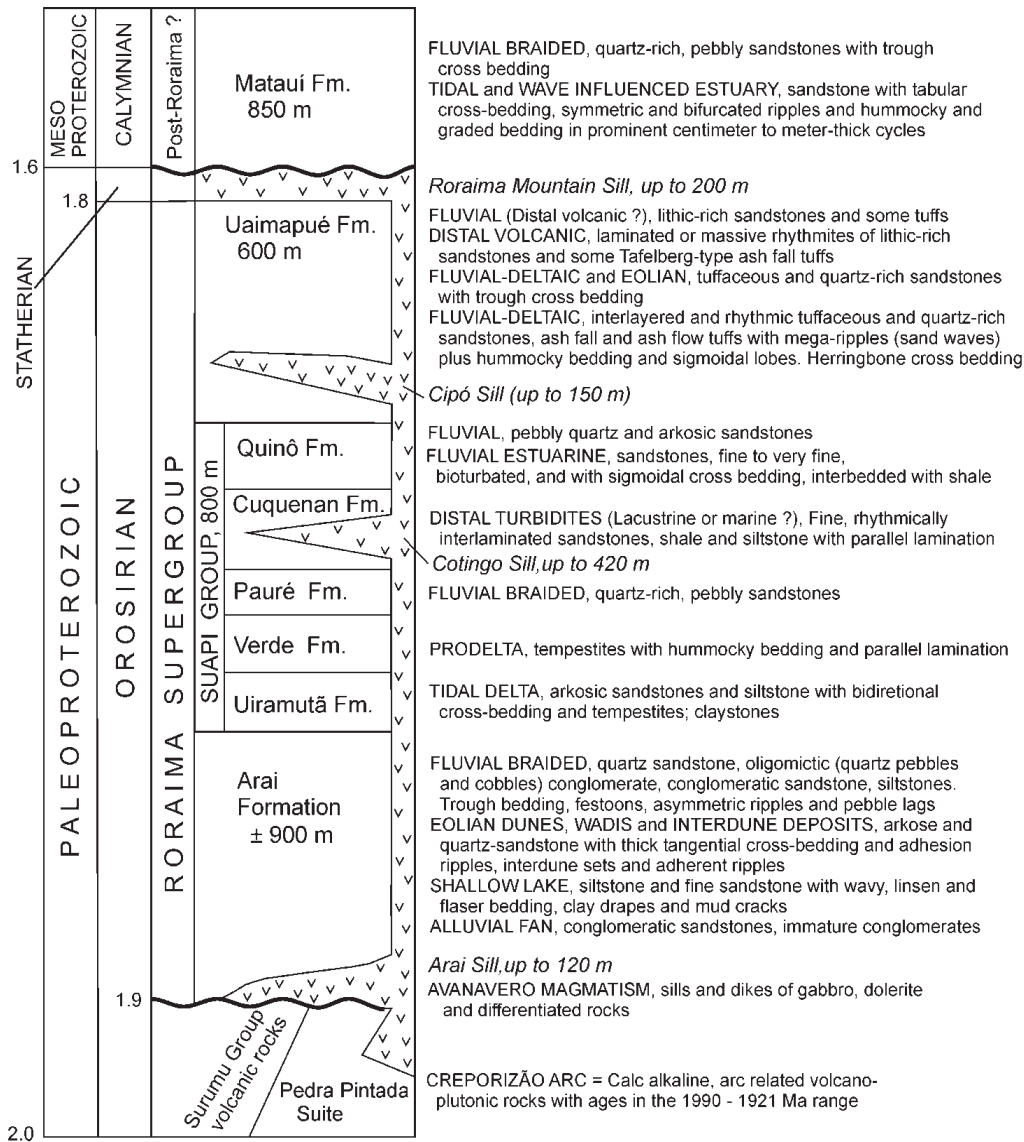


Fig. 4: Lithostratigraphic scheme of the Roraima Supergroup and its depositional systems. From Santos et al. (2003), slightly modified.

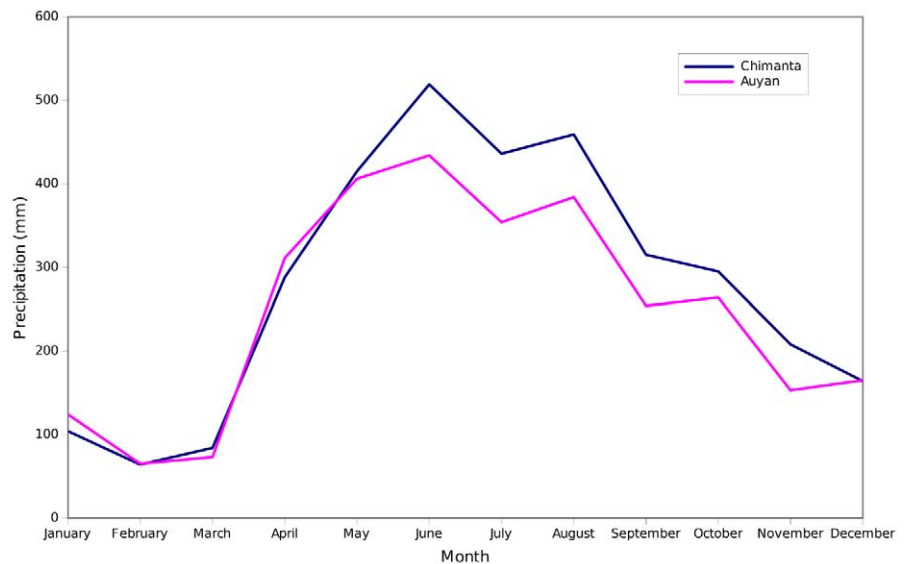


Fig. 5: Annual rainfall distribution on the mesetas of Chimantá Massif and Auyán Tepui, according to data published by Galán (1992).

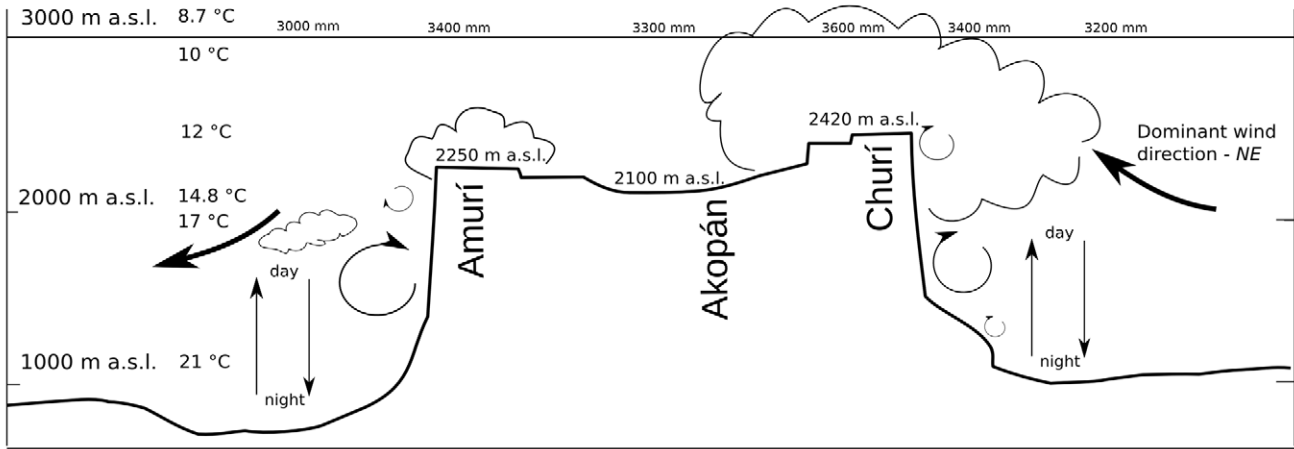


Fig. 6: Rainfall and temperature distribution in the area of the Chimantá Massif, according to Galán (1992).

stream of the Cueva Charles Brewer, where an average rainfall event can cause a water level increase of approximately 6 metres in a few hours (Fig. 7).

As mentioned above, there is very little data available for table-mountain climatic and hydrologic conditions, and, consequently, longer time-series data for temperature, rainfall, evapo-transpiration and stream discharges are unfortunately lacking. These data are necessary for evaluation of impacts from climatic changes and, in combination with hydrogeochemical

data, they are mandatory for correct evaluation of the overall mass transfer rate from the table-mountains to the lowlands.

2.2. HISTORY OF CAVE EXPLORATION ON TEPUIS

The table-mountains of the Guyana Highlands currently remain an ever-lasting treasure-trove for different types of scientific

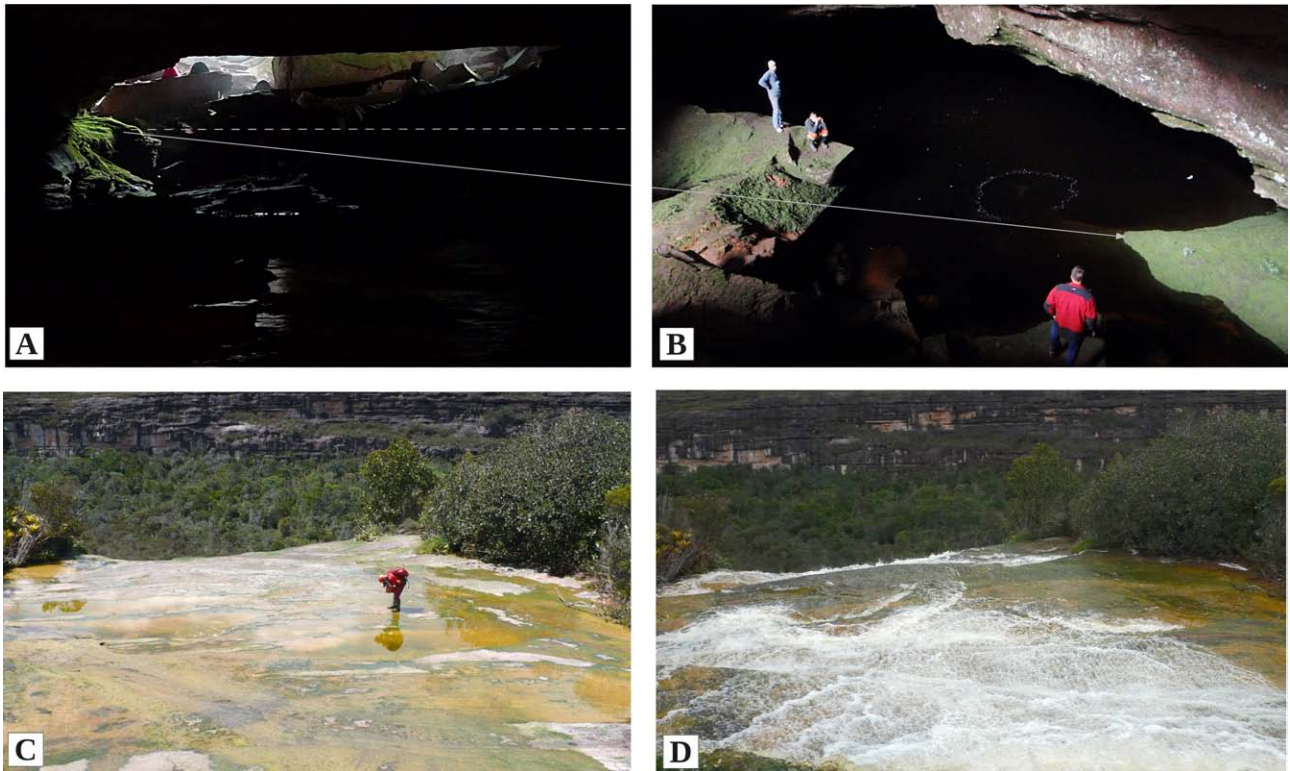


Fig. 7: Rapid water level changes in underground surface streams. A – View of the entrance of Cueva Charles Brewer; the dashed line denotes the approximate cave water level during the maximum observed water level a few hours after heavy rain. B – The water level in the stream close to the entrance of the Cueva Charles Brewer. The arrow points to the water level at the same site as in picture A. C – Río Olinka depicted during a dry period. D – Río Olinka shown shortly after heavy rain.



Fig. 8: Autana Tepui – where the Venezuelan quartzite speleology originated.

discoveries. They were first described by the royal surveyor Robert Schomburgk in 1838, and the first expedition to the Roraima Tepui meseta was led by Sir Everard im Thurn and Harry Perkins in 1884. Since then, several hundred general scientific expeditions, including tens of speleological expeditions, have explored these mountains, and fascinating discoveries including numerous novel species and unique caves have been made on virtually every trip.

Early speleological explorations of the quartzite massifs of the Guyana Highlands began on the Autana Tepui – a gigantic rock pillar towering 1,300 m above the Venezuelan Amazonia (Brewer-Carías, 1972, 1973^a, 1976^a; Colveé, 1972, 1973; Urbani & Szczerban, 1974; Szczerban & Gamba, 1973; Szczerban & Urbani, 1974; Galán, 1982; Pérez La Riva, 1976; Pérez La Riva & Reyes, 1976; Urbani, 1976^a; Owen, 1978). Speleological explorations then continued on the Jaua-Sarisariñama – an extensive meseta hidden in the deep jungle of the Río Caura River Basin (Urbani & Szczerban, 1974; Szczerban & Urbani, 1974; Szczerban & Gamba, 1973; Brewer-Carías 1973^b, 1976^b; Nott, 1975; Urbani, 1976^{b,c}).

The cave on the Autana Tepui (Fig. 8) was first described in 1757 as a portal resembling a large stone eye set in the 800 m southern wall (Gilij, 1780). Although this was visible from a long distance, no further detailed explorations were performed in those days. The first actual speleological expeditions were led by the naturalist Charles Brewer-Carías in the early 1970s. To the amazement of the entire party, they discovered that this

cave consisted of several fascinating horizontal passages up to 395 m in length. These entered the walls from several different locations, suggesting inter-connections throughout the entire mountain range (Brewer-Carías, 1970, 1972).

Further speleological explorations were then described by other intrepid explorers, including Urbani & Szczerban (1974) and Brewer-Carías (1976^b). During these expeditions, the Venezuelan scientists made several important discoveries, including the new mineral $KAl_7[Cl](OH)_8[(NO_3)_2]_2 \cdot 8H_2O$, named *sveite* after La Sociedad Venezolana de Espeleología (SVE) (Martini, 1980; Martini & Urbani, 1984). The Cueva del Cerro Autana became the first quartzite cave explored in great detail. The unique nature of this cave raised many intriguing questions, such as; i) was the cave created by an underground river, as indicated by erosion marks on the cave walls?; ii) when was the cave created – was it during a time when the surrounding land was eroded several hundred metres deep?; iii) where did the river flow?; and above all, iv) do other similar caves exist, also formed by this ancient river on other table-mountains in this area, and also in other parts of the world?

These intriguing questions will hopefully be answered by future explorations of the other table-mountains throughout the world. However, it was obvious from the start that this would not be an easy quest because the many expected difficulties were indeed encountered. The first problem, of course, was limited access to the area, with helicopters supplying the only means of overcoming the 900 m steep walls of the Autana Tepui to reach the Cueva del Cerro Autana. Moreover, this helicopter had to be small enough to land and manoeuvre on the meseta, so that the exploration party could descend 150 metres on a rope-ladder to the cave entrance.

The surface of the extensive meseta of the Sarisariñama Tepui is covered by dense jungle vegetation at 2,300 m a.s.l. Although it looks flat, the meseta is in fact characterized by huge vertical depressions with diameters up to 350 m and by steep walls of this same depth (Fig. 9). The huge passages running off these depressions form entrances into the rock massif, thus making it obvious that discovery of these unique caves would have been impossible without such manoeuvrable helicopters.

The depressions of Sima Mayor with depth of 314 m and Sima Menor with depth of 248 m on the Sarisariñama Tepui are drained by springs several kilometres distant (e.g. Brewer-Carías, 1973^b, 1976^{b,c}; Urbani & Szczerban, 1974; Szczerban & Urbani, 1974; Szczerban & Gamba, 1973). Detailed mapping of these depressions showed that based on the total measured volume of 18 million m³, the Sima Mayor Abyss can be classified as one of the largest known karst cavities in the world. Two cave segment branches enter in opposite directions from the lowest part of the smaller depression known as Sima Menor (or Sima Martel *sensu* De Bellard, 1974^{a,b}, 1975; or Sima Gibson *sensu* Brewer-Carías, 1974, respectively). These are called Cueva de la Cascada and Cueva de los Guácharos. Another huge karstic collapse called Sima de la Lluvia Cave is situated close to these sites. This one is 1,352 m long, including its Cueva de los Cristales branch. Due to the unique nature of these caves, two expeditions explored this site within a short period. The first expedition was led by Charles Brewer-Carías



Fig. 9: Sarisariñama Tepui plateau with the huge Sima Mayor Shaft 300 m in diameter.

who, together with his team, described their work in papers written in the 1970s (e. g. Brewer-Carías, 1973^b, 1976^b) and in a beautiful popular-scientific book (Brewer-Carías, 1983). Another, Polish-Venezuelan expedition was led by Franco Urbani. Their work is described in various speleological papers (as in Zawadzki et al., 1976; Dyga et al., 1976; CEDV, 1976), and also in popular-scientific papers and short notes (Kuczynski, 1976^{a,b}; Koisar & Solicki, 1977^{a,b}).

Several additional caves have been discovered on other Venezuelan table-mountains, as briefly summarized below in chronological order:

- The G1-G3 caves, with overall length of 130 m on the Guaiquinima Tepui, were described by Szczerban et al. (1977) and Urbani (1977).

- Several caves (assigned with the Bo. 4 – Bo. 7 – numbers according to the list of the Bolívar State in the National Speleological Cadastre) on the uplands of the Sierra Pacairima (Pacaraima) are described in papers by Urbani (1977) and Pérez La Riva (1977).

- Cueva (Sima) Kukenán in the mountain of Kukenán (Matuái) Tepui was described by Pérez La Riva et al. (1986^a), Michelangeli et al. (1993), and Doerr (1999).

- All caves discovered on Yuruaní Tepui (Galán, 1986), Sierra

Marutani (Bo. 9 – Bo. 19), Kukenán Tepui (Bo. 22 – Bo. 25), Acopán and Amurí tepuis (Bo. 40 – Bo. 53), Cerro Chirikayén (Bo. 90 – Bo. 91) as well as the short caves in the Río Aponguao River Basin (Bo. 20 – Bo. 21). These caves are described by the National Speleological Cadastre – Catastro Espeleológico Nacional (earlier Catastro Espeleológico de Venezuela).

- Several different caves (Galán, 1988) on mountains and partial massifs of Sarisariñama (3 caves), Guaiquinima (9 caves), Eutoarima (1 cave), Aonda (8 caves), Urutany (2 caves), Auyán Tepui Norte (1 cave), Tramén (1 cave), Aguapira (15 caves), Kukenán (5 caves), Roraima (1 cave) and Yuruaní (2 caves), in the foreground of the table-mountains near Santa Elena de Uairén – El Paují (4 caves) and on the mountain of Aponguao (2 caves), Serranía Pereña (2 caves), Chimantá (1 cave) and Autana (3 caves). 60 quartzite caves with 14,504 m overall length were located in the Estado Bolívar (57) and Territorio Federal Amazonas (3), according to Galán (1988).

- One large cave which is considered insignificant due to doubt over its continuation was discovered on the Ilú Tepui (Bo. 33), and there are also several abris (crepuscular caves) and pseudokarst caves noted; for example in the Distrito Cedeño (Bo. 56 – Bo. 82).

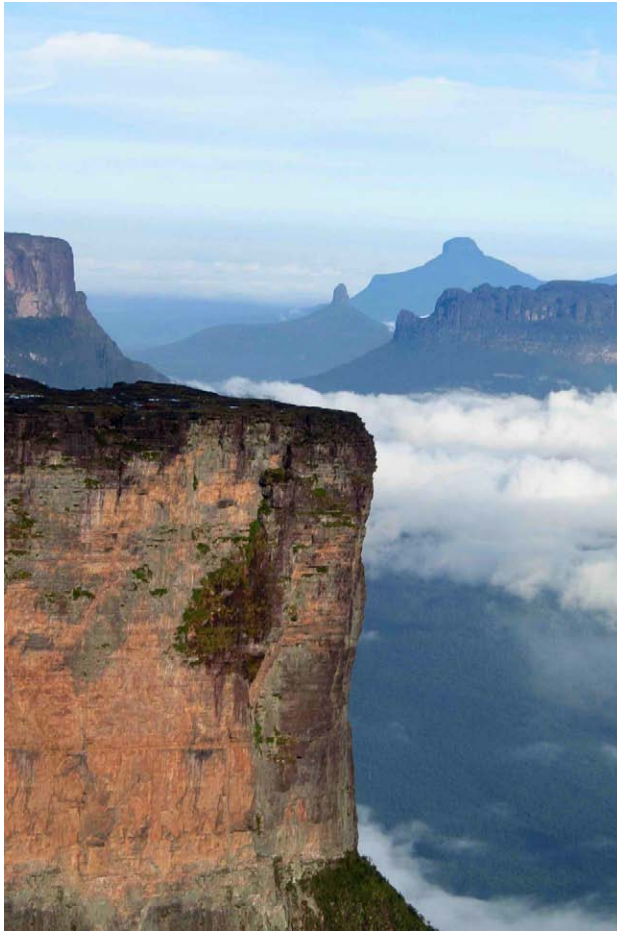


Fig. 10: Roraima Tepui table-mountain, “the Prova” northern vertical wall is 600 m high.

– Some caves have also been discovered on the Chimantá Massif (Maeztu et al., 1995; SVE, 1994) and Roraima (Fig. 10).

– Approximately 100 quartzite caves were listed by Ghneim (1999) in his bibliography of the Venezuelan caves. Of these, 91 were located in Bolívar State (names marked with the abbreviation Bo.). The remainder were located in the territory of Amazonas (names marked with Am., as in the Cueva del Cerro Autana). Since then, other quartzite caves have been discovered in the same area. For example, according to the Catastro Espeleológico Nacional, there were 107 known caves in Bolívar State in 2006, and most of these were formed by vertical cracks and/or short underground passages.

Thanks to international expeditions led by Venezuelan, Italian and Polish research leaders, cave research in this area has expanded continuously since the 1980s. During this period, several novel fascinating caves and cave systems were discovered. These included deep tectonic valleys and crevices, up to several hundred metres in depth and inter-connected by underground passageways. Their water was derived from rainwater draining from the surface along the impermeable base of the table-mountain. Some of these expeditions received public attention, especially the discovery of the Sima Aonda Cave located on the meseta of the Auyán Tepui (2,560 m a.s.l.). With its 383 metre

depth, this was considered the deepest quartzite cave in the world for many years.

The caves from the Auyán Tepui were described by Galán (1983^{ab}, 1984), Pérez La Riva et al. (1986^b), Inglese & Tognini (1993), Pezzolato (1993, 1996), Piccini (1994), Gori et al. (1993), Bernabei et al. (1993), Carreño (1996), Piccini et al. (1994), Mecchia et al. (1994) and also in the monographic issue of the journal *Progressione* (Bernabei, 1994). In the 1990s the Sima Aonda Superior Cave with its dimensions of 2.1 km length and 320 m depth (later re-evaluated to 362 m) (Bellomo et al., 1994; Forti, 1994; Martínez, 1989; Tognini et al., 1995; Urbani & Bordón, 1997) was surpassed by the Sima Aonda 2 Cave with its depth of 325 m, and also by Sima Aonda 3 Cave with its depth of 335 m which were discovered by Italian speleologists. Later, the 2,950 m long and 370 deep Sima Auyán Tepui Noroeste assumed supremacy in size (Bernabei et al., 1993; Bernabei, 1994; De Vivo et al., 1997; Piccini, 1995; Mecchia & Piccini, 1999). Urbani (1993) listed six quartzite caves longer than 1 km and 13 caves longer than 2 km, together with 13 caves deeper than 200 m and 13 caves deeper than 250 m. These impressive publications by the Italian speleological group La Venta showed that the Auyán Tepui caves are in fact an extensive system of gigantic tectonic crevices, called “grietas” in Spanish. These grietas are interconnected by smaller-scaled sub-horizontal channels. The draining function of this underground system is quite clear, however there are some disputes about whether the above-listed localities are “caves” or “karst phenomena”. According to recently accepted classification, only the channels interconnecting the grietas can be acknowledged as karstic caves. Their documented depths and lengths are enlarged by adding the vertical sectors of the grietas.

At the end of the 1990s Brazilian cavers explored the following caves; (1) the two crevice caves Grutta do Centenario (3.8 km long, 481 m deep) and Grutta da Bocaina (3.2 km long, 404 m deep, which are ranked the 4th and 5th longest quartzite caves in the world). These are located on the massif Pico do Inficionado in Minas Gerais State; (2) the Gruta Alaouf Cave (1.2 km long, 294 m deep) was also described there (Faverjon, 2003; Auler, 2002, 2004; Rubbioli, 1996, 1998, 2001, 2003; Dutra 1996^b, 1997; Hirashima, 1997; Perret, 2001; Sausse, 2001; Chaimovicz, 2001; Rodríguez & Silverio, 2002; Dutra et al. 2005); and (3) other quartzite caves were described in the southern part of the Minas Gerais State (as in Dutra, 1996^b). According to Rubbioli (1996) the first map of a quartzite cave was prepared in 1952. This cave is currently known as Grutta do Centenario and its characteristics suggest a tectonic origin, with only secondary contributions to its morphology from dissolution processes.

Although it had previously been referred to controversially as “pseudokarst” in some parts of Europe, quartzite karst has now been described in many sites throughout the world under its correct title. Although quartzite caves can also be found in other territories besides the Guyana Highland, most of these are rather small. Examples of these small caves include; (1) the quartzite caves on the Mato Grosso Upland and in the state Minas Gerais of Brazil (as in Travassos et al., 2008; Wernick et al., 1977; Auler, 2002; Willems et al., 2005, 2008); (2) the 1.4 km long Caverna Aroe Jari Cave in the Mato Grosso Plateau was described by Borghi & Moreira, (2000, 2002); and (3) caves of this type have



Fig. 11: Gladys Lake at the end of a shallow rocky valley on Roraima Tepui – the ponor zone of Cueva de los Vencejos which was explored by Charles Brewer-Capriles and José Miguel Pérez in 1990.

also been discovered in several African states, including Chad, Niger, and Algeria (as in Busche & Erbe, 1987; Sponholz, 1989, 1994^{a,b}; Willems et al., 1996). However, several large quartzite caves have also been found at locations other than the Guyana Highland. These include those in South Africa, which harbours twenty of the longest quartzite caves, including Magnet Cave (2,490 m; Martini, 1990, 1994) and a Bat's/Giant's/Climber's Cave System (1,632 m; Truluck, 1996; Martini, 1981, 1982, 1984, 1985, 2000). The Czech Republic boasts the 27.5 km long crevice system in quartz sandstones called Poseidon (Mlejnek & Ouhrabka, 2008), which is predominantly open to surface, thus not a real cave. The Meghalaya area on the India/Bangladesh border has the famous 1,297 m long Krem Dam Cave (Oldham, 2003). Although the megtourism.gov.in website states that the Krem Dam Cave was formed in a coarse-grained facies of limestone which looks almost like sandstone, Breitenbach et al. (2010) reported only sandstone caves in the Meghalaya State.

These are in fact sandstones with quartz grains and carbonate matrix mixed with sandy limestones with quartz grains. In addition, pseudokarstic features have also been reported from Queensland, Australia (Wray, 2009).

An important year for quartzite speleology was 2002, when a unique cave was discovered by Slovak and Czech cavers Zoltán Ágh and Marek Audy on the meseta of the Roraima Tepui – Cueva Ojos de Cristal (Šmída et al., 2003). This meseta has a highest peak of 2,810 m a.s.l., and it borders three countries: Venezuela, Brazil and Guyana (Guayana Essequiba, the Reclamation Zone claimed by Venezuela). Although Roraima is very well-known due to Charles Brewer-Carías' text (Brewer-Carías, 1978), the real boom in quartzite cave discoveries began with the Czech-Slovak expedition in 2003 (Audy, 2003, 2008; Audy & Šmída, 2003; Šmída et al., 2003; Vlček, 2004). This team discovered a very unique extensive continuation of the cave, together with other horizontal underground passages on the table-mountain. This



Fig. 12: The main passage close to the entrance of Cueva Ojos de Cristal on Roraima Tepui.

discovery was a historical break-through, because it presented a much better approach to understanding the quartzite karst phenomenon in the Guyana Highland. Such an extensive inlet/outlet cave system, with its huge variety of morphological forms as described by the Czech-Slovak team is unique on a world scale. Besides the Cueva Ojos de Cristal, no other fluvial active system of horizontal passages measuring several kilometres was known in any massif in the world (Fig. 12). This cave was explored in great detail during the 2003 and 2007 expeditions. For a time, it was regarded as the longest in Venezuela (surpassed recently by the discovery of the 18,200 metre long Cueva El Samán limestone cave), and it was classified as the longest quartzite cave in the world shortly after its discovery. After 2006, its dimensions were documented at 15,280 m long and 73 m deep (Vlček & Šmída, 2007). Shortly after presentation of exploration results from the Cueva Ojos de Cristal in 2004/2005, a Venezuelan-Spanish-English speleological team re-mapped the same cave at 10,580 metres and renamed it Cueva Roraima Sur. This was despite the name Cueva Ojos de Cristal having been codified since 2003 and already quoted in all English-language literature (Šmída et al., 2005^{a,b}). Their exploration results were published (with foredate) in the Bulletin of the SVE (Galán & Herrera, 2005; Galán et al., 2004^{a,c}; Carreño & Urbani, 2004; Carreño & Blanco, 2004) and also in short notes in publications such as the Bulletin of the South American Speleological Federation (FEALC; as in Pérez & Carreño, 2004; Carreño et al., 2005; and Galán & Herrera, 2005).

In parallel with these discoveries, several other smaller crevice caves were discovered by Venezuelan cavers (Carreño et al.,

2002) on the Wei-Assipu Tepui, which is the “smaller sister” of Roraima and called also Roraimita (2,400 m a.s.l.). While Venezuelans documented caves on Aprada Tepui (Fig. 13), a Slovak team found shorter horizontal fluvial active caves on the Kukenán Tepui in 2006 (Vlček & Šmída, 2007).

Shortly after the discovery of Cueva Ojos de Cristal, other caves were also described on the Chimantá Massif (2,698 m a.s.l.). Although exploration of the mesetas of this massif commenced in the early 1990s (Briceño & Schubert, 1992^{a,b}), these newly discovered caves were explored and documented between 2004 and 2007 by Venezuelan and Czech-Slovak speleological teams led by Charles Brewer-Carías. The Charles Brewer Cave (Cueva Charles Brewer) with its two gigantic branches measuring 4,800 metres was volumetrically the largest quartzite cave in the world (Brewer-Carías, 2005^a). The quadratic profiles of its domes are typical for quartzite caves, and these are up to 100 m wide and up to 40 m high (Fig. 14). The volumes created in this manner are comparable with the biggest chambers in the limestone systems of Borneo, Vietnam and New Guinea (Owen, 2011). Several papers have been dedicated to this cave, and while most of these were published in prestigious speleological journals (Šmída et al., 2005^{a-c}), some also appeared in popular-scientific literature (Audy et al., 2004; Šmída et al., 2004; Audy & Šmída, 2005^{a,b}; Šmída & Brewer-Carías, 2005). A special monographic issue of the Bulletin of the Slovak Speleological Society (Spravodaj Slovenskej Speleologickej Spoločnosti) has also been dedicated to this cave (Šmída et al., 2005^h).

In addition to the Charles Brewer Cave, other relatively large caves were also discovered and documented on the Chimantá Massif during both the 2007 expedition (Audy et al., 2008; Šmída et al., 2007; Šmída et al., 2008^{a,b}; Vlček et al., 2008) and the 2009 expedition (Audy et al., 2010; Lánčzos et al., 2009^{a,b}, 2010^{a,b}; Šmída, 2009, 2010; Šmída et al., 2009, 2010^{a-c}; Vlček & Šmída, 2009; Vlček et al., 2009^{a-c}). The following new caves were also discovered and documented in the Chimantá Massif during these two expeditions; Cueva Juliana (3.0 km long), Cueva Zuna (2.52 km long), Cueva Yanna (1.08 km long) and Cueva Colibrí (4.0 km long). At the same time, a cave system 7.5 km long was formed by connecting the Cueva Charles Brewer and Cueva del Diablo caves. The Czech members of the 2007 expedition discovered and explored the 2.5 km long Sistema de las Arañas, and this has been described by Audy & Tásler (2007), Audy (2008) and Brewer-Carías & Audy (2010). The last two expeditions in 2009 discovered the important Muchimuk Cave, which was connected to the previously discovered Cueva Colibrí to form the Sistema Muchimuk–Colibrí cave system. Its dimensions then were 8.0 km long with 160 m denivelation (Šmída, 2009). This cave system is genetically connected with Cueva Charles Brewer. Since results from the last survey show that the ends of their main passages are located just a few metres apart, the explorers led by Charles Brewer-Carías consider that all these caves are inter-connected in the one 17.8 km cave system (Audy et al., 2010; Brewer-Carías & Audy, 2010). This system has recently been distinguished as the largest quartzite cave system in the world. It has been eponymously named the Charles Brewer Cave System, and it contains the 400,000 m³ Gran Galería Karen y Fanny, and with passages, in the Cueva Charles Brewer sector, averaging 30 × 60 metres as well.

In 2009, the Italian La Venta team made two discoveries. One consisted of the new 3.5 km long corridors in Sistema Akopán – Dal Cin – Maripak located on the Akopán Tepui, which also forms part of the Chimantá Massif. The second was the Cueva Auchimpé on Churí Tepui (Cueva Eladio, 1 km long; De Vivo, 2009; La Venta, 2009; Mecchia et al., 2009). The Italian cavers in 2009 – 2010 also directed two expeditions to Auyán Tepui, where they explored the beautifully decorated 0.7 km long Cueva Guacamaya, and the 0.3 km long Cueva del Águila. These were both very similar to the Cueva Charles Brewer, but smaller in size.

An important and surprising discovery was made in 2006 on the Serra do Aracá in the Brazilian part of the Guyana Highlands. This was the Abismo Guy Collet Cave and its 670.6 m depth made it the deepest quartzite cave in the world (Epis, 2006; Ayub 2007, 2008). Due to the currently accepted potential of quartzite massifs world-wide, we expect that this will remain the deepest known cave for quite some time.

A new survey of the Cueva Ojos de Cristal extended the cave length to 16,140 m (Šmída et al., 2008^{a,b}) and the Charles Brewer Cave System was likewise revised to 17.8 km (Audy et al., 2010; Brewer-Carías & Audy, 2010). This latter revision created a new world record (Tab. 1).

Research summary shows that approximately 50 speleological expeditions have been so far conducted to the Venezuelan table-mountains. Therein, 20 quartzite-karst areas were explored and documented, together with over 160 quartzite caves with a total length of 60 km (Vlček, 2010).



Fig. 13: Giant entrance portal of Cueva El Fantasma on Aprada Tepui. Note the helicopters on the cave bottom.

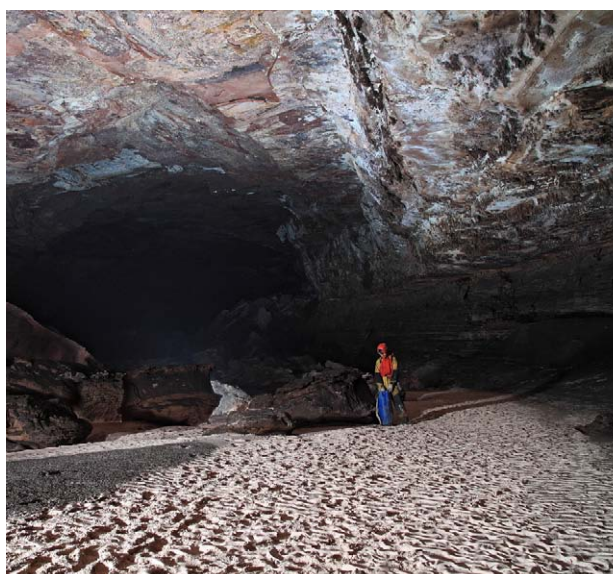


Fig. 14: The main passage in Cueva Charles Brewer branch, Charles Brewer Cave System.

Tab. 1: List of tepuis' quartzite caves longer than 1 km.

number	cave	length (km)	depth (m)	localization	state	explorers
1	Charles Brewer Cave System	17.8	160	Churí Tepui, Estado Bolívar	Venezuela	Ch. Brewer-Carías, M. Audy, B. Šmída et al. (SSS, ČSS, GE SVCN, 2004 – 2009)
2	Ojos de Cristal Cave System (Crystal Eyes Cave System, jaskynný systém Kryšťalové oči)	16.14	73	Roraima Tepui, Estado Bolívar	Venezuela	B. Šmída et al. (SSS, ČSS, GE SVCN, SVE 2003 – 2007)
3	Sistema de las Arañas	3.5		Churí Tepui, Estado Bolívar	Venezuela	M. Audy et al. (ČSS, GE SVCN, 2007)
4	Sistema Akopán – Dal Cin – Maripak	3.5		Akopán Tepui, Estado Bolívar	Venezuela	La Venta, 2009 – 2010
5	Cueva Juliana	3.0	45	Churí Tepui, Estado Bolívar	Venezuela	B. Šmída et al. (SSS, GE SVCN, 2007 – 2009)
6	Sima Auyán Tepui Noroeste	2.95	370	Auyán Tepui, Estado Bolívar	Venezuela	F. Urbani et al. (SSI, SVE, 1996)
7	Sima Aonda Superior	2.128	362	Aonda Tepui, Estado Bolívar	Venezuela	F. Urbani et al. (SSI, SVE, 1996)
8	Sima Aonda	1.88	383	Aonda Tepui, Estado Bolívar	Venezuela	SVE (1983), SSI, SVE (1993 – 1996)
9	Sima Acopán 1	1.376	90	Akopán Tepui, Estado Bolívar	Venezuela	UEV, SVE (1993)
10	Sima de La Lluvia de Sarisariñama	1.352	202	Sarisariñama, Estado Bolívar	Venezuela	FPA, SVE (1976)
11	Sima Menor	1.158	248	Sarisariñama, Estado Bolívar	Venezuela	FPA, SVE, GE SVCN (1976)
12	Cueva Yanna	1.08	40	Churí Tepui, Estado Bolívar	Venezuela	L. Vlček et al. (SSS, GE SVCN, 2009)
13	Sima Aonda 2	1.05	325	Aonda Tepui, Estado Bolívar	Venezuela	SSI, SVE (1993)

2.3. CHARLES BREWER CAVE SYSTEM

Localization: Chimantá Massif, partial massif Churí Tepui
Height a.s.l.: 2,100 m

Length: 17.8 km (formed by several cave sectors connected to each other on the Churí Tepui (sensu Brewer-Carías & Audy, 2010). However, the caves over the collapses to the west of Cueva Charles Brewer and also caves to its south do not form part of this cave system).

Depth: 160 m

Exploration: 2003 – 2010

2.3.1. Introduction

In 2002, Charles Brewer-Carías discovered an interesting depression with an underground entrance on top of the Chimantá Massif (Fig. 15). In the following year, the Grupo Espeológico de Sociedad Venezolana de Ciencias Naturales (GE SVCN – The Speleological Group of the Venezuelan Society of Natural Sciences) organized a scientific expedition to this site under the supervision of the Comisión Nacional para la Protección de los Tepuyes (National Commission for the Protection of the Tepuis). The leader of this expedition was Charles Brewer-Carías, who organized the following team of Venezuelan scientists and cavers; Charles Brewer-Capriles, Federico Mayoral, Alberto Tovar, Luis Alberto Carnicero, Fernando Tamayo, Alejandro Chumaceiro, Eduardo Wallis, Alfredo Chacón, Ricardo Guerrero and



Fig. 15: Aerial view to Churí Tepui from the northeast.

Francisco Delascio. After descending into the cave through the huge passage, they reached the first lake near the Cascadas de las Arañas waterfalls. Here, to their great astonishment they discovered the most amazing large quartzite cave. This cave, 4,482 m long and 110 m deep was eponymously named Cueva Charles Brewer. Several more expeditions led by Charles Brewer-Carías followed, and he invited experienced cavers to join him. These included Charles Brewer-Capriles, Federico Mayoral, Luis Alberto Carnicero and John Brewer together with Czech caver Marek Audy and the Slovak caver Branislav Šmída. Several scientific publications contained results from these expeditions (Audy et al., 2004; Šmída et al., 2004; Šmída & Brewer-Carías, 2005) and this unique research was highlighted in a special issue of the *Bulletin of the Slovak Speleological Society* 3/2005 (Šmída et al., 2005^b). Some of these studies met with criticism such as that from Urbani (2005), who had not explored this cave, and moreover, he had never visited it. Due to the many interesting discoveries, Charles Brewer-Carías organized several larger scientific expeditions, inviting additional members and scientists, not only from Venezuela (Federico Mayoral, Charles Brewer-Capriles, John Brewer, Roberto Brewer Martínez, Cesar Barrio-Amorós, Vicente Capriles, Hernán Biord, Luis Alberto Carnicero, Juan Carlos Godayol, Robert Cristobal, Francisco Delascio Chitty, Vincente Marcano, Roberto Brewer Mendoza, Francisco Delascio Chitty, Robert Rafael Eraso, Javier Mesa and

Ben Williams), but also from other countries including Slovakia (Branislav Šmída, Marián Majerčák, Erik Kapucian, Marcel Griflík, Zdenko Hochmuth, Ján Pavlík and Pavol Barabáš), and the Czech Republic (Marek Audy and Richard Bouda). The 2005 expedition discovered several new caves in the area near Cueva Charles Brewer. These included the 2.3 km long Cueva del Diablo, the 0.8 km long Cueva del Cañon Verde, and the 170 m deep Sima Noroeste. A sketch of the cave outlay taken from an aerial-view is shown in Fig. 16. Deeper explorations into Cueva Charles Brewer and Cueva del Diablo revealed additional spectacular discoveries including interconnections with a branch of Gran Galería de los Guácharos which increased the cave length by several hundred metres, to a total length of 4.8 km (Audy & Šmída, 2005^{a,b}; Barabáš, 2006; Brewer-Carías, 2005^{a,b}; Šmída et al. 2005^{a,b}). Many results from this expedition were widely popularized by the following researchers; Chacón et al. (2006); Chiappe (2006^{a,b}); Marbach & Fage (2006); Mayoral (2006); Hernandez (2005); Palmitesta Riveros (2006^{a,c}); Ramos Zibert (2006); Sánchez & Carnicero (2005); and Šmída et al. (2005^{a,b,c}).

A further expedition was organized in 2007 by the following speleologists; Branislav Šmída, Zoltán Ágh, Erik Kapucian and Lukáš Vlček from Slovakia, Marek Audy, Richard Bouda and Radko Tásler of the Czech Republic, Mladen Kuhta and Robert Dado from Croatia, and the Venezuelans Federico Mayoral and Igor Elorza. In addition to these, several other experts joined

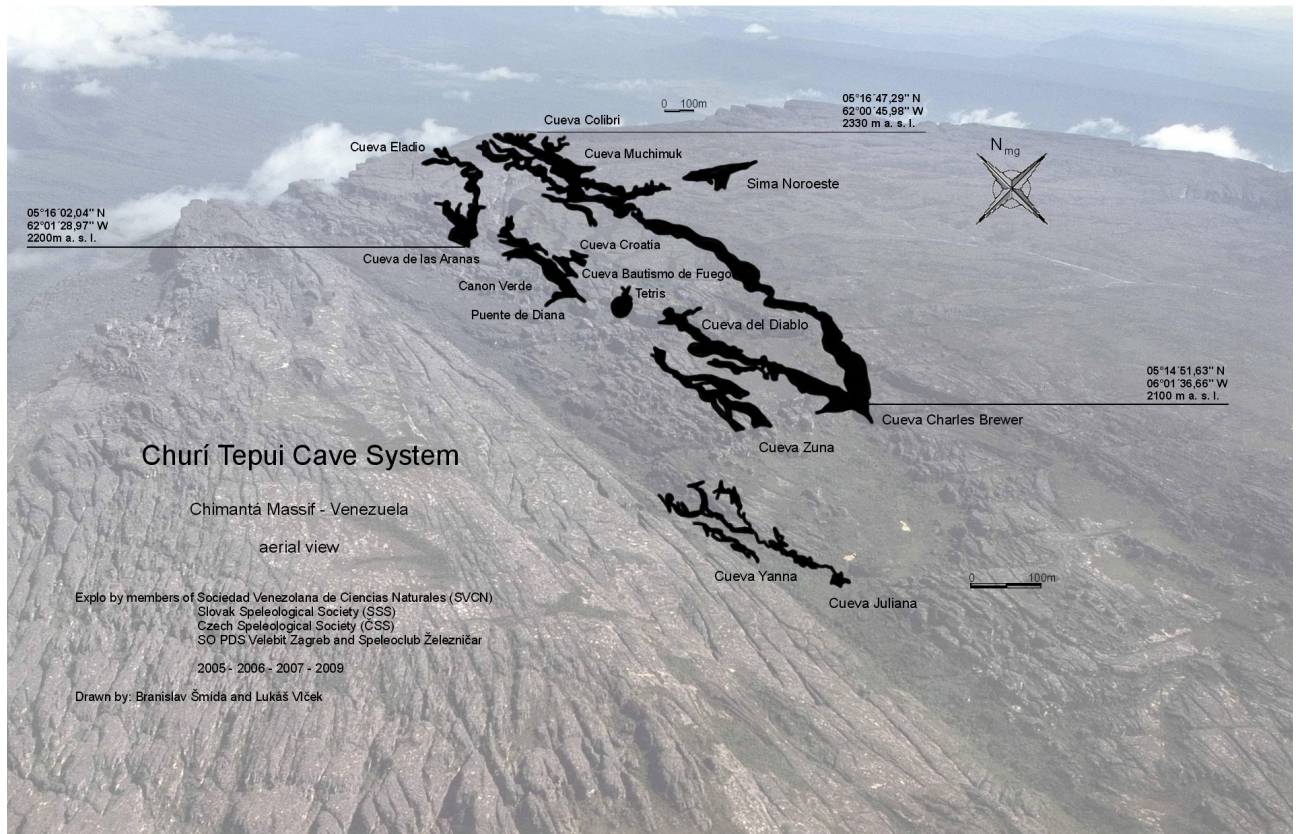


Fig. 16: Speleological sketch of the Charles Brewer Cave System and adjacent caves.

this team. These included Roman Aubrecht, Tomáš Lánczos and Ján Schlögl from the geological-geochemical team at the Comenius University in Slovakia, the Spanish herpetologist Cesar Barrio-Amorós and also a group consisting of Charles Brewer-Carías with a BBC film crew led by Roger Santo Domingo and Ian James representing the American Press. The aim of this expedition was to explore the northern part of Churí Tepui. This succeeded beyond expectation when several new caves were discovered on the Churí Tepui plateau. These supplemented those observed during a helicopter flight by Charles Brewer-Carías the previous year. The newly discovered caves were: Cueva de la Araña – Cueva la Cortina (2.5 km long), Cueva el Diente – Puente de Diana Cave (0.05 km long), Cueva Bautismo del Fuego (0.4 km long), Cueva Juliana (1 km long), Cueva Tetris (0.15 km long), Cueva Croatia (0.1 – 0.2 km long), Cueva Zuna (0.31 km long), Cueva con Columnas (0.2 km long), plus the Cueva Eladio and Cueva Colibrí which were merely observed from helicopter. All of these caves constitute different parts of a complicated cave system located parallel to Cueva Charles Brewer and west of its main passage. However, these are all isolated by different types of rock collapses of pre-existing cave ceilings. The results of these expeditions were described in several publications (Aubrecht et al., 2008^{a,b}; Audy et al., 2008; Barrio-Amorós et al., 2010; Lánczos et al., 2009^{a,b}, 2010^{a,b}; Šmída et al., 2007, 2008^{a-c}; Vlček et al., 2008, 2009^{a-e}). Some caves in this area, and particularly Cueva Auchimpé, which is currently known as the Cueva Eladio, were also explored by other caving expeditions in parallel with

the above expeditions. A contemporaneous example is the La Venta expedition noted on web link <http://www.tepui.info.com>.

Several expeditions explored the Churí Tepui plateau in 2009. These expeditions were organized by collaborating teams: a Slovak speleological team (Branislav Šmída, Erik Kapucian, Lukáš Vlček, Jaroslav Stankovič and Viliam Guľa), a general scientific team from the Slovak Comenius University (Roman Aubrecht, Ján Schlögl, Tomáš Lánczos and Tomáš Derka), a Croatian caver team (Darko Bakšić and Ana Bakšić) and the Venezuelan caver Javier Mesa.

The tasks of the speleological team were to land on the northern part of the meseta and reach the area expected for the logical continuation of Cueva Charles Brewer. Although some intended research could not be carried out as initially planned, this team made the following important discoveries; i) the junction between Cueva Charles Brewer and Cueva del Diablo was mapped, so that the total length of the system was extended to 7.5 km; ii) two caves were discovered to be longer than previously believed: Cueva Zuna with 2.52 km total length and Cueva Juliana with 3 km; iii) several new caves were discovered including the 0.2 – 0.3 km long Cueva de dos Machetes, the 1.08 km long Cueva Yanna and the 4.6 km long Cueva Colibrí. The most important of these is the giant Cueva Colibrí located in the northern part of the tepui. Since the water in the cave stream flows from the northern edge of the tepui southerly towards the Cueva Charles Brewer area, there was a distinct possibility that these two caves are joined.

Further evidence for this theory was obtained during the next expedition to Cueva Eladio by the team of Branislav Šmída, Marcel Grifflik, Charles Brewer-Carías, Federico Mayoral, Marek Audy, Richard Bouda, Pavol Barabáš and Ben Williams. In this expedition, another connecting giant cave was discovered that extended the Cueva Colibrí into the 8 km Cueva Muchimuk – Cueva Colibrí Cave System (Audy & Brewer-Carías, 2009; Šmída 2009, 2010; Šmída et al. 2009, 2010^{a-c}; Vlček & Šmída, 2009). Although a physical connection with the Cueva Charles Brewer was not possible because the southern end of this cave ended in a huge cave-fall (Šmída et al. 2010^c), topographically, this cave-fall appears identical to the one at the end of Cueva Charles Brewer. Therefore, Audy et al. (2010) and Brewer-Carías & Audy (2010) inferred that these caves should be regarded as one cave system. This particular cave-fall was thereupon inserted into a detailed map published by Audy et al. (2010). After these expeditions, the total length of the cave system named Sistema Muchimuk; sensu Audy et al. (2010) or Sistema Charles Brewer; sensu Brewer-Carías & Audy (2010), was registered at 17.8 km (± 230 m). Herein, it is referred to as the Charles Brewer Cave System, and this is currently recognized as the longest and most voluminous quartzite cave system in the world (Hernandez, 2010). However, these observations and conclusions are not indisputable. For example, Šmída (2010), Šmída & Vlček (2010) and Šmída et al. (2009, 2010^{a-c}) did not accept this junction, because not all interconnections had been physically proven. Therefore the maps and papers of Šmída & Vlček (2010) and Šmída et al. (2010^{a-c}) present the Muchimuk – Colibrí Cave as 8 km long and the Sistema Charles Brewer – Cueva del Diablo as 7.5 km long. The expedition also surveyed Cueva Eladio, which had been visited the previous year by Italian cavers who named it Cueva Auchimpé (Mecchia et al., 2009). According to research by Audy et al. (2010) and Brewer-Carías & Audy (2010), the 4 km ± 120 m Cueva de las Arañas Cave System was created by the physical junction of the following three caves: Cueva Cortina, Cueva de la Araña and Cueva Eladio.

Numerous scientific results and new biological research resulted from all expeditions, including those undertaken by Audy & Kalenda, 2010; Breure & Schlögl (2010); Derka & Fedor (2010); Derka et al. (2009, 2010); Robovský et al. (2007), and popular reports on this huge cave system on Chimantá were published by Ochoia Breijo (2011) and Rodrigues (2011).

Two additional expeditions were organized independently in 2009; i) by the Italian team (Corrado Conca, Tono De Vivo, Marco Mecchia, Francesco Sauro, Rolando Menardi, Fabio Negroni, Alessio Romeo, Pier Paolo Porcu, Andrea Pasqualini, Carla Corongiu, Vittorio Crobu; De Vivo – see La Venta, 2009; Mecchia et al., 2009); and ii) by the Venezuelan scientific-caver team led by Charles Brewer-Carías accompanied by scientists from Canada, U.S.A. and Austria (Lundberg et al., 2010^{a,b}).

2.3.2. Localization

The reported cave system is located in the Chimantá group of table-mountains, close to the northern edge of the Churí Tepui (2,100 m a.s.l.) (Fig. 16). Entrances to the cave system are situated between the middle of the central valley which divides the mountain into two parts, and the northern edge of the meseta.

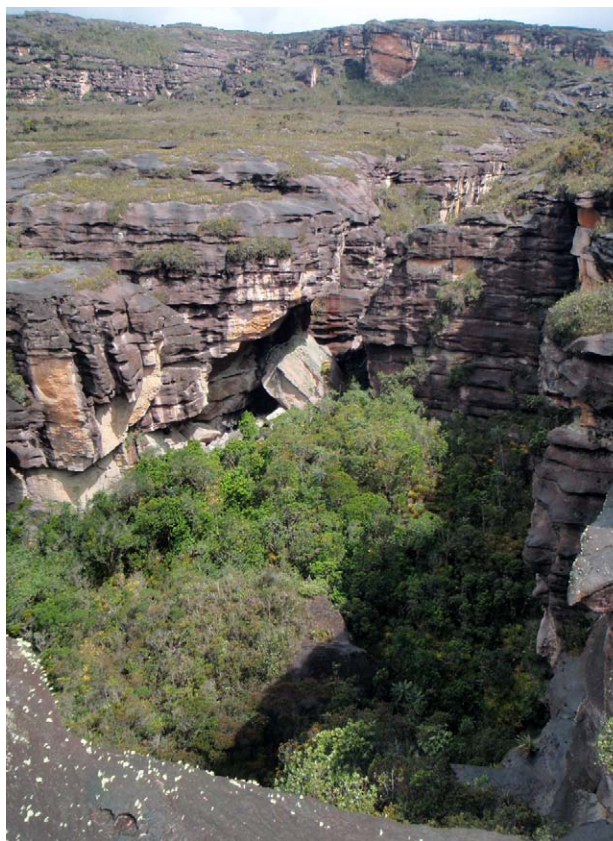


Fig. 17: Entrance to the Cueva Zuna sector in the Zuna Depression.

The main entrance forms the mouth of the discharge passage of the cave, draining most of the cave system's accumulated water from the northern and the central parts of the mountain. Other independent watercourses are distributed within the cave. The delta-like Cueva Muchimuk – Cueva Charles Brewer branches are situated north of these streams, while an underground watercourse flows parallel to these branches through the independent Cueva Eladio and Cueva de las Arañas. To the south, this flows through parts of the Charles Brewer Cave System (Cueva del Diablo and Cueva Zuna). Underground watercourses also flow through the separate Cueva Juliana and Cueva Yanna on a level below and to the south of the studied cave system. Along this path, the Charles Brewer Cave System splits into the spatially and genetically distinct sectors of Cueva Zuna, Cueva del Diablo, Cueva Charles Brewer, Cueva Muchimuk and Cueva Colibrí. Other caves which clearly form one genetic system are located in the vicinity (Fig. 16). All the above mentioned caves are situated relatively close to the surface. Following the gradual elevation of the terrain to the north, the southern sectors such as Cueva Zuna and the entrance to the Cueva Charles Brewer are only 50 – 80 m below the surface of the plateau, while the more northern cave parts are 100 – 120 m under it. Altogether, the cave system has 18 entrances; (1) 5 of these are in the northern wall of the Churí Tepui and 2 in the Colibrí Depression, forming the 7 entrances of the Colibrí sector; (2) 1 enters the Cueva Muchimuk sector from the south; (3) there is the main entrance situated in the Charles Brewer Depression; (4) 1 enters



Fig. 18: Interior of the 120 m wide entrance to the Cueva Charles Brewer sector, previously an independent cave.



Fig. 19: Passage in the Guácharo branch, Cueva Charles Brewer sector.

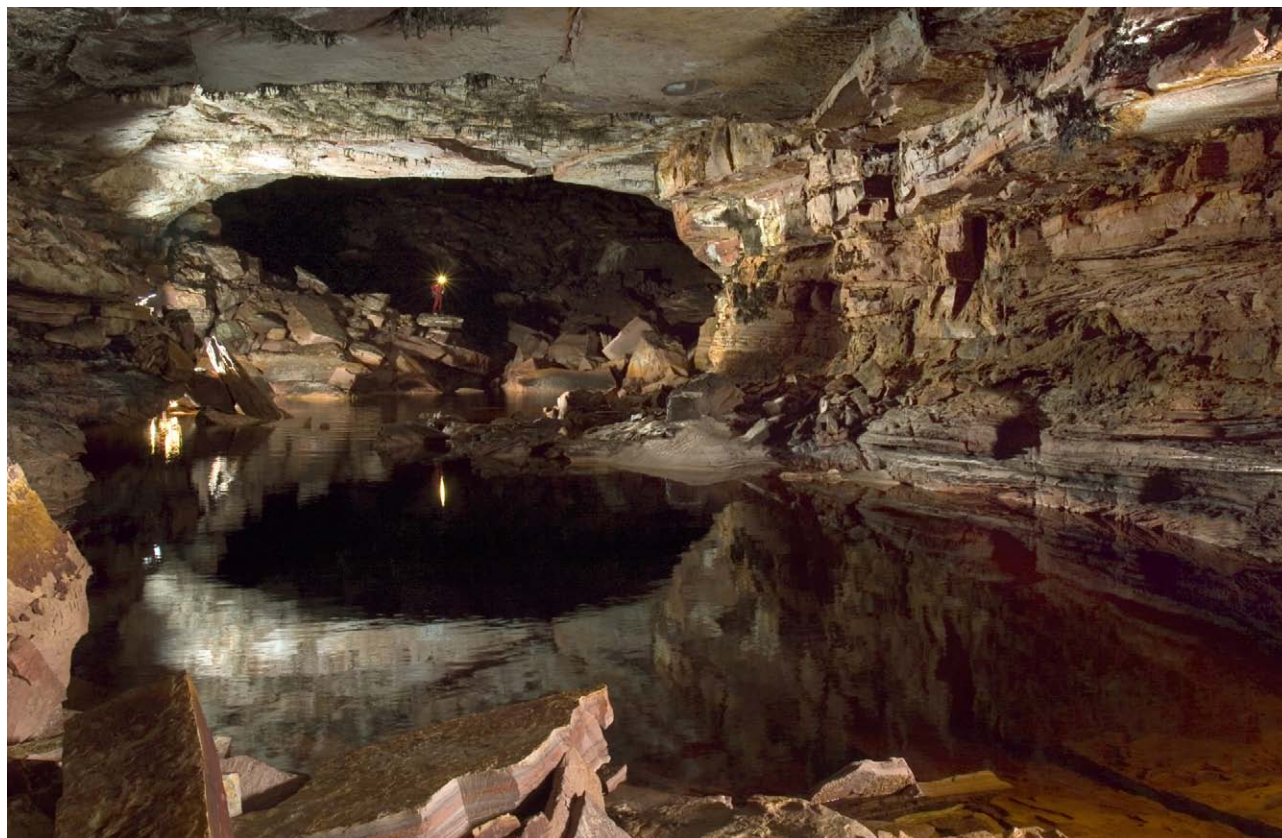


Fig. 20: An average corridor in the main passage of the Cueva Charles Brewer sector.

the Cueva Charles Brewer sector and a 2nd enters the Cueva del Diablo sector from the Guácharo Depression; (5) the Cueva del Diablo sector has two entrances situated in depressions dividing the partial massifs of rock towers east of the central valley, and referred to as the Diablo Depression; and (6) the Cueva Zuna sector has two entrances from the Charles Brewer Depression together with two from the Zuna Depression and one from the Diablo Depression.

2.3.3. Charles Brewer Cave System: basic description

2.3.3.1. Cueva Zuna

The Cueva Zuna sector has two entrances into the so-called Zuna South part from the Charles Brewer collapse depression, but these are partly blocked by stony debris. These passages then continue upstream to the north as two parallel branches connected by a labyrinth of side-branches until they end in the entrances of the Zuna Depression (Fig. 17). Meanwhile, the Zuna North entrance is in the opposite wall of the collapse depression. The Zuna North cave portion involves two adjoined branches which eventually form the surface opening of the Diablo Depression, which was previously called the Bromelia Vertical Cave. Part of the Cueva Zuna sector is situated only 50 – 60 m below the surface, and this has passages 1.5–2.5 m high and 2–5 m width. The Cueva Zuna is approximately 2.8 km long and it forms a continuation of the Cueva del Diablo through the Diablo Depression.

2.3.3.2. Cueva del Diablo

The Cueva del Diablo sector is formed by two spacious horizontal corridors opening onto the surface in several vertical crevices. These crevices cut the towers of the rock town, east of the Churí Tepui central valley. The Diablo North cave portion runs to the north and ends in rugged terrain between the towers south of Cueva del Cañon Verde, Cueva Croatia and Cueva Bautismo del Fuego. The direction of the Cueva Diablo South is southeast, and this opens into the Guácharo Depression through a rock-fall. This depression was formed by a ceiling collapse in a former huge cave passage which now separates the Cueva del Diablo sector from the Gran Galería de los Guácharos passage in the Cueva Charles Brewer sector. This sector's underground area is relatively superficial, at up to 100 m, with an average corridor height of 10 m and an average width of 30 m. The total length of the Cueva del Diablo sector is approximately 3 km.

2.3.3.3. Cueva Charles Brewer

The Cueva Charles Brewer sector has two entrances, with the dimensions of the main entrance, Boca de Mamut (the Mammoth's Mouth) 120 × 15 – 30 m (Fig. 18). This entrance is situated in the Charles Brewer Depression behind a huge rockfall formed by a cave ceiling collapse. This divides the cave here into two separate branches. One of these is the Guácharo branch (Gran Galería de los Guácharos), which runs northwest as a continuation of the Cueva del Diablo sector. The dimensions of the passage are up to 50 m in height and 80 m in width (Fig. 19).



Fig. 21: A corridor in the main passage of the Cueva Muchimuk sector.

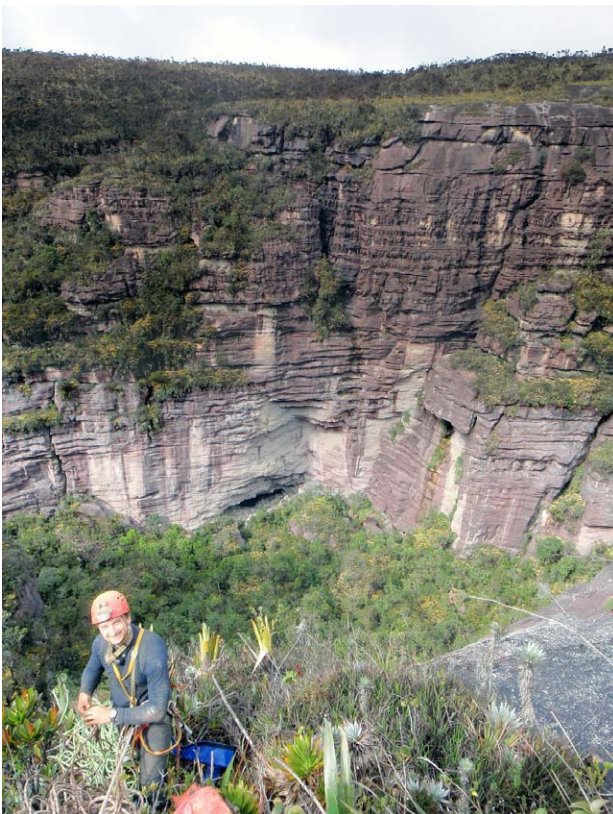


Fig. 22: Entrance to the Cueva Colibrí sector in the 120 m deep Colibrí Depression.

The second branch runs northeast against the stream flow direction and forms a simple, but huge, slightly meandering corridor leading into the massif. The average dimensions of this corridor are 40×15 m, with width approaching 80–100 m and height approaching 40 m (Fig. 20). There are several large chambers in this area with the largest of them named Gran Galería Karen y Fanny. This has a total volume of $400,000 \text{ m}^3$, which makes it one of the largest underground spaces in the world (Šmída et al., 2005^b). After 2 km, the corridor is divided into two branches, and both end in cave-falls, with a river discharging from them. The cave system then continues past these cave-falls into the Cueva Muchimuk sector. The total length of the Cueva Charles Brewer sector is 4.5 km.

2.3.3.4. Cueva Muchimuk

The entrance to Cueva Muchimuk is located in the vast Colibrí Depression at the northern part of the mountain. The cave runs in a southerly direction along the underground river, ending in the cave-fall which connects this cave to the Cueva Charles Brewer sector. Cueva Muchimuk divides into 4 huge corridors lateral to Cueva de las Arañas west of the area, close to Sima Noroeste. The streams in the corridors originate from the Colibrí Depression and join together as an underground river opening into a cave-fall at the end of the cave. The width of the corridors ranges between 20–50 m, and their height between 8 – 15 m (Fig. 21). The 4 km long Cueva Muchimuk sector is connected at its northern end to the Cueva Colibrí sector by a 120 m deep Colibrí Depression (Fig. 22).

2.3.3.5. Cueva Colibrí

The Cueva Colibrí sector forms a complicated two-dimensional labyrinth of an anastomosing corridor network that converges from the northern edge of the plateau into three cave branches. These branches are the Gran Galería de el Jaguar – Galería Yunek, Galería Ana – Renata and Galería Lagos y Cataratas de Čertík–Helen. The width of their corridors ranges between 20 m and 40 m and their height 8–15 m, with a most usual corridor size of approximately 20 m × 8 m (Fig. 23). They open into the Colibrí Depression (grieta), east of the entrance of the Cueva Eladio (Fig. 22). They have smaller side passages and are well watered by small streams. Five parallel entrances open on the northern wall of the tepui. The length of this sector is 3.5 km.

2.3.4. Cave spatial framework

The spatial framework of the cave systems on Churí Tepui shares similar geological patterns to Cueva Ojos de Cristal on the Mt. Roraima, and it follows the same principles as “classical” karst phenomena (Šmída et al. 2003). A crucial difference here is the anastomosing labyrinth of passages which converge into one large drainage pipeline characteristic of Churí Tepui caves, while the cave architecture on Roraima Mountain remains the same to its adit. We therefore presume that the Cueva Ojos de Cristal is in an earlier stage of evolution than the older and more spacious Charles Brewer Cave System. Water flowing through the

cave areas drains into them through vertical seepages along the crevices and grietas or by horizontal seepages along the bedding planes which dip to the southeast. The anastomosing corridor network forming the Cueva Colibrí sector is located in the area of the Colibrí Depression, then the network merges into two large draining branches of the Cueva Muchimuk sector. These then merge into one giant tube passing over the huge cave rockfall to the Cueva Charles Brewer sector. It is obvious that more of these large underground drainage systems must have existed on Churí Tepui in earlier times. This was proven by the discovery of a parallel cave system continuing in a southerly direction. This system included the following: Cueva Eladio–Cueva de las Arañas (which is considered one cave, Sistema de las Arañas), Cueva del Cañon Verde, Cueva del Diablo sector, Cueva Zuna sector, and the Guácharo branch of the Cueva Charles Brewer sector. Although these caves differ spatially, they form one drainage system. It is most likely that in the past they formed one continuous cave system, but today they are divided by huge collapses (Fig. 24). The largest collapse zone is located in a discharge zone between the systems which lie south of the Cueva Charles Brewer and Cueva Zuna sectors. We presume that a huge quartzite cave occurred here, and that it was most likely one of the largest of its kind in geological history until destroyed by reverse erosion of rivers flowing from the cave entrances. Today, the draining of the central part of the massif of the Churí Tepui continues a level below the Cueva Charles Brewer, as indicted



Fig. 23: One of the passages in the Cueva Colibrí sector.

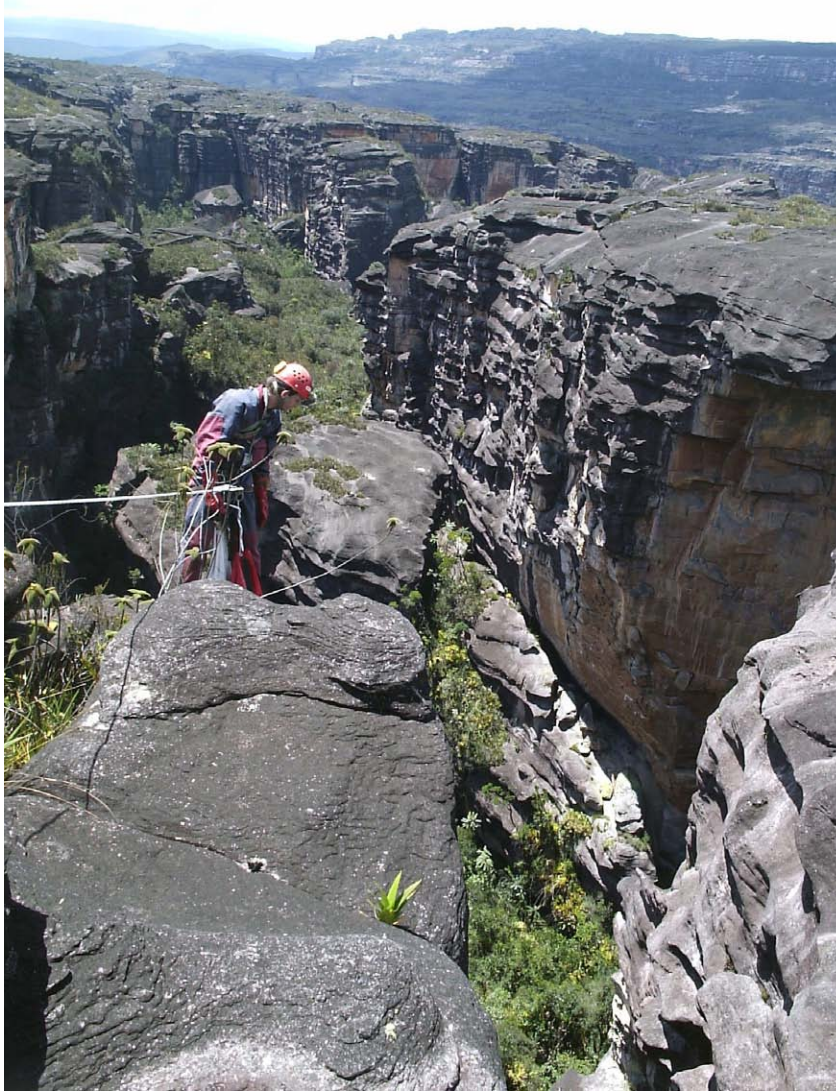


Fig. 24: Descent to the blocked area near Cueva Cañon Verde.

by young cave channels of Cueva Juliana and Cueva Yanna, situated approximately 60 m beneath the Cueva Charles Brewer opening. These caves possess considerably smaller corridors which strongly resemble the Cueva Ojos de Cristal passages on the Roraima Tepui.

2.3.5. Speleological perspectives

Since the speleological explorations undertaken until now have focused only on the central part of the massif, the remaining mountain underground is still less explored. Only the zone between Cueva Colibrí in the north and Cueva Juliana in the south has been relatively well documented in this area. The remainder, including a plateau with deep crevices, still awaits exploration, and we envisage that most of these unexplored areas will provide many interesting geological insights. One such area lies between the Cueva del Diablo and Cueva Charles Brewer sectors. Here, we postulate the existence of more than one huge cave branch which could form a lateral continuation of long passages into the Cueva Muchimuk sector far to the east and to Galería con 100 Lagos. In

addition, Cueva Juliana and Cueva Yanna, which lie at the lowest depths, have not been completely explored to the ends of their passages. When considering the caves' spatial structure and the denseness of their occurrence, it is obvious that the speleological potential of the Churí Tepui is far from entirely exploited. Further speleological investigation should unveil many further astounding discoveries, such as kilometres, or even tens of kilometres of additional passages. There is also great potential to discover many other interesting phenomena in this territory which will greatly stimulate many research areas, especially in the areas of geochemistry, mineralogy, hydrochemistry and geobiology.

2.4. OJOS DE CRISTAL CAVE SYSTEM

Localization: Roraima Tepui
 Height above a.s.l.: 2,630 m
 Length: 16.14 km
 Depth: 73 m
 Exploration: 2002 – 2007

2.4.1. Introduction

During 2002 two cavers, Zoltán Ágh of the Slovak Speleological Society and Marek Audy from the Czech Speleological Society, discovered an inconspicuous entrance to an inlet cave on the Roraima Tepui (Fig. 25). Since they lacked equipment required for more extensive exploration, they were only able to reach a horizontal passage approximately 300 m into an area with a lowered passage profile. This site was quite inaccessible and demanded tedious crawling for further advance. Since this cave contained numerous pot-holes on the floor, filled with rounded quartz crystals, it was named “Cueva Ojos de Cristal” (Crystal Eyes Cave, *Jaskyňa kryštálových očí*). Compared to previous descriptions of quartzite caves in other parts of the world, this cave proved to be quite unique, due to its unusual parent rocks and its horizontal course. Previously described quartzite caves were mainly characterized by deep vertical crevices which normally obtained water from the mountain surface, with this water then draining into external springs through the vertical outer mountain walls. Moreover, since this cave is situated close to the southern edge of the meseta and the cave water flows from south to north, there is at least the theoretical possibility of the existence of a cave traversing the entire mountain and ending at the springs situated in the northern walls of tepui.

A short Slovakian-Czech speleological expedition to the Roraima Tepui was organized in 2003 to explore this notion. The members of this group were Branislav Šmída, Erik Kapucian,

Marcel Griflík, Lukáš Vlček, Marek Audy, Zoltán Ágh and Marián Majerčák, and they had Venezuelan guides led by Antonio José Arocha Gonzales. During this week-long expedition, the cavers explored not only the Cueva Ojos de Cristal in greater detail, they also mapped 3.5 km of underground passages in the following 15 caves connected to this area; Cueva debajo del Hotel Principal, Cueva Asfixiadora, Cueva de Gilberto, Cueva Fragmento Marginal, Cueva con Bloques de Piedra, Cueva del Hotel Guácharos, Cueva 007, Cueva Papua, Cueva con Cataratita, Cueva 009, Grieta de Diablitos Volantes, Cueva con Puente, Cueva de Arañas Hidrófilas, Cueva Hipotética, Tuná Deutá, and Cueva El Foso. Fluvial corridors in the water flow direction in Cueva Ojos de Cristal measured an astonishing total length of 2.41 km. It had an elevation of 24 m, and contained an underground anastomosing passage system (Fig. 26) where the passages converged at the main water outflow in the vertical crevice. This particular site is named Pokémon (Šmída et al., 2003). These findings, together with the fact that this cave is characterized by a rather unique relatively horizontal direction, clearly suggested that Cueva Ojos de Cristal represented a new morphogenetic quartzite cave type, and also that it is one of the most prominent large quartzite caves in the world (for general scientific descriptions, see Audy, 2003, 2008; Audy & Šmída, 2003; Vlček, 2004; for a general overview see the special monographic issue of the Bulletin of the Slovak Speleological Society by Šmída et al., 2003). This discovery evoked heated debates about its legitimacy in several associations, including the International Union of Speleology – UIS and the Speleological



Fig. 25: View of the southern wall of Roraima Tepui from the ascent path, highlighting the highest point of El Maverick at 2,889 m a.s.l.

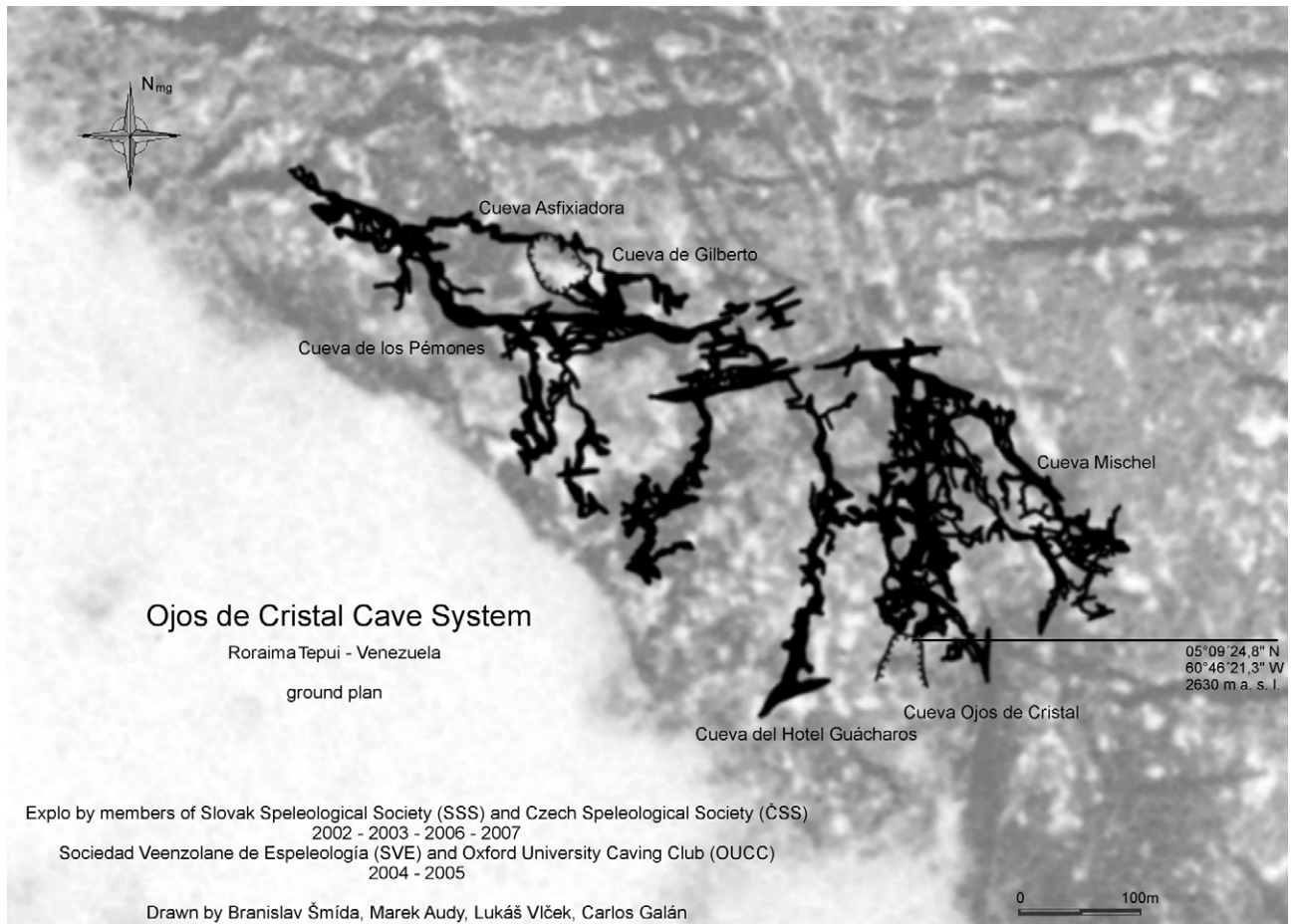


Fig. 26: Schematic speleological groundplan of the Ojos de Cristal Cave System. E –entrances, with numbers indicating the number of entrances when several are close to each other.

Federation of Latin America and the Caribbean – FEALC (see Geospeleology Commission of FEALC Newsletter – No. 60). However, the Czech-Slovak team gained respect thanks to expedition led by Charles Brewer-Carías to Cueva Charles Brewer on the Chimantá Massif in 2004. Marek Audy and Branislav Šmída also accompanied this expedition. This expedition then initiated fruitful cooperation between the Czech-Slovak and Venezuelan cavers associated in Grupo Espeleológico de Sociedad Venezolana de Ciencias Naturales – GESVCN. Another large cave, with 4,482 m length and 110 m denivelation, was discovered on this expedition to the Chimantá Massif, thus surpassing the acknowledged length of Cueva Ojos de Cristal (see Chapter 2.3).

Another Venezuelan-Czecho-Slovakian expedition was organized in 2005 by Charles Brewer-Carías, Federico Mayoral, Branislav Šmída, Marek Audy, and others. The goal of this expedition was to further investigate both Cueva Charles Brewer and Cueva Ojos de Cristal. Exploration of Cueva Ojos de Cristal was undertaken by the smaller team of Branislav Šmída, Erik Kapucian, Marcel Griflík and Marián Majerčák. They clarified the cave's continuation over the Pokémon crevice, and then recorded the length of the nearby Cueva de los Pémones at an astonishing 5.3 km. These results from the Chimantá Massif were published in several papers (Šmída et al., 2005^{a-e}; Šmída

et al., 2004; Audy & Šmída, 2005^{a,b}; Šmída & Brewer-Carías, 2005), and in a special monographic issue of the Bulletin of the Slovak Speleological Society dedicated to these discoveries on the Chimantá Massif (Šmída et al., 2005^b). This edition was published in both Slovak and Spanish languages. Exploration results from Cueva Ojos de Cristal have been published in papers by Šmída et al. (2005^{a,b}).

Cueva Ojos de Cristal was renamed Sistema Roraima Sur by the Venezuelan-British-Spanish team in 2004. During their 2004 and 2005 expeditions, this team also remapped the Cueva Ojos de Cristal Cave, and measured extensions of the Cueva de los Pémones passages at 10.82 km. Since the map published by this team contains some discrepancies, this caused confusion. For example, Young et al. (2009) unfortunately defined Sistema Roraima Sur and Cueva Ojos de Cristal as being two different caves. For completely reliable tracking of the order of events and the cave descriptions, please see the monographic issue of the Boletín de la Sociedad Venezolana de Espeleología (SVE) in 2005 (this issue was antedated to 2004; Galán et al., 2004^{a-b}; Carreño & Urbani, 2004; Carreño & Blanco, 2004). Shorter notes are also contained in scientific papers by Galán & Herrera (2005); Pérez & Carreño (2004); Carreño et al. (2005); Galán & Herrera (2006), and Barton et al. (2009).

A new expedition was organized to Kukenán and Roraima tepuis in 2006 to settle various disputes. This was undertaken by the Slovak cavers, Branislav Šmída, Lukáš Vlček, Peter Medzihradský, Jozef Ondruška, Peter Masarovič and Pavol Barabáš. They explored a few of short horizontal caves and descended to the Sima Kukenán shaft. After this, the group was divided into two parts on Roraima Tepui for detailed studies of Cueva del los Pémones and Cueva Ojos de Cristal. This led to the discovery and survey of several passages which increased the total length of the cave system to 15.28 km. Several interesting cave connections were discovered. The main was the interconnection of the above mentioned two caves through the Cueva del Hotel Guácharos, and the second was the discovery that Cueva del Gilberto and Cueva Asfixiadora were physically connected to this large cave system. The results of this expedition were published by Vlček & Šmída (2007), and also in a documentary movie called Matauí (Barabáš, 2007).

After the expedition to Chimantá Massif, a Slovak-Croatian-Venezuelan expedition to Roraima was organized in 2007 by the cavers Branislav Šmída, Lukáš Vlček, Erik Kapucian, Zoltán Ágh, Igor Elorza, Mladen Kuhta and Robert Dado. They also invited a Slovak scientific team from the Comenius University in Bratislava consisting of Roman Aubrecht, Tomáš Lánczos and Ján Schlögl. During this expedition, interconnections of Cueva

Ojos de Cristal with Cueva de Gilberto (including the former independent Fragmento Marginal Cave) and with Cueva Asfixiadora were discovered, thus the total length of the Cueva Ojos de Cristal was finally registered at 16.14 km with a denivelation of 73 m (Šmída et al., 2007, 2008^{a-d}; Vlček et al., 2008).

A further expedition was specially organized by Slovak and Croatian cavers, comprising Slovak cavers and scientists, Lukáš Vlček, Viliam Gula, Ján Schlögl and Tomáš Derka and the Croatian cavers Darko and Ana Bakšić. Its main goals were to visit Roraima and Cueva Ojos de Cristal and to take samples for scientific research (Šmída, 2010; Vlček & Šmída, 2009; Vlček et al., 2009^{a-c}).

The summary of current discoveries and their status in the history of cave explorations read as follows; the 16.14 km length established in 2006 for Cueva Ojos de Cristal surpassed the length of the limestone Cueva el Samán located in the neighbouring state of Zulia, and thus became the longest cave discovered in Venezuela. However, the prolonged mapping of Cueva el Samán completed by Venezuelan cavers the following year reversed this, and Cueva el Samán was re-established as the longest cave at 18.2 km (Herrera et al., 2006). Since a complete detailed map of Cueva Ojos de Cristal has not yet been published, its total length is still debatable; as in Audy (2008), and Brewer-Carías & Audy (2010).



Fig. 27: Ponor depression of Cueva Ojos de Cristal, where the cave was discovered.

2.4.2. Localization

Cueva de Ojos de Cristal is situated on the Roraima table mountain at 2,810 m a.s.l. close to its southern edge. The entrance which was discovered first, is located at one of the southernmost parts of the entire cave system (Fig. 27). It is formed by a sinkhole draining rainwater from an approximately 0.02 km² wide area, so that underground streams form several cave passages. Genetic aspects play an important role in discoveries of distinct parts of this system, so from a speleogenetic viewpoint this cave can be divided into five different sectors: Cueva Ojos

de Cristal, Cueva Mischel, Cueva del Hotel Guácharos, Cueva de los Pémones, and Cueva Asfixiadora with Cueva de Gilberto. Based on current discoveries, this cave has the following 23 entrances; 4 situated in the sink depression of the Cueva Ojos de Cristal; 5 in the outer wall of the Roraima Tepui at depths of up to 70 m below the plateau; 2 in the sink depression of the Cueva Mischel; 6 in two sink depressions of Cueva Asfixiadora and Cueva de Gilberto; 1 forming the huge portal of the Hotel Guácharos rock shelter; and the final 5 discovered on the vertical crevices named Pokémoms, whose basal portions are connected to deep horizontal passages.

Fig. 28: Entrance to the Cueva Mischel sector – previously the independent Cueva Mischel.



Fig. 29: The main passage of the Cueva Ojos de Cristal sector.



Fig. 30: Entrance to the Cueva del Hotel Guácharos sector – previously the independent Cueva del Hotel Guácharos.

2.4.3. Ojos de Cristal Cave System – basic description

2.4.3.1. Cueva Mischel

The Cueva Mischel sector begins as two sink entrances located in a huge flat-based sink depression which drains rainwater from a surrounding 0.05 km² area. The underground drainage flow direction is westward from this depression. Two entrances are situated under the western edge; a northern one among rock towers and a southern one which appears to form a visible sink entrance into compact rock (Fig. 28). The stream divides into two parts which sink into the massif and flow to the northwest, where they join again. After 100 metres, this cave sector joins Cueva Ojos de Cristal sector, this part of the cave is approx. 1 km long. The Cueva Mischel/Cueva Ojos de Cristal interconnection was surveyed in 2003, as reported in Šmída et al. (2003).

2.4.3.2. Cueva Ojos de Cristal

The Cueva Ojos de Cristal sector begins in the Ojos de Cristal sink depression in a surrounding area of approximately 0.02 km². Here, four sink entrances enter the underground passages. These generally run northerly with an inclination up to 5 degrees, and following the direction of the bedding plane dip. The cave terminates approximately 300 m from the entrance at its junction with the 30 m deep Pokémon 1 vertical crevice, which opens in the rock elevation north of the entrance. Water from the sinks flows northwards disappearing between the blocks in the base of Pokémon

1, and during high water levels as occurs in the rainy season, it also dissipates through horizontal apertures in the pokémon's base. The seeping water formed two confluent branches which flowed from the cave in a south-westerly direction. One of these is now dry, while the other remains an active stream (Fig. 29). These branches are connected to the Cueva Mischel sector. This sector is approximately 4 km long. A lateral horizontal corridor uniting Cueva Ojos de Cristal and Cueva del Hotel Guácharos deviates from the mid-section of these branches. The cave connections here were surveyed in 2005 by Šmída et al., (2005^{a-c}).

2.4.3.3. Cueva del Hotel Guácharos

The Cueva del Hotel Guácharos sector begins with a huge 50 m wide entrance with a maximum height of 5 m (Fig. 30). This entrance is generally used as a rock shelter by tourists and it therefore earned the nickname “hotel”, similarly as other rock shelters on Roraima Mt. Although this huge cave entrance has been frequently used for a long time, the first scientific reports about it were not published before 2003 (Šmída et al., 2003). The cave continues from the entrance along declining quartzite strata to a dry passage-way. After a distance of approximately 150 m, it connects with the Sala Con Catarata Dome (Waterfall Hall). This waterfall is formed by a stream flowing from an aperture throughout length of the ceiling. An eastern horizontal branch from the Cueva Ojos de Cristal sector connects to the main watercourse immediately above this hall, and the



Fig. 31: Descent into the Cueva de los Pémones sector through the vertical crevice Pokémon No. 3.

cave then continues as an active fluvial branch in a low passage along the watercourse. After extreme narrowing in its northernmost tip, the cave system continues into the Cueva de los Pémones sector. Although this narrow passage had previously been plotted by Venezuelan cavers in their 2005 map (Galán et al., 2004^a), this connection was physically explored for the first time by the members of the Slovak expedition in 2006 only (Vlček & Šmída, 2007). The Cueva del Hotel Guácharos sector is approximately 1 km long.

2.4.3.4. Cueva de los Pémones

The water from Cueva del Hotel Guácharos after its narrowing continues in a slightly declining, low passage toward the vertical 30 m deep Pokémon 2 crevice. The Cueva de los Pémones sector was first discovered at this site. An extensive branch with up to 30 m wide corridors, like the Sala de la Madre Sociedad Espeleológica de Eslovaquia, proceeds from this pokémon in a southerly to south-westerly direction against the flow of the stream which forms by water dripping down the cave walls. This branch ends in the southern wall of the tepui as a huge window which forms the southernmost of the five entrances to the Cueva Ojos de Cristal Cave System which are situated below the entrance of the Cueva del Hotel Guácharos sector. The stream flows in a northerly direction from Pokémon 2, which is actually a genetic continuation of Pokémon 1. The stream then reaches the Pokémon 3 vertical crevice (Fig. 31). The cave turns west – northwest above this pokémon before striking off in an easterly direction via low passages which are most likely connected to the higher situated Cueva con Bloques de Piedra and



Fig. 32: The main passage in the Cueva de los Pémones sector.



Fig. 33: One of the entrances to the Cueva de Gilberto sector – previously the independent Cueva de Gilberto Cave.

related crevices penetrating from the surface. Two extensive dividing branches run from the main thrust and end in the walls of the Roraima Mt. Cueva de Gilberto is situated above the labyrinth in this part of the cave sector, and is connected to the system through a crevice. An underground stream flows below the main thrust and parallel to it. This stream is fed by the above mentioned branches, and it forms a huge corridor (Fig. 32) ending in two rocky windows in the Roraima wall. A connecting branch from Cueva Asfixiadora occurs above a vertical step approximately 100 m from the end of this sector. This connection was discovered in 2006 (Vlček & Šmída, 2007). During high water level events, as occur in the rainy season, the river flowing through the Cueva de los Pémones makes impressive waterfalls flooding from a window in the wall. The total length of this most extensive sector of the Cueva Ojos de Cristal System is 8 km.

2.4.3.5. Cueva Asfixiadora and Cueva de Gilberto

The Cueva Asfixiadora and Cueva de Gilberto sector is located just above the Cueva de los Pémones section and forms an upper floor of the Ojos de Cristal Cave System. This sector is formed by three parts previously considered to be individual caves: Cueva de Gilberto, Cueva Asfixiadora and Fragmento Marginal (Šmída et al., 2003). These caves are connected by a 40 m × 70 m collapse

depression. Cueva de Gilberto drains part of the sink depression located south of the cave. This cave has four big entrances, all of which are suitable for underground camps (Fig. 33). The extensive Cueva de Gilberto has a complicated spatial arrangement connected to the Fragmento Marginal and Cueva de los Pémones. Cueva de Gilberto is located at the western edge of the collapse depression which limits continuation of its underground passages, while Cueva Asfixiadora has an entrance at the eastern edge of the depression, and this continues underground. This cave part is formed by a simple horizontal passage that ends in a shaft leading to the lower floor of the cave system. This connection was surveyed in 2007 (Vlček & Šmída, 2007), and the total length of Cueva Asfixiadora, Cueva de Gilberto and Fragmento Marginal sector passages was recorded at approximately 2 km.

2.4.4. Cave spatial framework

The first discovered entrance to the cave system is located at the southernmost part of the cave system. It is formed by a sink hole draining rainwater from the Ojos de Cristal sink depression. The water is then drained into underground streams which form various fingerlike passages connected to each other, all coursing toward the outflow. In the geological past, the sink was drained

by the now dry Cueva del Hotel Guácharo branch which was located superiorly. The Ojos de Cristal Cave System forms a superficial cave with passages running parallel to the sandstone strata of the Matauí Formation. It also has slight declination to the north – northwest, in keeping with the 75 m cave declination to the deepest north-western part of the system at approximately 150 m below the plateau surface. The ground-plan indicates that this cave can be categorized as an anastomosing system, similar to karstic maze caves as in Palmer (1991). The largest passages in systems such as this act as water-flow corridors, and the smaller side passages, which are mostly flat-shaped with sandy floors, only become fluvial during extreme inflow events (Fig. 34). Based on currently retrieved data and observations, we postulate that the most important parameters in the speleogenesis of these caves are the high energy storm waters which widen the cave system laterally into parallel channels and later connect the main corridors. Nine main corridors have been currently observed in this system. One of these forms a framework which delimits the Cueva Mischel sector from the north-east. Two other corridors form the framework of the Cueva Ojos de Cristal sector while another constitutes the Cueva del Hotel Guácharos sector, and four more compose the main thrust of the Cueva de los Pémones. The last corridor is mostly dry, and it runs through the Cueva Asfixiadora and Cueva de Gilberto sectors. The vertical part of the cave system – the so-called pokémons – act as a rapid water supply to the cavern underground. Although they normally drain small areas, Pokémon 2 drains a larger part of the sink depression south of Cueva del Gilberto from a surrounding area of approximately 0.025 km². The vertical crevices also act as expansion basins which can accumulate excess inflow during the high water level events. The pokémons and whole Cueva Ojos de Cristal Cave System can be considered as superficial karst phenomena, reaching only a few tens of metres below the tepui surface. Deeper structures are represented by grietas.

2.4.5. Speleological perspectives

Although five expeditions were undertaken to the Ojos de Cristal Cave System, not all of its physical extent has been properly surveyed. The system is delimited from the east by the Cueva Mischel sink depression and from the south by the Ojos de Cristal sink depression. While the vertical Pokémon 1 forms its northern limit, the system is cut off by the vertical wall of the Roraima Tepui in the southwest. Between the main thrust of the Cueva de los Pémones sector and the edge of the meseta, there is an area containing a large number of underground passages. Thus, the greatest possibility of discovering new passages most likely lies in the area between the southernmost branch of Cueva de los Pémones and the Cueva del Hotel Guácharos sectors. There is a potential to discover approximately 1.5 km of additional passages here. Other locations with great potential to contain unexplored cave systems or passages can be found in the area northeast of Pokémon 3 towards Cueva con Bloques de Piedra (Šmída et al., 2003). Currently, we postulate that this cave system continues to other inflow branches from inside the mountain, and this creates potential to uncover about a further 1.5 km of passages. The most challenging area for future explorations lies in the massif north of Cueva de los Pémones. The relief at the surface between the mesa El Maverick, which at 2,810 m a.s.l. is the highest point of the Roraima Tepui, and a mound north of the Cueva Asfixiadora, Cueva de Gilberto and Fragmento Marginal sector has disintegrated due to numerous vertical crevices. This rugged relief also contains several extensive flat-based depressions draining to the underground (Fig. 35). From this site, it is possible to enter a cave not necessarily connected to the Ojos de Cristal Cave System, although it may belong to the same compact system from a genetic point of view. There is added potential here to discover a further kilometres of cave passages. One of the most important questions which still requires explanation



Fig. 34: A smaller tributary branch in the Cueva Mischel sector.



Fig. 35: View from the highest peak of Roraima Tepui – El Maverick (2,880 m a. s. l.) to the surface. The Ojos de Cristal Cave System lies below this.

is whether all the water is drained exclusively by the windows in the outer walls of the tepui, or if they are also conducted to deeper parts of the rock massif and then rise in resurgence at the impediment of the mountain, similar to the Tuná Deutá or Doble Tubo del Agua on the southern Roraima slopes (Šmída et al., 2003). We presume that some water infiltrates deeper parts of the mountain through narrow cracks which are inaccessible to humans due to their small size.

2.5. HYDROGEOCHEMISTRY

Few scientific papers deal with the exogenous geochemistry of the tepuis. The soil and natural water geochemistry on Chimantá Massif was investigated by Briceño & Paolini (1992) and Barreto (1992); Aubrecht et al. (2008^a, 2011) researched geochemistry of the natural waters of Chimantá Massif and Roraima Mountain. In addition, geochemistry of the natural waters on the remaining table-mountains was published by Chalcraft & Pye (1984), and the chemistry of the Auyán Tepui waters was described by Mecchia & Piccini (1999) and Piccini & Mecchia (2009).

2.5.1. Sampling of natural waters and related fieldwork

The hydrogeochemical fieldwork consisted of taking water samples, examining their field parameters and performing

colorimetric analyses, as summarized in Table 2. Water samples were collected from underground streams, dripping from walls and speleothems, and also from surface streams, springs, ponds and swamps. Sampling and field analysis were performed during both the 2007 and 2009 expeditions. Sample amounts of 50 ml underwent colorimetric analysis performed at base camp on the collection day (Fig. 36C), and 15 ml of each sample was sealed in a plastic container and taken to a laboratory for $\delta^{18}\text{O}$ and $\delta^2\text{H}$ determination. Samples were filtered in situ using a 0.45 μm mesh diameter and each sample was run in duplicate (Fig. 36A). The pH and electric conductivity (EC) were established in the field by the WTW pH/Cond 340i SET field device (Fig. 36B). During the 2007 expedition, acidity and alkalinity measurements were done by titration, but this method was abandoned because all values fell under detection limits. The Merck Spectroquant Multy portable colorimeter was used for colorimetry analysis of Fe, Mn, $\text{SiO}_2\text{-Si}$, Al, $\text{PO}_4^{3-}\text{-P}$, $\text{NO}_3\text{-N}$, $\text{NH}_4^+\text{-N}$ and N.

2.5.2. Results of geochemical investigations

The pH values of all water samples were slightly to moderately acidic, between 3.3 and 5.6, with the pH values above 5 being registered for samples of cave drippings and ponds on Churí Tepui.

The values of electric conductivity (EC) were also very low, ranging between 2 and 28 $\mu\text{S}\cdot\text{cm}^{-1}$ (Figs. 37, 38). Considerable differences were noted in this relatively narrow interval for samples

Tab. 2: Table summarizing field water analysis during the sampling campaigns in 2007 and 2009.

Sample name	Site name	Site type	Expedition	pH	Conductivity ($\mu\text{S.cm}^{-1}$)	Fe (mg.l^{-1})	SiO ₂ -Si ($\mu\text{S.cm}^{-1}$)	Al ³⁺ (mg.l^{-1})	PO ₄ ³⁻ P (mg.l^{-1})	NO ₃ -N (mg.l^{-1})	Mn (mg.l^{-1})
CH-C-1	Churí, Cueva de Bautismo del Fuego	underground river	2007	4.09	22	0.04	0.49		0.01	6.2	
CH-C-2	Churí, Cueva Cañon Verde	underground river	2007		22	0.01	0.27				
CH-C-3	Churí – Cueva Charles Brewer, the fairst point of the cave (Gallery of Adina)	underground river	2007	2.54	20	0.07	0.22		0.28	<0.5	
CH-C-4	Churí – Cueva Charles Brewer, Orinoco Gallery	dripping water	2007	2.52	6	0.03	3.05		0.09	0.05	
CH-C-5	Churí – Cueva Charles Brewer, Lago Carnicero	underground river	2007	2.47	20	0.09	0.22		0.25	<0.5	
CH-C-6	Churí – Cueva Charles Brewer, Planetario de Cesar Barrio	underground river	2007	2.51	20	0.11	0.21		0.19	<0.5	
CH-C-7	Churí – Cueva Charles Brewer, the outlet of the underground river	underground river	2007	2.52	20	0.12	0.2		0.14	<0.5	
CH-S-1	Churí – surface	creek	2007	3.91	19	0.22	0.54		0.13	<0.5	
CH-S-2	Churí – surface	swamp	2007	5.64	23	0.25	0.51		0.52		
CH-S-3	Churí – surface	creek	2007	3.93	18	0.15	0.77		0.15	<0.5	
CH-S-4	Churí – surface	spring – seepage from a swamp	2007	5.48	25	0.08	0.5		0.16	<0.5	
CH-S-5	Churí – surface	spring – seepage from a swamp	2007		26	0.06	0.41		0.03	1.1	
CH-C-1-09	Churí – Cueva Charles Brewer, Cascadas de Moravia	dripping water	2009	5.2	7	0.01	3.35		0.04	0.8	
CH-C-2-09	Churí – Cueva Charles Brewer, the outlet of the underground river	underground river	2009	4.58	9	0.01	0.08	34	0.04	0.4	0.06
CH-C-3-09	Churí – Cueva Juliana	underground river	2009	4.38	18	0.1	0.56	39	0.02	0.3	0.18
CH-C-4-09	Churí – Cueva Juliana	dripping water (barro rojo)	2009	5.26	24	1.7	3.26	106	0.1	0.9	0.06
CH-C-5-09	Churí – Cueva Juliana	dripping water	2009	5.3		0.89	3.26	153	0.03	0.7	0.13
CH-C-6-09	Churí – Cueva Charles Brewer, Gran Galeria Karen y Fanny	water dripping from a speleotheme	2009		28		16.03				
CH-S-4-09	Churí – surface, Río Rojo	river	2009	3.3	25	0.07	0.02	92	0.02	1.3	<0.02

CH-S-5-09	Churí – surface, northern part of the plateau	creek	2009	4.58	2	0.03	0.16	<20	0.03	<0.5	0.07
CH-S-6-09	Churí – surface, northern part of the plateau	creek	2009	4.54	9	0.04	0.12	<20	0.03	<0.5	<0.02
CH-S-7-09	Churí – surface, northern part of the plateau	creek	2009	4.56	11	0.07	0.21	18	0.05	<0.5	<0.02
CH-S-8-09	Churí – surface, valley below the entrance of the Cueva Charles Brewer	creek	2009	4.38	14	0.03	0.28	69	0.1	0.8	0.06
Ro-C-1	Roraima, Cueva de los Pemones	underground river	2007		12	0.05	0.97		0.14	0.7	
Ro-C-2	Roraima, Cueva de los Pemones	dripping water	2007		2	0.03	2.3		0.09	1.2	
Ro-C-3	Roraima, Cueva de los Pemones	underground river	2007		14	0.03	1.01		0.13	1.9	
Ro-C-4	Roraima, Cueva de los Pemones	underground river	2007		18	0.05	1.36		0.16	5.6	
Ro-C-5	Roraima, Cueva Ojos de Cristal	underground river	2007		10	0.02	0.79		0.08	<0.5	
Ro-C-6	Roraima, Cueva Ojos de Cristal	underground river	2007		13	0.02	0.74		0.1	1.2	
Ro-C-7	Roraima, Cueva Ojos de Cristal, 20 m far from the portal	underground river	2007		13	0.04	0.73		0.15	1.6	
Ro-S-1	Roraima, Tuná Deutá	spring	2007		19	0.01	1.01		<0.01	<0.5	
Ro-S-2	Roraima, lake beneath the Valle de los Cristales	lake	2007		5	0.03	0.09		0.04	<0.5	
Ro-C-1-09	Roraima, Cueva de los Pemones	underground river	2009	4.9	8	0.07	0.19	265	0.03	<0.5	0.08
Ro-C-3-09	Roraima, Cueva de los Pemones	dripping water	2009	5.65	3	0.03	2.27	<20	<0.01	<0.5	<0.05
Ro-C-5-09	Roraima, Cueva Ojos de Cristal, 100 m from the entrance	underground river	2009	4.71	8	0.04	0.14	21	<0.01	<0.5	<0.05
Ro-S-2-09	Roraima, Tuna Damu	creek	2009	5.05	8	0.04	0.47	<20	<0.01	<0.5	<0.05
Ro-S-4-09	Roraima, Tuná Deutá	spring	2009	4.76	5	0.06	0.16	<20	<0.01	0.3	0.04

collected from the different sources of streams, springs and cave wall drippings, and also in the sample collection time. There was an overall tendency for higher electrical conductivity values for the surface and cave streams and spring samples collected in the 2007 expedition than those recorded in 2009. The 2007 expedition registered 18 – 27 $\mu\text{S}\cdot\text{cm}^{-1}$ in the samples from Churí and 5 – 19 $\mu\text{S}\cdot\text{cm}^{-1}$ in the samples from Roraima, while 2 – 18 $\mu\text{S}\cdot\text{cm}^{-1}$ were recorded for the Churí samples and 5 – 8 $\mu\text{S}\cdot\text{cm}^{-1}$ for the Roraima samples in 2009. It is quite obvious that the stream and spring samples collected on Churí had higher electrical conductivity values than those on Roraima. Low and stable values were typical for samples of the water dripping from the cave walls: 7-8

$\mu\text{S}\cdot\text{cm}^{-1}$ for samples from Cueva Charles Brewer and Cueva Juliana on the Churí Tepui. Considerably lower electrical conductivities were observed in the cave drippings of the Cueva de los Pemones sector on Roraima: 2-3 $\mu\text{S}\cdot\text{cm}^{-1}$. Analyses were performed on water samples dripping from the red mud in Cueva Juliana on Churí Tepui and on another dripping from a large inorganic opal stalactite in Cueva Charles Brewer, and these had higher electrical conductivity values at 24 $\mu\text{S}\cdot\text{cm}^{-1}$ from the red mud source and 28 $\mu\text{S}\cdot\text{cm}^{-1}$ from the speleothem. An overview of the studied speleothems is recorded in Aubrecht et al. (2008^{a,b}).

With the exception of the cave drippings results, all SiO_2 -Si concentrations in Churí samples ranged between 0.08 – 0.77

mg.l⁻¹ with slightly higher concentrations in samples collected during the first expedition (Fig. 38). While the SiO₂-Si concentrations in samples collected from similar sources on Roraima during the first expedition ranged from 0.73 to 1.36 mg.l⁻¹, one sample from a pond representing the Río Arabopó spring source contained extremely low concentration of 0.09 mg.l⁻¹. This water sample also registered the lowest electrical conductivity measured in streams at 5 µS.cm⁻¹. While SiO₂-Si concentrations in the samples collected in the 2009 expedition had a narrower interval of 0.14 – 0.47 mg.l⁻¹, there was a considerably higher range of 3.05 to 3.36 mg.l⁻¹ recorded in samples dripping from the Cueva Charles Brewer walls. A similar concentration of 3.26 mg.l⁻¹ was registered in the water sampled from red mud in Cueva Juliana, while samples dripping in the Cueva de los Pémones sector on Roraima were slightly lower at 2.3 and 2.26 mg.l⁻¹. However, the highest SiO₂-Si concentration of 16.03 mg.l⁻¹ was recorded in the water dripping from the opal stalactite in Cueva Charles Brewer.

Fe concentrations in all samples ranged between the detection limit of 0.01 mg.l⁻¹ and a maximum concentration of 1.7 mg.l⁻¹ (Fig. 39). Samples collected on the 2007 expedition from surface and underground streams, ponds and Churí Tepui cave drippings had slightly higher maximum concentrations of 0.22 mg.l⁻¹ compared to the 0.07 mg.l⁻¹ in 2009. Little difference in the ranges of Fe concentrations was noted in the samples collected on Roraima. These values were 0.01 – 0.05 mg.l⁻¹ in 2007 and 0.03 – 0.07 mg.l⁻¹ in 2009. Extreme Fe concentrations recorded in the cave drippings from the “Barro Rojo” (red mud) in Cueva Juliana were 0.86 – 1.7 mg.l⁻¹ in 2009. The Fe concentration in the small creek flowing near the red mud in Cueva Juliana was 1 mg.l⁻¹.



Fig. 36: Hydrogeochemical field work. A – Water sampling and filtering through a 0.45 µm mesh in Cueva Charles Brewer, Churí Tepui. B – Measurement of the pH and electrical conductivity in water samples, Cueva Ojos de Cristal, Roraima. C – Colorimetric analyses in the Northern Camp, Churí Tepui.

A comparison shows cave drippings collected from the “pure” quartzite cave walls containing Fe in the range of 0.01 to 0.03 mg.l⁻¹.

Al concentrations were measured only in samples from the 2009 expedition (Fig. 40). Concentrations in all samples from Roraima and small creeks in the northern Chimantá swamps were below the detection limit of 20 mg.l⁻¹. Moderately higher concentrations were recorded in Cueva Charles Brewer sector underground streams and Cueva Juliana, at 34 and 39 mg.l⁻¹, respectively. Al concentrations in the stream of the deep tectonic valley (probably draining cave systems of the Churí Tepui) in the western part of the Churí Tepui were up to 69 mg.l⁻¹ and 92 mg.l⁻¹ in the water of Río Rojo, the river of unknown origin which most likely drains the valley. The highest Al concentrations were measured in red mud dripping samples collected in Cueva Juliana at 106 and 153 mg.l⁻¹ respectively.

The Mn concentrations in the surface stream samples ranged between the detection limit of 0.02 mg.l⁻¹ and 0.06 mg.l⁻¹, while those from the underground caves and drippings were moderately higher at between 0.06 and 0.18 mg.l⁻¹.

2.5.3. Processes influencing water chemical composition

Natural waters on the table-mountains’ mesetas are influenced by the following main factors:

- precipitation water composition
- processes in soils and peats
- rock-water interactions

Although rainwater composition was not investigated during our expedition, Briceño & Paolini (1992) reported the composition of several samples collected on different mesetas of the Chimantá Massif. According to their findings, these precipitation waters were quite acidic, at average pH of 4.59 and range of 4.0 to 5.09. They also contained very low dissolved matter content with an average conductivity value of 7.4 µS.cm⁻¹ with a range of 4.6 to 9.7 µS.cm⁻¹. Other measured contents included; the Ca and Mg concentrations were below the detection limits, while the average Na and K contents were both 0.06 mg.l⁻¹ and the average Cl content was 0.35 mg.l⁻¹. Mecchia & Piccini (1999) recorded a wider interval in pH and electrical conductivity values in the rainwater samples collected on Auyán Tepui, the pH value range was 3.8 to 6.5, and the electrical conductivity values ranged from 1.3 to 15.9 µS.cm⁻¹. Variations in pH and electrical conductivity values generally depend on the acidic gases CO₂, SO₂ and NO_x, and also on dust content in the atmosphere. The Gran Sabana area is considered remote with a minimum of industrial factors influencing rainwater composition. In addition, because of low variability in the geology of the general Gran Sabana area, dust composition is most likely not responsible for these pH and electrical conductivity variations. Therefore, the variations may have been influenced by rainwater sampling methods.

Although rainwater is one of the few primary sources of nutrients such as Ca, Mg, K, their content there is often below the detection limit. The concentrations of these nutrients are increased due to evaporation and pre-concentration in plant bodies due to multiple recycling of organic debris. The greatest influence on

Fig. 37: The pH – EC relationship in natural water samples.

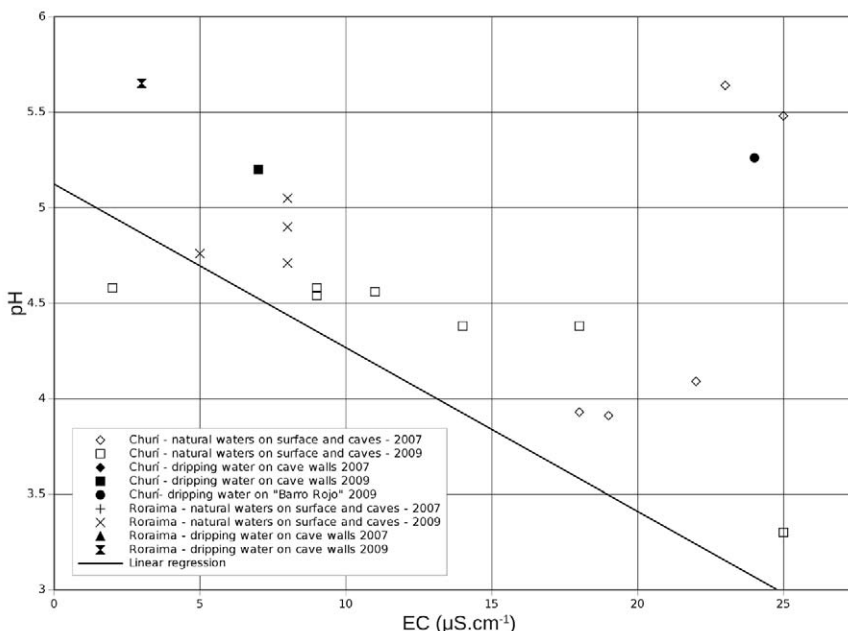
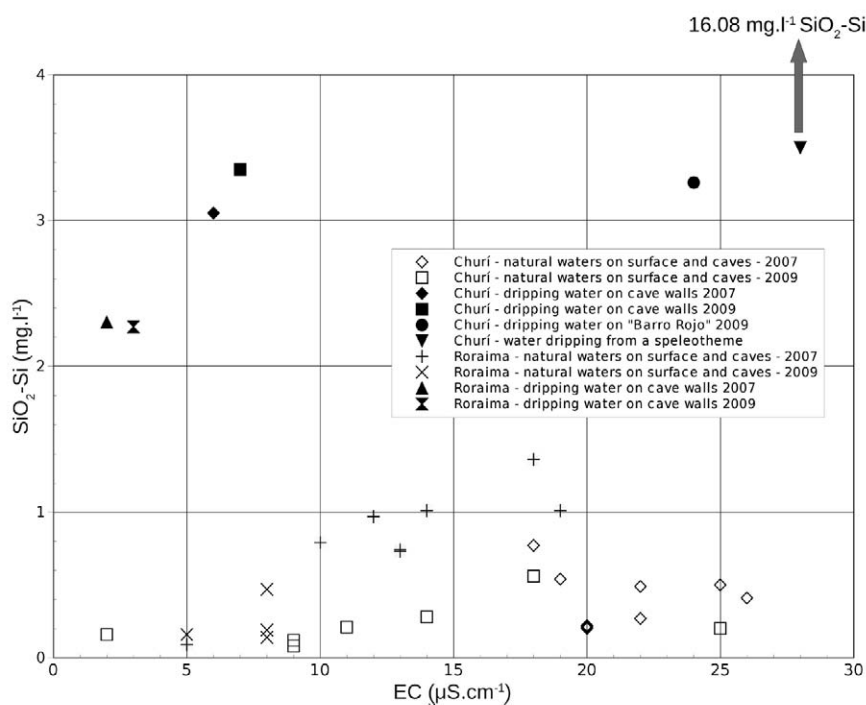


Fig. 38: Relationship of electrical conductivity and Si contents of natural waters.



the table-mountains' natural waters is the dilution effect during the rainy season as this provides more effective dissolution processes. The rainwater collected in small pools (opferkessels, kamenitzas) has an effect on sandstone weathering, because it is mediated by cyanobacteria (Fig. 43A). Naturally, since water completely evaporates from these pools, it cannot contribute to the groundwater and surface water systems in tepuis.

The effect of rainwater is demonstrated on the EC/pH relationship (Fig. 37). This graph depicts the negative dependency of electric conductivity (EC) on pH. This dependence for the Chimantá Massif's natural waters was also described by Briceño & Paolini, (1992). The graph clearly indicates that waters diluted

by rainwater typically have higher pH and lower EC values, while more evaporated waters possess higher EC and lower pH values. The highest pH values and lowest EC values were registered in samples taken from water dripping down the quartzite cave walls. Their pH show a generalized equilibrium with atmospheric CO₂, while their low EC values highlight the lack of minerals dissociating to ions in their dissolution processes (see the next chapter). The slightly higher pH and lower EC values in the water samples from Roraima in the 2009 expedition were caused by the high rainfall which occurred on Gran Sabana in that January and February. Samples collected on Churí Tepuy at the same time had wider EC and pH value intervals, as depicted in Figure 37; samples from

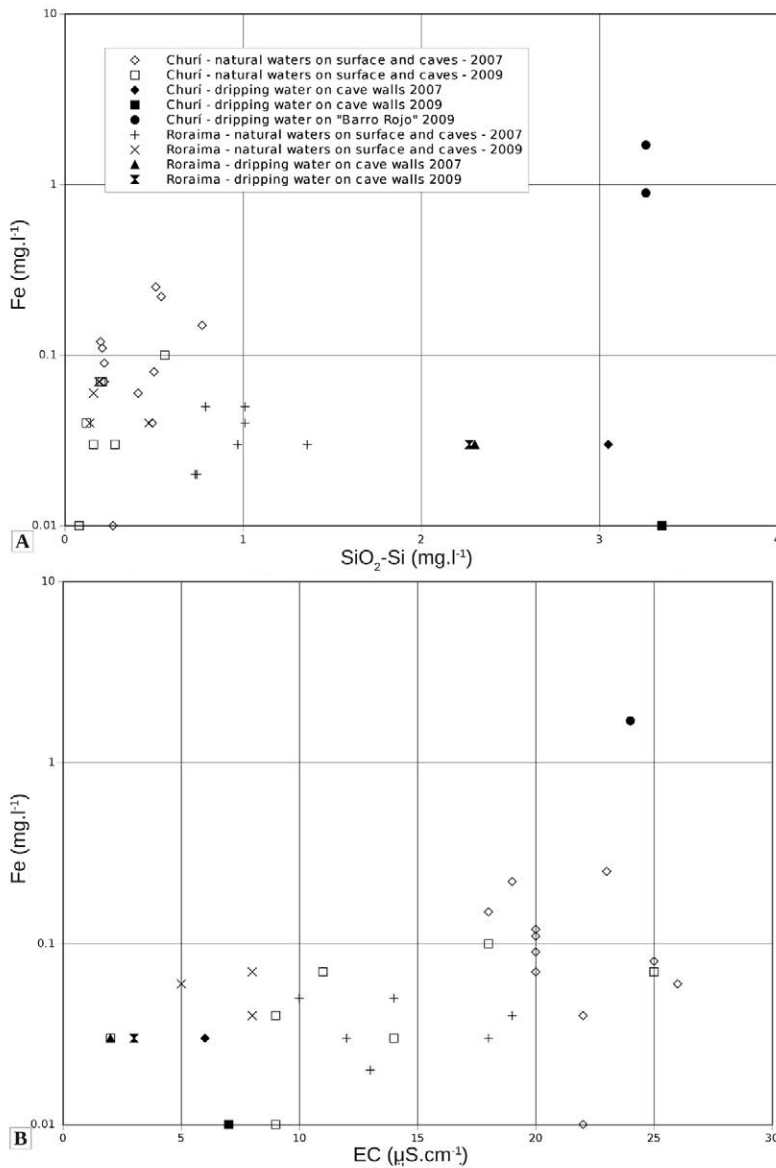


Fig. 39: Relationships of concentrations of Fe with Si (A) and electric conductivity (B).

small creeks close to the northern edge of the meseta following heavy rainfall are shown on the left, while a sample from the Río Rojo in the lowest part of the deep valley below the Cueva Juliana entrance appears on the right. Samples from Churí Tepui in 2007 are grouped below those of 2009, because they are more influenced by evaporation increasing organic acid and dissolved salts concentrations. Similar trends are apparent in the Si-SiO₂ contents and EC relationship in samples collected from the streams (Fig. 38).

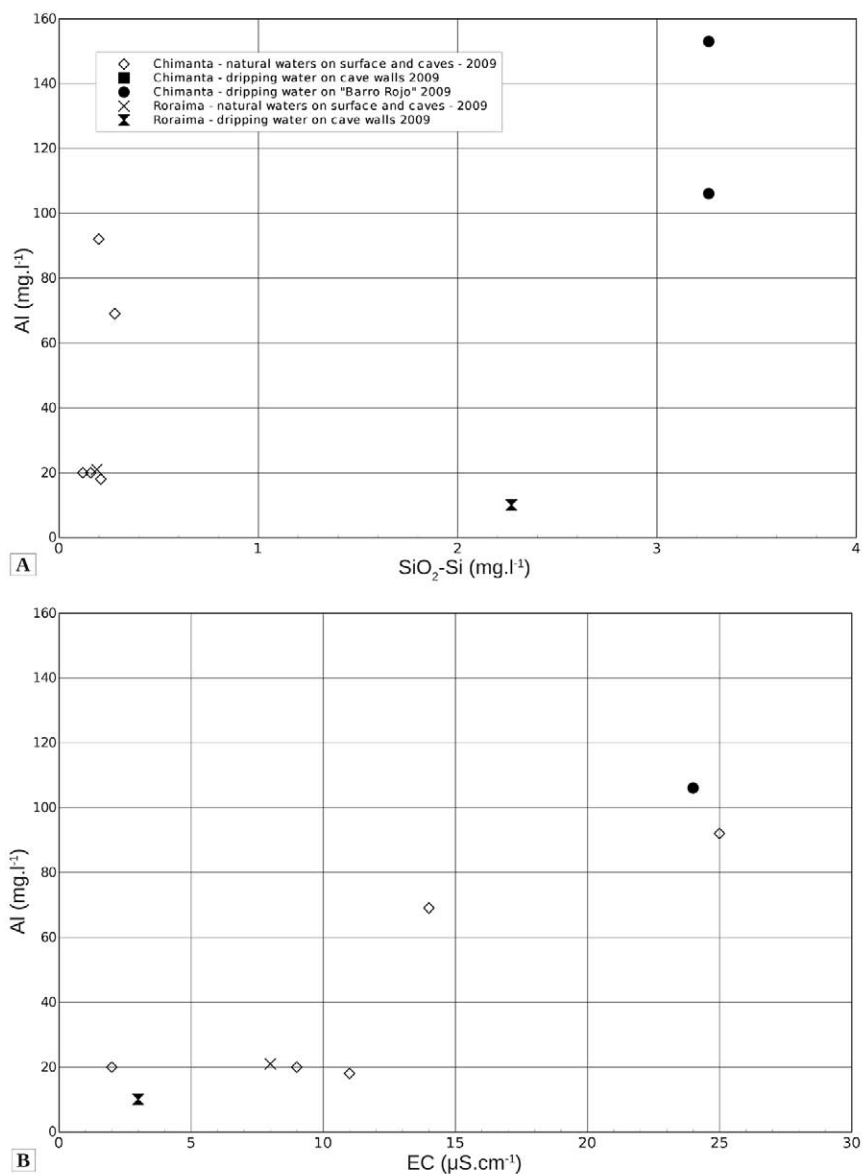
Peatbog geochemistry on the Chimantá Massif was described by Briceño & Paolini (1992), and its pedology was discussed by Barreto (1992).

Peat normally occurs in lower situated zones covered by dense savanna vegetation (Briceño & Paolini, 1992). The organic debris is in different stages of decomposition and water content is usually over 85%. Its maximum thickness on Chimantá is 2.1 m, as recorded on Akopán Tepui. The upper (fibrous) layer consists of living and dead plant roots and plant detritus, while the lower (hemic) layer is composed of decayed products from organic debris. The Ca, Mg, Na, K and Si concentrations in the plant

and peat material decrease with the depth of the peat layer due to their utilization by plants (Briceño & Paolini, 1992). These nutrients are leached from the substrate in very low amounts, and while they are primarily utilized from the rainwater and substrate leachate they are secondarily recycled from decayed organic debris. Although the above chemical concentrations all decreased, the Fe content increases with depth due to its higher redox potential values (Briceño & Paolini, 1992).

Barreto (1992) identified three soil types on the mesetas of the Chimantá Massif: entisols, histosols and ultisols. Histosols occur in lofty places and have 0.60 m thickness while ultisols in the deeper valley can be up to 2 m thick. These latter consist of two layers, the upper 0.30 – 0.40 m thick layer is composed of less decomposed organic materials, while the remainder consists of totally decomposed organic debris. These soils are quite acidic, with pH below 5, and their potassium, calcium and magnesium contents are extremely low, thus causing the very low fertility found in these soils. Despite these deficiencies, organic nitrogen, phosphorus and carbon contents are very high.

Fig. 40: Relationships of concentrations of Al with Si (A) and electric conductivity (B).



Since the soils and peatbogs represent environments with the highest water retention capacity, they serve as a relatively stable water source for numerous springs and watercourses draining the surrounds (Fig. 41A). The influence of the soils and peatbogs on the chemical composition of the surface and groundwaters of Chimantá Massif, and other table-mountains is mainly manifested by high amounts of organic acids and humic substances. These cause the yellow-brown-red colouring of waters (Fig. 41C), and the thick yellow foam which is quite apparent below waterfalls (Fig. 42). Higher amounts of organic acids contribute to the overall acidic character of these waters. Other effects of intensive organic matter decay are CO₂ production and dissolving carbonic acid which contribute further to lowering of pH values (Fig. 41B). These processes are highlighted in Figure 37. The negative dependency between pH values and electrical conductivity is also due to higher organic acid content in the evaporated waters. A typical example is the Río Rojo in the lowest part of the deep valley beneath Cueva Juliana entrance (Fig. 41C). This river most likely drains a larger

area on the western part of the Churí Tepui, because the high content of organic acids cause a reddish river water colour and a low pH of 3.3.

The rock-water interactions in the table-mountains involve the dissolution of quartz and aluminosilicate minerals. A numerical dissolution model for quartz, anorthite and amorphous silica by USGS PHREEQC geochemical modelling software was prepared to demonstrate the effects of mineral dissolution (Parkhurst & Appelo, 1999). The results of the model concur with the experimental data of Correns (1949) (cf. Fig. 44). The dissolution of quartz in water under natural conditions is a simple hydration process resulting in the formation of silicic acid:



The silicic acid then dissociates ionically to give:



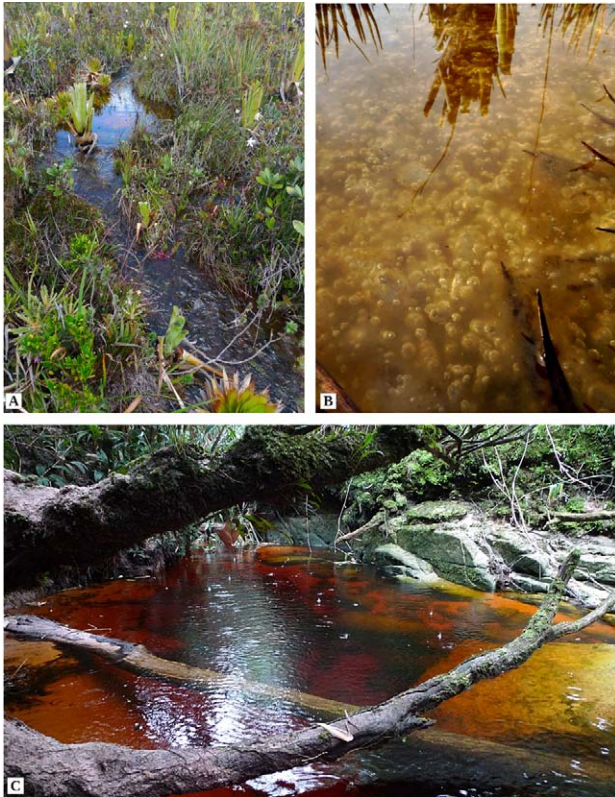


Fig. 41: A – One of the springs from a small creek draining a swamp area on the northern part of Churí Tepui. B – Gas bubbles emanating from organic debris decomposition in a small pool in the swamp, Churí Tepui. C – The typical yellow-reddish color of waters on the tepuis is caused by organic acids from organic debris decomposition processes in Río Rojo, Churí Tepui.

Reaction (2) significantly increases the solubility of the quartz, but only in a pH above 9. Below this value, the solubility is slightly affected by pH and water ionic content (Fig. 44). Complexing silicic acid with certain organic acids increases quartz solubility (Bennett, 1991).

In dynamic systems with high energy, such as karstic aquifers, the mineral dissolution is often controlled by reaction kinetics, as also occurs in relatively soluble minerals, including calcite. The dissolution of quartz at room temperature is extremely slow, and is controlled by the breaking of bonds and hydration of the silica on the mineral surface (Dove & Rimstidt, 1994). The dissolution rate can be increased from 10^{-17} moles $\text{cm}^2 \cdot \text{s}^{-1}$ at 25 °C in pure water (Bennett, 1991) to 10^{-14} moles $\text{cm}^2 \cdot \text{s}^{-1}$ at high pH values and in a concentrated NaCl solution (Dove & Rimstidt, 1994), and also by the presence of organic compounds such as citrate to $10^{-15.5}$ moles $\text{cm}^2 \cdot \text{s}^{-1}$ (Bennett, 1991).

The foregoing makes it clear that quartz dissolution is a long-term process and long-lasting exposure to a tropical humid climate is necessary to remove larger amounts of SiO_2 (Doerr & Wray, 2004). Although little data is available on water chemical composition in Venezuelan table-mountains, very low silica



Fig. 42: A – Dense and stiff foam remnants on rocks in a creek on Churí Tepui. B – Foam accumulated on an unnamed river flowing from the Cueva Charles Brewer sector. C – Foam remnants following a decrease in water level in Cueva Charles Brewer.

concentrations have been reported in the water drained from quartzite in the Roraima Supergroup. Chalcraft & Pye (1984) reported that silica contents are below $1 \text{ mg} \cdot \text{l}^{-1}$ in streams sampled on the table-mountains tops. Similar results were registered by Piccini & Mecchia (2009) for Auyán Tepui. The silica contents of streamwater sampled by our team both on the surface and in the caves concur with literature data, and in only two cases did they slightly exceed $1 \text{ mg} \cdot \text{l}^{-1}$. The silica contents and electric conductivity values in these samples appear to be considerably affected by hydrological conditions, as they were slightly higher in samples collected at the beginning of 2007 when the rainfall was lower than in our second expedition two years later. The different values occurred even though both of the expeditions were conducted during the dry period of January and February (Fig. 38).

The pH of water at the top of the tepui is quite low. According to Briceño & Paolini (1992) this ranges between 3.4 and 6.0 for natural waters at Chimantá Massif, while Mecchia & Piccini (1999) and Piccini & Mecchia (2009) reported pH values from 3.5 to 4.9 for waters sampled on the Auyán Tepui. Our samples had pH values ranging from 3.3 to 5.5, and the combination

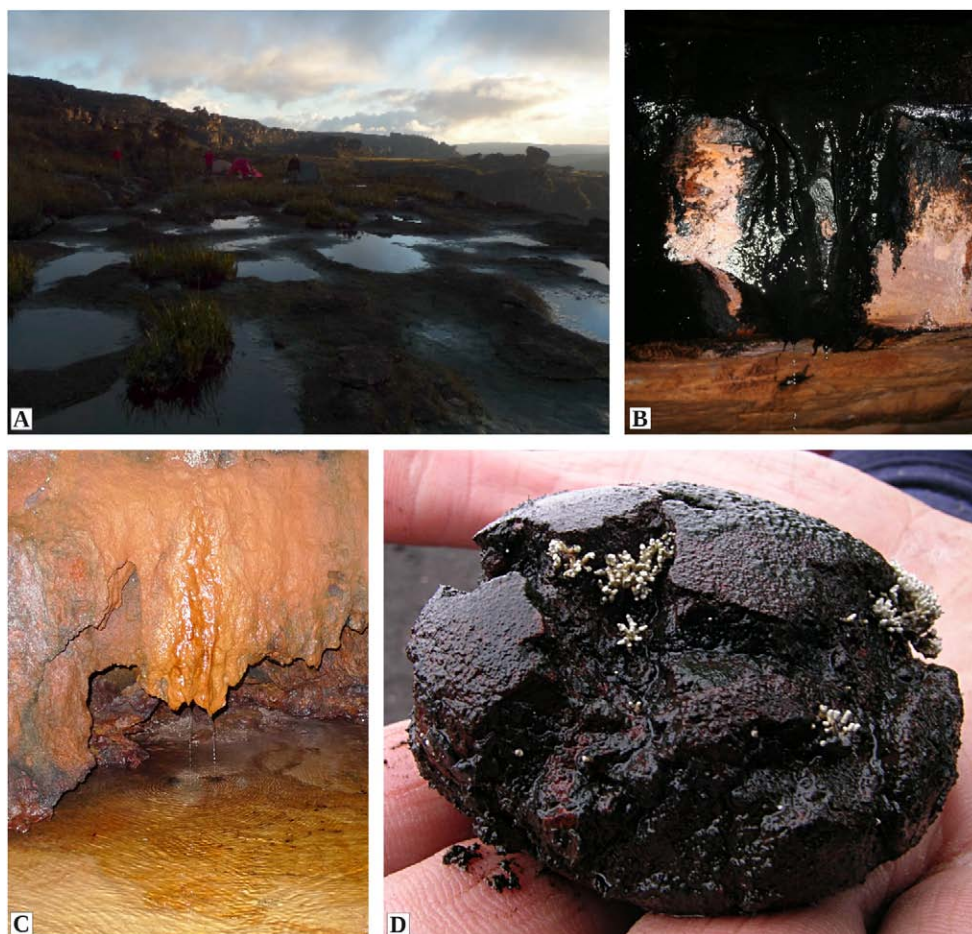


Fig. 43: A – Small pools in the sandstone surface filled with water following heavy rain. Intensive microbially intermediated weathering is evident in these pools on Churí Tepui. B – Condensed water dripping from a cave wall in Cueva Charles Brewer, Churí Tepui. C – Water dripping from “Barro Rojo” accumulated in Cueva Juliana, Churí Tepui. D – Depiction of a probably bio-corroded quartz pebble on Roraima.

of all these values indicates that pH values in natural surface waters uninfluenced here by human activity are extremely low. This phenomenon is common for natural waters of the quartzite terrains of the Gran Sabana (Briceño et al., 1991). It is caused by; lack of aluminosilicates and carbonates which act as acidity buffers; the presence of organic acids from organic debris decomposition in surface swamps; and the CO_2 production in organic matter decomposition. An interesting negative relationship was identified between the pH and EC values in the water samples, and this relationship was also reported by Briceño & Paolini (1992). In addition to the effects of rainwater on the soil and peatbog described above, rock-water interactions also affect this relationship, where high precipitation diminishes the neutralization effect of the aluminosilicate dissolution. Consequently, natural waters in these areas are generally strongly undersaturated compared to aluminosilicates, even in extremely low pH conditions where their solubility is lowest (compare Figs. 37, 38 and 44). Very high organic acid concentrations did not significantly increase quartz solubility because silica complexing by organics is effective only at high pH (Ingri, 1977). The highest Si content of 16.03 mg.l^{-1} was recorded in the water sample

dripping from the opal stalactite in the Cueva Charles Brewer sector. This extreme concentration was above the equilibrium concentration with quartz, and it was also associated with the highest conductivity value of $28 \mu\text{S.cm}^{-1}$, which indicates that this is due to water evaporation on the cave walls rather than a consequence of dissolution. The most effective quartz dissolution process was observed on the cave walls, where air moisture precipitates and causes corrosive dissolution due to strong undersaturation, compared to that of SiO_2 in the precipitated water. This process was recognized in samples of water dripping from the cave walls (Fig. 43B-C). The origin of the dripping water from condensed air moisture is apparent from the higher silica content of $2.3 - 3.3 \text{ mg.l}^{-1}$ and very low electrical conductivity values of 2 to $7 \mu\text{S.cm}^{-1}$ presented in Fig. 38. Further evidence is provided by the 5.3 to 5.6 pH values of the dripping water, which are close to the 5.6–5.7 pH value of distilled water in equilibrium with atmospheric CO_2 . These values illustrate a process of almost pure SiO_2 dissolution in distilled water, as proven by the accompanying extremely low electrical values described above. These occur because silicic acid, which is a dissolution product of SiO_2 , does not dissociate below a pH of 9, and therefore it

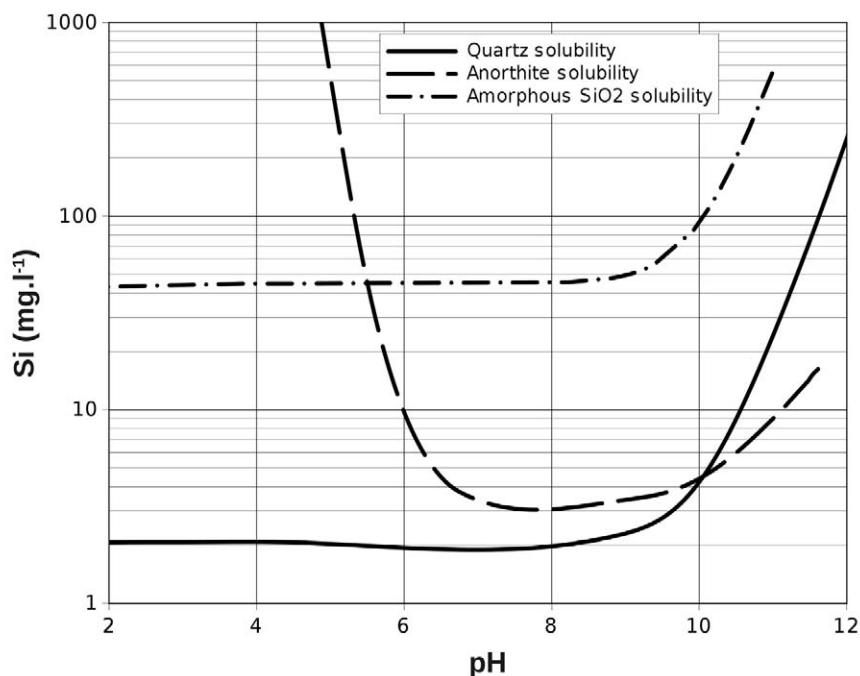
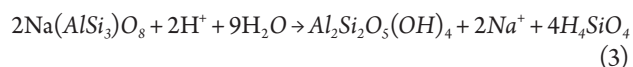


Fig. 44: Solubility of quartz, amorphous SiO₂ and anorthite from the thermodynamic model constructed in PHREEQC.

does not contribute to the electric conductivity. Despite this, although the dissolution process is extraordinarily effective, it has only a local importance because it occurs only in specific circumstances. The circumstances required here are that the moisture can precipitate in a well developed underground area with minimum air flow, so that water vapour is not blown away. Since the amount of dissolved and mobilized silica is volumetrically negligible, its importance as a key process in speleogenesis is also negligible.

Some arenites, such as arkoses and subarkoses, also contain aluminosilicate minerals, mainly micas and feldspars. These aluminosilicates dissolve in acidic water more effectively than quartz (Fig. 44; see also diagrams in Valetton, 1972; experiments of Franklin et al., 1994). The dissolution, or weathering process, of aluminosilicate minerals is an incongruent process where

insoluble remnants are formed during the dissolution process. These remnants are secondary minerals including clays such as montmorillonite, illite and kaolinite and various Fe and Al oxides and hydroxides. Here, released silica may further precipitate as opal-A. The types of secondary minerals depend on the water pH, temperature and ion content and also the composition of the primary aluminosilicate. A typical example of an aluminosilicate dissolution reaction is the following albite dissolution with the secondary kaolinite mineral:

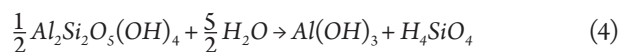


The presence of aluminosilicates in the tepui rocks is apparent in thin sections and in the samples from less lithified quartzite layers examined by SEM (cf. Fig. 61). Under humid and warm tropical conditions, the incongruent dissolution processes together with other silicate rock weathering processes result in laterite formation. In many cases, there are white, heavily kaolinized arkosic arenites with red lateritic caps, as are visible in Gran Sabana. The red mud found in excessive quantities in both examined cave systems registered a mineral composition of goethite, kaolinite, illite, quartz and pyrophyllite, thus representing true laterite (Tab. 4). It is reasonable to presume that the mud accumulations observed in the caves are only remnants left by the subterranean streams and that the original amount of red mud was much higher. The dissolution processes in the laterite bodies have considerable influence upon water chemistry but this was manifested only in water dripping from the laterite bodies. Si content was recorded up to 3.26 mg.l⁻¹ in such samples in Cueva Juliana on Churí Tepui, and although this content is quite similar to that in other dripwater samples, the electric conductivity here was 24 μScm⁻¹ (Figs. 35, 36). This was most likely due to the higher concentrations of ions originating in aluminosilicate dissolution reactions,



Fig. 45: Field measurements of rock hardness by Schmidt hammer in Cueva Juliana.

and also presumably from kaolinite and/or other secondary phyllosilicate dissolution under conditions of low pH:



Relatively high concentrations of Al^{3+} in water samples dripping from the red mud registered 106 and 153 $mg.l^{-1}$, and this is 3-8 times higher than in the surrounding stream water. These were a consequence of gibbsite and/or other aluminium oxides/hydroxides dissolution under acidic conditions:



Higher Fe^{2+} concentrations in these dripping water samples are a sign of goethite dissolution.



Stream waters at the table-mountain pediment are affected by dissolution processes in arkosic arenites. For example, there are silica concentrations up to 3.4 $mg.l^{-1}$ in Río Carrao (Piccini & Mecchia, 2009), which may indicate that the lateritization in the existing cave passages occurred in its final stages.

2.6. SPELEOGENESIS OF THE CHARLES BREWER AND OJOS DE CRISTAL CAVE SYSTEMS

2.6.1. Introduction

Several aspects must be considered and several methods used in order to explain the speleogenesis of Charles Brewer and Ojos de Cristal cave systems – the two largest sandstone cave systems in the world. However, results of this speleogenetic research go beyond the initial target and help us to better understand the geomorphological evolution of tepuis. It is first necessary to emphasize the extreme difficulties encountered in establishing the genesis of sandstone and quartzite caves, because the origin of the arenitic caves in Venezuelan tepuis has created scientific disputes all over the world. Caves and karstic phenomena are common in limestone terrains and in other areas containing rocks with similar or greater solubility, including gypsum and salt. In this regard, there is also the quandary on caves formed in other rocks, such as silicates. All karst-like phenomena that evolved in non-carbonate environments were initially attributed to the pseudokarst category, but the term “karst” was later extended to some non-carbonate rocks (see Doerr & Wray, 2004 for overview). Most recent definitions state that dissolution is the determining factor of karstic phenomena (Jennings, 1983; Wray,

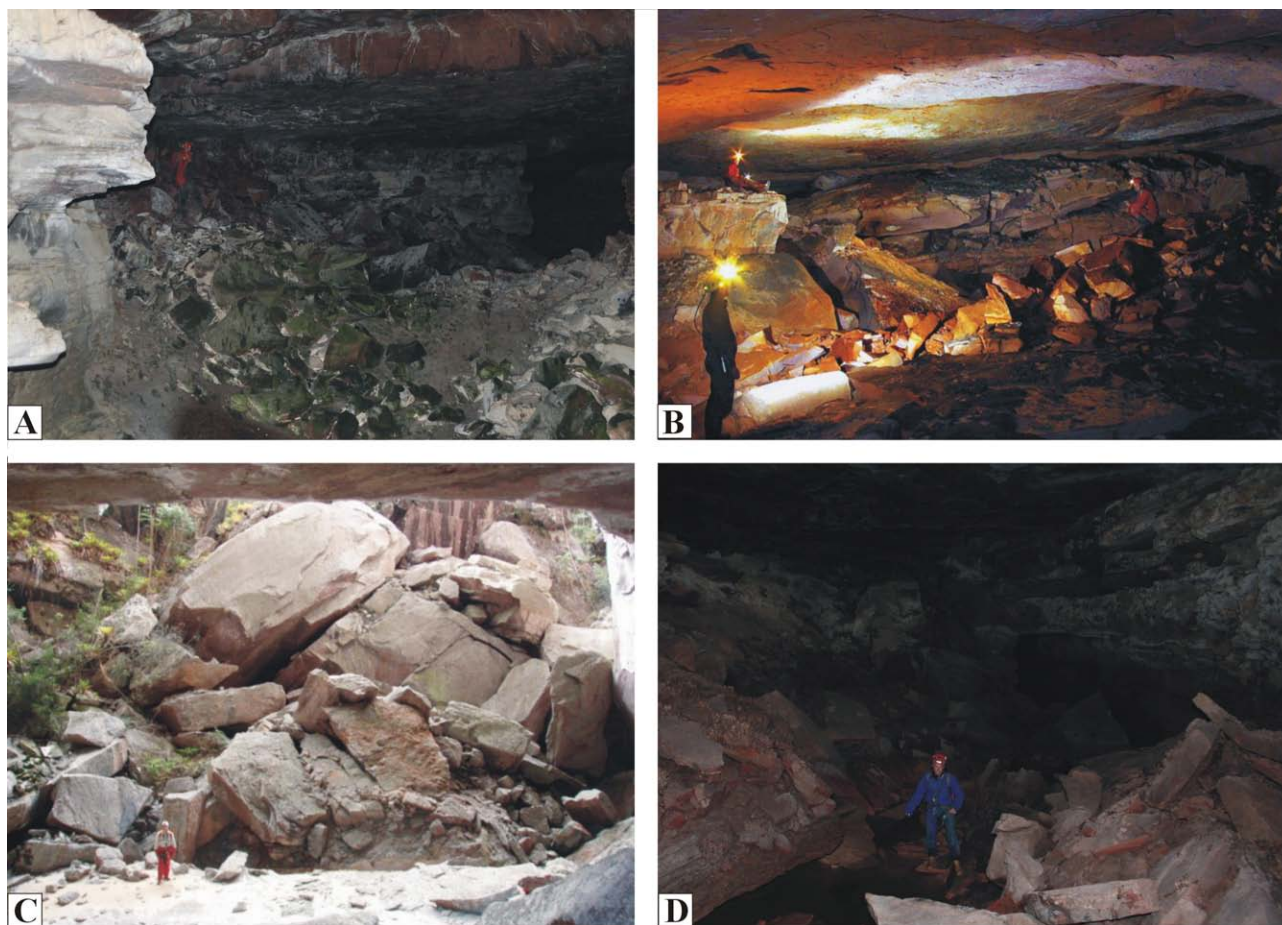


Fig. 46: Rockfalls represent the main cave-forming process in later stages of speleogenesis. A – Cueva Colibri, B – Cueva del Hotel Guácharos in the Ojos de Cristal Cave System, C – Collapsed entrance of Cueva Tetris, D – Cueva Cañon Verde.

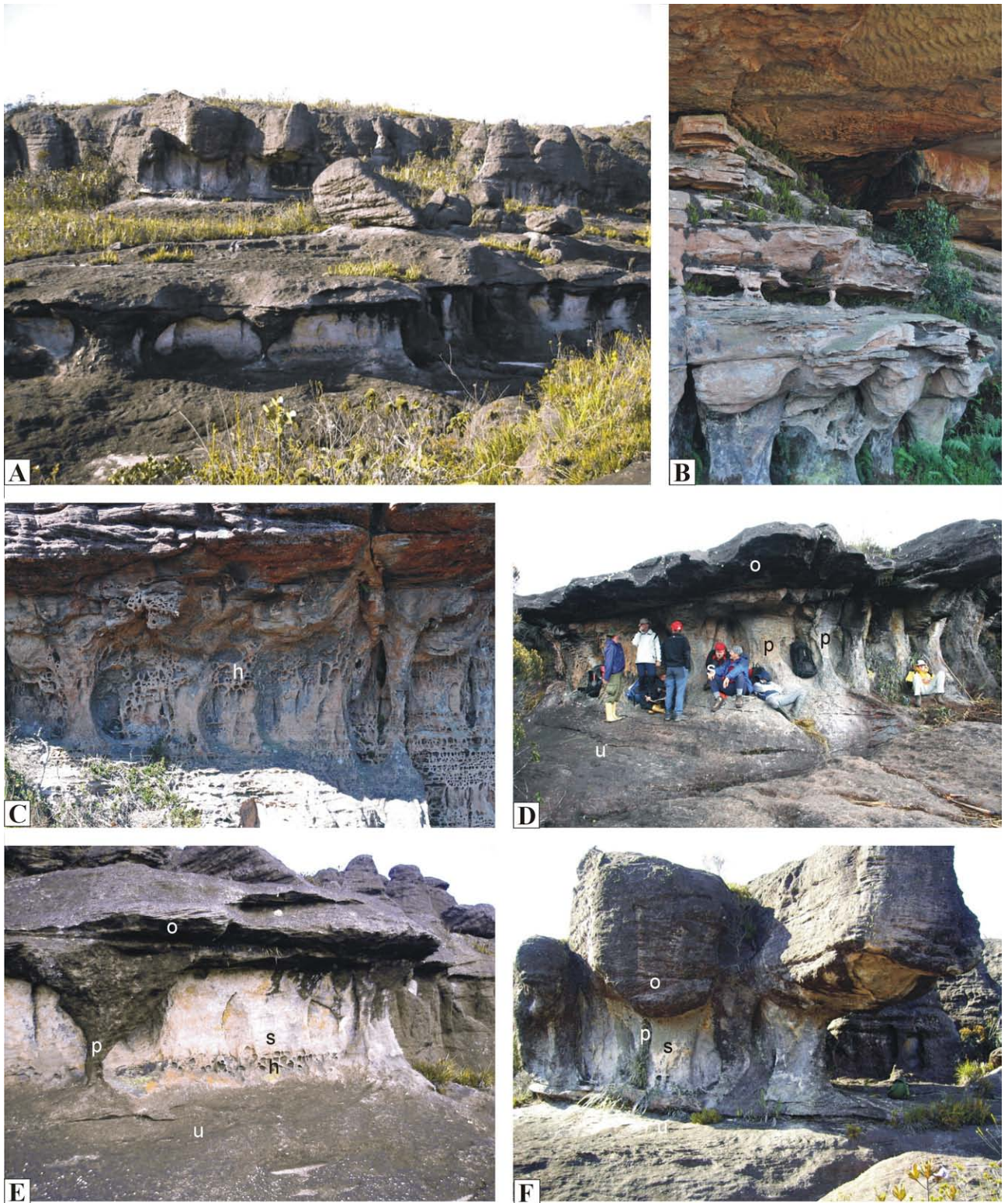


Fig. 47: Horizons of poorly-lithified arenites on the tepui surfaces. A – Two superimposed horizons with poorly-lithified arenites, forming the depressed relief between well-lithified quartzites on Churí Tepui close to base camp, served as sampling sites for petrographic studies in 2007. B – Superimposed poorly-lithified horizons on Roraima. Typical features are “finger-flow” pillars. C – Another poorly lithified horizon on Roraima. “Finger-flow” pillars are combined by “honeycomb”-like vein network (h). D-F – Typical features of poorly-lithified horizons on Churí: o – overlying quartzite bed, h – “honeycomb”-like vein network, u – underlying quartzite bed, p – “finger-flow” pillar, s – poorly lithified sand. (D) base camp in 2007; (E-F) locality figured in 47 A .

1997^b; Doerr & Wray, 2004; Martini, 2004). Silicate rocks generally have very low solubility, and therefore caves which formed in silicate rocks were considered to be pseudokarst, as most workers believed that dissolution does not play an important role in their formation. However, many works later emerged which applied the term karst to silicate caves which occurred either in granites (Willems et al., 2002; Twidale & Vidal Romani, 2005; Vidal Romani & Vaqueiro Rodrigues, 2007; Cioccale et al., 2008), or else in sandstones (see reviews in Wray, 1997^{a-b}, 1999). According to these authors, dissolution is definitely the main process forming these caves, regardless of how slowly this progresses. The term “arenization” was then coined to describe silicate rock weathering. Martini (1979) used this term for sandstone rocks, extending its meaning to dissolution of the cements in arenitic rocks. Accordingly, this turns quartzites to the so-called “neo-sandstone” (see Martini, 2004). This loose sand material, when eroded and winnowed, provides subterranean spaces. If this arenization theory was accepted, most sandstone caves might be attributed to karst because this dissolution is considered to be a triggering stimulus for cave formation. The main evidence that dissolution occurs in silicate caves is provided by the silica speleothems which occur in most silicate caves. These are mostly composed of opal-A, which slowly turns into opal-CT (crystalite-tridymite) and then into microcrystalline quartz (cf. Aubrecht et al., 2008^a and discussion on speleothems in this volume). The question is whether the silica dissolution is so important that the Venezuelan arenitic caves can be correctly ranked among karstic ones. Our team presents a different view on the genesis of sandstone caves where we challenge their karstic origin on the basis of preliminary results from our two speleological expeditions to the Venezuelan Gran Sabana (Aubrecht et al., 2008^b). Although it was accepted that dissolution may be quite important, this dissolution involved feldspars, micas and clay minerals in a process of lateritization, rather than quartz dissolution (Aubrecht et al., 2011). In this volume we provide further data and illustrations to support this view, and consequences of this premise on the geomorphological evolution of tepuis.

2.6.2. Material and methods

Our geological, geomorphological and speleological observations were focused on phenomena relevant to the solution of the speleogenetic problems. This mainly centred on the differential weathering of the various kinds of arenites on the tepuis surfaces and caves in the Matauí Formation, and also on morphological aspects of the various stages of speleogenesis and its final manifestations on the surface. Sites with different arenite lithification and erosion provided 40 samples for petrographic analysis in thin-sections and under SEM. Differences in rock hardness were observed empirically, and 23 sites were measured by Schmidt hammer (Fig. 45). The Schmidt hammer enables a simple and quick field test of the rebound hardness of rock, delineation of the horizons of various weathering/alteration stages along a given profile, and also assessment of the characteristics of the rocks' strength. The rebound is measured by touching the rock firmly with the Schmidt hammer and releasing the strained spring with a cylinder inside the hammer. The cylinder rebounds depending

on the rock hardness and this is recorded mechanically on a paper scroll which the mechanized version of the hammer shifts after each straining. The measurements (159 measured points) were focused on soft, poorly lithified layers, hard overlying and underlying layers and also on the “finger-flow” pillars penetrating the soft layers, which are discussed in later chapters. Most of the measured rocks were wet, but not completely saturated with water. Hardness at each point was measured 10 to 15 times and the average values were estimated, following exclusion of the extreme values. Since there was insufficient number of arenite samples, the measured rocks uniaxial compressive strength was calculated from the rebound values.

Mineralogical composition of the samples was determined optically and also by X-ray diffraction analysis (XRD). The mineral composition of selected samples of sandstones and the clay fraction of red mud were established by X-ray powder diffraction analysis using a Philips PW 1820 diffractometer fitted with a graphite monochromator and Cu tube. Scanning steps of 0.02 °2θ with counting time of 1 s per step from 4 – 74 °2θ were used for sandstone samples. Oriented and non-oriented specimens were prepared for analysis. The XRD data for oriented specimens were obtained in air-dry and ethylene-glycol-solvated (EG) states.

Selected samples were also studied by infrared spectroscopy, Raman spectroscopy and electron microprobe analysis. Polished thin-sections of each speleothem were prepared for microscopic investigations under polarized light.

2.6.3. Results and interpretations

2.6.3.1. Field geomorphological and geological observations and their importance in speleogenesis

Erosion and rockfalls, which recently prevail in the Charles Brewer and Ojos de Cristal cave systems have concealed their true speleogenetic processes (Fig. 46). The sandstone beds have angular edges and the caves are full of fallen angular blocks. The signs of dissolution in the sandstone beds smooth edges and bizarre etching patterns are too rare to explain recent stages of the caves' evolution. All the trigger and structural factors acting during initial stages of the caves' evolution are now obliterated in the mature parts of the cavern systems. While our observations of surface geomorphology of these tepuis and their subterranean spaces have supplied some clues to their speleogenetic processes, many of these clues emanated also from caves which are still in their initial stages of evolution.

The sandstone surfaces of tepuis are very uneven and bizarre, obviously due to an inhomogeneous lithification of the Proterozoic arenites. This is especially apparent in areas where arenite beds form overhangs (Fig. 47). The overlying and underlying beds are hard, well-lithified rocks formed by sandstones to quartzites, so that sampling was possible only with strong hammering. However, the beds inbetween are only slightly lithified or completely unlithified soft sands and sandstones, so that it was almost impossible to take lithified samples for petrographic microscopic study, even after digging 30 cm deep by hand. These poorly lithified beds are penetrated by perpendicular pillar-shaped bodies. These are narrower in the middle, but they have

funnel-like widening at either end, with the lower funnel less developed than the upper one (Fig. 47C-E). They are relatively well-lithified rocks, ranging from sandstones to quartzites, and the combination of overhangs and pillars provides attractive decoration for most tepui surfaces (Fig. 48).

The origin of these pillars is purely diagenetic and their presence proves that the softness of the poorly lithified beds is primary rather than being secondary. The pillars are considered to originate by a “finger flow” mechanism (cf. Aubrecht et al., 2008^b, 2011). The main factors influencing diagenetic variability were the differing hydraulic properties of the sediment in different layers which influenced its hydraulic conductivity. The diagenetic fluids most likely penetrated vertically from the overlying strata as a descending diagenetic fluid flow. In finer-grained sediments, these diagenetic fluids filled the intergranular spaces evenly and resulted in the formation of diagenetically well-lithified beds, resistant to weathering. In coarse-grained arenites with higher hydraulic conductivity below the fine-grained beds, the evenly distributed descending diagenetic front divided into “fingers”, where the fluid flow accelerated and formed separate, finger-like flows. This process has been described in detail by various authors working with transport processes in unsaturated zones of sandy aquifers and also in soils (Bauters et al., 2000; Liu et al. 1994). A similar process is seen in snow penetrated by descending water as it leaks from melted snow above (Marsh, 1988: fig. 2). Liu et al. (1994) considered that when these finger flows are generated in originally dry sandstones they are conserved as the most preferred method of infiltrating solutions. This is the way pillars originated in the unlithified sands. The upper diminishing funnel shape of the upper part of the pillar originated from flow acceleration, which continued until it decelerated when approaching the less permeable bottom. This retardation process is manifested in the reversely oriented funnel shape of the pillar bottom (Aubrecht et al., 2008^b).

The poorly lithified beds form distinct horizons in tepui geomorphology, and these can be traced and correlated for long distances (Fig. 49A-C). The overlying and underlying beds protect the unlithified sand from rainfall, but they are easily eroded when accessed by horizontally flowing water streams. When the overlying protective beds become weathered, broken or dissected by clefts, water can then penetrate as deep as the unlithified beds, thus forming a horizontal cave (Fig. 49E-F). Observations in the Charles Brewer and Ojos de Cristal cave systems show that pillars are present in most of the caves and in their galleries, which are still in younger stages of their evolution (Fig. 49D-H). These usually possess low ceilings and strictly maintain one distinct layer. Relic finger-flow pillars were also observed in the marginal, uncollapsed parts of the larger galleries (Fig. 50). In some caves, incomplete “finger-flow” pillars occurred where only the upper funnel was developed. Speleologists named these forms “tetras” (teats – Fig. 51)

When several superimposed winnowed horizons evolve together, a second collapse stage follows, leading to formation of much larger subterranean spaces (Fig. 52A). Galleries in the Charles Brewer Cave System are typically 40 metres wide, but they can also be much larger. The largest chamber found in the cave is Gran Galería Karen y Fanny. This is 40 metres high, more than 355 metres long and 70 metres wide, giving a volume of approximately 400,000 cubic metres (Fig. 52B). The initial

cave-forming stages of this cave system were clearly related to the laminated clay-bearing sandstones which now persist in the lower parts of the cave (Fig. 52C). In addition to being primarily poorly lithified, their clay mineral content makes them prone to lateritization (see below). These initial stages were followed by collapses of strongly lithified quartzites overlying the laminated sandstones (Fig. 52D).

The final stages of cave evolution often lead to huge collapses, and these are apparent on the tepui surfaces (Fig. 53). One of the largest collapse zones is present on Churí Tepui in the Chimantá Massif (Aubrecht et al., 2008^b: pl. III, fig. 3). This collapse zone is sunken and the sandstone mass is dissected into large blocks which slope in different directions (Fig. 53F). These blocks were evidently “undercut” by erosion of the poorly lithified sand layers so that they then collapsed. No other processes, including dissolution or arenization involving breakdown of cement and release of sand grains, or even weathering would be capable of creating such a huge collapse zone. The linear course of this zone highlights that it is related to tectonic fault activity (cf. Briceño & Schubert, 1992^a), but this most likely served only as a trigger for the collapse, by enabling drainage of flowing water and erosion of the unlithified strata. Collapses of the cave spaces, from which the poorly lithified arenites were winnowed, obviously led to the creation of the large abysses in the Sarisariñama Plateau (Sima Mayor and Sima Menor – Fig. 9), or the well known depression El Foso on Roraima Plateau (Fig. 54A). On the basis of these observations, winnowing of the unlithified or weakly lithified sands fulfils the trigger role in the formation of the sandstone caves in tepuis, and it also influences their further evolution.

Although the signs of quartz dissolution forming smooth edges of sandstone beds or bizarre etching patterns are relatively rare (Fig. 55A-C), some of these signs can be found in the caves and on the tepui surfaces. Here, the uneven, bizarre patterns may be due to etching from the increased alkalinity produced by microbial colonies (cf. Büdel et al., 2004; Brehm et al., 2005; Barton et al., 2009). Some even form photokarren, which can be seen oriented parallel to the sunlight near the entrance of Cueva Charles Brewer (Lundberg et al., 2010^b). This same process may also be responsible for the pitted surface of the tepuis. There are numerous small pools on the surface which host various species of cyanobacteria (Fig. 55D-F). Such depressions were formerly also considered to be initial karst forms (White et al., 1966).

From other aspects which contribute to cave-forming processes, the presence of considerable quantities of lateritic red mud (Spanish: “Barro Rojo”) were observed. It is a ubiquitous phenomenon here, and large quantities can be found in all the explored Churí and Roraima caves (Aubrecht et al., 2011). This mud usually leaks from fractures and bedding planes (Fig. 56) and when desiccated it forms mounds or even speleothems, including flowstones, globules and small stalactites (Fig. 57). Its colour can also sometimes be black (Fig. 56E, 57F), so that broken speleothems often show alternating red and black laminae (Fig. 57G).

2.6.3.2. Hardness measurements

Measurements were performed to objectively verify the obvious hardness differences existing within the Matauí Formation's arenites. These were verified empirically (Aubrecht et

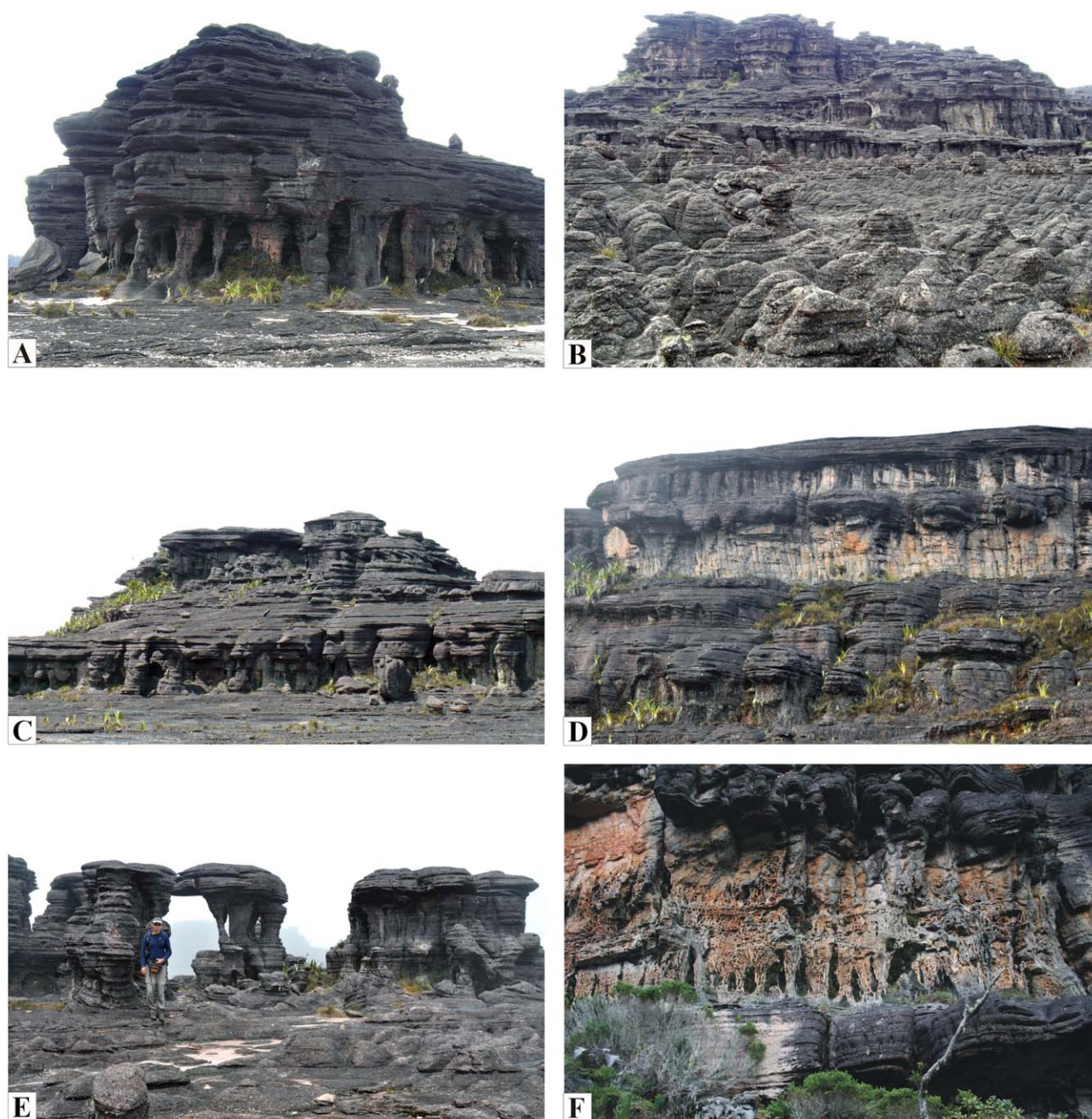
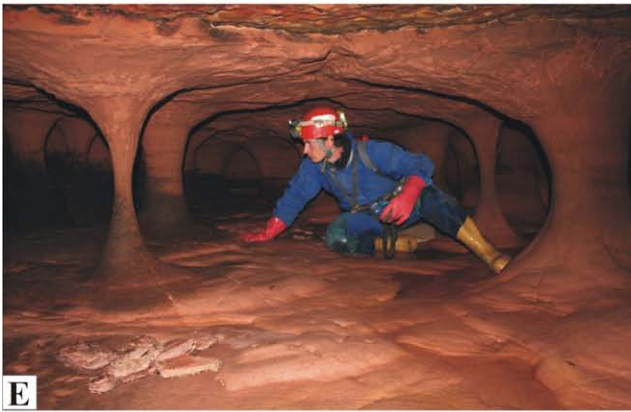


Fig. 48: Horizons of “finger-flow” pillars are typical decoration of Roraima surface geomorphological forms.

al., 2008^b) and also by objective measurements enabled by the Schmidt hammer (Aubrecht et al., 2011). The measurements showed different values between the hardness of loose sands in the poorly lithified beds, and that of the well lithified overlying and underlying beds and “finger flow” pillars. The hardness differences are also clearly highlighted in the average and median values of the entire set of measurements. In the scale of 0 to 100, the rebound hardness of the poorly lithified arenites ranged from 18 to 37.67 in 49 measurements; with an arithmetic average of 23.49, a median of 22.27, and a standard deviation of 4.74. The

derived uniaxial compressive strength ranged from 25 MPa to 150 MPa, with the majority of values falling below 47 MPa. Although the rebound strength of the overlying and underlying beds varied, at most measured sites, it exceeded the values of the corresponding poorly cemented interlayer at each site (Fig. 58). Hardness values ranged from 18 to 63.11 in 57 measurements, with an average of 34.49, median of 31.67, and a standard deviation of 12.19. The derived uniaxial compressive strength ranged from 26 MPa to 270 MPa, with the majority of values less than 90 MPa. The measured hardness of “finger flow” pillars ranged



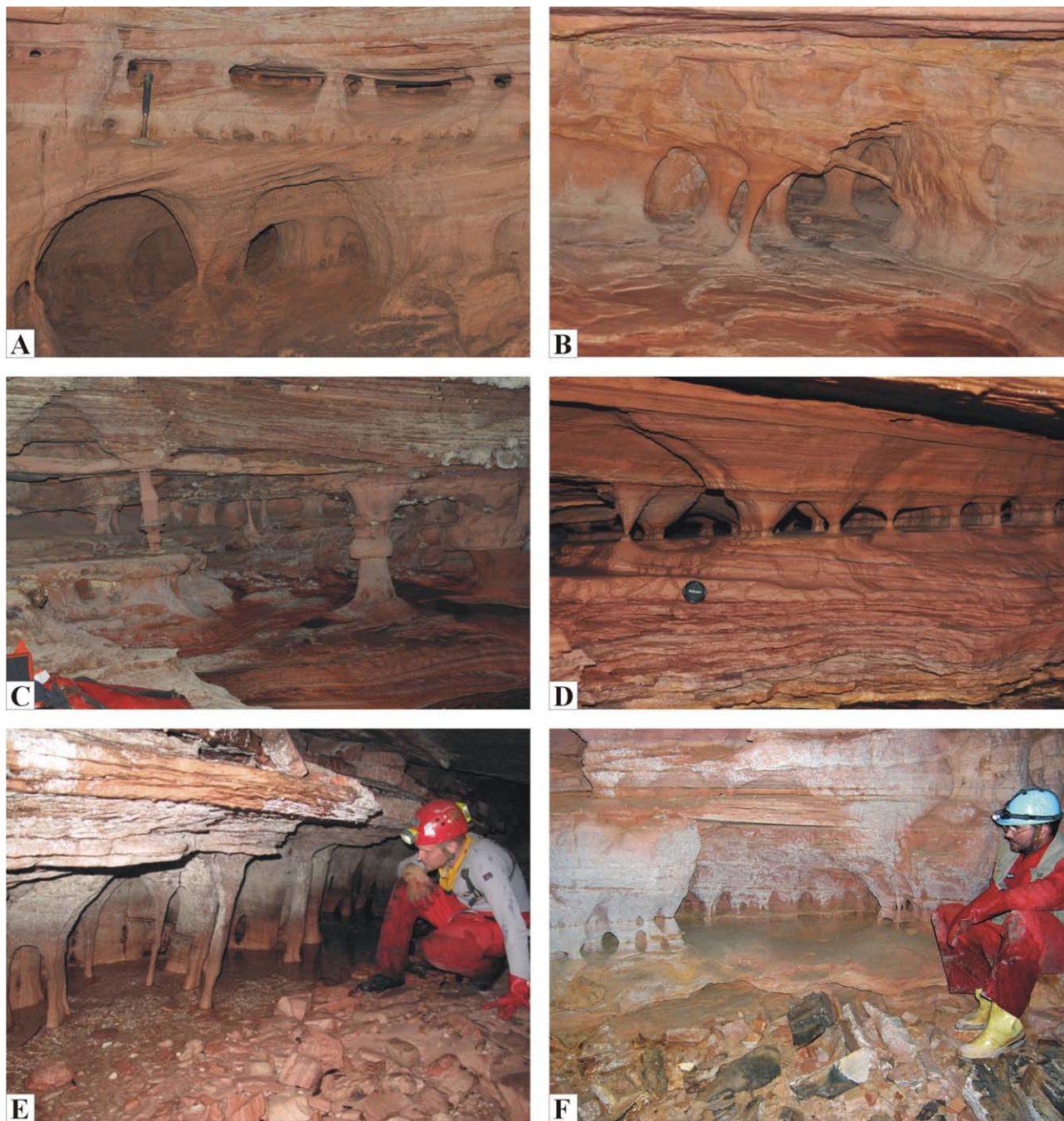


Fig. 50: "Finger-flow" pillars preserved in uncollapsed parts of the sides of large corridors. A, F – Cueva de los Pémones sector, B, C, E – Cueva Colibrí sector, D – Cueva Charles Brewer sector.

Fig. 49: A-C – Poorly lithified beds are clearly visible on the tepui surfaces and they can be correlated for long distances (A – multiple collapsed and poorly lithified horizons between Cueva Charles Brewer and Cueva Cañon Verde, close to the 2007 base camp, B – collapsed poorly lithified horizon in the Guyana part of Roraima Tepui, C – multiple poorly-lithified horizons above Cueva Colibrí). D-H – well preserved "finger-flow" pillars in the uncollapsed main corridors of cave parts during early stages of their speleogenesis (D – Cueva Colibrí sector, E-F – Cueva Cañon Verde, G – Cueva Zuna, H – Cueva Charles Brewer sector).

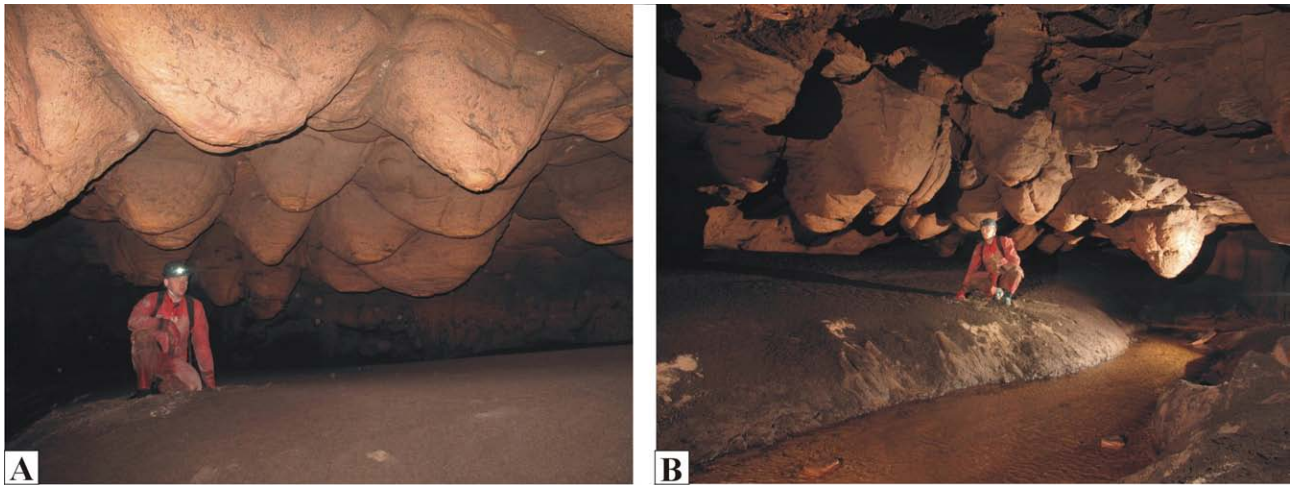


Fig. 51: Imperfectly developed “finger-flow” pillars, called “tetras” by cavers. These represent the upper funnels, and other remains of the pillars in this Cueva Muchimuk sector were insufficiently lithified to be preserved.

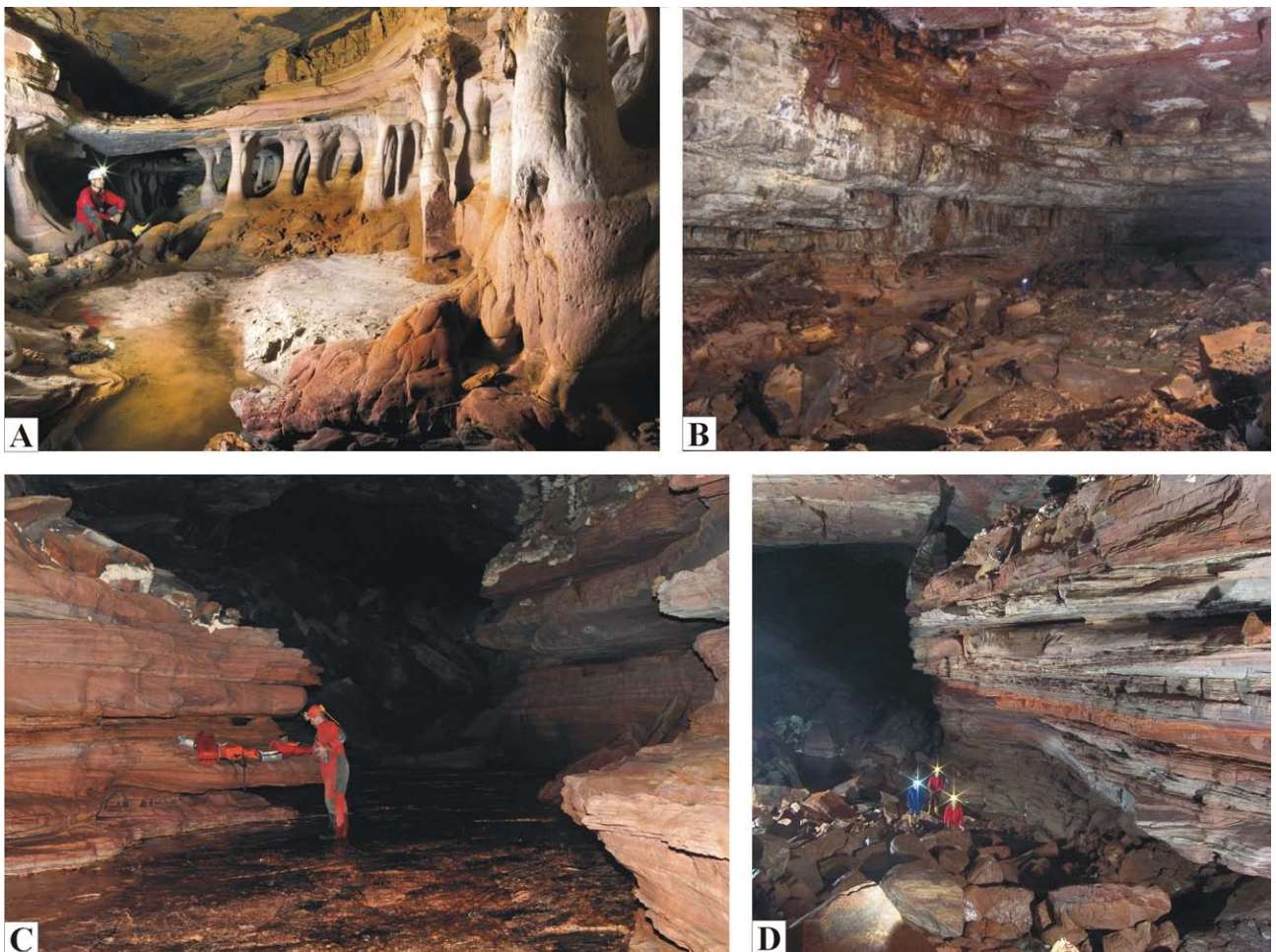


Fig. 52: A – Two horizons with winnowed poorly-lithified arenites supported only by the “finger-flow” pillars in Cueva de Arañas. B – Gran Galería Karen y Fanny in the Cueva Charles Brewer sector represents the world’s largest cavity in arenites and it is also one of the ten largest natural subterranean spaces in the world. The latest stages of its development are clearly dominated by rockfalls and gradual ceiling collapse. C, D – Laminated, soft, clay-rich arenites in the lower part of the Cueva Charles Brewer sector were responsible for the initial stages of this cave’s speleogenesis which was followed by successive rockfalls.

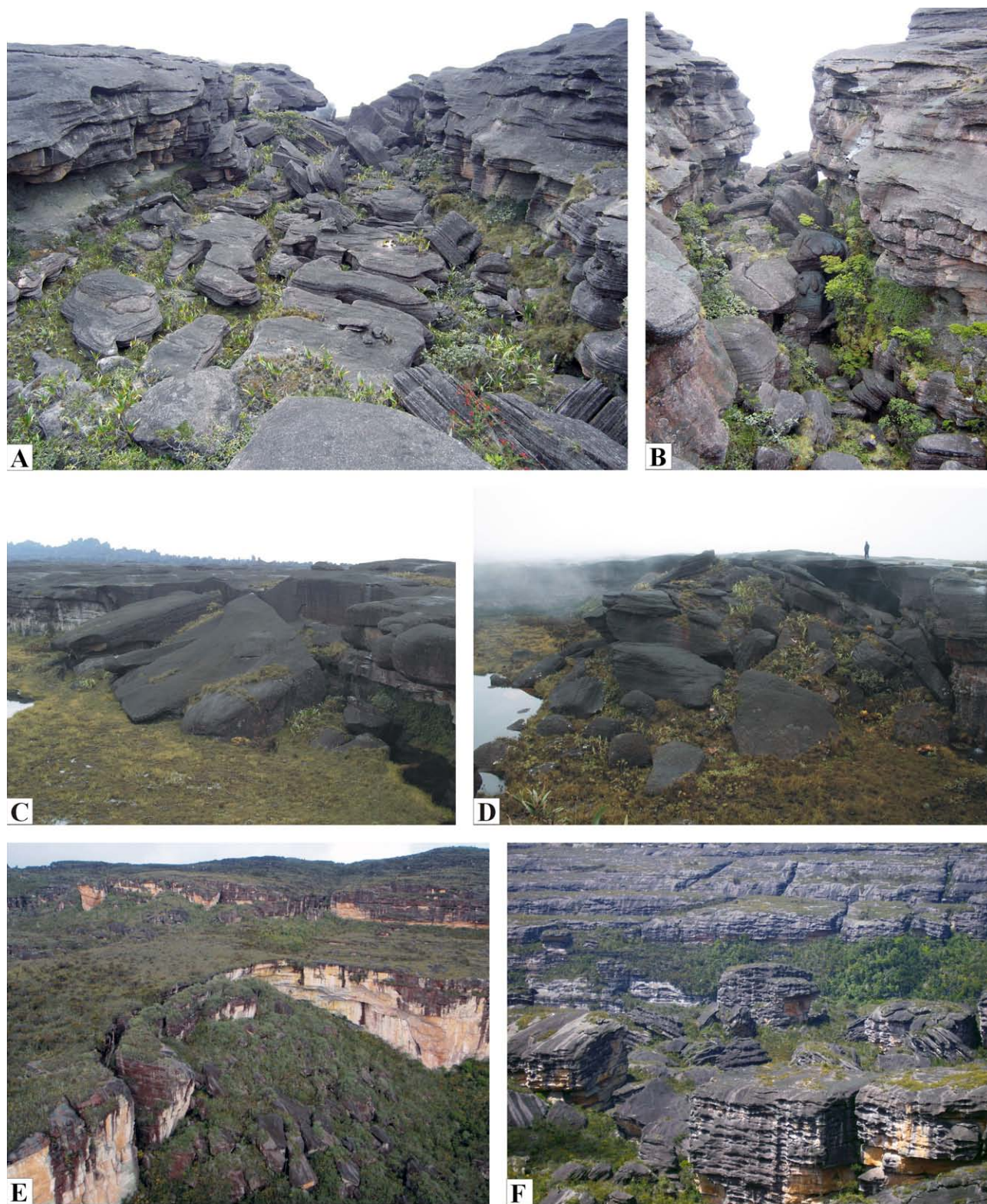


Fig. 53: A, B – Collapsed linear caves in the Guyana part of Roraima. C, D – This collapsed huge cave space created the well-known Lake Gladys in the Guyana part of Roraima. E – Recent entrance to the Cueva Charles Brewer sector was created as a huge collapse. F – Large collapse zone in Churí Tepui. This collapse zone was most likely also influenced by winnowing of poorly-lithified sediments, as shown by the inclined megablocks in the collapse zone.

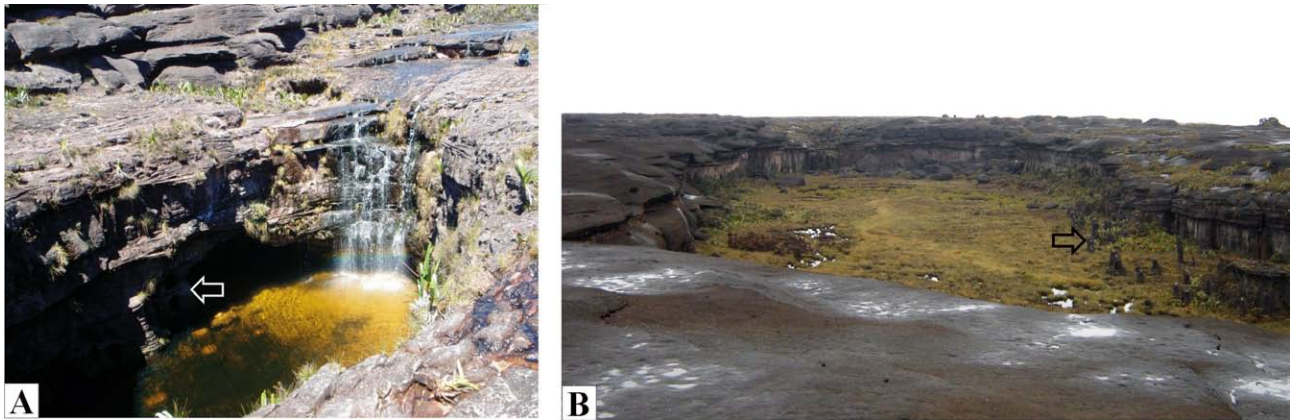


Fig. 54: A – The well-known depression El Foso on Roraima caused by cave collapse. Some remaining “finger-flow” pillars are visible at the bottom of the depression (arrow). B – Rests of the “finger-flow” pillars are also visible in Lake Gladys (arrow).

from 18.08 to 45.75 in 52 measurements, with an average of 28.47, median of 27.17, and a standard deviation of 7.03. The derived uniaxial compressive strength ranged from 25 to 80 MPa, with the majority of values below 60 MPa. It should be noted that the value of the derived uniaxial compressive strength increases with its increasing dispersion. The relatively high fluctuations within this strength parameter are closely linked to the effect of hidden discontinuities in the rock massif interior.

These uniaxial compressive strength values show that most of the measured arenites ranged from weak sandstones to indurated sandstones, while the true quartzites with uniaxial compressive strengths above 200 MPa were rare at the measured sites (cf. Young et al., 2009: p. 22-24) (Fig. 58B).

2.6.3.3. Mineralogy and petrology of arenites and red muds

The Matauí Formation is the topmost part of the Roraima Supergroup and it shows a wide lithification variability in its arenites. It ranges from loose sands through sandstones to very hard quartzites. The loose sands are least common, as they are rarely preserved due to erosion. The sandstones and quartzites dominate this formation and form the main mass of the tepuis, with the current proportion of individual types representing recent-stage relics remaining after long-term weathering and erosion. It is presently unclear if this same ratio also applied to the eroded part of the formation (see Discussion). Our observations show that the recent remnants of the Matauí Formation are dominated by quartzose arenites, and subordinately by arkoses and lithic to sublithic arenites (cf. White et al., 1966; Reid, 1972). The arenite grain size varies depending on original sedimentary conditions. Here, it ranges from very fine, well-sorted arenites which are mainly of aeolian origin to very coarse arenites and conglomerate layers, which are most likely fluvial in origin (Fig. 59A-B). The aeolian origin of the fine arenites is indicated by well-abraded sand grains, and by cross-bedding with angles greater than 30° (Fig. 59C-F). Water-formed ripple marks are common on the cave ceilings and floors (Fig. 59G-H).

Our research focused on beds with contrasting hardness on the formation’s surface and in its caves. The hardness correlates

to the arenite lithification stage, and the contrast between the poorly lithified arenites and the overlying and underlying well-lithified arenites, including “finger-flow” pillars, was so great that these two end-member lithologies had to be treated by separate methods. The samples from loose arenites usually disintegrated into individual grains and their mineralogical composition was determined by XRD, under binocular lens and SEM. The hard samples of well-lithified arenites were also studied in thin-sections. The petrographic study showed that arenites were first compacted. Compaction is the main lithification agent, common to all samples, including the poorly lithified arenites. The arenitic grains are tightly packed together, with common interlocked and jigsaw-like grain boundaries. This compaction caused partial mobilization of SiO₂, and syntaxial rims grew into the free pores (Fig. 60). Cementation of the remaining pores in the aforementioned two end-members was different. The poorly lithified arenites showed no further cementation stages or else they were cemented only with kaolinite (Fig. 60E-F; confirmed also by the XRD results – see below). Table 3 provides an overview of the diagenetic phenomena in all examined lithotypes. The remaining porosity of the arenites from the overlying and underlying beds was filled with silica (Fig. 60A-B). The “finger-flow” pillars mainly displayed quartz syntaxial overgrowths, pervasive silica cementation and some kaolinite (Fig. 60C-D). The SEM observation of some incompletely disintegrated grain clusters of poorly lithified arenites illustrated that the boundaries between the grains are still open, porosity remains high and the grain boundaries show no evidence of being formed by dissolution (Fig. 61A-B). In contrast, the well-lithified arenites show larger amounts of silica (Fig. 62A) and quartz (Fig. 62B-C) and their grain boundaries are mostly obliterated by cementation, with low subsequent porosity (Fig. 61C-D). It is important to note that there were no signs of quartz dissolution in any of the samples, and the quartz grains displayed no pits or notches typical of quartz dissolution (cf. Hurst, 1981; Hurst & Bjorkum, 1986). The only alteration observed was kaolinization of mica scales (Fig. 62D) and feldspar crystals (Fig. 62E).

The XRD analysis was focused on both friable and lithified sandstones. Mineralogical constituents of samples from the

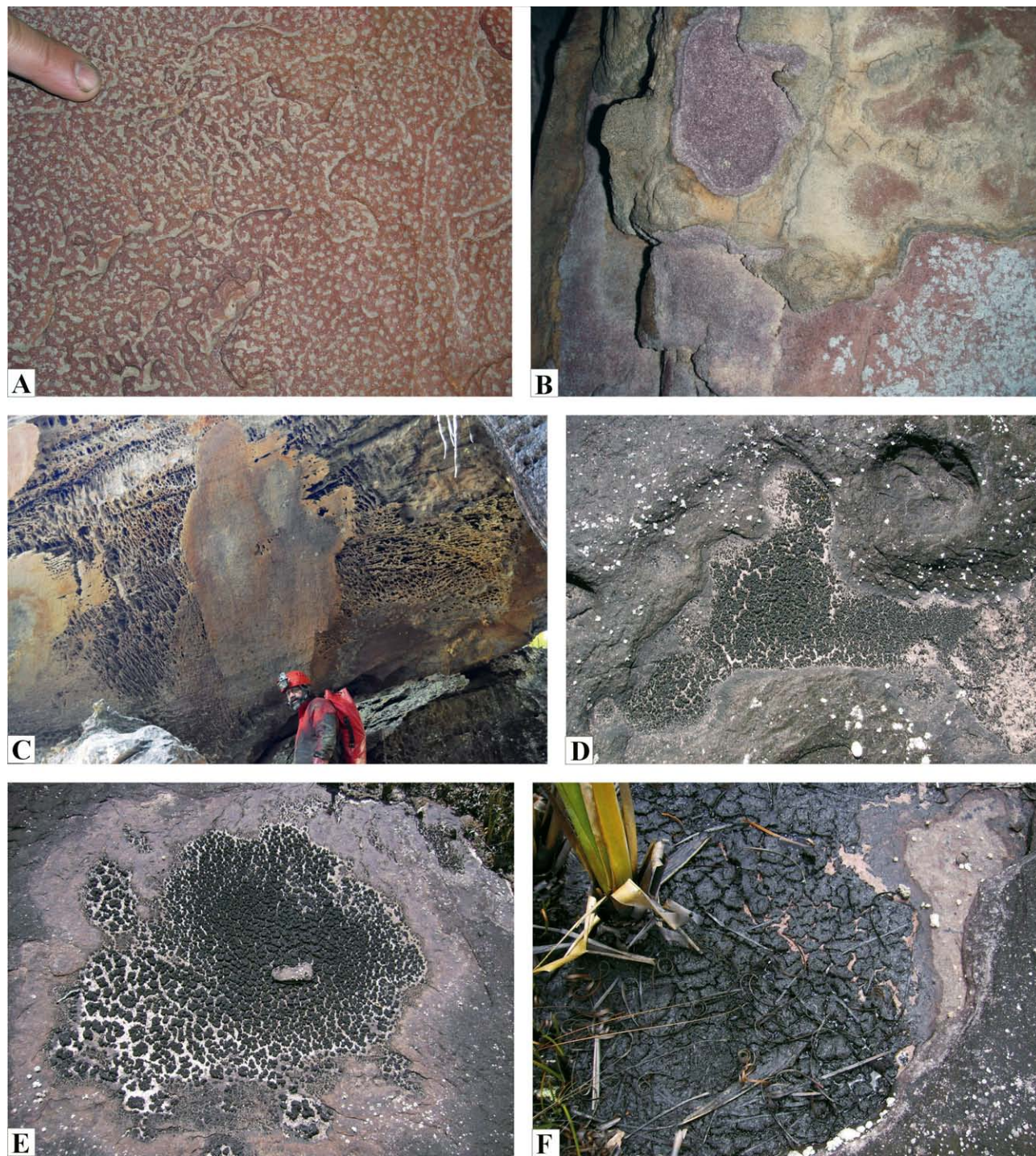


Fig. 55: A – Bizarre patterns on the surface of a sandstone block in the Cueva Charles Brewer sector which may have originated from microbial etching. B – Additional dissolutional forms found in Cueva de los Pémones (Ojos de Cristal Cave System). C – Bizarre weathering structures on quartzitic blocks forming the collapse zone between Cueva Charles Brewer and Cueva Juliana. Their origin is uncertain. Their equal orientation indicates that they originated in a similar manner to photokarren described by Lundberg et al. (2010^o). D-F – Pools with cyanobacteria on the surface of Churí Tepui. The shallow depressions could be due to etching from the cyanobacterial alkalization in this environment.

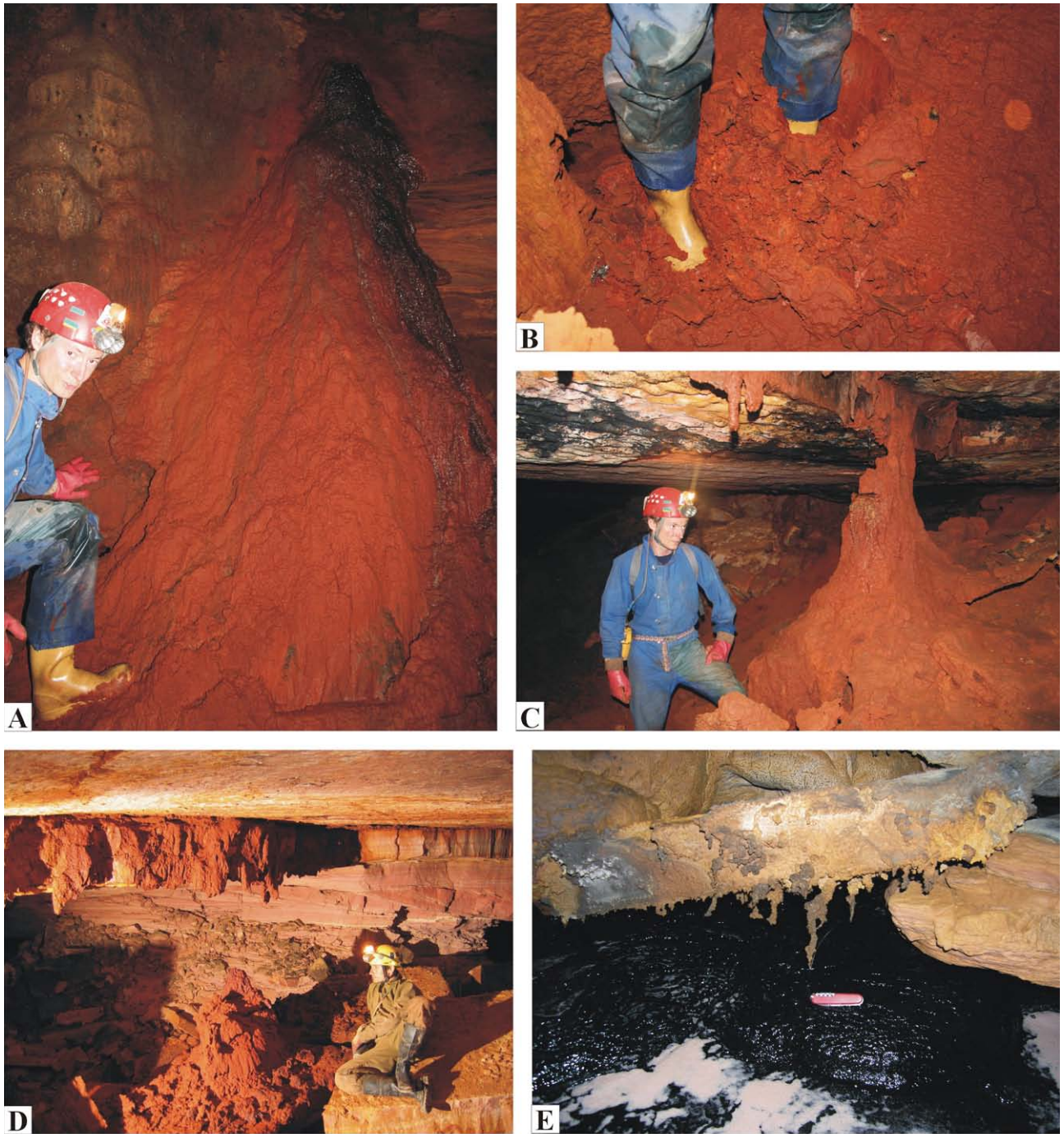


Fig. 56: A-D – Forms of leaking and the accumulation of lateritic products (“Barro Rojo”) in the studied caves. E – “Barro Rojo” can be black in some places. A,B,C,E – Cueva Charles Brewer sector, D – Cueva de los Pémones sector.

plateaus over the Cueva Charles Brewer and Cueva Colibrí sectors are listed in Table 4. Samples of laminated friable sandstone come from the laminated sandstones of the beds with “finger-flow” pillars, and these were collected from the pillars themselves and also from the surrounding loose sandstone. Meanwhile, samples of lithified sandstones were collected from overlying beds of massive to laminated quartzites. The main mineralogical components of both types of sandstones are quartz and various clay minerals (Tab. 4; Fig. 63A-B). Although the samples analysed by XRD

did not contain any feldspars, their presence was detected petrographically in some other samples. Although clay mineral content differs in these sandstones, kaolinite and pyrophyllite are typical in all samples of the loosely lithified sandstones (Fig. 63A) while the well-lithified massive sandstones from the overlying beds of massive quartzite consist almost exclusively of pure quartz. The very weak shoulder between $18 - 28^\circ 2\theta$ may reflect the presence of amorphous silica (opal-A) in the composition of sandstones lacking clay minerals (Fig. 63B; CK5-5). Pyrophyllite and traces

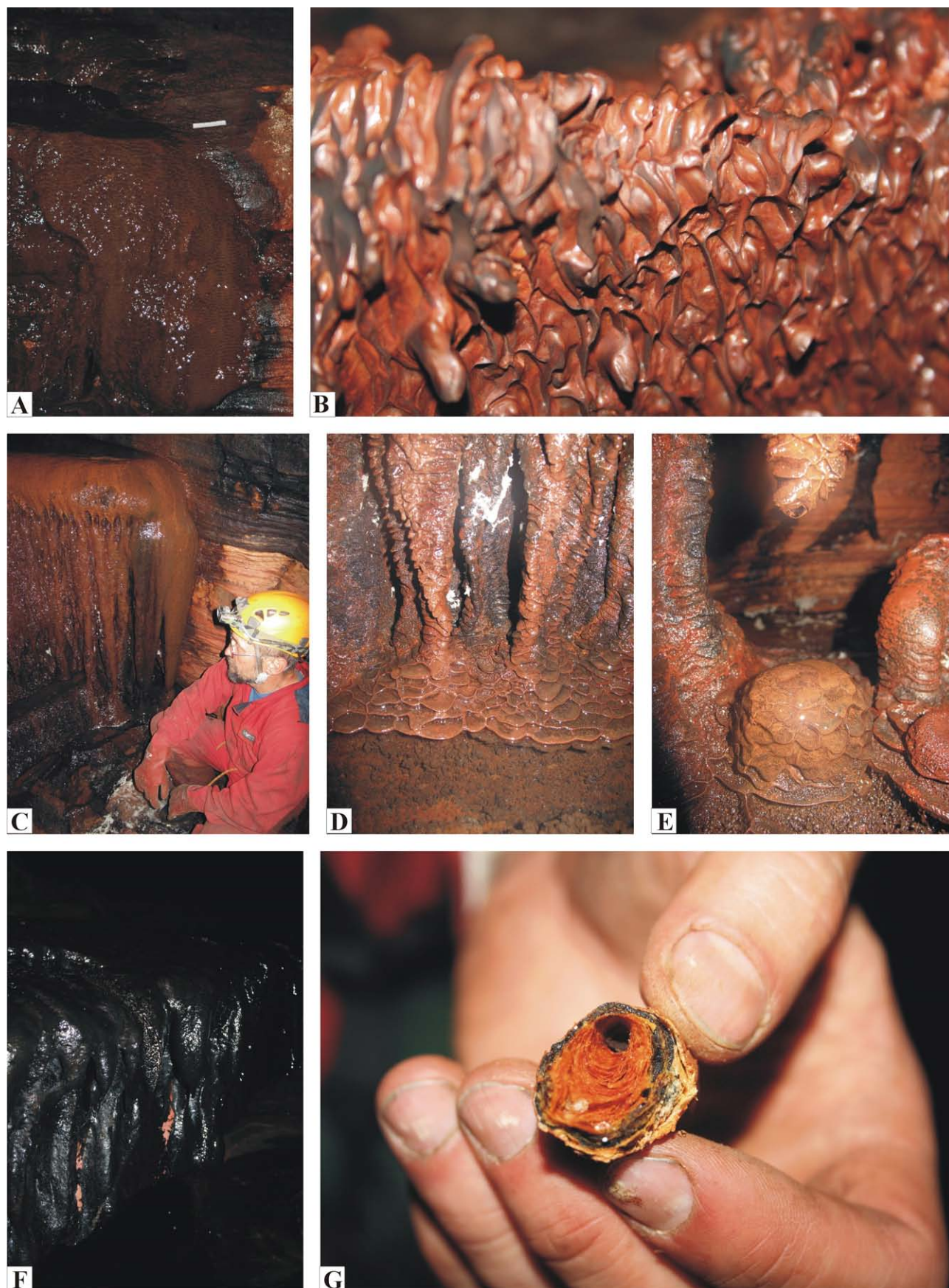


Fig. 57: A-F – Speleothem forms produced from lithified “Barro Rojo”. Note that the colour changes from red to black (A-B, F – Cueva Charles Brewer sector, C-E – Cueva Colibrí sector). G – A broken “Barro Rojo” stalactite in the Cueva Charles Brewer sector revealing concentric structure with red and black laminae.

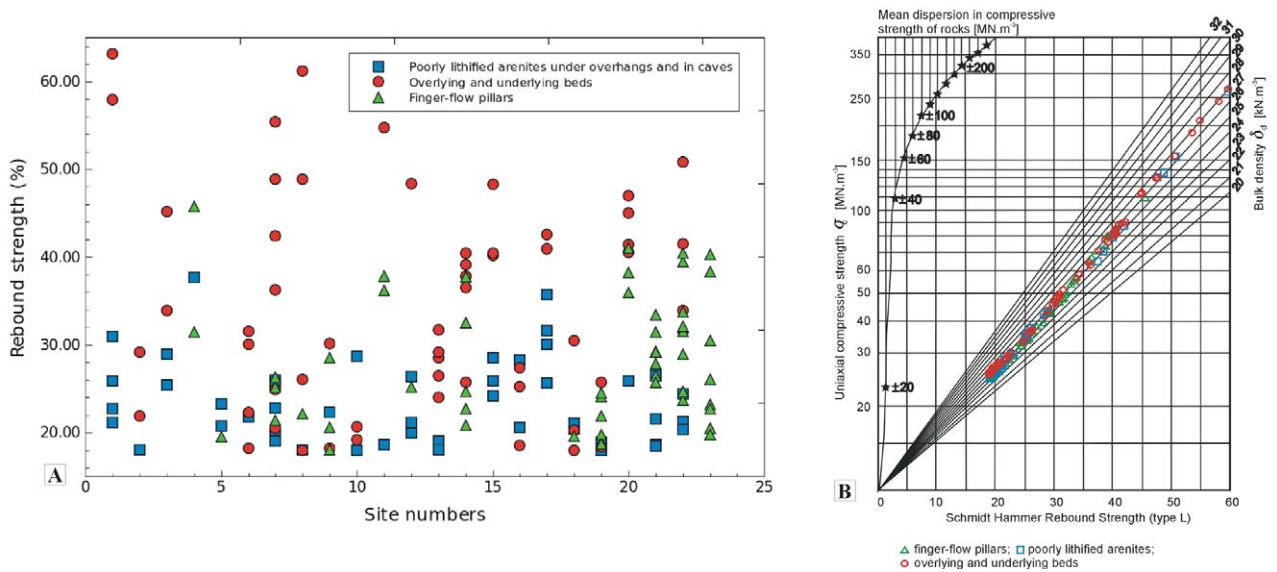


Fig. 58: A – Diagram showing the differences in hardness of poorly-lithified rocks, overlying and underlying beds and the “finger-flow” pillars at individual sites, measured by Schmidt hammer. B – Diagram showing relationships between Schmidt hammer rebound strength, bulk density and derived uniaxial compressive strength.

of kaolinite were also identified in the mineralogical composition of some samples from the lowermost parts of the overlying beds which possess a transitional composition (Fig. 63B; CK5-14).

Mineralogical constituents of the red mud are listed in Table 4, and the main clay mineral identified by XRD is kaolinite (Fig. 63C). Minor amounts of pyrophyllite and quartz were identified in the mineralogical composition of the separated clay fraction (<2 μm). The broader hump between 17 and 30 $^{\circ}2\theta$ reflects the presence of iron oxy-hydroxides, which are most likely poorly crystallized (Fig. 63C), and the identified diffraction peaks reveal the presence of goethite.

Particularly important is itacolumite, a special flexible sandstone which commonly occurs in the Ojos de Cristal Cave System, and also in some parts of the Charles Brewer Cave System (Fig. 64A-B). Its flexibility is possible due to lack of cement but interlocked quartz grains enable some movement (Dusseault, 1980). There are several theories concerning this lack of cement, with some authors considering it to be a secondary characteristic caused by dissolution of clay minerals or micas (see Kerbey, 2011 for review). Only Suzuki & Shimizu (2003) have inferred that the missing cement is etched quartz cement. Microscope views show that clay minerals, presumably kaolinite, are present in the itacolumite specimen from the Ojos de Cristal System (Fig. 64C-E). The possibility of dissolution of clay minerals is supported by the fact that itacolumite was sometimes connected with the discharges of red mud (Fig. 64F). However, thin-section and SEM studies make the whole genesis of itacolumite more complex. At first glance, thin-section shows no porosity preserved in the rock (Fig. 65A). However, under larger magnification, thin rims around the quartz grains are visible. In some places these appear empty (Fig. 65B), but in others they contain colour and extinguishing of neighbouring quartz grain (Fig. 65C). The rim is actually an empty space, and the gap noted in this latter

instance is just masked by overlapping quartz grain edges. The empty spaces at the grain/grain boundaries are clearly visible under SEM (Fig. 65D-E). These thin spaces between the grains are the reason for the itacolumite flexibility. The SEM study also revealed that unlike other examined arenite samples, the itacolumite specimen displays obvious signs of dissolution (Figs. 66, 67). Thin-lamellate phyllosilicates, which are most likely kaolinite, are also ubiquitous, thus confirming microscopic studies (Fig. 67). However, they rest on a substrate formed by quartz grains with etching, but the fact that they are intact indicates that the cement phase is secondary, post-dating the quartz etching. There is no clear relationship between this etching and the aforementioned thin gaps between the quartz grains, and the grain boundaries bear no signs of irregularities caused by such etching. To the contrary, they appear to match each other, and this suggests an origin due to hydraulic dilatation. A similar process was inferred by Wirth (1989), who suggested that itacolumite originated from the overpressure of fluids during heating of the quartz/kaolinite system to produce pyrophyllite and water. The common presence of pyrophyllite revealed in sandstone samples in our XRD analysis may substantiate this assumption.

2.6.4. Discussion

2.6.4.1. Cement dissolution versus non-cementation

Besides lava tunnels, which are especially common in basaltic lava volcanic areas, silicate caves are the most exceptional due to very low SiO_2 solubility (Hill & Forti, 1986; Wray, 1997^{a,b}, 1999). The novel results concerning speleogenesis described in this volume and in previous papers (Aubrecht et al., 2008^b; Aubrecht et al., 2011) explain the cave-forming processes in arenites using examples from the two largest sandstone cave

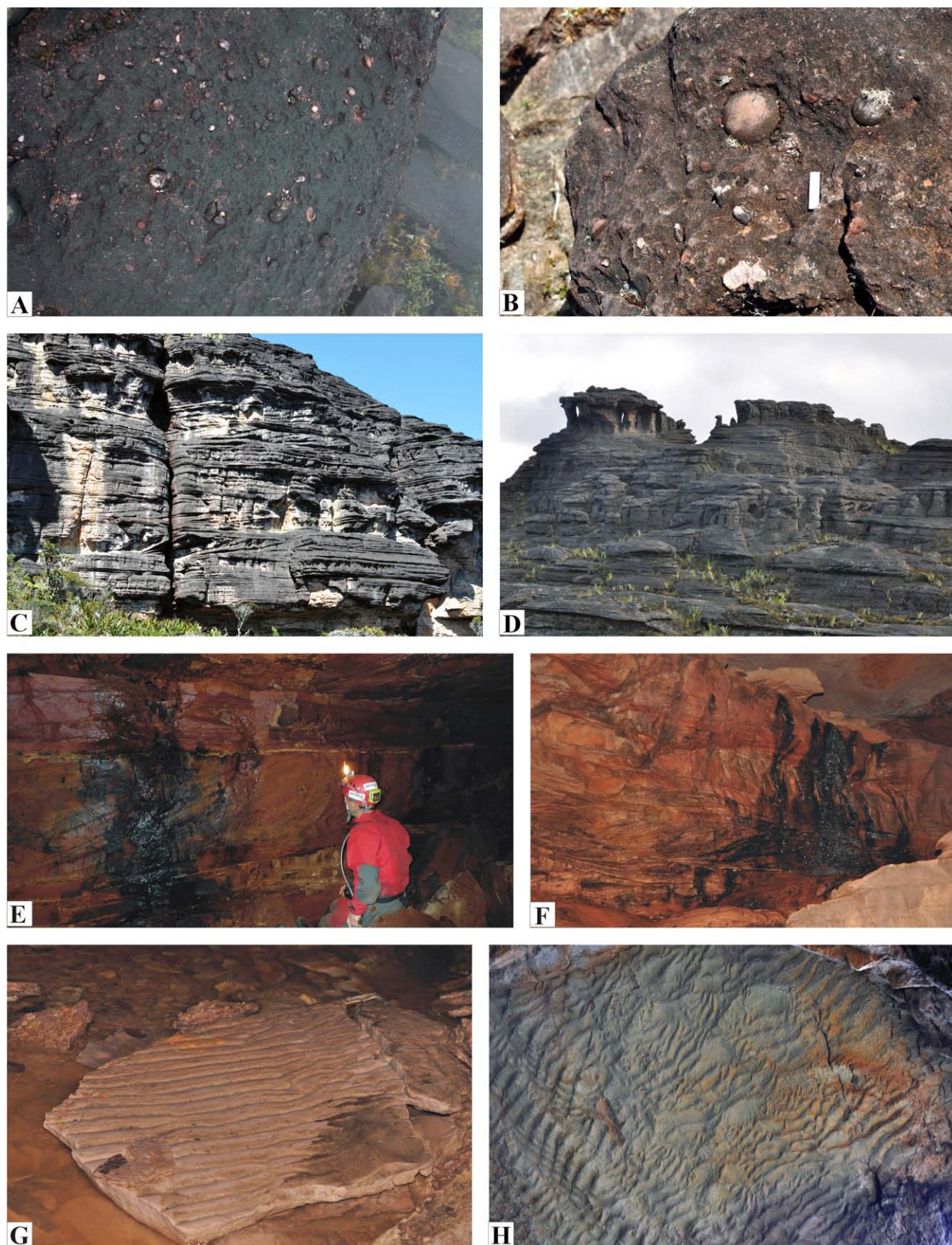


Fig. 59: A-B – Conglomerate layers in the Matauí Formation on top of Roraima. These are most likely of fluvial origin. C-D – High-angle cross-bedding in the Matauí Formation in arenite beds on top of Roraima, highlighting their aeolian origin. E-F – Similar high-angle cross-beddings in Cueva de los Pémones. G-H – Ripple marks in the Matauí Formation arenites showing their deposition in the aquatic environment. (G) Cueva Charles Brewer, (H) Cueva Juliana.

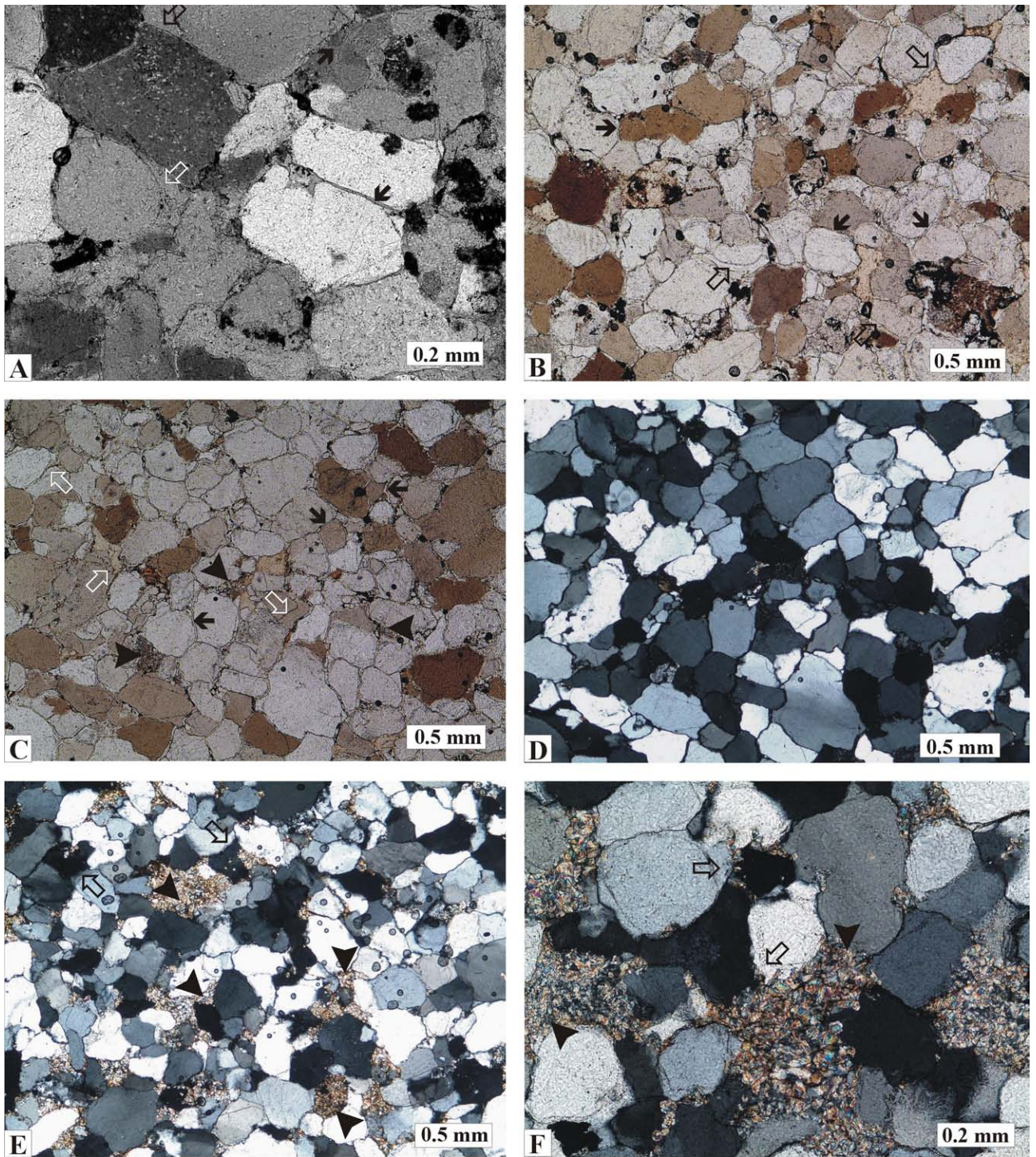


Fig. 60: Thin-section photos comparing diagenesis of the hard quartzites from the overlying and underlying beds of the poorly lithified horizons (A-B), “finger-flow” pillars (C-D) and the poorly-lithified arenites (E-F). Empty arrows point to syntaxial quartz overgrowths originated during the initial compaction. Black arrows point to additional, later opal cement and triangular arrows indicate kaolinitic, clay-mineral cement. These samples were taken from the top of Churí Tepui at the locality depicted in Figure 47A.

Tab 3: Table summarizing the diagenetic phenomena present in the investigated forms of arenites.

arenite formation	diagenetic feature			
	jigsaw-like boundaries	syntaxial quartz	kaolinite cement	opal cement
poorly cemented arenites	+	+	+	-
underlying and overlying beds	++	++	+	++
“finger-flow” pillars	++	++	+	++

systems in the world: the Charles Brewer and Ojos de Cristal cave systems. Most authors (e.g. Urbani, 1986; Galán, 1988; Piccini, 1995; Wray, 1997^{a,b}, etc.) explain the origin and evolution of the quartzite karst by chemical dissolution processes in various climatic conditions, combined with long-term exposure to chemical weathering. This model was even previously used by Galán et al. (2004^b) for the Ojos de Cristal System (called therein the “Roraima Sur System”). The following theories have been advanced to explain the dissolution mechanism; (1) temporarily increased alkalinity of the groundwaters caused by lateritic weathering (Marker, 1976); (2) local alkalization of the micro-environment caused by microbes (Büdel et al., 2004; Brehm et al., 2005; Barton et al., 2009); (3) quartz hydration to opal (White et al., 1966); (4) the change of quartz to opal by microbial activity (Vidal Romani & Vaquero Rodrigues, 2007); (5) hydrothermal alteration along bedding planes and fractures (Zawadzki et al., 1976; Szczerban et al., 1977); and (6) karstification via intergranular cement dissolution (Martini, 1979; Urbani, 1986; Briceño & Schubert, 1990; Doerr, 1999). Martini (2004) considered the newly formed rock soft and prone to erosion, and he named it “neosandstone”.

The results presented by our team show that quartz dissolution is not necessarily the main speleogenetic factor in the Venezuelan tepuis. The hardness measurements showed that the caves’ side walls and the beds under overhangs on the surface are really soft, and the petrographic research showed that this softness may be primary. There is an evident lack of the characteristic signs of quartz dissolution and the soft and hard beds show different stages of cementation. While the soft beds have compaction or cementation only with kaolinite cement, the harder beds also possess opal to quartz cementation. Meanwhile, itacolumite has obvious quartz etching which may have been caused by increased alkalinity due to lateritization. The secondary kaolinite cement resting on this etched quartz could be an intermediate product in the weathering chain: aluminosilicate-clay mineral-laterite. It is not currently clear, whether the thin empty spaces between the quartz grains were also caused by etching, but the matching grain/grain boundaries do not support this view.

The “finger-flow” pillars also provide evidence of lithification differences. They occur not only in the cave systems investigated by our team but also in the caves on Kukenán Tepui (Doerr, 1999: fig. 11), on sandstone terrains in other continents including South Africa (Marker, 1976: figs. 2, 4) and in collapsed caves, such as El

Foso (Fig. 54A) or Gladys Lake (Fig. 54B). Their origin is obviously related to the main phase of arenite cementation in upper parts of the tepuis by descending diagenetic fluids which converted the overlying and underlying beds to hard quartzite. Splitting of the fluid front into “fingers” ensured that these fluids did not fill the entire bed. Meanwhile, the strongly lithified overlying and underlying beds caused their isolation and protected the uncemented beds from further fluid infiltration. This premise is supported by the horizontal course of most of the caves, which have perfectly straight ceilings and floors and are almost rectangular in cross-section. Other evidence are smooth surfaces of many “finger-flow” pillars. Martini (2004) summarized this arenization/neosandstone theory as ‘weathering first, followed by mechanical removal of sand’. According to this idea, the beds in which the caves formed were originally well cemented, as in the other beds or else the dissolution may have occurred in lithified beds with higher porosity (Wray, 1999). If this was true, lithified portions of rock would change to unlithified rock gradually, and no sharp demarcation would be visible. This would certainly result in uneven tops and bottoms of the caves and also irregular pillar shapes. Assuming that the pillars were not formed by “finger-flow” diagenesis, but were only erosional remnants (or corrosional – see Doerr, 1999), these pillars should have shapes which are elongated in the flow direction, with many irregularities and projections. Such elongated pillars were already observed in some parts of the stream corridors, as in Cueva Colibrí, and they are easily distinguishable from the true “finger-flow” pillars which originated diagenetically (Fig. 68). A secondary penetration of these “finger-flows” to already weathered “neossandstone” is quite unlikely.

Hydrogeochemical results also discredit quartz dissolution as an important cave-forming process in the examined caves (see Aubrecht et al., 2011 and the hydrogeochemistry chapter in this volume). The dissolution of quartz at room temperature is extremely slow and it occurs best in alkaline environments. Several authors including Briceño & Schubert (1990) and Piccini & Mecchia (2009) proposed an arenization model involving the dissolution of the more soluble opal sandstone matrix. However, true, mature quartzite does not contain any matrix; it consists of a compact mosaic of quartz crystals and rims. Following Martini (1979, 2000), Chalcraft & Pye (1984) and Wray (1997^b), quartzite arenization is caused by quartz grain dissolution along the crystal joints, preferably along sediment joints and bedding planes.

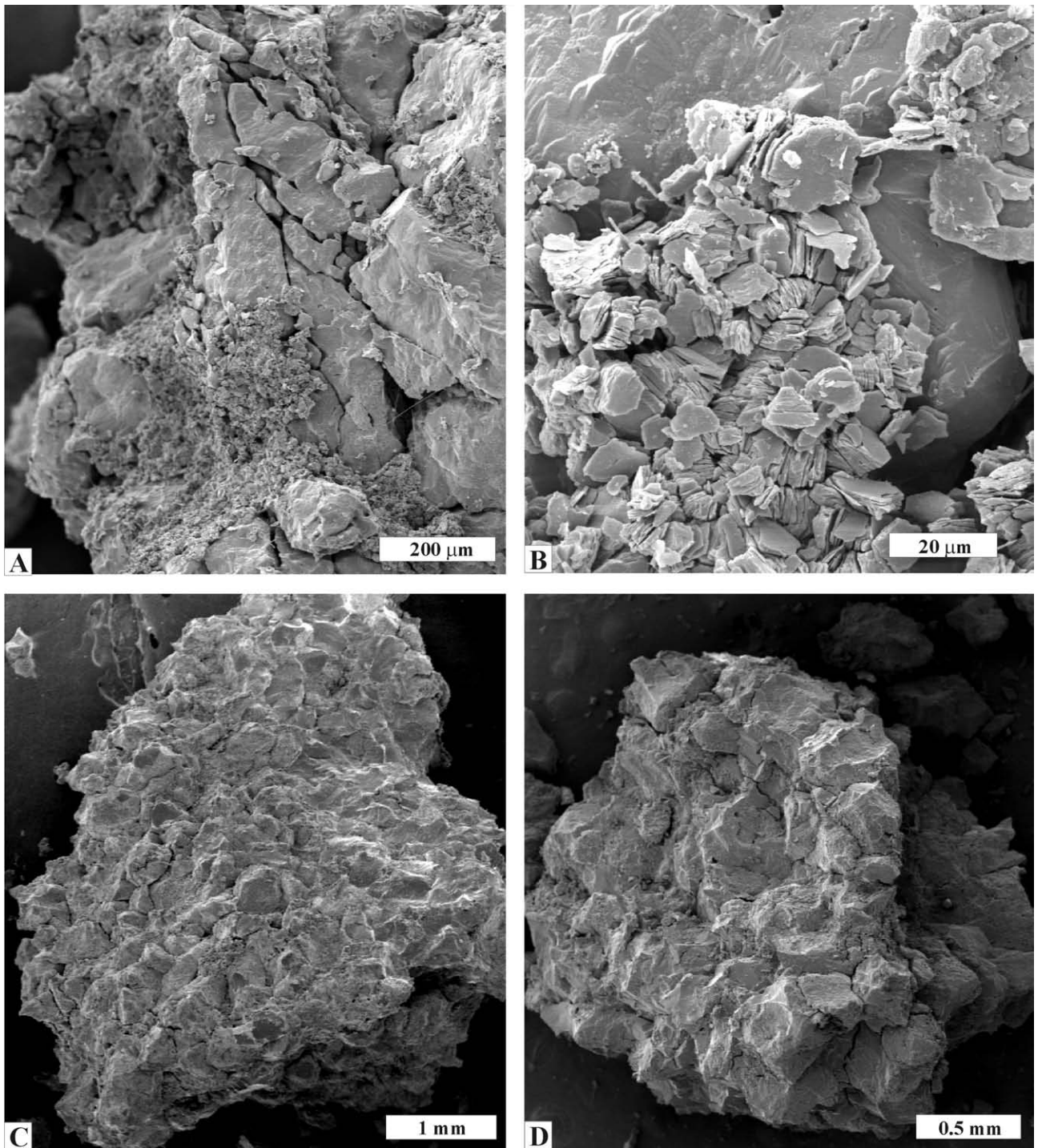


Fig. 61: A – SEM photo of kaolinite-cemented soft arenite (the same bed as Fig. 60E-F). Note the remaining pores are still open. B – Enlarged view of the previous. Kaolinite, forming tiny idiomorphic scales, is the only cement in this rock. C–D – SEM of the strongly lithified quartzite specimens from the top of Churi Tepui. Note that the remaining porosity is low and most intergranular boundaries have been obliterated.

The poorly lithified quartzite samples showed no evidence of quartz cement remnants following dissolution. In addition, solution pits and notches on quartz grains were not observed in thin sections or under SEM as described by Burley & Kantorowicz (1986) and Hurst (1981). In contrast to reports by Martini (1979, 2000), and Chalcraft and Pye (1984), signs of quartz grain

corrosion along the crystal joints did not appear in our thin sections. Consequently, quartz dissolution cannot be considered a dominant force or a trigger process in the speleogenesis of these examined caves.

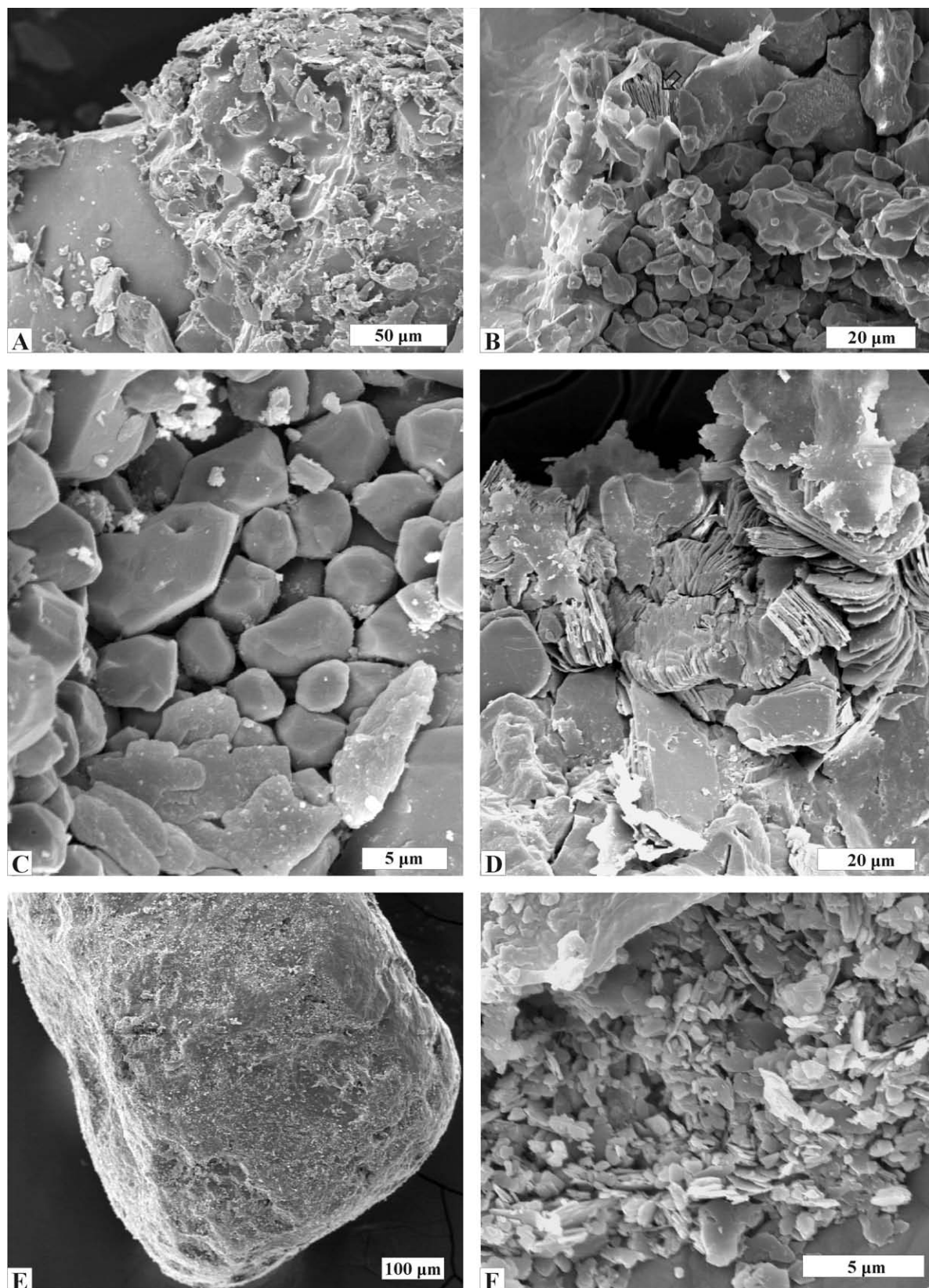


Fig. 62: A – Opal cement on the surface of quartz grain from strongly lithified quartzite from the top of Churí Tepui. B – Opal cement recrystallized to microcrystalline quartz and partly intergrown with the kaolinite (arrow). Sample from top of Churí Tepui. C – Microcrystalline quartz crystals originated by recrystallization of opal cement. The strongly lithified quartzite from top of Churí Tepui. D – Kaolinite (smaller scales, top) originating at the expense of mica (larger scales, bottom). The strongly lithified quartzite from top of the Churí Tepui. E – Grain of kaolinized feldspar from the surface of Roraima. F – Enlarged view of 62E, showing the feldspar kaolinization in detail.

Tab. 4: Overview of mineralogical composition in selected samples of sandstones and muds from various localities. The mineralogical composition was identified with the help of X-ray powder analysis (PXRD).

Sample	Locality	Rock type	Quartz	Goethite	Kaolinite	Pyrophyllite	Opal-A
PCHB2-5	Cueva Charles Brewer	friable sandstone	+	-	+	+	-
PCHB2-8	Cueva Charles Brewer	friable sandstone	+	-	+	+	-
RP2-9	Cueva Charles Brewer	friable sandstone	+	-	+	+	-
CK5-5	Cueva Colibrí	lithified sandstone	+	-	-	-	?
CK5-6	Cueva Colibrí	lithified sandstone	+	-	-	+	-
CK5-10	Cueva Colibrí	lithified sandstone	+	-	-	+	-
CK5-14	Cueva Colibrí	lithified sandstone	+	-	-	+	-
CK5-16	Cueva Colibrí	lithified sandstone	+	-	-	+	-
BR001	Cueva Charles Brewer	Barro Rojo	+	+	+	+	-
BR002	Cueva Charles Brewer	Barro Rojo	+	+	+	+	-

2.6.4.2. Importance of “Barro Rojo”

Some examined arenites, such as arkoses and subarkoses, also contain aluminosilicate minerals. Here, they mainly comprise micas and feldspars and these aluminosilicates dissolve in the acidic waters much more easily than quartz does (cf. diagrams in Valetton, 1972, and experiments of Franklin et al., 1994). Weathering of feldspars, micas and clays release more silica than does quartz dissolution (Young et al., 2009). For aluminosilicate minerals this dissolution, or weathering, is an incongruent process, so that insoluble remnants such as secondary minerals are also formed during the dissolution process. These secondary minerals include various clay minerals such as montmorillonite, illite and kaolinite, as well as Fe and Al oxides and hydroxides. Resultant types of secondary minerals depend on pH, temperature and ion content of the water, as well as on the composition of the primary aluminosilicates. The presence of aluminosilicates, especially in the less lithified quartzite layers of tepui rocks, is apparent in both thin sections and SEM examination. Under such humid and warm tropical conditions, the combination of incongruent dissolution processes and silicate rock weathering results in laterite formation. White, heavily kaolinized arkosic arenites with red lateritic caps are common in the Gran Sabana, (Fig. 69A-B). The SiO₂ released by the lateritization process causes local hardening of laterites (Fig. 69C), or it can freely precipitate in the form of jasper. A great example is the famous Quebrada de Jaspe (Jasper Creek), approximately 35 km north of Santa Elena de Uairén (Fig. 69D-E), where the red colour portrays its lateritic origin. The red mud found in excessive quantities in the examined cave systems consists of goethite, kaolinite, illite, quartz and pyrophyllite, thus making it a true laterite. The

mud accumulations currently in the caves are only remnants not removed by water, and therefore the original amount of red mud was obviously much higher. Strongly lateritized arkosic and also greywacke arenites occur in some parts of these caves. These are prone to easy erosion (Fig. 70A-C) and they are so soft that they are easily cut by knife (Fig. 70D). The continuing dissolution processes within the laterite bodies have a considerable influence upon the water chemistry, but this is manifested only in the water dripping from the laterite bodies, as noted in the hydro-geochemistry chapter herein. At the pediment of the table-mountains, the stream waters are affected by the dissolution processes in arkosic arenites. An apt example of the results of such processes is silica concentrations of up to 3.4 mg.l⁻¹ in Río Carrao (Piccini & Mecchia, 2009). We therefore presume that lateritization within the existing cave passages is in its final stages.

The lateritization in the examined cave systems is a very important process. It is responsible for up to 30% of the empty space, and can therefore obviously trigger speleogenesis. This view is not entirely new, and is shared by authors including Corrêa Neto (2000), who stated that the alteration of mica and feldspar to argillaceous minerals and hydroxides is a very important speleogenetic factor. Although his statement concerned caves with similar formation in Brazil, he did not emphasize its role with respect to the quartz dissolution. Yanes & Briceño (1993) also admitted the role of feldspar weathering as an accompanying process to the quartz dissolution. Iron-rich speleothems are common in the areas formed by sandstones (see the review in Young et al., 2009, p. 138-140), and other cave explorers have also reported their existence in Venezuelan tepuis (Dyga et al., 1976; Zawadzki et al., 1976).

Lateritization not only creates empty subterranean spaces, but it also provides the great amount of dissolved SiO_2 necessary to form large opal speleothems. Feldspars and micas are much more soluble in acidic tropical waters, and with their much more rapid dissolution than that of quartz, they contribute to both, cave formation and speleothem-forming processes.

Finally, the role of biologically induced dissolution should be mentioned, too. The role of different biological growths such as lichens, algae and cyanobacteria in sandstone dissolution and/or disintegration has been described in numerous scientific papers. The effect of lichen organic acids on chemical weathering has already been described by Viles & Pentecost (1994), Bjelland & Thorseth (2002), Duane (2006) and others. Although the solubility in this case was enhanced by creation of organic-silica complexes, more effective dissolution processes are most likely due to the cyanobacteria induced bio-alkalization. Büdel et al. (2004) explained exfoliation processes occurring in South African sandstone by bio-alkalization caused by cryptoendolithic cyanobacteria. This type of exfoliation was not seen in sandstones on the Matauí Formation. Brehm et al. (2005) investigated the influence of the biofilms created by cyanobacteria, diatoms and heterotrophic bacteria on the quartz surfaces on Roraima. There they noted that the associated biofilms can create a localized shift in the pH from 3.4 to more than 9, which is sufficient for quartz dissolution. The quartz covered with biofilm is partly perforated to a depth of more than 4 mm (Brehm et al., 2005). This process is also apparent on the surface through the formation of the typical small pools on the quartzite surface (Fig. 43A, 55D). The corrosion of quartz grains or pebbles is often clearly visible (Fig. 43D).

Dissolution of quartz, even when enhanced by microbe alkalization (Büdel et al., 2004; Brehm et al., 2005; Barton et al., 2009) as seen in solution pits on the table-mountains' rocky surfaces plays a subordinate role in speleogenesis *sensu stricto*. However, if we concede that lateritization is a true dissolution process, the arenitic caves in the Venezuelan tepuis may be really ranked as karst.

2.6.4.3. Descending diagenetic fluid flow and possible origin of tepuis

Summarizing the results of the speleogenetic research of our team, several important points surfaced concerning the origin of the tepuis. Although the research elucidated many aspects of the speleogenetic process, it also created new questions and problems. The most conspicuous finding was that the Matauí Formation is formed not only by quartzites but that its arenites show various degrees of lithification. Our research provided evidence of variability in vertical profiles. But what about the lateral variability? Are tepuis with a dominant presence of hard-lithified quartzites typical examples of the Matauí Formation? What about the larger, missing portion of the formation which was removed by erosion? Why are tepuis usually isolated islands rising up from the flat Gran Sabana? And also, why there are no "ruins" of tepuis formed by accumulations of quartzite boulders dispersed throughout the Gran Sabana?

Answers to these questions are currently purely theoretical as the missing, eroded portion of the Matauí Formation can no

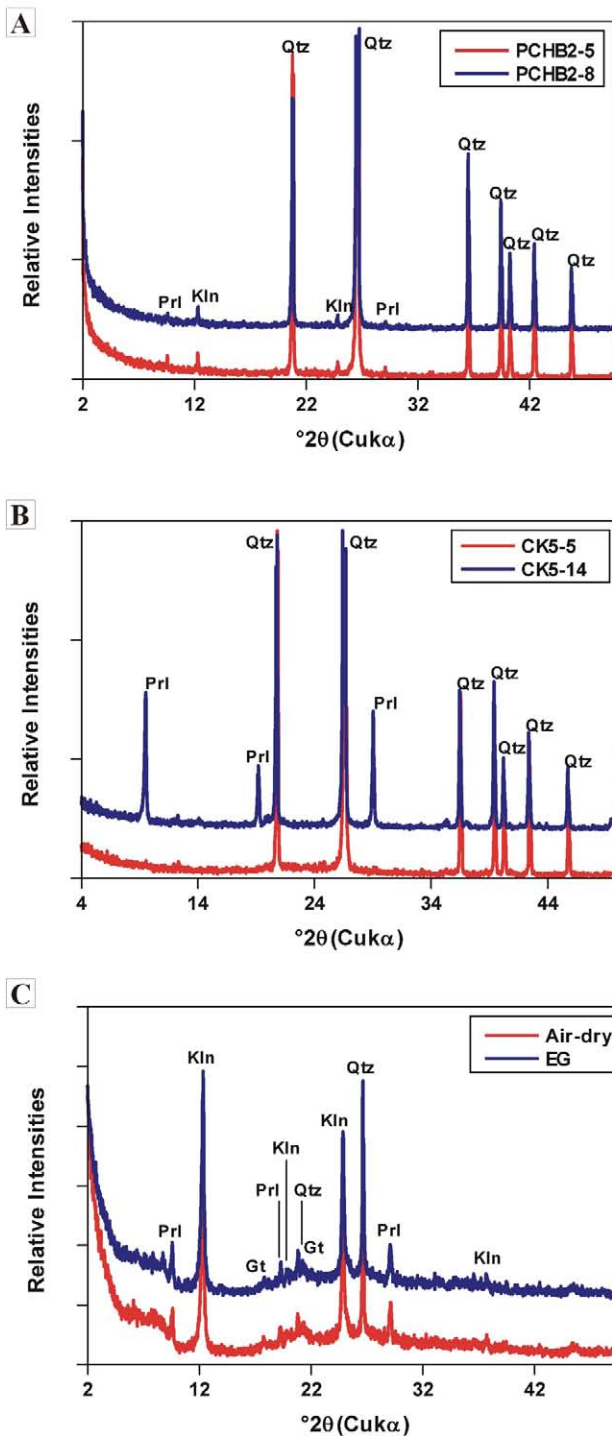


Fig. 63: A – X-ray powder diffraction (PXRD) pattern of friable sandstones from the plateau over the Cueva Charles Brewer sector. Prl – pyrophyllite, Kln – kaolinite, Qtz – quartz. B – A most representative PXRD pattern of the well lithified massif (CK5-5) and laminated (CK5-14) sandstones from the Cueva Colibrí sector. The PXRD pattern of CK5-5 sample shows a very weak shoulder between 18 – 28 $^{\circ}2\theta$; this may refer to the presence of amorphous silica (opal-A). C – PXRD pattern of samples of "Barro Rojo". The broader hump between 17 and 30 $^{\circ}2\theta$ may reflect the presence of poorly crystallized iron oxi-hydroxides. Only presence of goethite (Gt) has been definitely confirmed.

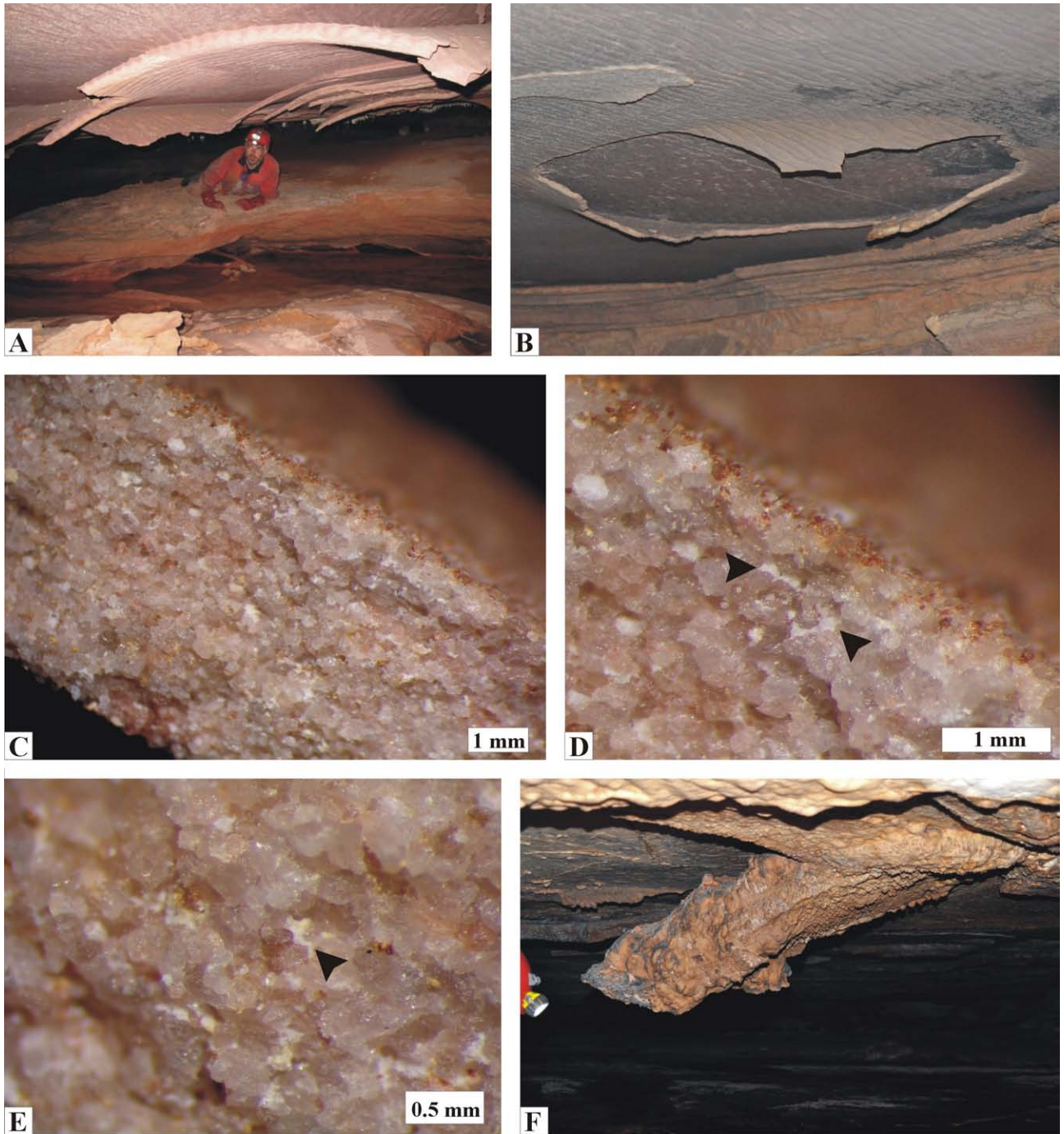


Fig. 64: A-B – Plates of flexible sandstone (itacolomite) scaled from the cave ceilings (A – Cueva Juliana, B – Cueva de los Pémones sector). C – Itacolomite sample from Cueva de los Pémones sector seen under binocular lens. The sediment is formed by quartz grains (glassy), with remnants of clay-mineral cement (most likely kaolinite – white spots). D – Enlarged view of the previous, showing two intergranular voids with white clay-mineral cement (arrow). E – A further void with clay-mineral cement (arrow). F – A well scaled itacolomite plate covered with the “Barro Rojo” laterite in Cueva Juliana.

longer be examined. However, knowledge gathered from our research of this formation’s remnants can be united under one common image which entails a new theory of the origin of tepuis.

“Finger-flow” pillars in the arenites forming these tepuis indicate that the descending flow of silica-bearing diagenetic fluids provided induration of arenites to very hard quartzites. This flow penetrated deeply enough to lithify hundreds of metres

of arenites in a vertical profile, and the indurated rocks then protected less lithified portions of the formation below. Most of the tepuis are limited by vertical cliffs, and undercutting of these cliffs often occurs because the lower parts of the rock are less lithified (see also Young et al., 2009: p. 58-60). Undercutting and the subsequent rockfall are responsible for creation of the rock talus around tepuis (Montañas al pie del escarpado – see

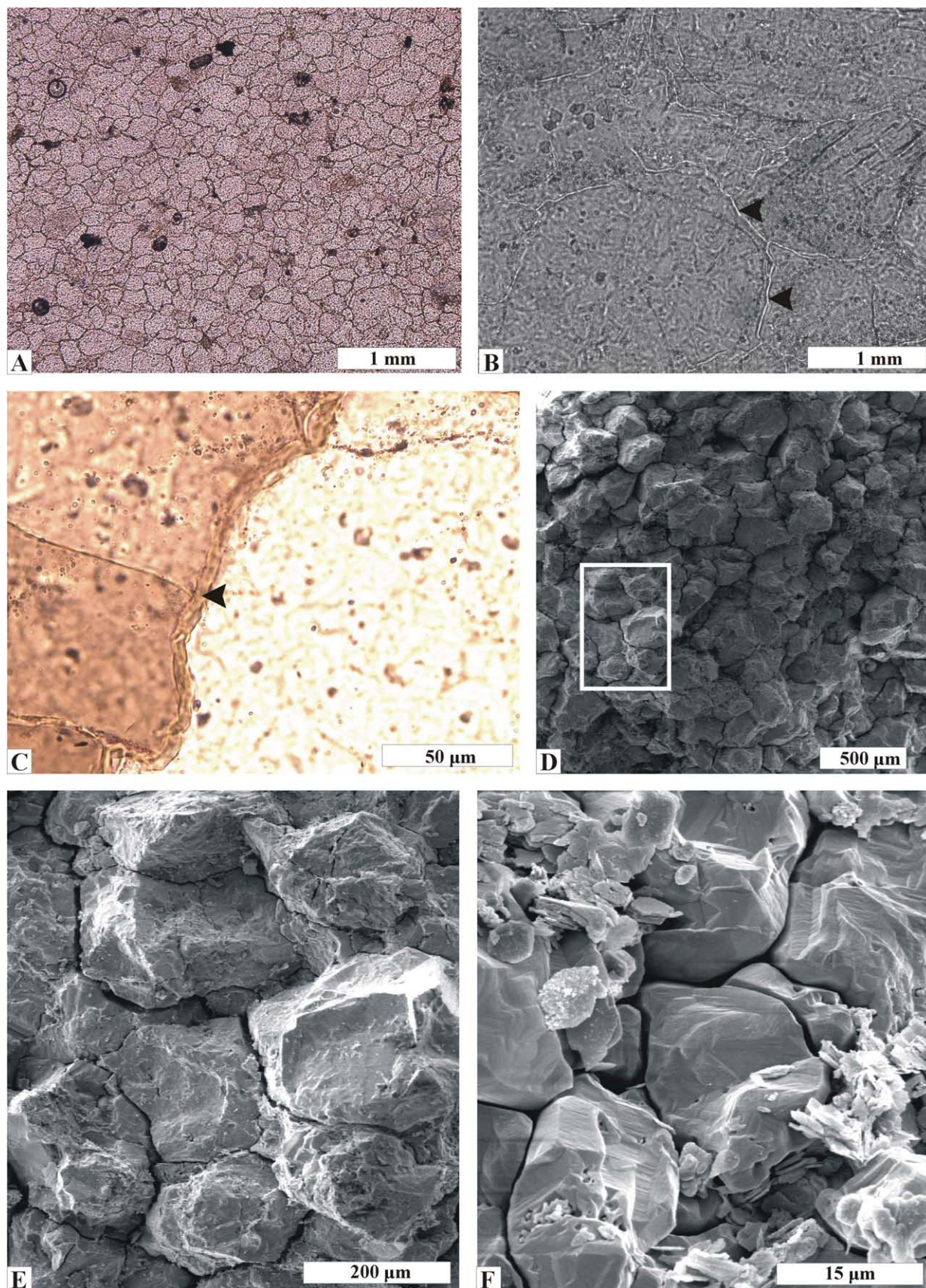


Fig. 65: A – A thin-section view of the itacolumite sample showing quartz arenite with interlocked grains which apparently lack porosity. B – The thin intergranular empty spaces are revealed under higher magnification (arrows). C – An apparently filled space which is actually an overlap of quartz grain edges (arrow). D-F – SEM confirming the presence of thin empty spaces between the quartz grains in the Cueva de los Pémones sector, Ojos de Cristal Cave System.

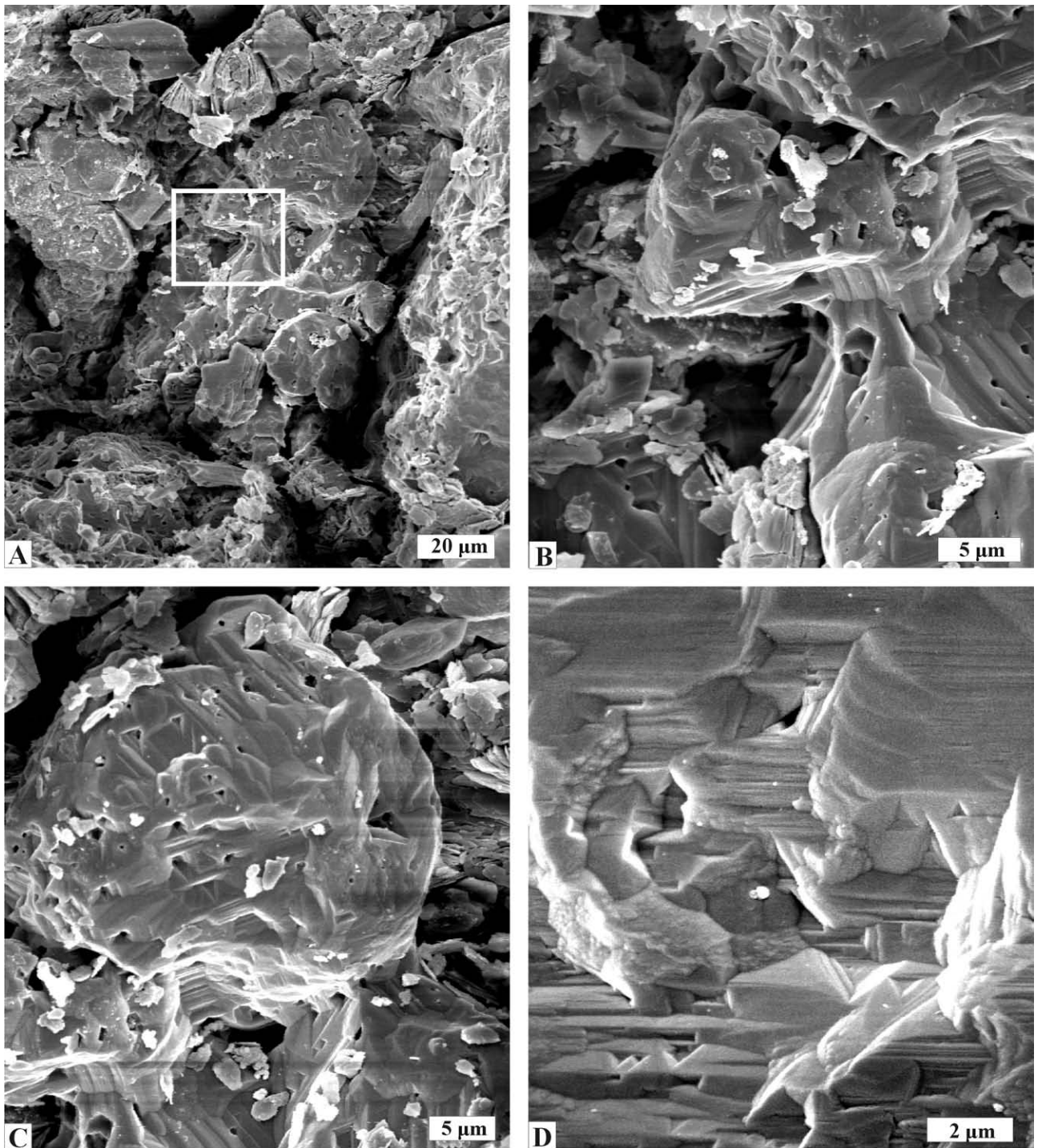


Fig. 66: A-D – Signs of dissolution of quartz grains in the itacolumite sample. The rectangle in A marks the area which is enlarged in B.

Briceño & Schubert, 1992^b: fig. 4.3). The talus then passes to flat country surrounding the tepuis, without retaining any remnants of quartzite boulder accumulations. Moreover, closer inspection of the talus around Roraima indicates that it is formed by less lithified, soft arenites of the Roraima Supergroup, which most likely underlie the sandstones and quartzites, rather than by fallen quartzite blocks (Fig. 71A-C). Erosion of these soft arenites causes undercutting of the Roraima cliffs and keeps them steep.

All these observations indicate that the patchy distribution of tepuis in Gran Sabana was formed long ago by vertical lithification of the Matauí Formation. This lithification required a voluminous source of soluble SiO_2 and sufficient fluids. Exactly as expected today, the best source of SiO_2 then was the clay and rocks with micas and feldspars above the Matauí Formation. These were easily affected by lateritization, which most likely occurred after the Late Carboniferous, when the northernmost

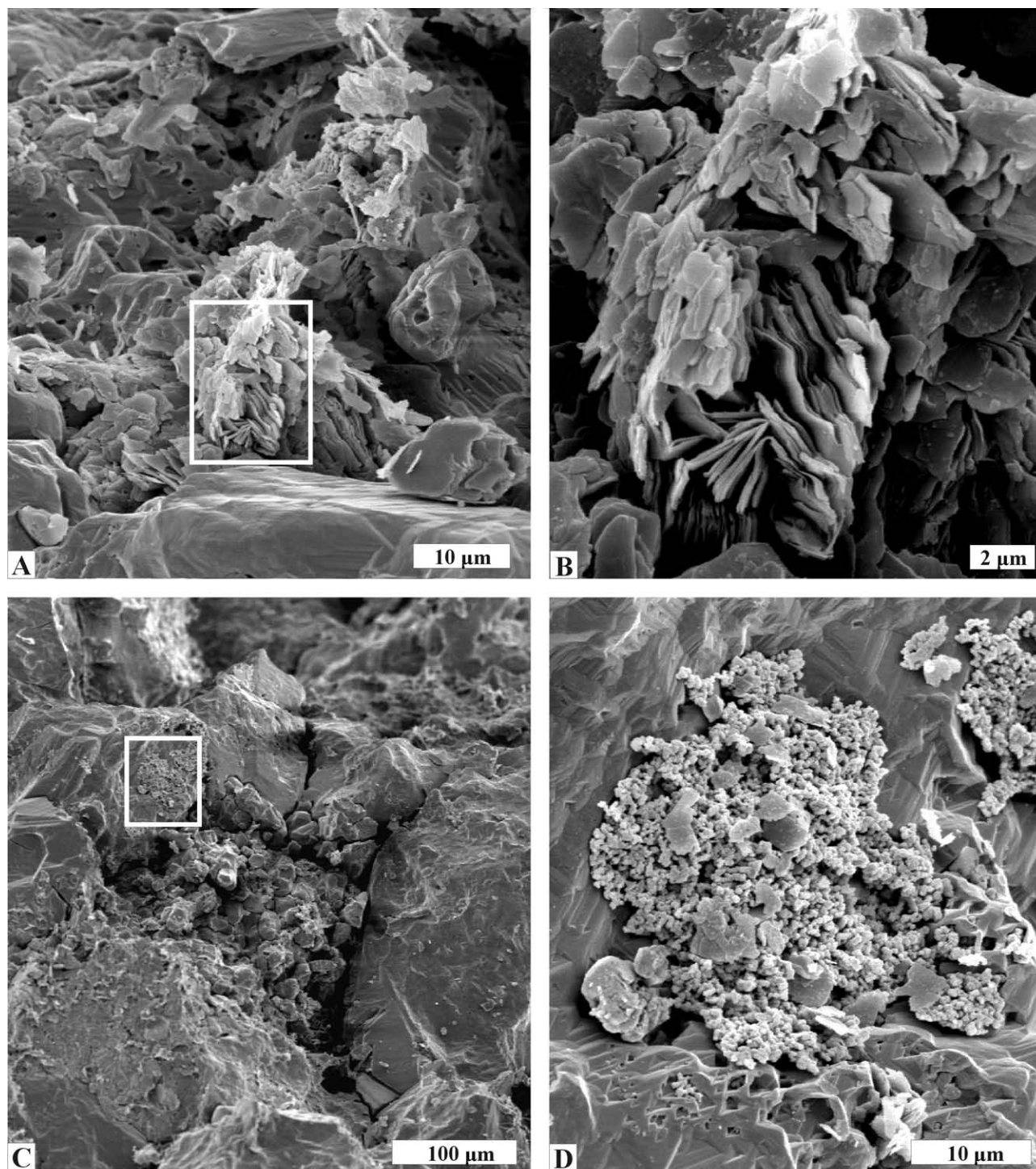


Fig. 67: A – Newly-formed phyllosilicate minerals (most likely kaolinite) resting on the etched quartz grains (clearly visible in the upper left part of the photo). The rectangle indicates the area enlarged in the next photo. B – Enlarged phyllosilicate minerals from the previous photo. C – Unknown clay minerals with very small crystals (in the rectangle – enlarged in D) resting on the etched quartz grains. Newly formed, euhedral quartz grains are present in the centre of the photo. These grains most likely formed from recrystallization of silica cement. D – Enlarged clay minerals from the previous photo. Itacolumite sample, Cueva de los Pémones sector, Ojos de Cristal Cave System.



Fig. 68: Erosional pillars formed by flowing water can be easily differentiated from the “finger-flow” pillars by their elongated shapes parallel to the stream course, Cueva Colibrí sector, Charles Brewer Cave System.

part of South America reached the tropical zone (see Scotese, 2001). The best source of fluids would undoubtedly have been water reservoirs on the surface, and thus the recent distribution of tepuis may have copied the distribution of ancient lakes and rivers (Fig. 72). Alternative explanations for the erosion of the missing portions of the Roraima Supergroup include the inference of Galán et al. (2004^a: fig. 1) that this erosion mainly affected tectonically disrupted parts of the Roraima Supergroup. However, this contradicts the lack of boulder accumulations on Gran Sabana. Moreover, the disrupted parts of the Roraima Supergroup had to be more widespread than the undissected ones, and this is considered most unlikely.

This theory is currently based on a limited set of data and further research is necessary. Although new data may support or refute our theory, it is very satisfying to provoke future research in this area.

2.7. SPELEOTHEMS

2.7.1. Introduction

Speleothems are special cave formations caused by secondary mineral deposits and are generally ubiquitous in limestone caves, since the rates of dissolution and reprecipitation of calcite and aragonite are relatively high (Appelo & Postma, 2005). However, caves formed in silicate rocks such as the caves in the Venezuelan tepuis contain siliceous speleothems instead (Urbani, 1976, 1996; Webb & Finlayson, 1984; Vidal Romani & Vilaplana, 1984; Wray, 1999; Léveillé et al., 2000; Willems et al., 2002; Forti et al., 2003; Cioccale et al., 2008; Vidal Romani et al., 2010). Siliceous speleothems are usually small, rarely exceeding 2 cm in size (e.g. Webb and Finlayson, 1984). The mineralogical composition of the siliceous speleothems is quite simple, since they all consist of various types of opal, mainly opal-A, opal-CT or quartz. In addition to this, the opal may also contain various enclosures of minerals such as kaolinite, dickite, sepiolite, or gypsum (Webb & Finlayson, 1987; Wray, 1999; Forti et al., 2003). Interestingly, these siliceous speleothems share many structural similarities

with the siliceous sinters precipitated from hot springs (Jones et al., 2001^a; Konhauser et al., 2001; Konhauser et al., 2003).

In contrast to most carbonate speleothems, the precipitation of siliceous speleothems is often mediated by microbes (e.g. Willems et al., 2002; Urbani et al., 2005; Urban et al., 2007; Aubrecht et al., 2008^a). This feature is also common in the hot-spring siliceous sinters (Jones et al., 2001^b; Jones et al., 2002; Jones et al., 2003), but the prevailing hypothesis is that the hot-spring siliceous sinters might contain other biotas (e.g. a high amount of autotrophic cyanobacteria) than the siliceous speleothems. It is a well established fact in paleontology that siliceous microbialites are generally typical features of the Precambrian era and that they provide evidence of early prokaryotic life. Several studies have been dedicated to the comparison of microbial communities in Archean time and the recent hot-spring siliceous sinters (e.g. Konhauser et al., 2003). Examination of siliceous speleothems may therefore provide an interesting supplementary approach to explore the siliceous stromatolites that originated from non-photoc environments. Furthermore, in the longer context, such studies may also provide interesting models for research into the biology and evolution of extremophiles (organisms living under extreme conditions) as well as for astrobiology in general, since many extreme cave or karst systems may serve as models for how life might appear on other planetary bodies such as Mars (Léveillé & Datta, 2009; Lee et al., 2012).

The Charles Brewer and Ojos de Cristal cave systems, which are separated from each other by a distance of about 200 km, contain many types of speleothems (Carreño & Urbani, 2004; Aubrecht et al., 2008^{a,b}). Most of these are siliceous speleothems, consisting of virtually all minerals generally encountered in siliceous speleothems, from amorphous opal-A, through opal-CT to microcrystalline quartz (chalcedony). However, there are also non-siliceous speleothems in these caves, such as the desiccated “Barro Rojo” (consisting mainly of goethite – see speleogenesis chapter – 2.5.). It is important to note that the term “non-siliceous” used in this context denotes speleothems which originate from materials other than silica, although they may contain some silicate minerals, such as kaolinite and pyrophyllite. In addition, other minerals have also occasionally



Fig. 69: A – The white kaolinic weathering crust developed on the Roraima Supergroup arkosic arenites, capped by a red lateritic weathering crust. Sierra de Pakaraima at the Venezuelan/Brazilian border. B – Lateritic weathering crust with the remnants of kaolinite at Sierra de Pakaraima. C – Remnants of silicified laterites are typical for the Gran Sabana area. D-E – Jasper layers precipitated from silica emanating from lateritic processes. Quebrada de Jaspe (Jasper Creek).

been identified in the explored caves including gypsum and sanjuanite (see section 2.7.4.).

These speleothems were formed in different ways: some were most likely formed by inorganic precipitation from water solutions, while others represent only insoluble residua (e.g. “Barro Rojo” – see section 2.6.3.3.), but the vast majority of the speleothems do appear to bear signs of microbial mediation during at least some stages of their development. Interestingly, most of these speleothems represent the largest known cryptic stromatolites grown in cave habitats, and the largest siliceous

stromatolites in non-aquatic environments (Aubrecht et al., 2008^{a,b}). Generally, the Charles Brewer Cave System contains larger speleothem formations than the Ojos de Cristal Cave System. A plausible explanation for this may be the obvious size differences between these two cave systems and, consequently, different amounts of dissolved SiO₂. In this subchapter, we describe the research performed so far on various types of speleothems (non-microbial versus microbial siliceous speleothems) in more detail. This description was supported by the mineralogical and petrographical methods normally used in

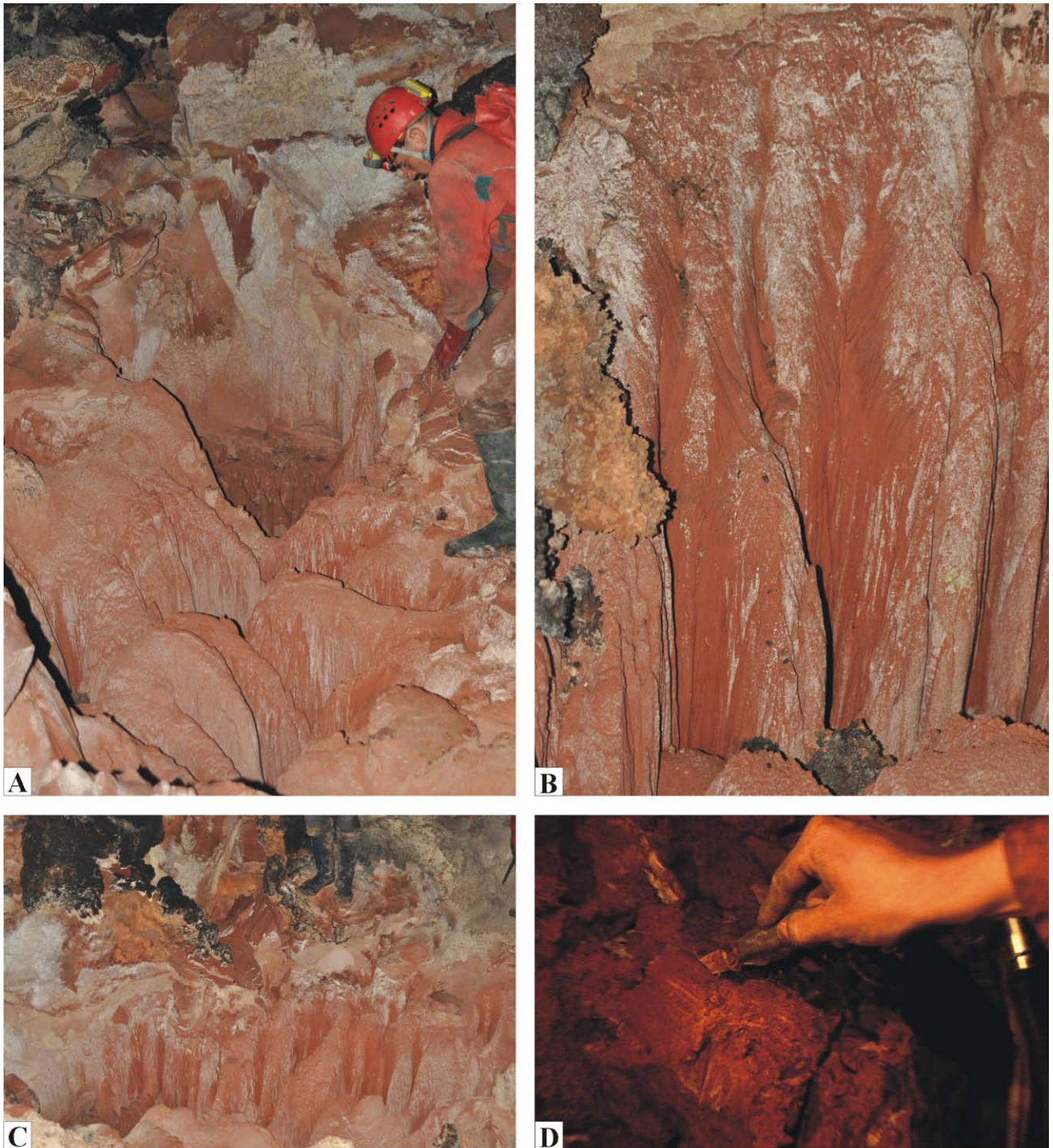


Fig. 70: A-C – Soft lateritized greywacke arenites with evolved erosional forms in the Cueva Colibrí sector (Charles Brewer Cave System). D – Lateritized arenites are so soft that they can be cut by knife. Cueva Cañon Verde.

analysis of speleothems, comprising thin-section, SEM and XRD studies, together with different types of biological investigations. Unfortunately, these studies have only currently been performed on a limited number of samples, because great caution has been taken to prevent excessive damage to the speleothem decoration of the caves during various expeditions. Therefore, almost all samples used for these studies were taken from speleothems which were already detached from the surface or partly damaged

by previous cave visitors. Although the number of samples may produce some biased results, nevertheless each item of information is paramount in gaining a first glimpse into the origin and composition of these speleothems. Based on these results, we hope that future sampling can then be planned more efficiently for more penetrating, holistic studies.



Fig. 71: A – A view on Mt. Roraima (and Mt. Kukenan – left). The mountain consists of quartzites, which form steep cliffs (C) and surrounding talus (T). B-C – The talus is not formed only of fallen quartzite blocks but mostly of soft, uncemented arenites prone to erosion. Photos from the tourist access trail to Roraima.

2.7.2. Inorganic siliceous speleothems

In this subchapter, we describe siliceous speleothems that are generally not obviously mediated via microbes or other organisms, but which may occasionally contain or become influenced by organic material. Although non-microbial speleothems are rather rare in the Charles Brewer and Ojos de Cristal cave systems, their shapes are very similar, differing only in their average size.

2.7.2.1. Siliceous stalactites

Stalactites are one of the most common forms of non-microbial siliceous speleothems in the examined caves (Fig. 73). The various stages of their development can be observed in slabs of old mature stalactites (Fig. 74). In their initial stages, they form mostly smooth, soda-straw-like stalactites (Fig. 73A-B; see also Carreño & Urbani, 2004: p. 33) hanging from the ceilings in cave areas where SiO₂-saturated, or semi-saturated, water drips down. Unlike limestone speleothems, these usually do not have stalagmitic counterparts on the ground, and only planar flowstone crusts cover the substrate (see the following section 2.7.2.2.). The structure of these speleothems can change over a period to bizarre, atypical forms, reminiscent of carrots and turnips, firstly with regular wavy constrictions (Fig. 73C-D), and later with a pustular surface (Fig. 73E-F). Analysis of cross-sections of such speleothems indicated that these structures were caused by uneven precipitation of silica directly on the stalactite before dripping and forming small cascades, overhangs, lumps and bulbs (Fig. 74A-B). The more uneven the surface, the longer the trajectory of the water drop becomes, so that the water most likely evaporates before it reaches the stalactite tip. This phenomenon therefore often induces a finely-laminated inner structure (Fig. 75A-B).

Although non-recrystallized opal is the main component of these stalactites, relatively long needle-like gypsum crystals can also occasionally be found in them (Fig. 75C-D). Some stalactites can also contain a rich sandy admixture, so that agglutinated sandy stalactites may form when excessive sand is present (Fig. 74C-D).

2.7.2.2. Flowstone crusts

Flowstone crusts are from several mm to 1cm thick. These are usually laminated (Fig. 76A) and a gradual recrystallization of originally amorphous phases to quartz can be observed on some of them (Fig. 76B). Microscopic observations show that most analyzed specimens are characterized by spheroidal forms, with undulose, fan-like extinguishing in crossed polars (Fig. 76C). This may indicate that the transformation is still an ongoing process, most likely transforming from opal-CT to chalcedony. The individual spheroids are usually very finely laminated (Fig. 76D), possibly due to the diagenetic oscillation of opal with various water contents (see Jones & Renaut, 2004). Speleothems as a whole are commonly zonal due to the numerous opaque inclusions that form the above-mentioned lamination. Under microscope examination, some speleothems show bizarre structures including numerous voids, or alveolar “bubbles” (Fig. 76E). Some voids are filled by younger, non-recrystallized generations of silica compounds, and needles of currently unidentified, low-birefringence mineral enclosed in silica are commonly observed (Fig. 76F). These speleothems

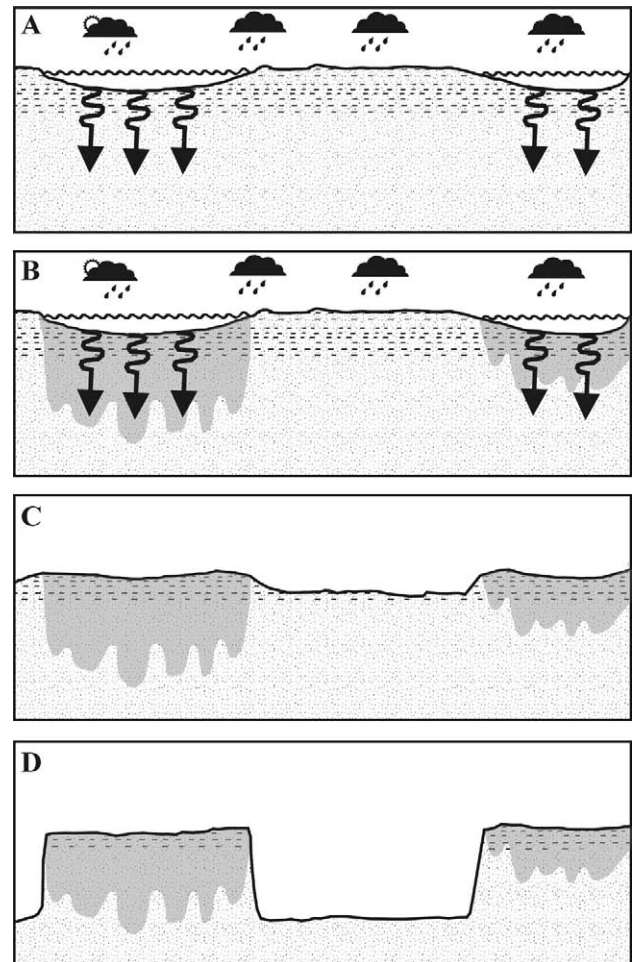


Fig. 72: The newly proposed model of the origin of the tepuis. A – The Roraima Group was originally capped by sediments rich in micas, feldspars or clay minerals which were prone to lateritization. This lateritization may have begun in the Late Carboniferous when the northern part of present South America reached tropical areas (Scotese, 2001). B – The lateritization occurred mostly in the areas with excess fluids, such as rivers and lakes. The descending fluids brought silica from the lateritization zones downwards, causing additional cementation of the Matauí Formation. This cementation was patchy, and concentrated only in the zones with sufficient water. C-D – In the later geomorphological evolution stages, the uncemented portions of the Roraima Supergroup were subjected to erosion and the cemented, quartzitic parts were preserved, together with the softer, uncemented parts protected below them. The steep cliffs of the tepuis are maintained by erosion of the softer, uncemented arenites below with subsequent undercutting of the quartzite layers.

may also contain occasionally sand accumulations, or they might even become combined with microbial speleothems (e.g. overgrown by stromatolites).

2.7.2.3. “Cobweb stalactites” (telerañas)

“Cobweb stalactites” occur in both examined cave systems. They do not represent truly inorganic speleothems as they are formed via opal encrustation of spider webs hanging from the ceilings (Fig. 77). The very fine structures of some “cobweb stalactites”,

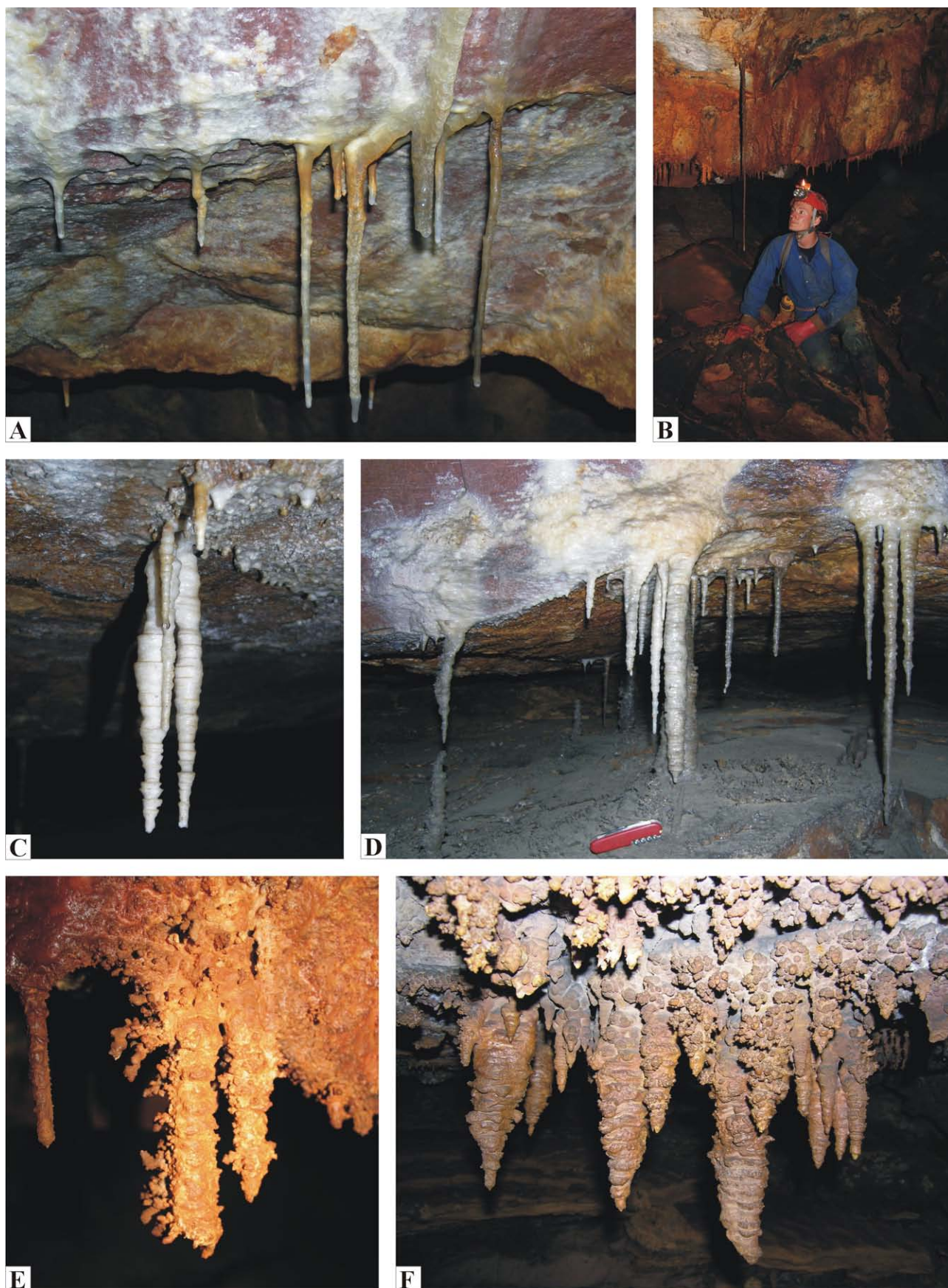


Fig. 73: Typical evolution of inorganic opal stalactites. The initial stages are straight, soda-straw-like stalactites (A-B), which attain more bizarre forms with wavy constrictions (C-D), and later with irregular pustules (E-F). Cueva Charles Brewer sector (Charles Brewer Cave System).

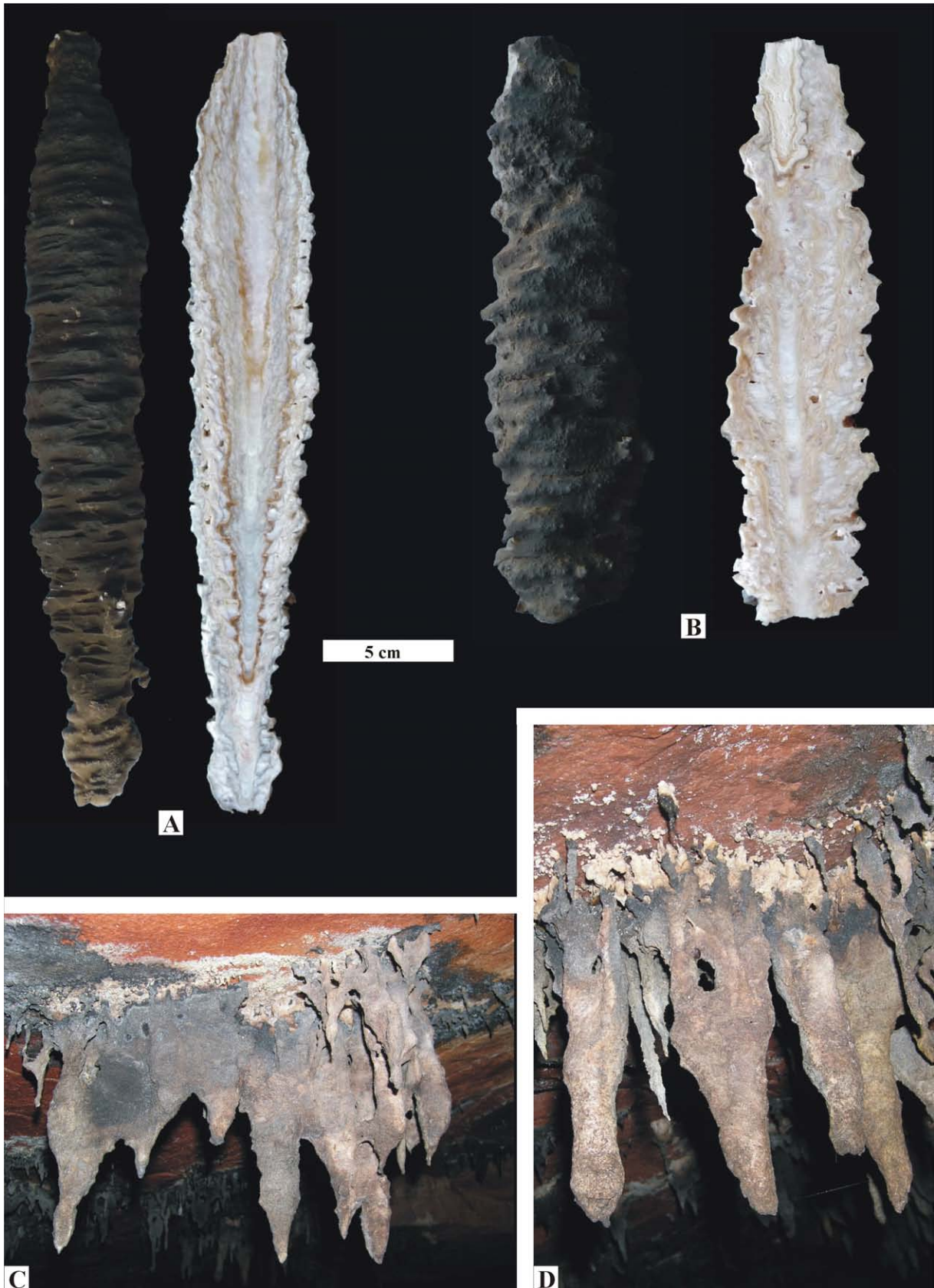


Fig. 74: A-B – Slabs showing longitudinal cross-sections through two specimens of inorganic opal stalactites from the Cueva Charles Brewer sector (the specimens were not in growing position as they were already detached from the substrate). The growth zones highlight the irregular formation of the speleothems, attaining more and more bizarre shape with elongation of the trajectory of the water droplets. C-D – Mixed, sandy-opal stalactites may form in the excess of free sand grains. Cueva de los Pémones sector (Ojos de Cristal Cave System).

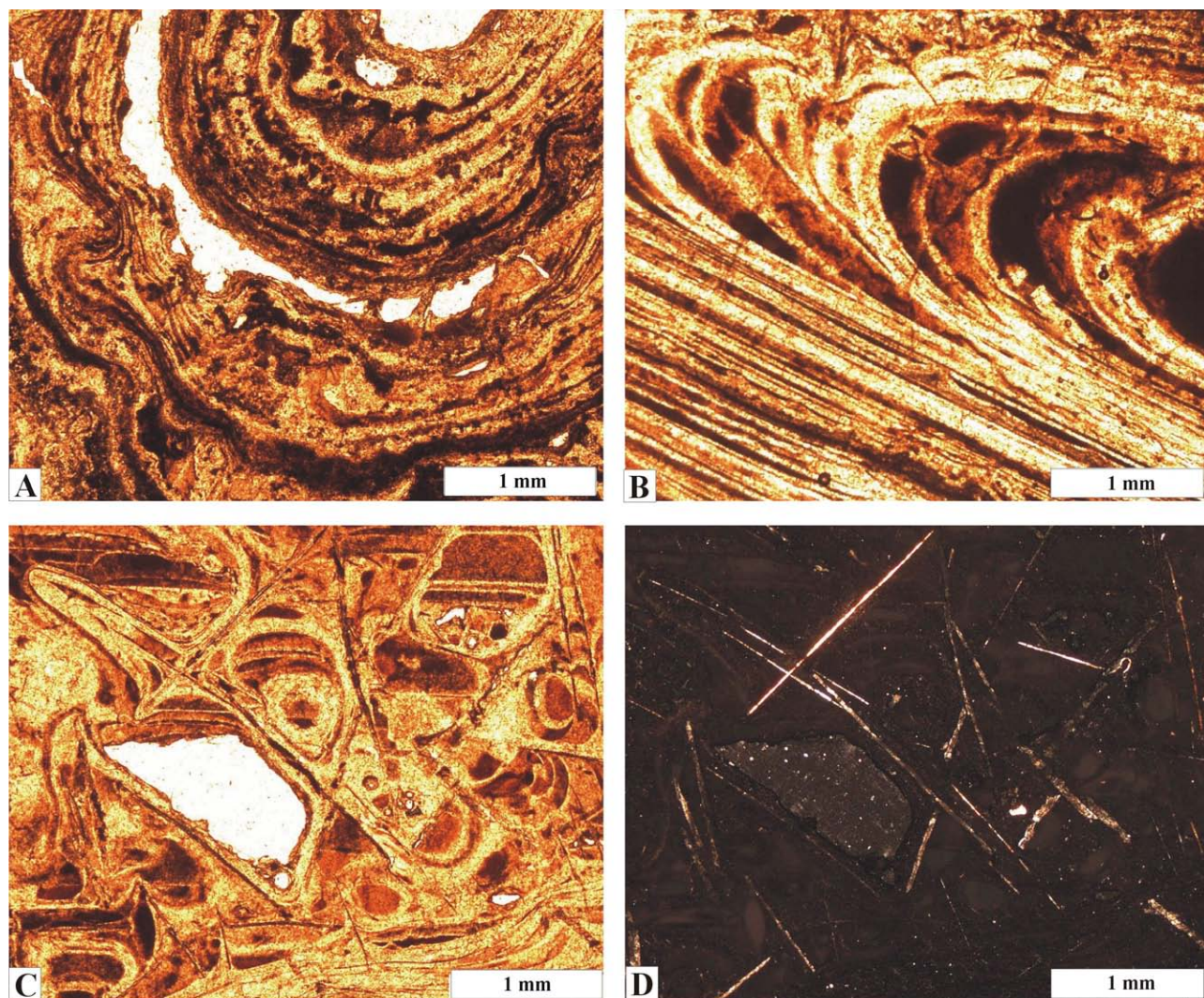


Fig. 75: Microphotos of the inorganic opal stalactite. A,B – Fine-laminated structure of the stalactite. C,D – Thin needle-like gypsum crystals in the stalactite (C – plane polarized light, D – crossed polars).

with tips commonly inclined towards the air draught, imply that their encrustation was not caused by seeping water but more likely by aerosols (Fig. 77F). One reason for this is that seeping water would make the cobweb too heavy, and consequently it would hang more vertically from the ceiling.

Microscopic studies of cobweb stalactites showed that these structures are almost exclusively characterized by a laminated opal form, resembling columnar stromatolite but of inorganic origin (herein we consider stromatolites as being exclusively of biogenic origin). Four different growth subzones can often be distinguished in the speleothem specimen (Fig. 78): the middle zone (m), central zone (c), alveolar zone (a), and outer zone (o). The middle and central zones are discontinuous in 2-D view, possibly caused by initial scrolling of the stalactite during its growth. The middle zone consists of brownish (colours as they appear in thin-section), cloudy to semi-opaque, non-laminated opal. In contrast, the central zone consists of finely laminated opal (resembling siliceous stromatolite) which is much clearer and transparent. Under higher magnification, thin spider threads

can be observed in the latter two zones (Fig. 78B). Since these filaments are very thin and discontinuous and often extend beyond the plane of the thin-section, this may indicate that they are linear rather than planar bodies, and therefore they represent threads rather than tiny fractures.

The alveolar zone is formed by laminated opal, which is cloudy in some places with numerous alveolar to globular voids resembling fenestral pores in intertidal limestones and dolomites (Fig. 78C-D). A rich sandy admixture can be observed with the spider threads in this zone.

The outer zone is predominantly composed of clear, or sometimes turbid finely laminated opal. In some places, the lamination is convex from the stalactite, giving the appearance of an inward growing stromatolite (Fig. 78D). Spider threads are present in this zone, which also contains considerably less fenestral pores and detrital sand grains.

In some other samples of “telerañas” the non-microbial opal encrusting spider threads may also be combined with some microbial, stromatolitic zones.

2.7.2.4. Mineralogical composition of siliceous speleothems

The mineralogy of speleothems in sandstone caves does not vary as much as for those in granitic caves, which can contain opal-A, evansite, bolivarite, struvite, pigotite, tanarakite, allophane, hematite or goethite in different areas (Webb, 1976; Macías Vásquez et al., 1980; Hill & Forti, 1995; Forti et al., 2003; Vidal Romani et al., 2010). Although speleothems from the examined sandstone cave systems show different forms and types, their mineralogy is quite uniform. These samples usually exhibit a concentric or botrioidal texture in thin section. Needle-like crystals with low interference colours were detected in samples of speleothems with concentric structure (Fig. 76F). Due to their small size it was not possible to identify them, but the low birefringence of these minerals indicates that they could represent barite or apatite. There were also some higher-birefringence needles, which most likely represented gypsum (Fig. 75C-D).

XRD patterns of the speleothems were compared with published data, and mineralogical identification and characterization of impurities enclosed in the opal was also performed. According to X-ray powder diffraction results, all analyzed speleothems had a large hump centered at approximately 4.0 Å in a pattern typical for opal-A (Jones & Segnit, 1971; Floerke et al., 1991; Graetsch, 1994). In addition to opal-A, there was also quartz in some samples, likely some of this was detritic (Fig. 79A).

The opal-A samples from the studied speleothems differ in FWHM index (listed in Tab. 5). The FWHM index was not calculated for samples containing quartz, because the broad hump in opal-A coincides with quartz diffraction peaks. An approximation of the structural state of a particular opaline silica sample is available from the FWHM index of the above-mentioned distinctive 0.4 nm diffraction line or band (Herdianita et al., 2000). This method is analogous to the one used to measure clay crystallinities (Moore & Reynolds, 1997).

SEM images of samples from the studied sandstone caves revealed the presence of smooth silica spheres typical for opal-AG (Fig. 79B-C). These opal spheres are commonly elongated and often imperfectly shaped. They are also disordered, and differ in size in the range of from 1 to 2 µm. The freshly broken surfaces of selected samples showed none of the concentric layered spheres reported by Darragh et al. (1966) and Gaillou et al. (2008).

Siliceous speleothems were also analyzed using Raman spectroscopy in thin section and freshly broken chips. A typical feature of all the analyzed samples was a high level of fluorescence which effectively swamped any Raman photons. When bands were observable, these tended to be broad and ill defined, and therefore their interpretation was not possible. Since some of the fluorescence background appears to reside in the disordered and amorphous state of opal-A itself (Splett et al., 1997), the obtained Raman spectra most likely represent opal-A. Moreover, the fluorescence of opal-A may be caused by the presence of specific chemical compounds such as aluminum or iron.

Despite the opal strong fluorescence, the most characteristic Raman signals identified quartz (Fig. 80A-B). Quartz was confirmed by the presence of most characteristic Raman signals (Fig. 80B). Subsequently, the obtained spectrum of quartz was compared with the published data, and it correlated perfectly

(www.rruff.info – R040031, Kingma & Hemley, 1994). According to these results it appears that quartz is a very common “inclusion” in the examined opal speleothems.

2.7.3. Biospeleothems

In this subchapter we describe speleothems mediated via microorganisms. Most of these represent true stromatolites as described in the literature, with the latest overviews being contained in the volume edited by Reitner et al. (2011). Unlike most of the stromatolites described previously, stromatolites in these two examined large cave systems mostly did not form in an entirely aquatic environment. As such, they are unique and deserve a detailed description.

Many bizarre biospeleothem forms were discovered in both the Charles Brewer and Ojos de Cristal cave systems, thus highlighting the striking similarities between these two systems. They were found in many different locations in the caves, especially close to flowing water systems, and there were vast quantities in all cave zones, from well illuminated entrance zones to completely dark inner ones. One of the most common forms encountered was mushroom-shaped speleothems, sometimes termed “dolls” (Spanish: muñecos – Fig. 81A-B). These are over 10 cm high, and their main features are the white stems and dark brown caps. However, there are also several other forms, such as the “black corals” (Spanish: corales negros), characterized by a more bizarre, branching shape (Fig. 81C-E), and also “guácimos” which have branching shapes, but otherwise resemble muñecos (Fig. 81F). All these are coralloid speleothems types, which are the most common types of speleothems encountered in silicate caves in other parts of the world (Swartzlow & Keller, 1937; Urbani, 1976; Zawadzki et al., 1976; Wray, 1999; Cioccale et al., 2008).

Many of the biospeleothems in the Charles Brewer and Ojos de Cristal cave systems are often found in amazingly large arrangements on bedding-planes, joints and the lower sides of overhanging quartzite beds. These may be lined up in massive numbers of ball-shaped speleothems called “champignons” (Fig. 82A-G), or in kidney-shaped speleothems (Spanish: riñón – Fig. 82H), or other mushroom-like speleothems (Fig. 83A-C). Some of these “champignons” are hollow, with a thin crust on their top, which may have originated from the encrusting parts of a microbial mat unattached to the previous microbial layers (Fig. 82G). Some stalagmitic forms also resemble ice-creams (Spanish: helados – Fig. 83D-E). Older, strongly lithified champignon-like speleothems prevail in the Ojos de Cristal Cave System, including stalactites with strange shapes similar to wide cones (Fig. 83F), while others have surfaces with bizarre patterns resembling panther fur (Fig. 83G). This latter type is also present in the Charles Brewer Cave System.

“Muñecos”, “corals” and “champignons” are the most common forms of biospeleothems in the Charles Brewer and Ojos de Cristal cave systems, and although most resemble the classical stalactites and stalagmites in limestone caves, they differ in structure and origin. Despite their bizarre and variable shapes, the microbial speleothems often show a common principal texture corresponding to various stages of their evolution (Fig. 84). They consist of the following two main components, commonly

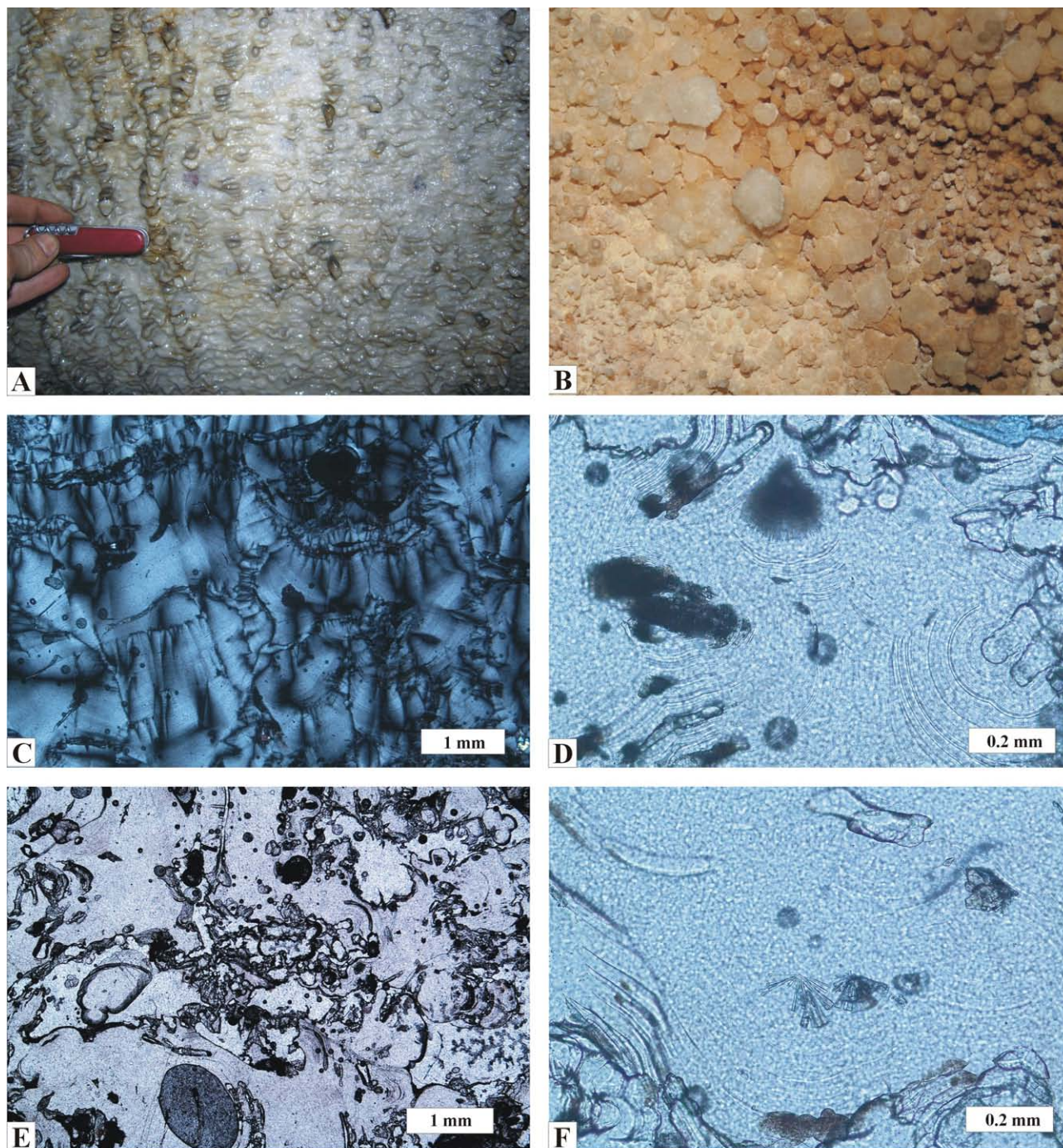


Fig. 76: A – Inorganic, drapery-shaped opal flowstone crust. Cueva Charles Brewer sector. B – Old flowstone crust recrystallized to quartz crystals in the Cueva de los Pémones sector. C-F – Microphotos of the flowstone crust from the Cueva Charles Brewer sector. C – This fan-like undulatory extinguishing of the flowstone crust in the thin-section indicates the initial recrystallization of originally amorphous opal. This stage may represent opal CT. D – Very fine spheroidal lamination in the flowstone may be caused by oscillating contents of water. E – Bizarre alveolar bubbles trapped in the siliceous flowstone. F – Newly formed low-birefringence needle-like crystals in the flowstone, depicted in the centre of the photo.

occurring in the same speleothem; 1) a laminated columnar stromatolite, consisting of non-porous compact opal which forms most of the speleothem internal zone; and 2) a strongly porous stromatolite formed by white chalk-like opal, which appear to contain an accumulation of microbial-like peloids, usually forming the outer speleothem zone.

In some biospeleothems, these zones are irregular and can alternate, or else they can occur separately, thus forming speleothems consisting exclusively of one type of microbial structure. For some currently undiscovered reason, samples from the Charles Brewer Cave System contain both types of microbialites, whereas those from the Ojos de Cristal System have only the

porous or peloidal type (see below). Since this latter finding may be caused by insufficient sampling, a columnar stromatolite-type presence in the Ojos de Cristal System cannot be excluded.

Detailed observations of the anatomy of both types of stromatolites were performed by petrographic, thin-section study, and also by SEM study of fresh, broken, cut or hydrofluoric acid (HF) etched speleothems. Longitudinal thin-sections through various specimens of microbial speleothems revealed that their inner structure usually mainly consists of the two principal types (Fig. 85A); the branching, fine-laminated columnar stromatolite (s) and the porous peloidal stromatolite (m) form the majority

of the “muñeco” specimen. These are accompanied by a thin, fine-laminated outer stromatolitic zone (o).

Columnar stromatolites from the Churí Tepui caves samples are finely laminated, with alternating laminae of clear and brownish opal (Fig. 85B-C), which appear alveolar in cross-section (Fig. 85D). Dense bundles of radial filaments formed by microbial builders are clearly apparent in these stromatolites (Fig. 86A-C), and spherical enclosures, most likely of organic origin, can be found trapped in some parts (Fig. 86D).

Apical portions of the “black coral” and “guácimo” samples from the Cueva Charles Brewer sector, which most likely represent the

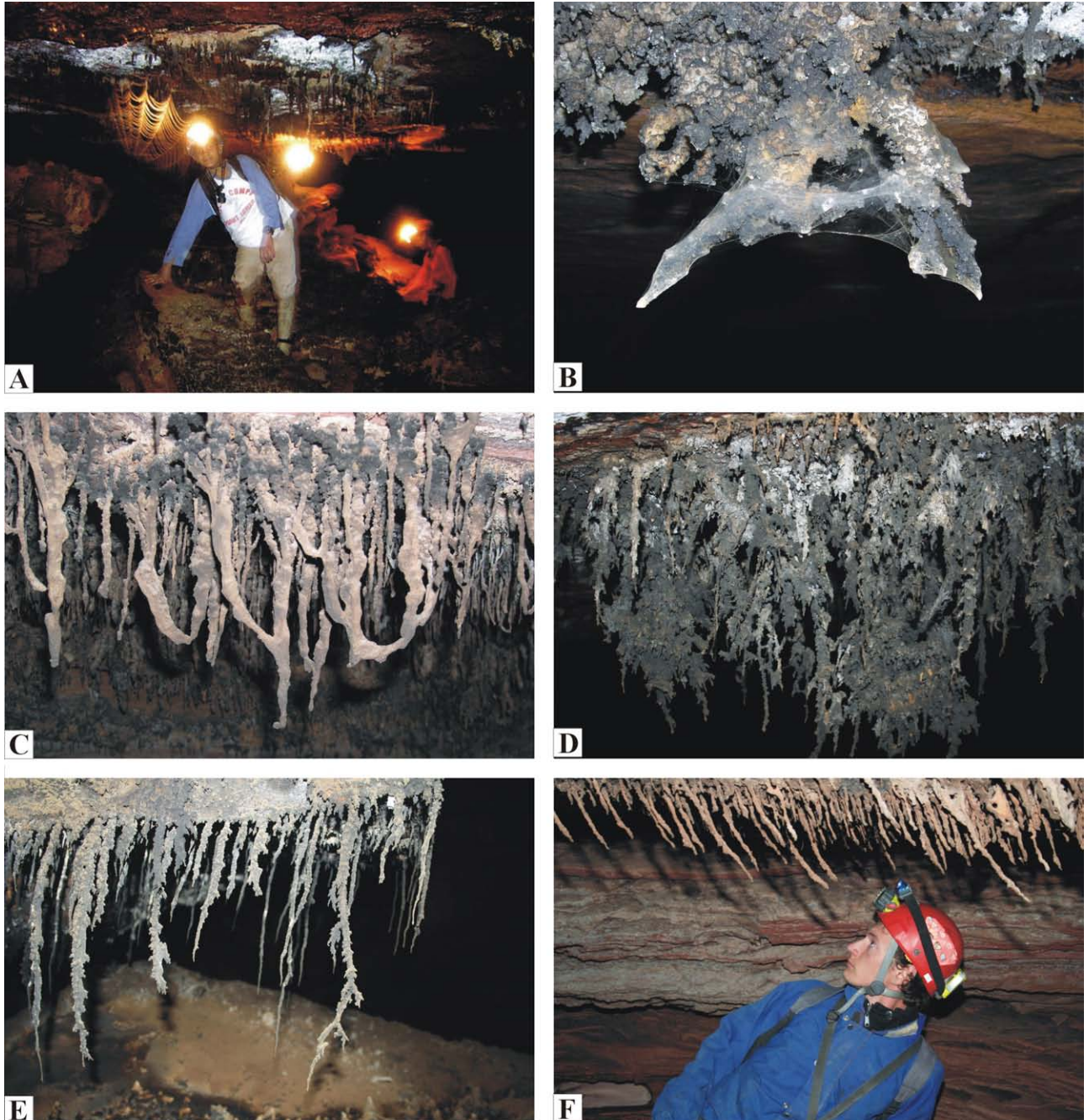


Fig. 77: A-E – Various forms of cobweb stalactites (“telerañas”) originating from encrustation of spider threads by opal. F – Due to the supporting fine cobweb structure, the speleothems are often inclined in the direction of the draught. A-B – Cueva Charles Brewer sector, C,F – Cueva Cañon Verde, D,E – Cueva Colibri sector.

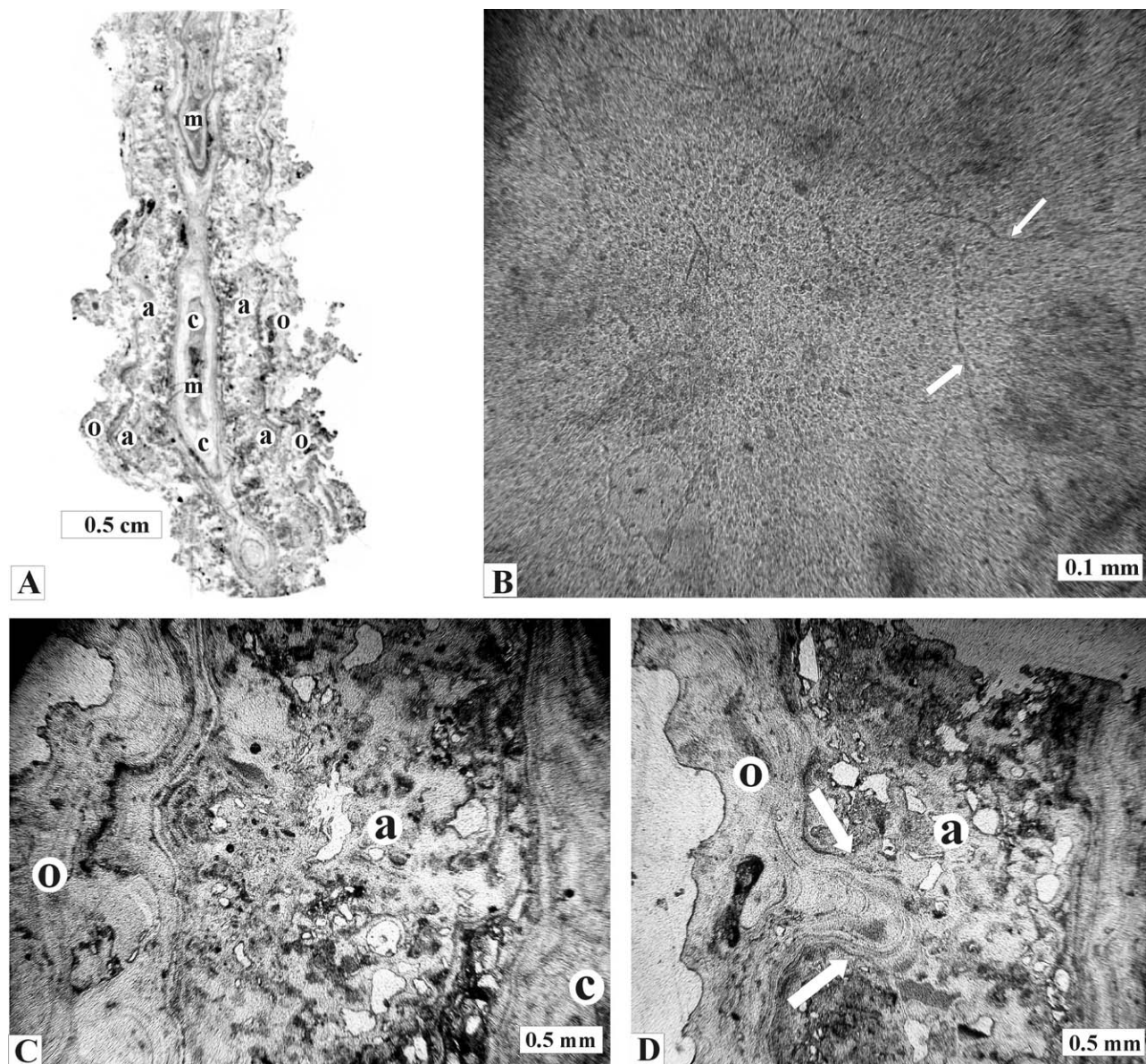


Fig. 78: Thin-section images of a "cobweb stalactite" from the Cueva Charles Brewer sector. A – Scanned overview image of a longitudinal thin-section of a "cobweb stalactite". The letters indicate zones: middle (m), central (c), alveolar (a) and outer (o). B – Spider threads (arrowed) preserved in the clear opal of the central zone. C – Alveolar zone (longitudinal cross-section), bordered by central (c) and outer (o) zones. Note the bizarre fenestral pores and quartz sand grains trapped within this zone. D – Convex stromatolitic offspur (arrows) projecting inward from the outer zone, implying the possible inward growth of the entire stalactite.

active, living/evolving parts of the columnar stromatolite, appear under SEM as bizarre, branching, coral-like bodies (Fig. 87A-D). It is likely that other animals, especially spiders, contributed to these structures, since spider-like threads can often clearly be seen emerging from the opal (Fig. 87E). These are readily distinguished from the fungal hyphae which are usually thicker, curved and branching (Fig. 87F). In situ field observations in the Cueva Charles Brewer sector revealed considerable spider activity, not only on the "cobweb stalactites" but also on stalagmitic forms. Some of the observed growth planes of these speleothems appear to be agglutinated from detrital material (Fig. 87G-H).

SEM study of etched surfaces of the fine-laminated columnar stromatolite showed that it consists mainly of thin concentric

laminae (Fig. 88). Most of the lamination appears to be related to the presence of microorganisms, since many densely packed, parallel tubular casts of filamentous-like microbes can be observed (Figs. 88, 89). This is also supported by thin-section petrographic studies. However, it is also possible, for example, that at least some of the laminae may be of abiogenic origin, precipitated directly from water. The abundance and distribution of the microbial and abiogenic laminae vary within the speleothems (Fig. 89C-F).

SEM study of the filamentous-like microbes shows that their tubes are 50-80 μm long, straight and unbranched. They have circular cross-sections, measuring 5-10 μm in width. In longitudinal section these appear as simple tubes, but small remnants of septa

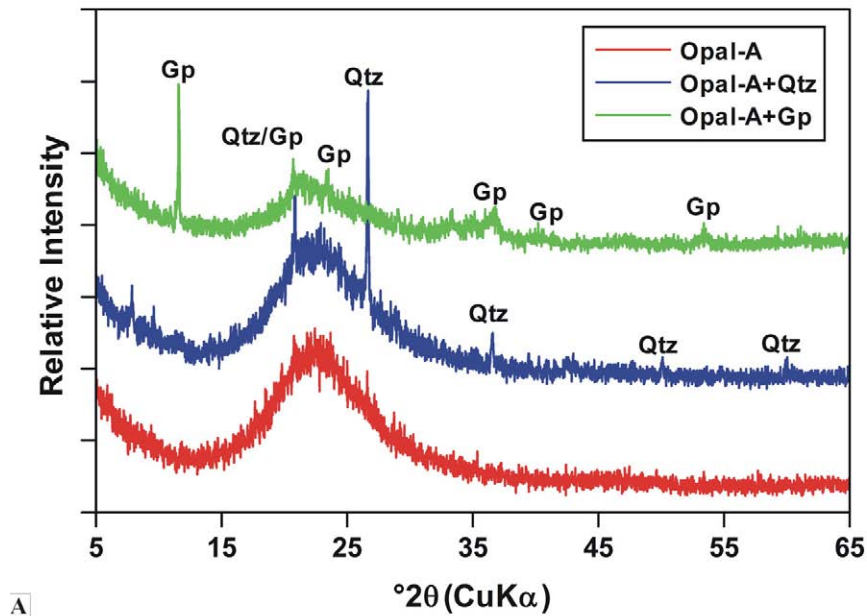


Fig. 79: A – X-ray powder diffraction patterns of various opal speleothems. Some opal speleothems contain only one mineral, but some also include quartz (Qtz) or gypsum (Gp). B-C – SEM image of opal-AG spheres.

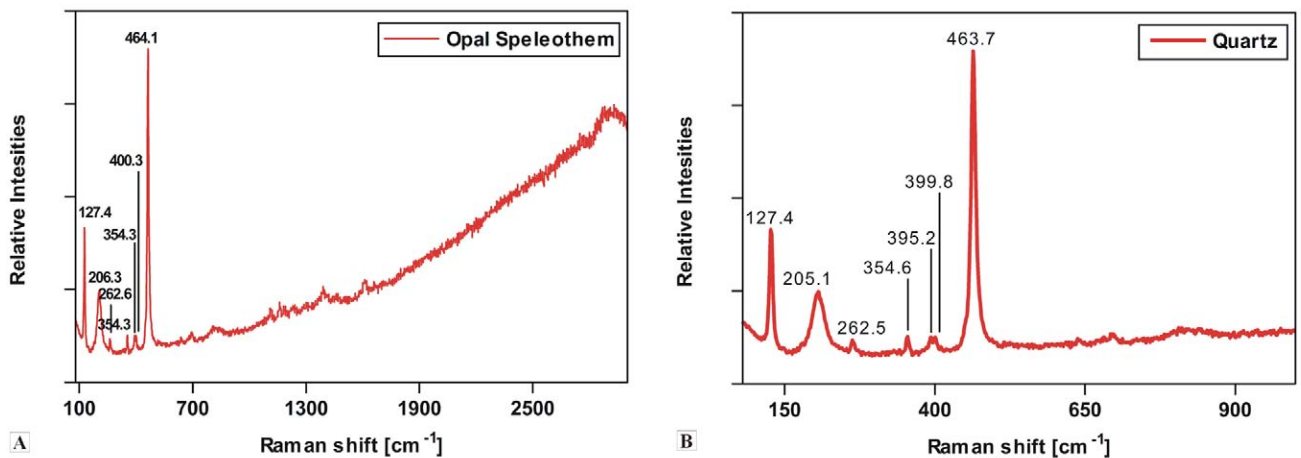
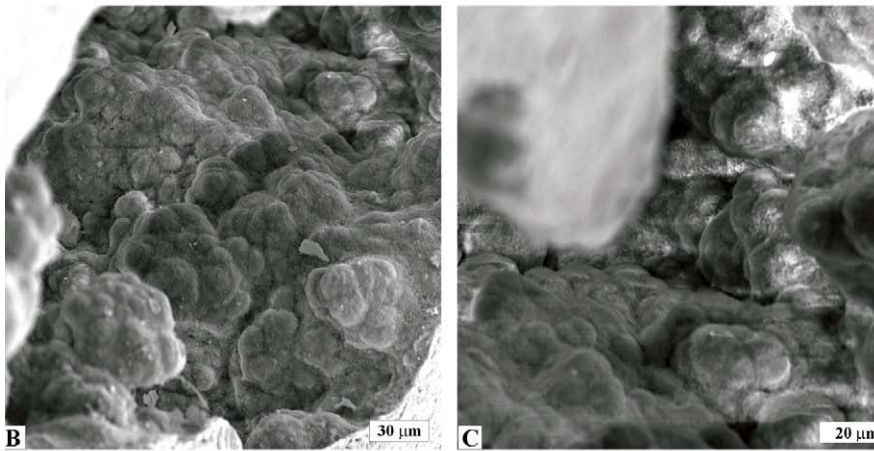


Fig. 80: A – The Raman spectra of opal speleothems are influenced by strong fluorescence which effectively swamped Raman photons. This strong fluorescence is characteristic for opal-A with certain amount of aluminum or iron. B – Raman spectra of quartz grains which occur as inclusions in speleothem opal.

Tab. 5: Overview of identified mineralogical composition of opal speleothems analyzed by X-ray powder diffraction. The FWHM (full width at half maximum) index was calculated using Winfit software for all samples. Cueva Charles Brewer sector.

Sample	Opal type	Other minerals	Calculated d-spacing [nm]	Peak position ($^{\circ}2\theta\text{CuK}\alpha$)	FWHM index
Ven-1	opal-A	–	0,415	21,417	2,098
Ven-2	opal-A	–	0,416	21,351	2,391
Ven-3	opal-A	–	0,416	21,377	2,355
Ven-4	opal-A	–	0,411	21,621	2,747
Ven-5	opal-A	–	0,416	21,366	3,780
Ven-6	opal-A	–	0,414	21,490	3,008
Ven-7	opal-A	–	4,168	21,319	5,229
Ven-8	opal-A	Qtz	–	–	–
Ven-9	opal-A	Qtz	–	–	–

are visible on their inner surfaces (Fig. 90). The spaces between the septa are regular at approximately 2.5 μm . These structures may represent the same microbes that form the surface alveolar bodies observed on the unetched speleothem surfaces of SEM prepared specimens (see above – Fig. 87). Irregular, and often oval-shaped double-layered cross-sections of silicified microbe tubes were revealed within some parts of the columnar stromatolite (Fig. 91). Their diameters are more variable than those of the previous casts, ranging from 10 to 35 μm . In other parts of the stromatolite, the etching revealed network-like structures (Fig. 92A), which are also likely related to microbial activity and which contribute to formation of the columnar stromatolites alveolar zone. Etching of the columnar stromatolite also revealed other, sheet-like structures trapped in the opal. These structures showed certain similarities to remnants of plant tissues or the chitin of insect remnants (Fig. 92B).

The porous peloidal stromatolite in both cave systems consists of relatively uniform ovoid peloids (Fig. 93A-D), which are densely packed and arranged in concentric laminae. Near the columnar stromatolite, they are usually packed more loosely, with interstitial pores filled with pure opal. The size of the peloids ranges from 0.1 to about 0.3 mm. In some places, well-defined peloid areas connect to areas of obliterated peloidal structure which resemble mud-cracks (Fig. 93E). In some parts of the “champignon” samples from the Cueva Charles Brewer sector, larger spheroidal bodies, with irregular sizes varying from 250 to 520 μm , can be observed (Fig. 93F). In the central zone of the “muñeco” specimen, the peloidal structure is disturbed by fenestral shaped pores and trapped quartz sand grains. Some silicified organic remnants, which appear as thin tubes and tube meshworks are apparent in the central zone. These may be affiliated to trapped insects, spiders or plant remnants (Fig. 94A-B).

Similar structures have also been found in some speleothems in the Ojos de Cristal Cave System (Fig. 94C). A common structure in many of the speleothems is the chitin remnants of arthropods, ranging from common insects to spiders, and even scorpion exuvia (Fig. 94D).

Unlike columnar laminated stromatolites, the peloidal types are usually less cemented. Stronger cementation was frequently observed in the samples from the Ojos de Cristal Cave System (mainly from the Cueva de Gilberto sector) but more rarely in the samples from the Charles Brewer Cave System (the Cueva Charles Brewer sector). The well-cemented peloidal microbialites are usually older, as shown by Lundberg et al. (2010³) who estimated that the age of “riñón” (see the specimen in Fig. 82H) lies between 290-390 KA.

The peloids of most of the younger samples studied via SEM are predominantly loosely packed, with open pores between the peloids (Fig. 95A-C). When these structures become cemented and the boundaries between the peloids are obliterated, some porosity usually remains (Fig. 95D-E). To determine the portion of porosity in the speleothems and the ability of capillary forces to moisturize the speleothems, we invented the simple staining experiment of dipping the bottom part of longitudinally cut “muñeco” into ink for one day. The gradual rise of the liquid was then documented by a series of photos. This procedure showed that the ink reached the extreme apical part of the speleothem after several hours, and even its surface became wet (Fig. 96). Interestingly, this simple laboratory experiment explains the field observation of wet speleothem surfaces with drops of water on the tips, in caves where humidity was not excessively high. In some cases, even a small amount of water is sufficient to moisten an entire small speleothem up to 10 cm in height and to provide water to non-encrusted organisms, such as bacteria residing on its surface.

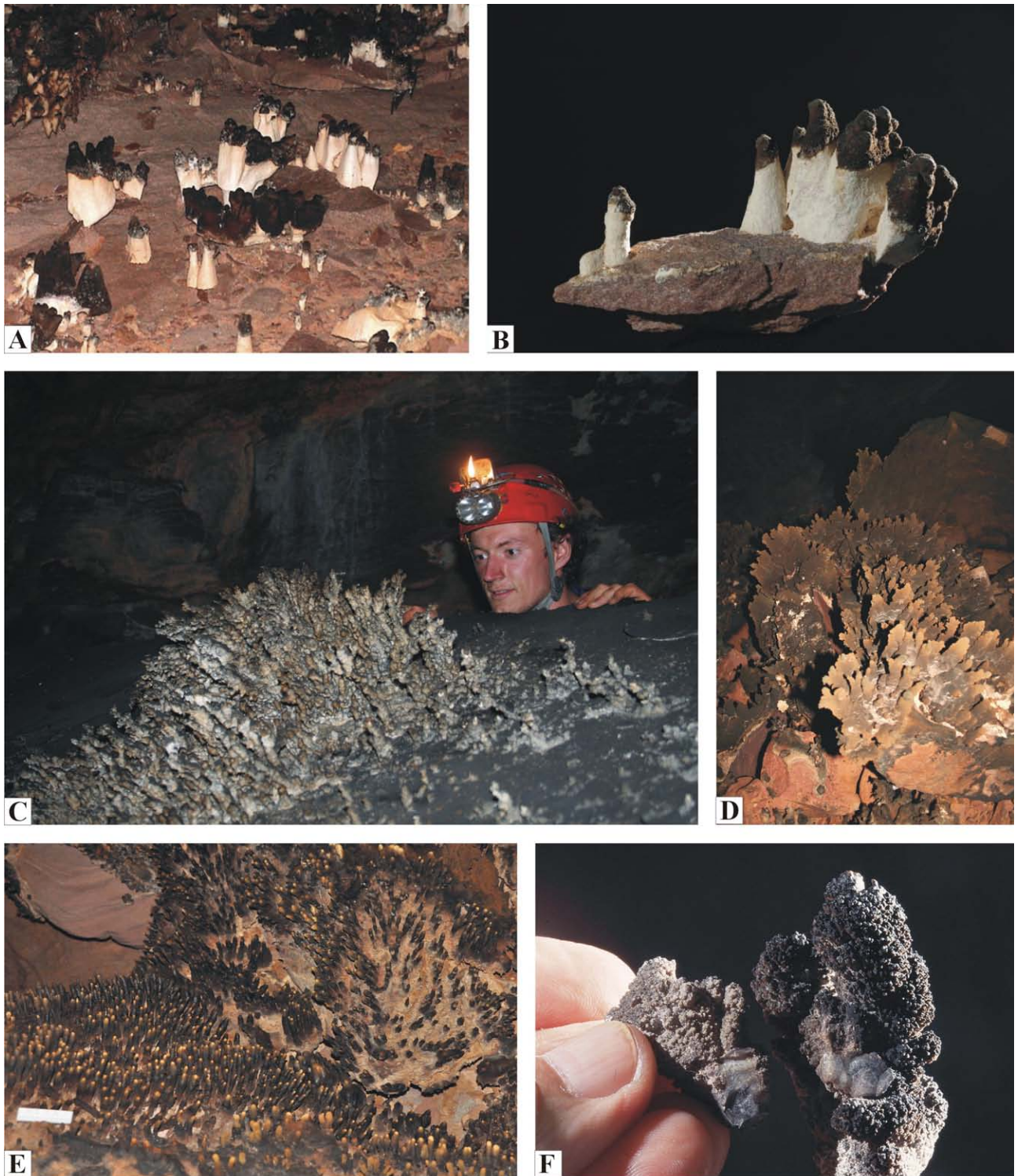


Fig. 81: The most common forms of stalagmitic microbial speleothems: A-B – “Muñecos”. C-E – “Black corals”. F – “Guácimo”. A,B,D,F – Cueva Charles Brewer and C – Cueva Colibrí sectors, E – Cueva Juliana.

Fig. 82: Various forms of champignon-like microbial speleothems. A-D – “Champignons” in Cueva Charles Brewer sector. E – “Champignons” from Cueva Juliana. F – “Champignons” in the Cueva Colibrí sector. G – Some “champignons” are hollow, with thin crusts preserved on top, Cueva Charles Brewer sector. H – An old, well-lithified specimen of a champignon-like speleothem called “riñón” (kidney speleothem), Cueva Charles Brewer sector. This specimen was analyzed and dated by Lundberg et al. (2010).



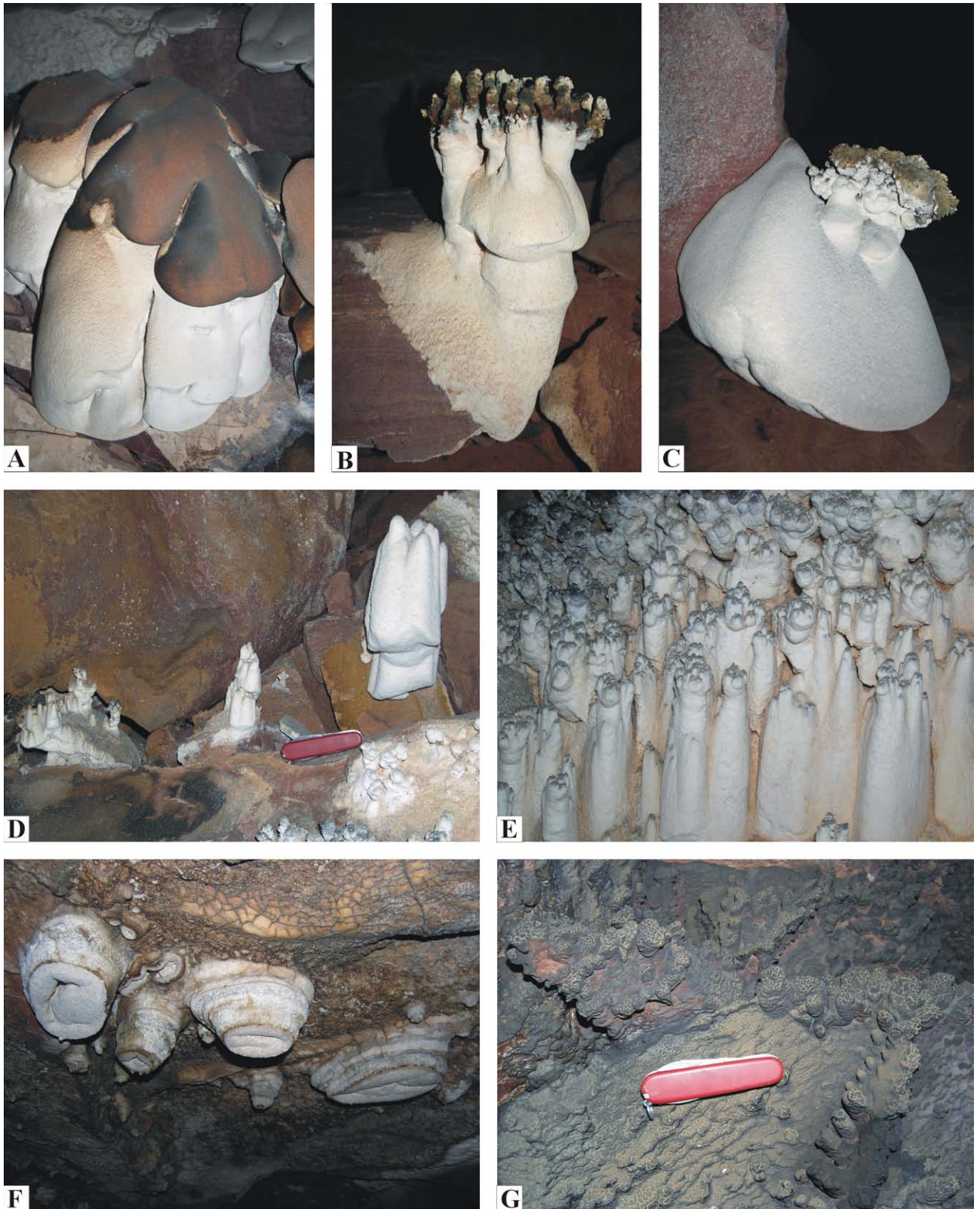


Fig. 83: A-C – Additional examples of mushroom-like microbial speleothems from Cueva Charles Brewer sector. D-E – Ice-cream-like speleothems (“helados”), Cueva Charles Brewer sector. F – Old, well lithified microbial speleothems with shapes of wider truncated cones in Cueva Ojos de Cristal sector. G – Strange microbial speleothems with their surfaces resembling panther-fur pattern, seen in the Cueva Charles Brewer sector.

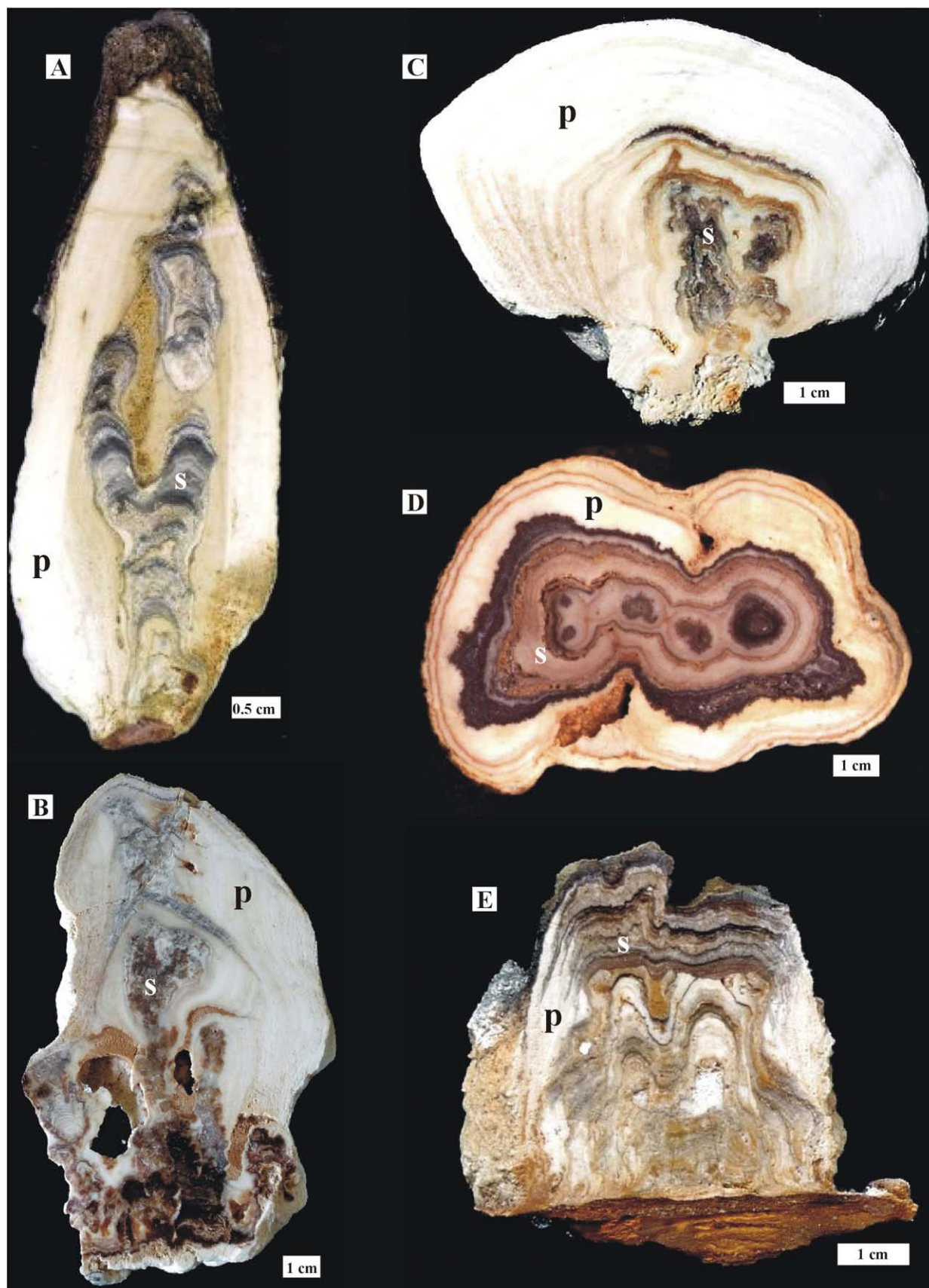


Fig. 84: Slabs showing the internal structure of microbial speleothems from Cueva Charles Brewer sector. A – “Muñeco”, B-C – “Champignons”, D – “Riñón” (the same specimen as in Fig. 82H), E – “Guácimo”. The principal common structure consists of columnar stromatolite (s) formed by filamentous microbes with white, chalky pelloidal stromatolite (p) formed by *Nostoc*-like microbes.

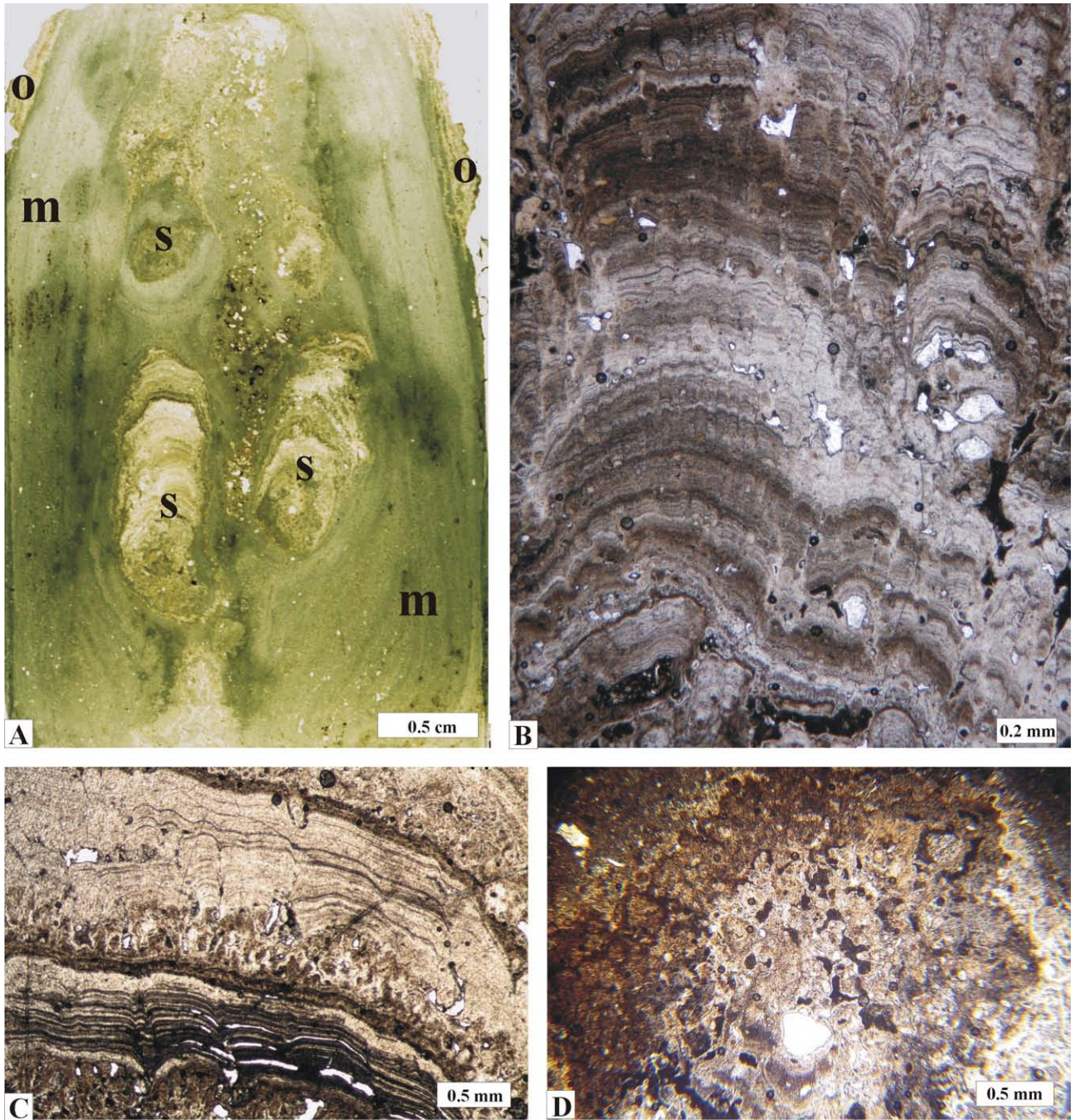


Fig. 85: A – Scanned longitudinal thin-section of the “muñeco” specimen from the Cueva Charles Brewer sector (see Fig. 81A). The zones visible in thin-section are: s – columnar stromatolites, m – laminated peloidal microbialites, and o – outer stromatolitic zone. B – Longitudinal cross-section of the columnar stromatolite. C – Another image of the columnar stromatolite showing alternation of fine laminae of brownish and clear opal. A speleothem with a panther-like pattern on its surface in the Cueva Charles Brewer sector. D – Tangential cross-section of columnar stromatolites showing alveolar-like structure.

The internal structures of peloids are often obliterated by progressive diagenesis and contain less microbial-like structures. The peloid surfaces from the inner, well lithified parts show only tiny irregular spherules (Fig. 97A-B). Internal microbial-like structures can only be identified after scraping away the outer, less silicified zones. A similar observation is apparent in thin section examination of the outer zones. The peloids and also larger spheroidal bodies consist of short microbial

filaments which usually have a uniform cell size, with 1.3-1.4 μm diameter (Fig. 97C-F, 98), although larger cells 1.8-1.9 μm in diameter are sometimes present (Fig. 98C). These cells bear a certain resemblance to heterocysts normally associated with nitrogen fixing *Nostoc*-type cyanobacteria (cf. Fig. 99). The microbial structures can also be observed by SEM, although the inner structure is less clear here due to silica encrustation (Fig. 98D-F).

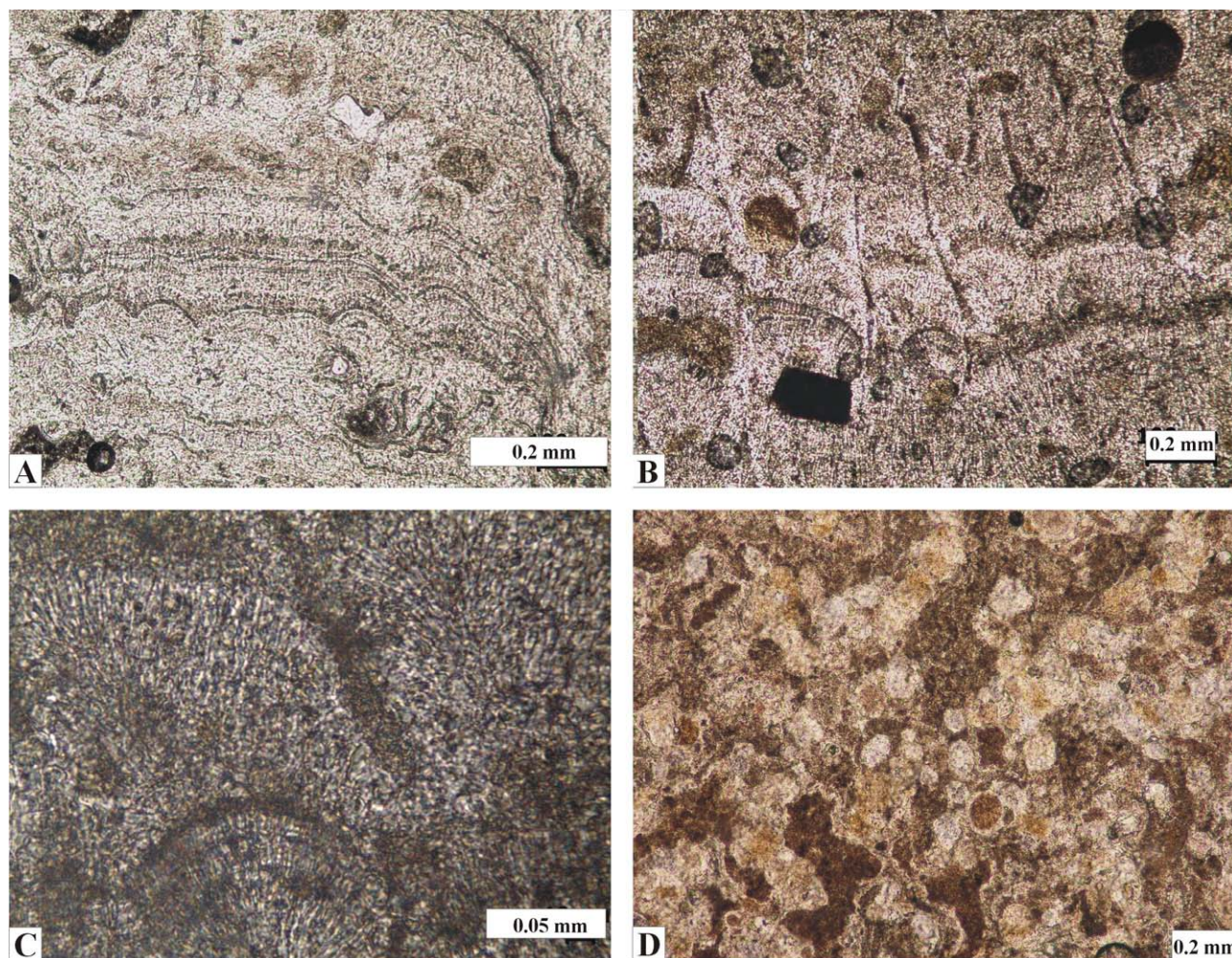


Fig. 86: A-C – Filamentous microbes in the columnar stromatolite visible under higher magnifications. D – Spherical enclosures trapped in the stromatolite. These are most likely of organic origin. Cueva Charles Brewer sector.

White mats on the rock surfaces were commonly observed in both examined cave systems. These represent initial colonization of the surface by the microbes that form the peloidal zones of the speleothems (see previous paragraph). In the initial stages, they form mats (Fig. 100A), shrubs (Fig. 100B-C) and also irregular swarms (Fig. 100D) which cover the underlying arenites. The similarity between this kind of microbe and those from the peloidal speleothem types was microscopically verified (Fig. 100E). While the microbial filaments are commonly encrusted with white silica, the surrounding arenites remain intact. This may be an indication of microbial mediation of the silica precipitation (cf. Aubrecht et al., 2008^b), caused either by microbe metabolism or modified physico-chemical conditions. While such microbial mediated processes can often be observed in limestones, it was unclear if this is also valid for silica precipitation, so this has been widely debated (see overview in Konhauser, 2007).

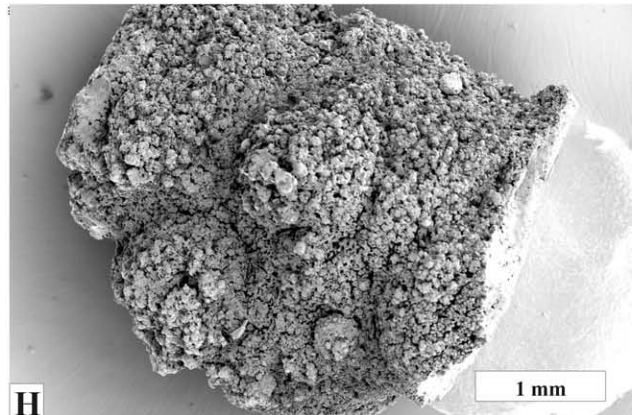
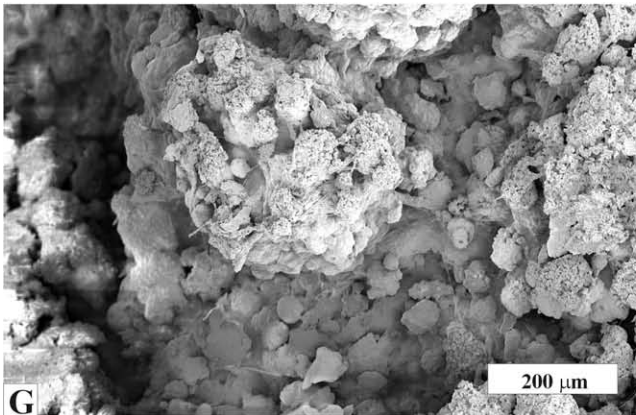
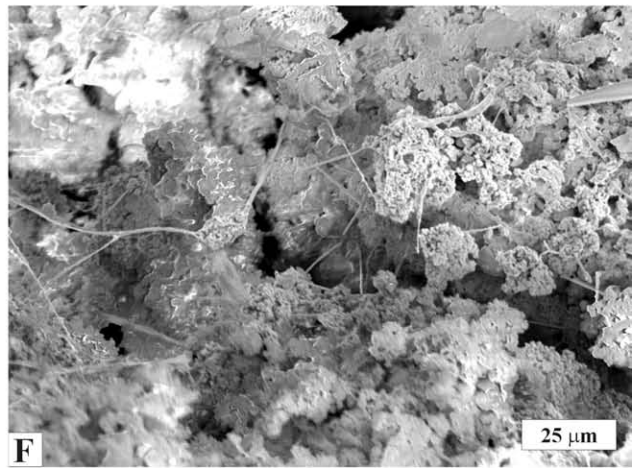
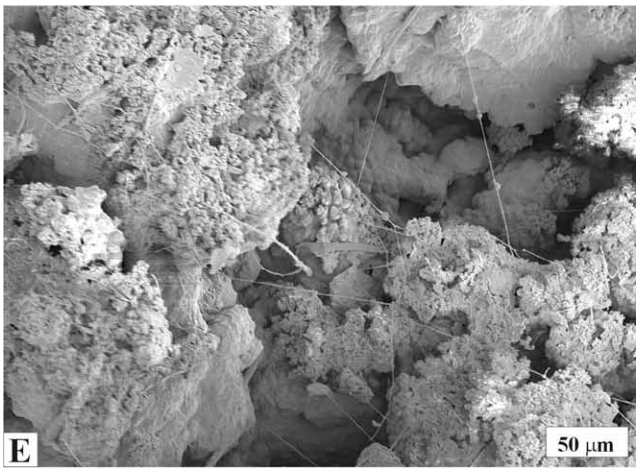
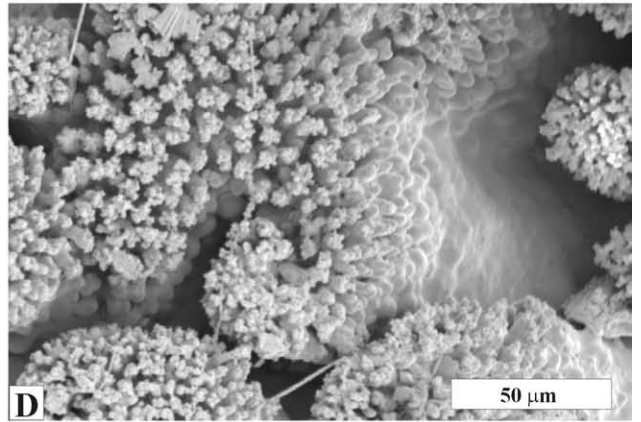
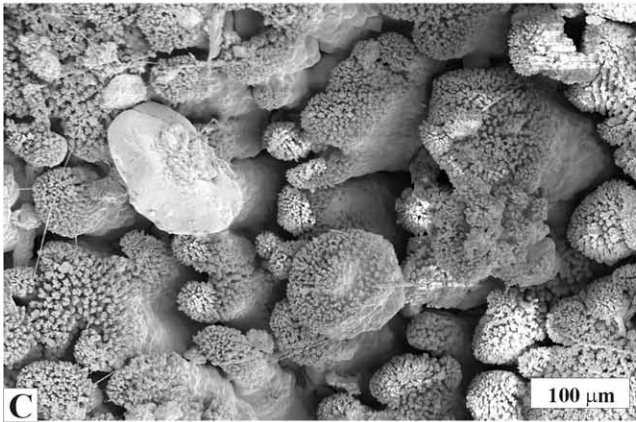
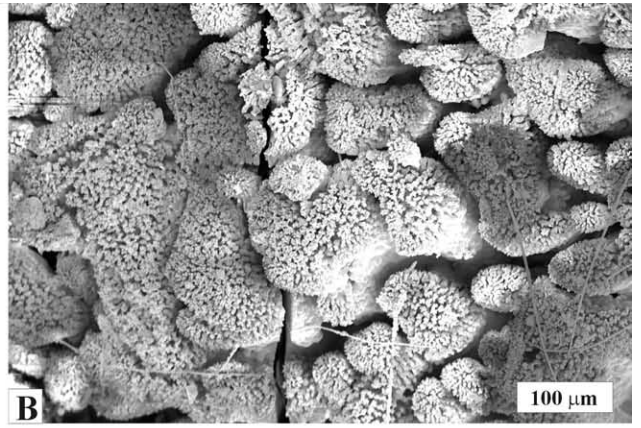
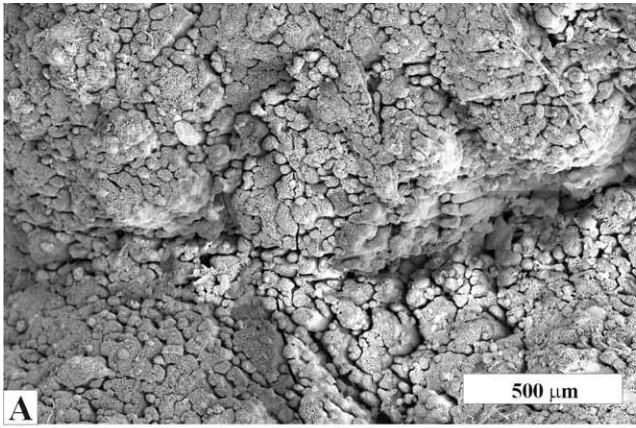
2.7.4. Non-siliceous speleothems

In addition to the siliceous speleothems, a wide range of non-siliceous speleothems, including gypsum, pigotite, evansite,

struvite, taranakite, goethite, sanjuanite and natrolite have been reported in different silicate caves (Webb, 1976; Macías Vásquez et al., 1980; Hill and Forti, 1995; Forti et al., 2003; Vidal Romaní et al., 2010). Some of these can also be observed in both our cave systems. A short overview on currently observed non-siliceous speleothems in the explored cave systems is now provided.

2.7.4.1. “Barro Rojo”

Since the mineralogical composition and macroscopic forms of this speleothem type were covered in the speleogenesis chapter (2.6.), this section concentrates on its microscopic characteristics. Red mud (“Barro Rojo”) stalactites are relatively soft and therefore it is quite difficult to prepare thin-sections from them. In the thin-sections which could be prepared for microscopy studies, the laterite often appears laminated and is either brown or black in colour. Although it was not possible to distinguish any obvious microbial-like forms in these kinds of stalactite samples, microscopy examination of a temporary preparation of an un lithified “Barro Rojo” mud from the Charles Brewer Cave System revealed ubiquitous forms similar to the cell strings seen in the peloidal zones of other speleothems (Fig. 101A-B). In



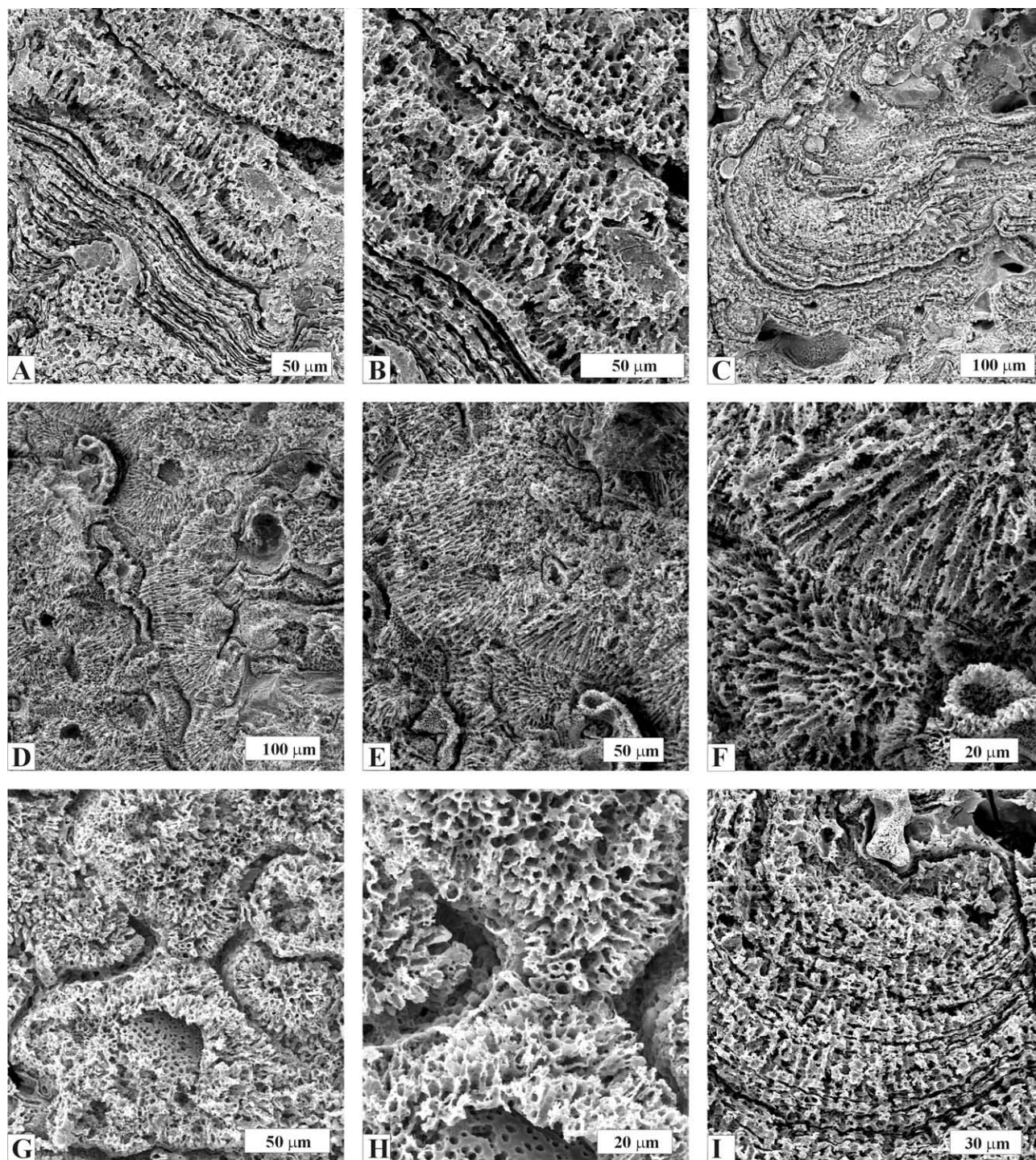


Fig. 88: A-I – SEM views on filamentous microbe casts from columnar stromatolites from the “muñeco” specimen (see Fig. 81A). Cueva Charles Brewer sector.

Fig. 87: SEM images of the surface of “black coral” (Cueva Charles Brewer sector). A – Surface of “black coral” formed by bizarre stromatolitic bodies, possibly representing a surface with protruding filamentous microbes. B-D – Enlarged alveolar surface from the previous photo, resembling tiny coral bodies. Thin spider threads emerging from the speleothem are also visible. E – Another part of the surface of the growing portion of the “black coral” with spider threads emerging from the opal surface. F – Branching fungal hyphae visible on the speleothem surface. These are thicker than the spider threads. G-H – Surface of the growing part of the speleothem formed by agglutinated detritic material.

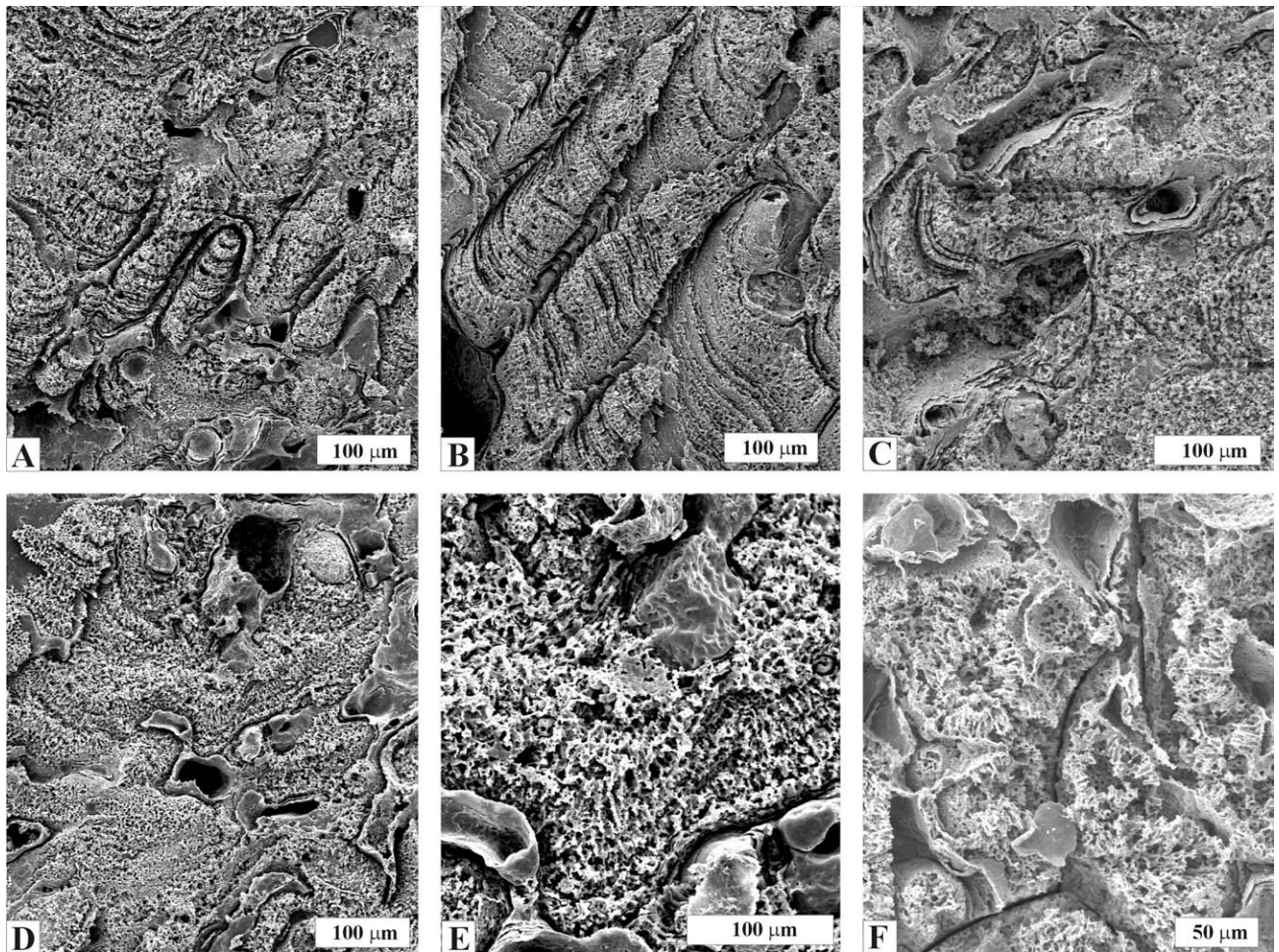


Fig. 89: Filamentous microbe casts from columnar stromatolites in the “muñeco” specimen. Note that some laminae are inorganic, formed by pure silica (C-F). Cueva Charles Brewer sector.

addition to these, numerous thin, green filamentous structures could also be observed (Fig. 101A-D) and the laterite itself forms tiny globules among meshworks of these filaments (Fig. 101C-D). The green filaments appear as small twisted tubes under SEM (Fig. 101E-F), and these remnants' morphology has similarities to stalks of Fe-oxidizing bacteria *Gallionella ferruginea* (see e.g. Ridgway et al., 1981; Kim et al., 2003; Schieber & Glamoclija, 2007; Hofmann et al., 2008). It is most likely that these microbes do not play an active role in the early stages of lateritization such as decaying phyllosilicates and feldspars, but they may possibly become active in the final, iron-oxidizing stages.

2.7.4.2. Gypsum

Gypsum (calcium sulphate – $\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$) is a common cave mineral in all normal limestone caves (Hill & Forti, 1986) but it also occurs in silicate caves (Sanjurjo et al., 2007; Vidal Romani et al., 2010), and has also been reported from arenitic caves on tepuis (Forti, 1994)

Mineral samples which range from the needle to platy or coralloid morphology (Fig. 102A-B) and the fibrous to earthy aggregates sampled in the studied cave systems were subjected to basic mineralogical study based on powder X-ray diffraction.

This study revealed that two distinctive minerals could be distinguished in these samples. The first group includes needle to flat or coralloid-like mineral aggregates which showed a distinctive powder X-ray diffraction pattern. These patterns are typical for gypsum (Fig. 102C). Although various gypsum crystal morphotypes show a large diversity, as discussed above, in most cases all analyzed aggregates appear mono-mineralic (Fig. 102C). Further studies, based for example on stable isotopes, are required to provide a more detailed understanding of these speleothems. Isotopic study of sulphur can reveal its potential source. The examined arenites mostly lack sulphur and there were no signs of hydrothermal activity. On the other hand, presence of biological activity in the cave systems infers that the sulphur may be of biogenic origin.

2.7.4.3. Sanjuanite

The second group of non-siliceous minerals includes needle-like or fibrous to earthy aggregates (Fig. 103A-B), mostly of white colour. According to the X-ray diffraction pattern, they consist of associations of sanjuanite – $\text{Al}_2(\text{PO}_4)(\text{SO}_4)(\text{OH}) \cdot 9(\text{H}_2\text{O})$ and gypsum (Fig. 103C). So far, this mineral has only been detected at a few localities around the world (see e.g. Abeledo

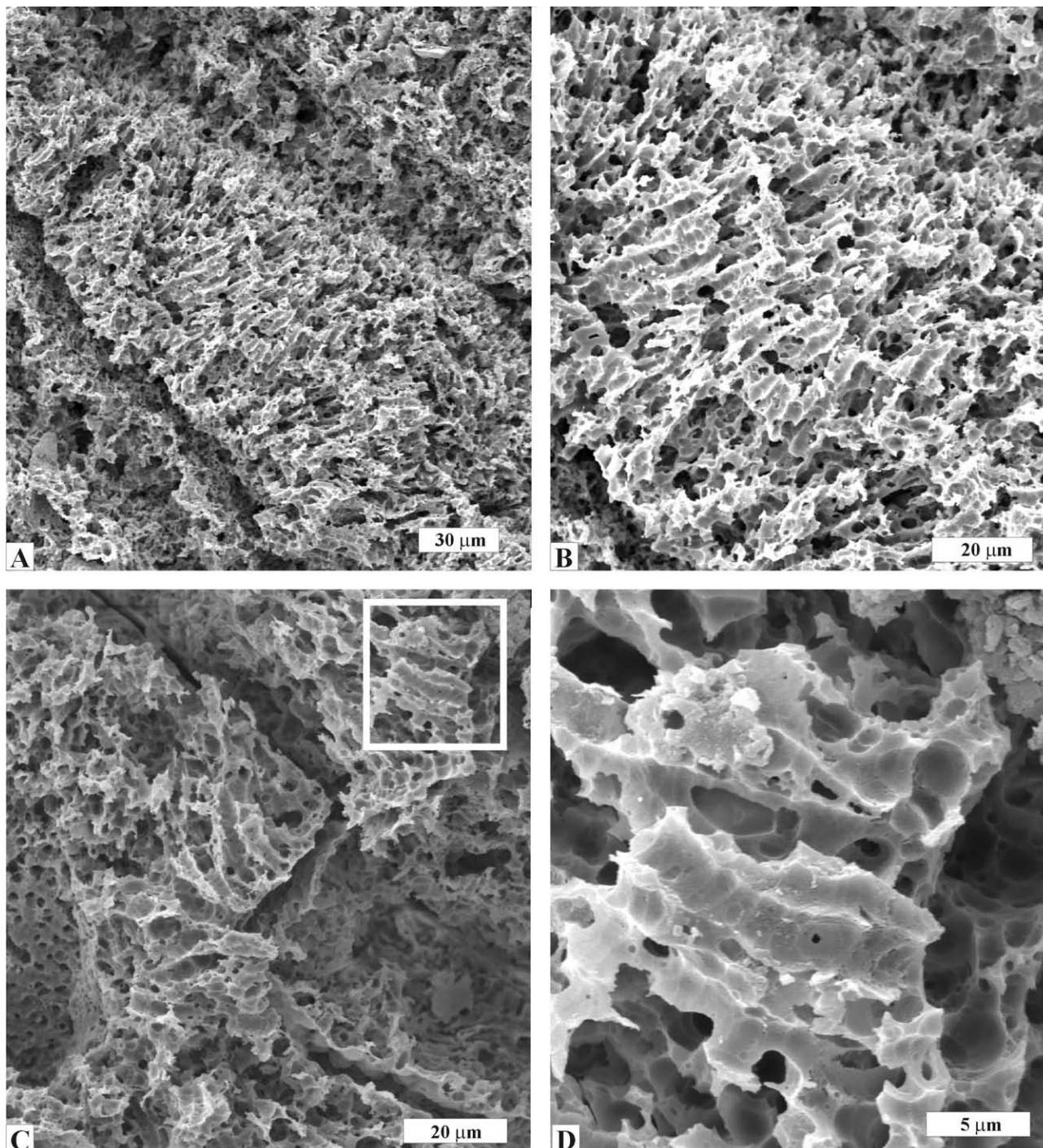


Fig. 90: Details from filament casts showing regular septate structure. Cueva Charles Brewer sector. The white rectangle in C depicts the area enlarged in D. Note that some septae in the casts are oblique to the filament orientation. This is apparent in the centre of D.

et al., 1968 who described sanjuanite from plant-bearing slates located on the ridges of Sierra Chica de Zonda and San Juan Precordillera). The veinlets of sanjuanite are often bounded by thin gypsum layers, and sanjuanite occurs as white, chalk-like compact masses with dull to silky lustre. In comparison, sanjuanite from the arenitic caves appears as white, fibrous or earthy aggregates, which are often friable. The association of sanjuanite and gypsum has also been observed in samples

from the studied arenitic caves (Cueva Charles Brewer, Cueva Colibrí – Charles Brewer Cave System) where they usually appear as small, several centimetre-sized aggregates with sharp boundaries. These aggregates are usually oval and are chaotically distributed in the deeper levels of the caves. Although the main elements of sanjuanite are sulphur and phosphorus, it is almost certain that they do not originate from hydrothermal activity. Instead, it is more likely that these two elements came from

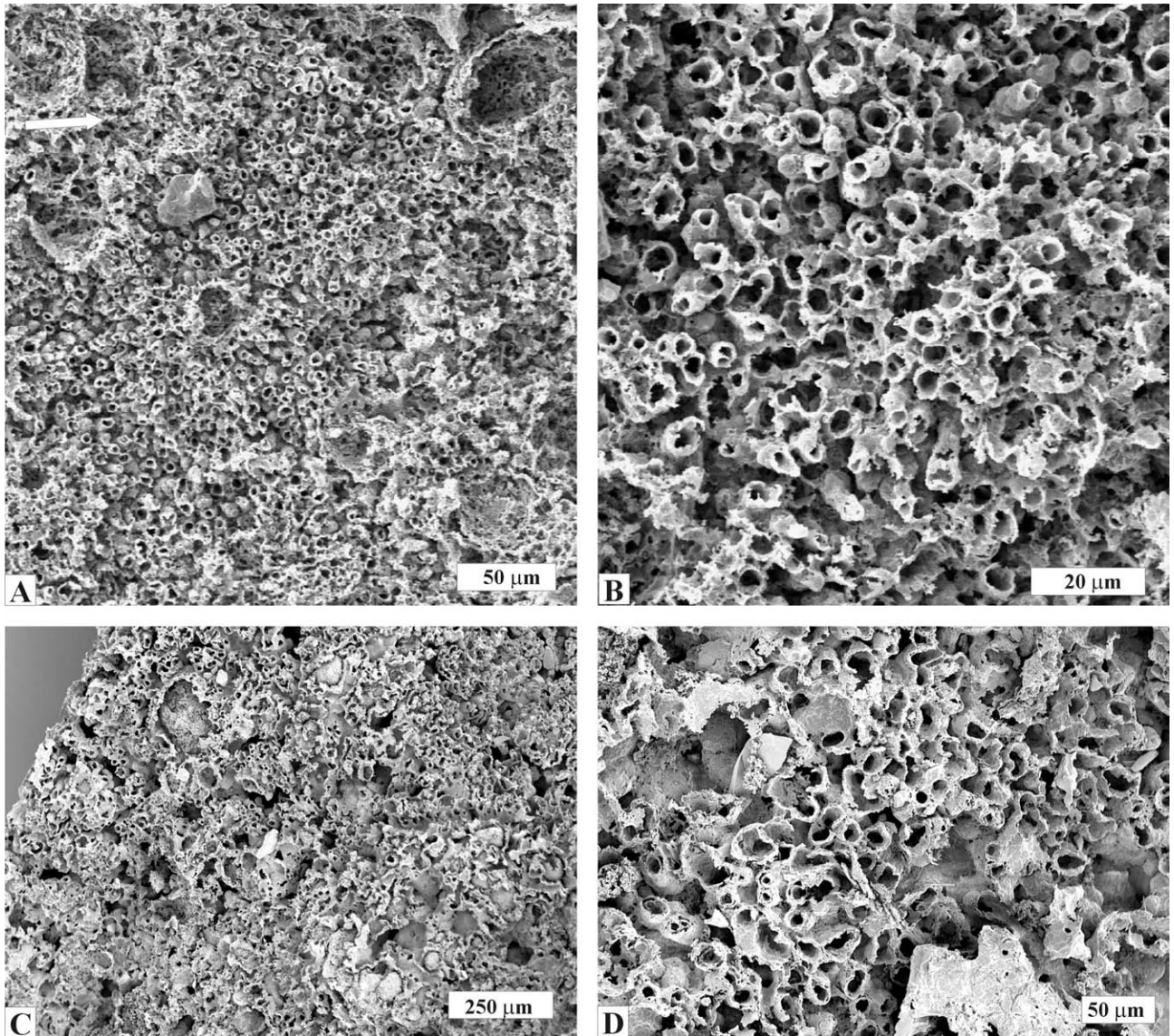


Fig. 91: Irregular double-layered cross-sections of tubes representing casts from different filamentous microbes. "Black coral" (A-B) and mushroom-like speleothem (C-D), Cueva Charles Brewer sector.

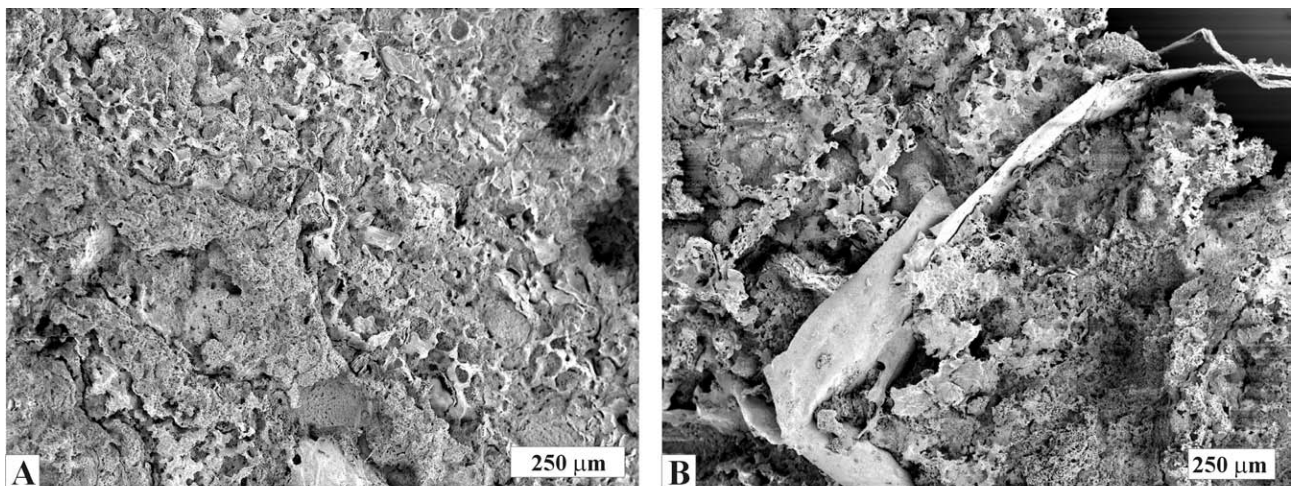


Fig. 92: A – Irregular network structure contributing to the formation of the alveolar zone of the columnar stromatolite. B – Sheet-like structures protruding from the opal. These most likely represent remnants of plant tissue or chitinous insect remains. "Black coral" specimen in the Cueva Charles Brewer sector.

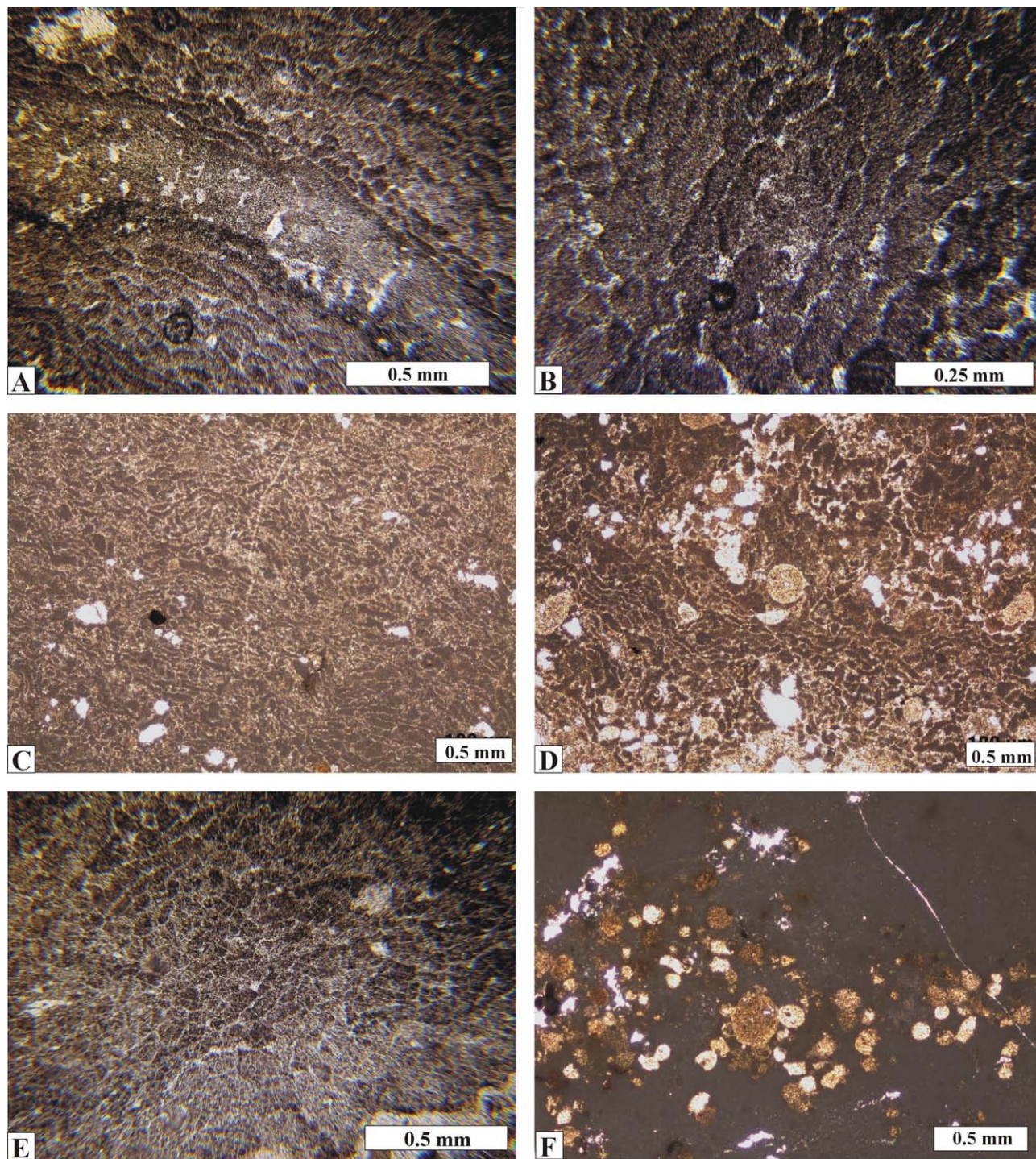


Fig. 93: A – Concentric laminae of peloids in the peloidal zone of the “muñeco” specimen (Cueva Charles Brewer sector). B – Detailed view of these peloids. C-D – Similar peloidal stromatolites are also typical in champignon-like speleothems at Roraima (Cueva de Gilberto sector). E – View of portion of the peloidal zone, with the structure replaced by mud-crack-like appearance in the “muñeco” specimen. Cueva Charles Brewer sector. F – Spheroid bodies in the “champignon”. Together with peloids, these mostly resemble spherical bodies formed by *Nostoc* colonies. Cueva Cañon Verde Cave.

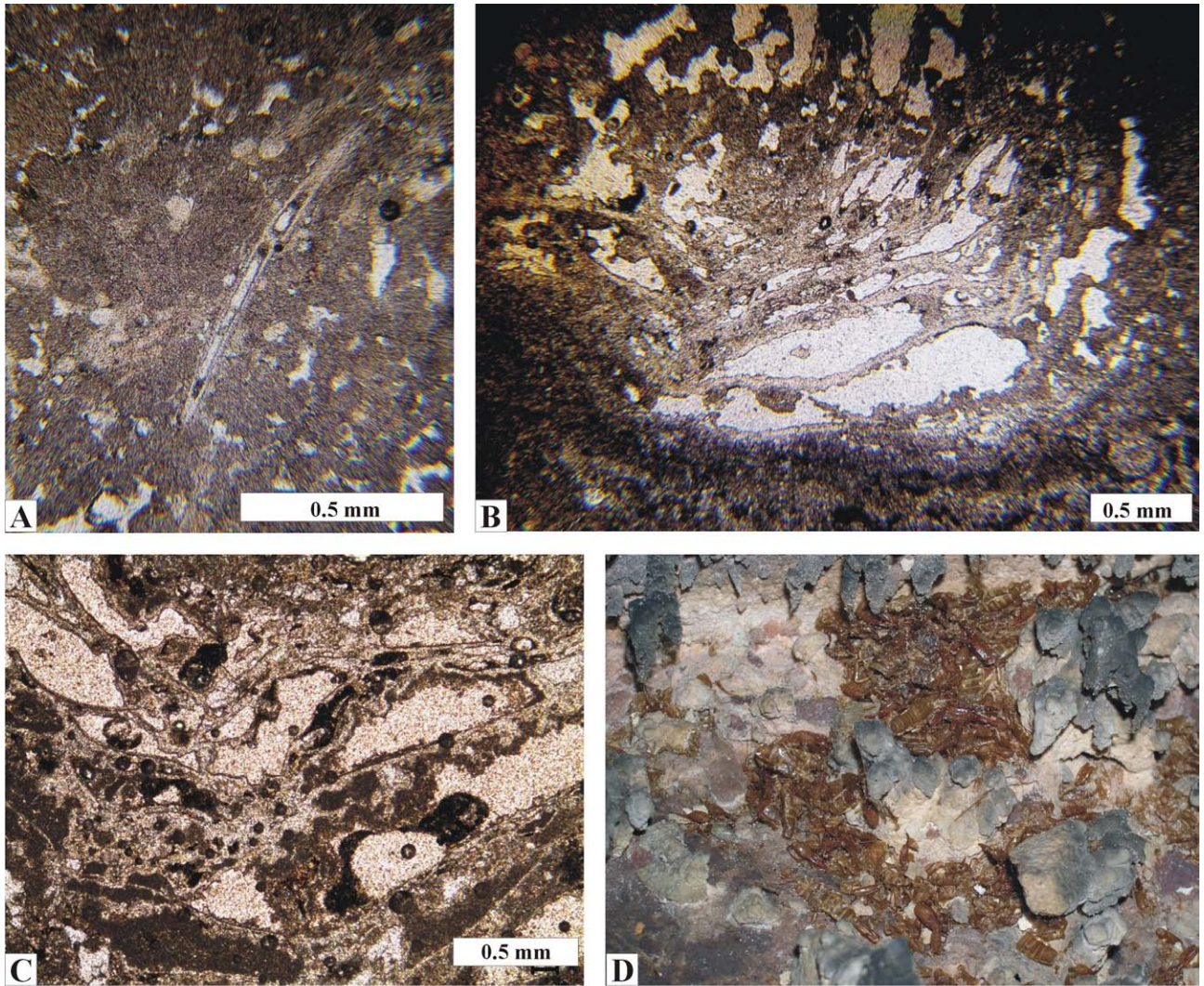


Fig. 94: A-C – Silicified relics of organic structures trapped in the speleothems. These are most likely from arthropods or plants; A-B – “Muñeco” specimen, Cueva Charles Brewer sector, C – Mushroom-like microbial-sandy speleothem (Cueva Ojos de Cristal sector). D – Accumulation of scorpion exuvia encrusted by silica in the Cueva Charles Brewer sector.

organic residues such as guano or from an accumulation of dead animal bodies, such as insects. However, this hypothesis needs further exploration based on a wide field of studies, including mineralogical and geochemical analyses.

2.7.5. Discussion

2.7.5.1. Speleothem size

Siliceous speleothems are ubiquitous not only in Venezuelan caves, such as in the Roraima Supergroup (Zawidzki et al., 1976; Urbani, 1976, 1996; Forti, 1994; Urbani et al., 2005), but also in silicate caves throughout the world (e.g. Webb & Finlayson, 1984; Wray, 1999; Léveillé et al., 2000; Gradziński & Jach, 2001; Willems et al., 2002; Forti et al., 2003; Urban et al., 2007; Vidal Romani et al., 2010). Although the silicate speleothems in the Venezuelan cave systems are rather unique, they show certain resemblances to other silicate speleothems, and particularly to the coralloid speleothems first described

by Swartzlow & Keller (1937). However, the greatest majority of siliceous speleothems currently described in silicate caves outside Venezuela have been rather small specimens, and they mainly represent flowstones several millimetres thick. The only exception so far is the 28 cm opal column from Bilemat Kul lava cave in Korea (Hill & Forti, 1986: p. 105). In contrast to silicate caves in other parts of the world, the siliceous speleothems in the Cueva Charles Brewer sector, for example, often exceed 10 cm in length and can reach up to 50 cm. Although the speleothems from the Ojos de Cristal Cave System are somewhat smaller, usually not exceeding 10 cm, they are still larger than the average speleothem size in silicate caves in other parts of the world. A quite plausible explanation for this difference in size between the silicate speleothems in the Charles Brewer and Ojos de Cristal cave systems compared to other world silicate caves could be that these two Venezuelan caves are currently the largest described sandstone cave systems on Earth. Logically, the large cave size will be able to

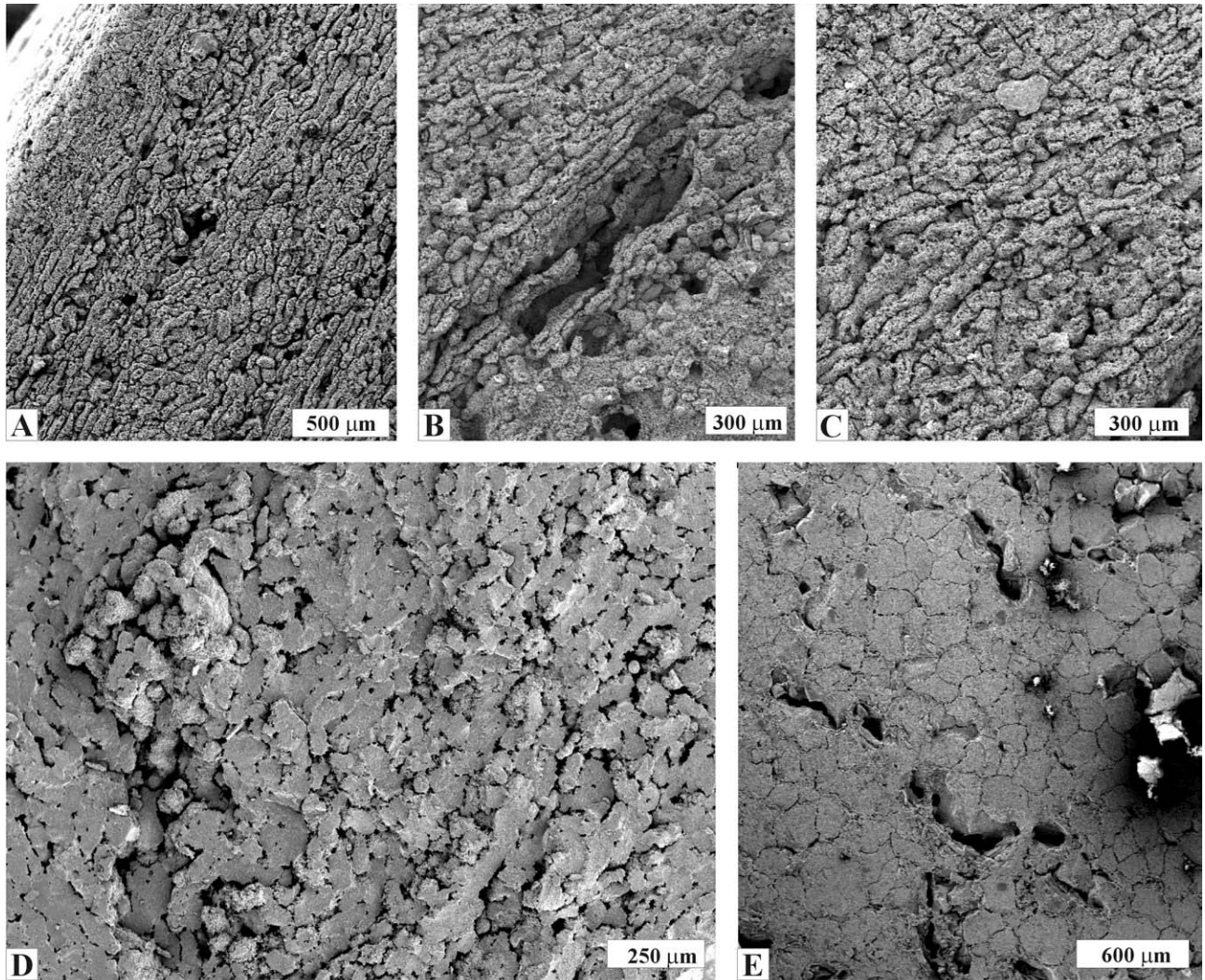


Fig. 95: A – Etched surface of the “muñeco” specimen revealing the peloidal layer. These peloids and the porosity between them are well preserved, but the microbial structures are obscured. Cueva Charles Brewer sector. B-C – detailed view of the previous sample. D – Part of the peloidal layer underwent stronger opal cementation, but its considerable porosity is still preserved. “Black coral” in the Cueva Charles Brewer sector. E – Part of the stronger lithified peloidal stromatolite, with deformed peloids which resemble mud-cracks in cross-section. Cueva de Gilberto sector.

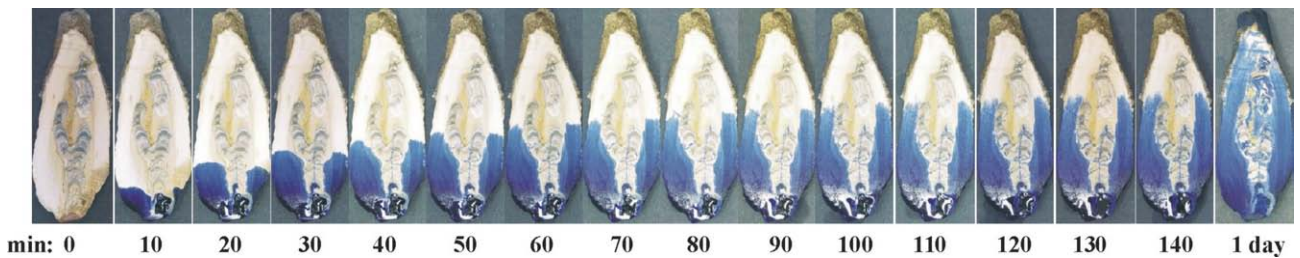


Fig. 96: Results of experiments from staining the “muñeco” slab with ink. It is obvious that the liquid is able to penetrate the pores in the peloidal layer by capillary force to the height of the speleothem’s apical portion. Only the central columnar stromatolite, mostly formed by compact silicite, remained less coloured. Cueva Charles Brewer sector.

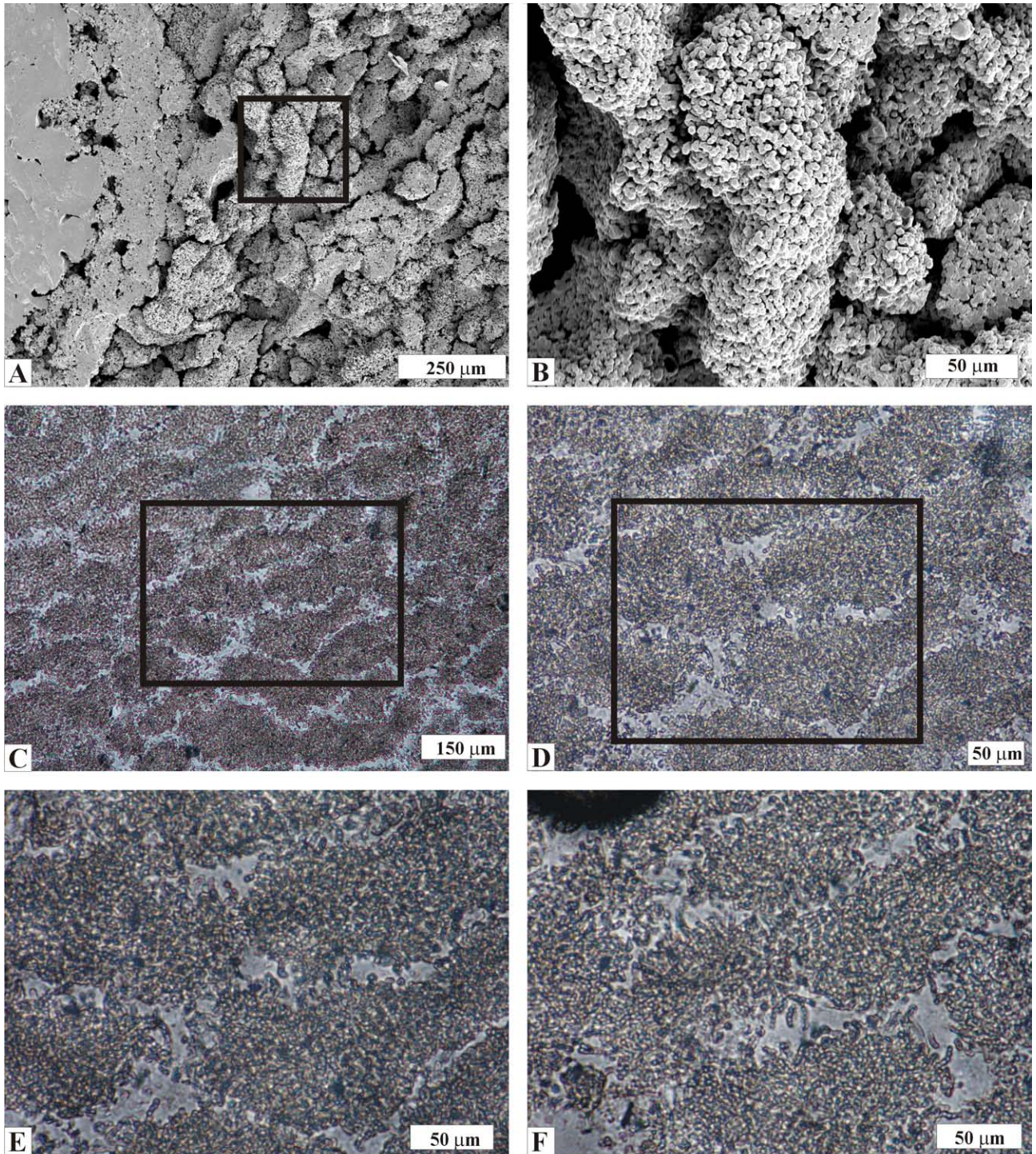


Fig. 97: A – SEM images of the peloidal layer of the “black coral” sample showing loosely packed ovoidal peloids. The rectangle marks the portion enlarged in the next photo. Cueva Charles Brewer sector. B – Enlarged view of the peloid in the previous photo. Irregular tiny spherules are visible on its surface. C-E – Gradually enlarged views of peloids from the outer layers of the “champignon” specimen (Cueva Charles Brewer sector) revealing microbial structure of peloids. These peloids are formed by short-filamentous microbes which have a meshwork arrangement. F – A further enlarged view of these peloids.

provide larger volumes of dissolved and re-precipitated SiO_2 over a period of time. However, more detailed future studies are required to confirm if there is a significant correlation between cave size and speleothem size. Despite these large cave dimensions, the growth rate of various types of siliceous

speleothems, including the microbial speleothems, is very low. Lundberg et al. (2010^a) concluded that the maximum growth rates of speleothems are 0.37 ± 0.23 mm/ka. This indicates that approximately 270,000 years is required for a speleothem to reach a height of 10 cm!

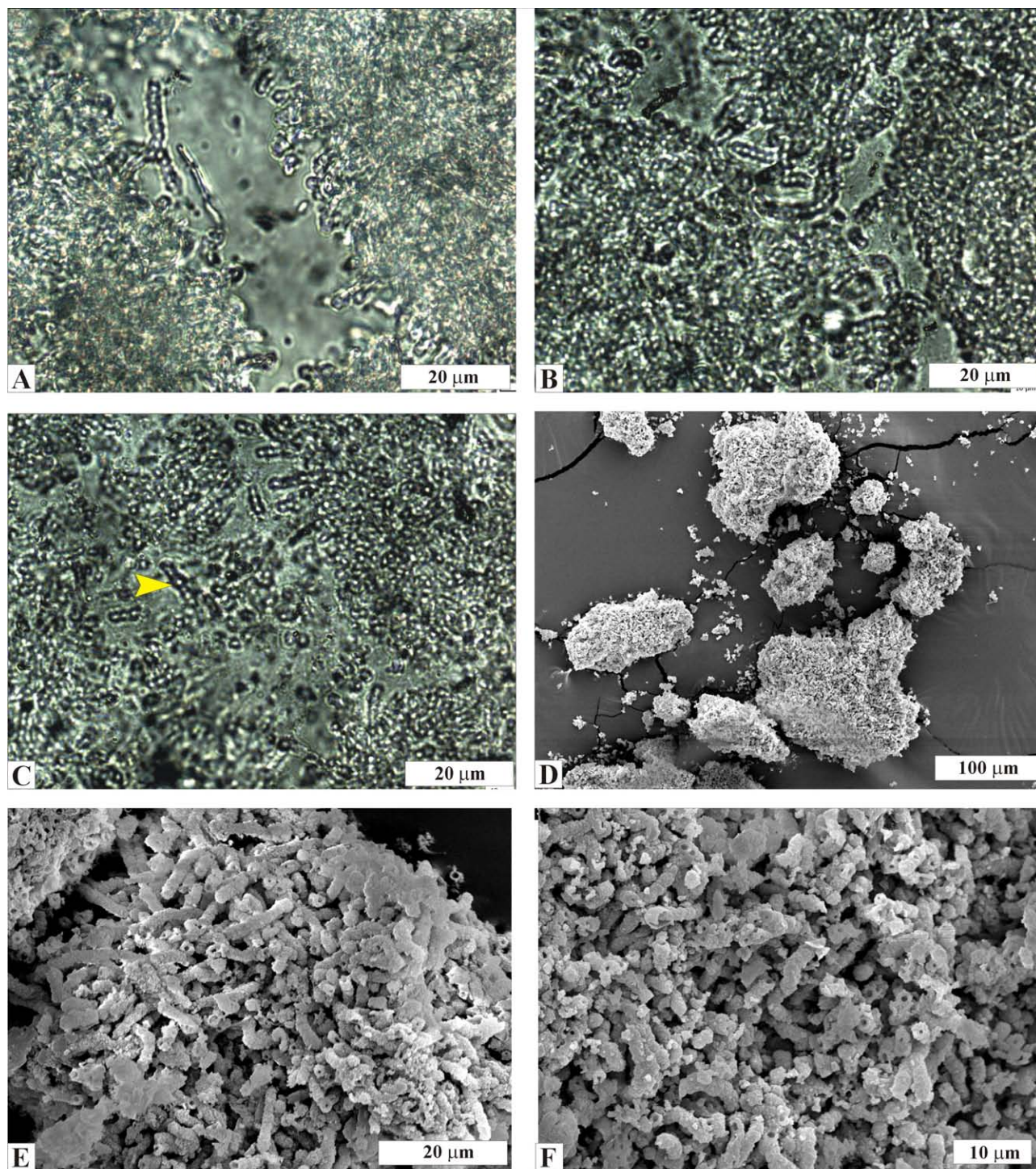


Fig. 98: A-B – Strongly enlarged thin-section views of the peloids from the outer zones of the “champignon” specimen, showing detailed appearance of the microbes. Cueva Charles Brewer sector. C – Similar view, revealing also some enlarged cells (heterocysts) in some microbial strings (yellow arrow). D – SEM view on the detached peloid from the outer zone of the “champignon” specimen. E-F – Details of the previous sample revealing meshwork of the microbial filaments. However, the inner structure of microbes is not visible under SEM.

2.7.5.2. Sources of silica

Four principal types of natural sources contribute silica compounds to speleothem formation. The two following can be regarded as primary; subterranean rivers and water seeping from the surface, while two additional sources can be derived from

these: water spray and condensed moisture on cave walls. Our current hypothesis is that the two latter sources serve as the main agents for distribution of silica to the speleothems, since most of them are beyond the reach of flowing water, and dissolved silica concentration in subterranean streams and seeping waters

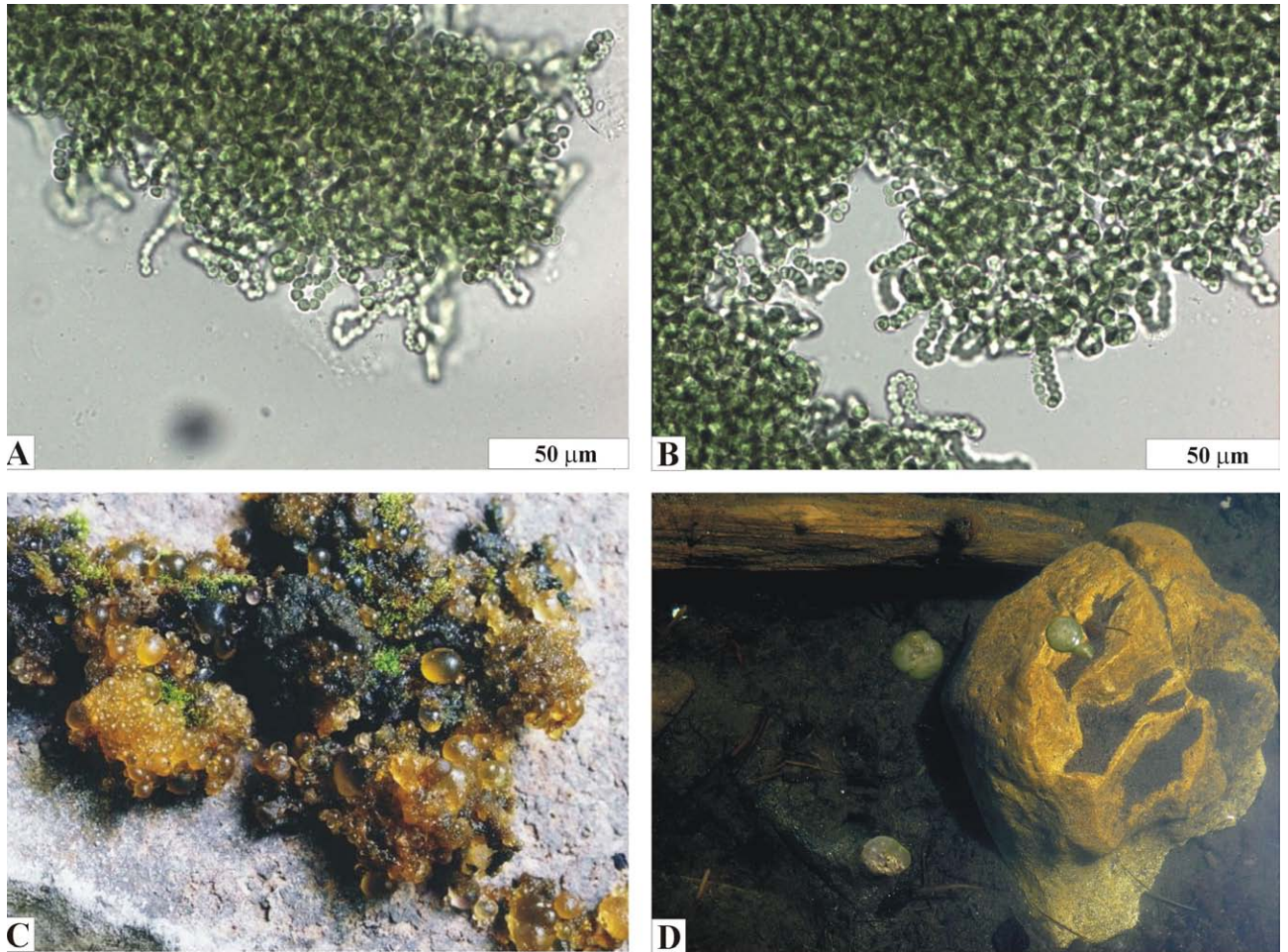


Fig. 99: Images of living *Nostoc* colonies for comparison purposes. A-B – Normal soil *Nostoc* colony cultivated in lab (compare it with Fig. 98A-C). C – Macroscopic view of spherical *Nostoc* colonies. D – Spherical *Nostoc* colonies in Laudachsee Lake, Austria.

is quite low (see Ipiña, 1994; Láncoz et al., 2007; Aubrecht et al., 2008^b, 2011; and section 2.5. in this volume).

This hypothesis is further supported by hydrogeochemical analysis of the small pools of dripping condensed water. This showed that despite low overall concentrations of dissolved substances, silica concentration there is considerably higher than in all other measured water sources (see the hydrogeochemistry chapter; section 2.5. herein). Based on this, we propose that the mechanism for the speleothem development is initiated by a “hydrocorrosive action” of the condensed water on surfaces, which will then induce a regular release of sand grains over a period of time. These sand grains are then transported via droplets or small streams of this water onto the speleothem surfaces irrespective of whether these are dripstones or erected forms. This hypothesis may provide a simple explanation for several mysterious phenomena, such as why so many sand grains can be found on the speleothems (some of these might even have been formed via agglutination of sand grains), and why so many speleothems can be found even under the ceilings of large galleries. This is also a proof that “arenization” is really present, but only in mature stages of the speleogenesis. Another possible strong silicifying agent could also be the water released from

lateritization, as indicated by analysis measured in pools which are formed in “Barro Rojo”.

Although generally undersaturated with respect to SiO_2 , the primary water flowing and seeping from the surface can also be an important source of silica as evaporation occurs. Generally, silicification can result from evaporation of any kind of water, regardless of how high the initial concentration of dissolved silica is. Evaporation modifies the cave waters’ hydrochemistry significantly, so that the concentration of dissolved compounds can increase in the small isolated pools over a period of time. This evaporation can then also act on the speleothems themselves. The dye experiment reported in section 2.7.3. herein showed that the peloidal layer can serve as an excellent conduit for water and that capillary forces are strong enough to provide moisture to most of the speleothem volume, even when only a small volume of water is available (Fig. 96). This moisture can therefore not only support growth of microbial mats, but its evaporation from speleothem surfaces also causes precipitation of SiO_2 over a period of time.

Fine water spray and aerosols which pervade the caves’ atmosphere can also provide an equally perfect source of silica. These aerosol droplets cannot be observed with the naked eye but they can be revealed on photographs using a flash light (Fig.

104). Evaporation of tiny spray droplets can greatly increase the silica concentration, and this process is most likely the main contributor to the development of the “cobweb stalactites” (see also section 2.7.2.3.). The fine structures of these special stalactites with tips inclined towards the air draught imply that their encrustation was not due to the seeping water, but rather to aerosols because seeping water would have made the cobwebs so heavy that they would have hung more vertically from the ceiling.

2.7.5.3. Geomicrobiology

During the last decades, concepts of the potential role of different types of organisms in caves expanded significantly. These include micro-organisms, and also macro-organisms such as fungi and smaller animals. Although it is acknowledged that some types of organisms and communities have contributed significantly to cave developmental processes, including the formation of speleothems, our knowledge of these processes remains extremely limited (Lee et al., 2012).

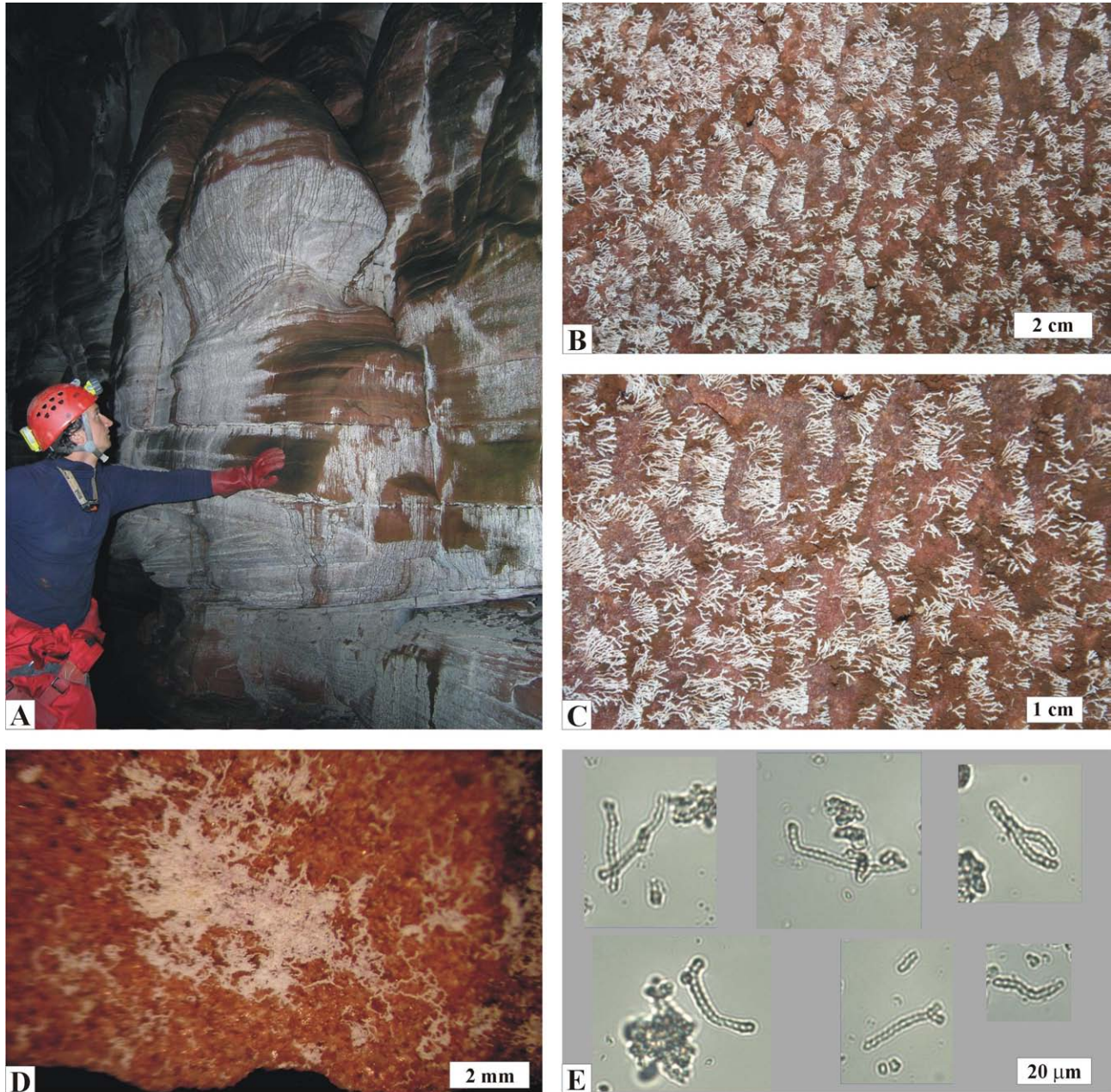


Fig. 100: A – Silica-encrusted microbial mats represent the initial microbial colonization on the cave walls. Cueva de los Pémones sector. B-C – Detailed views of the initial microbial colonization of the rock substrate. The microbes are arranged in regular shrub-like formations. Note that the white coloured silicification affected only the microbes, and not the surrounding quartzite. Cueva Cañon Verde. D – Another view of the initial microbial colonization, lacking regularity in its filament arrangement. Cueva Charles Brewer sector. E – Collage of microphotos of the microbial cell strings from the microbial mat highlighted in the previous photo. The filaments strongly resemble those in the outer layers of the “champignon”.

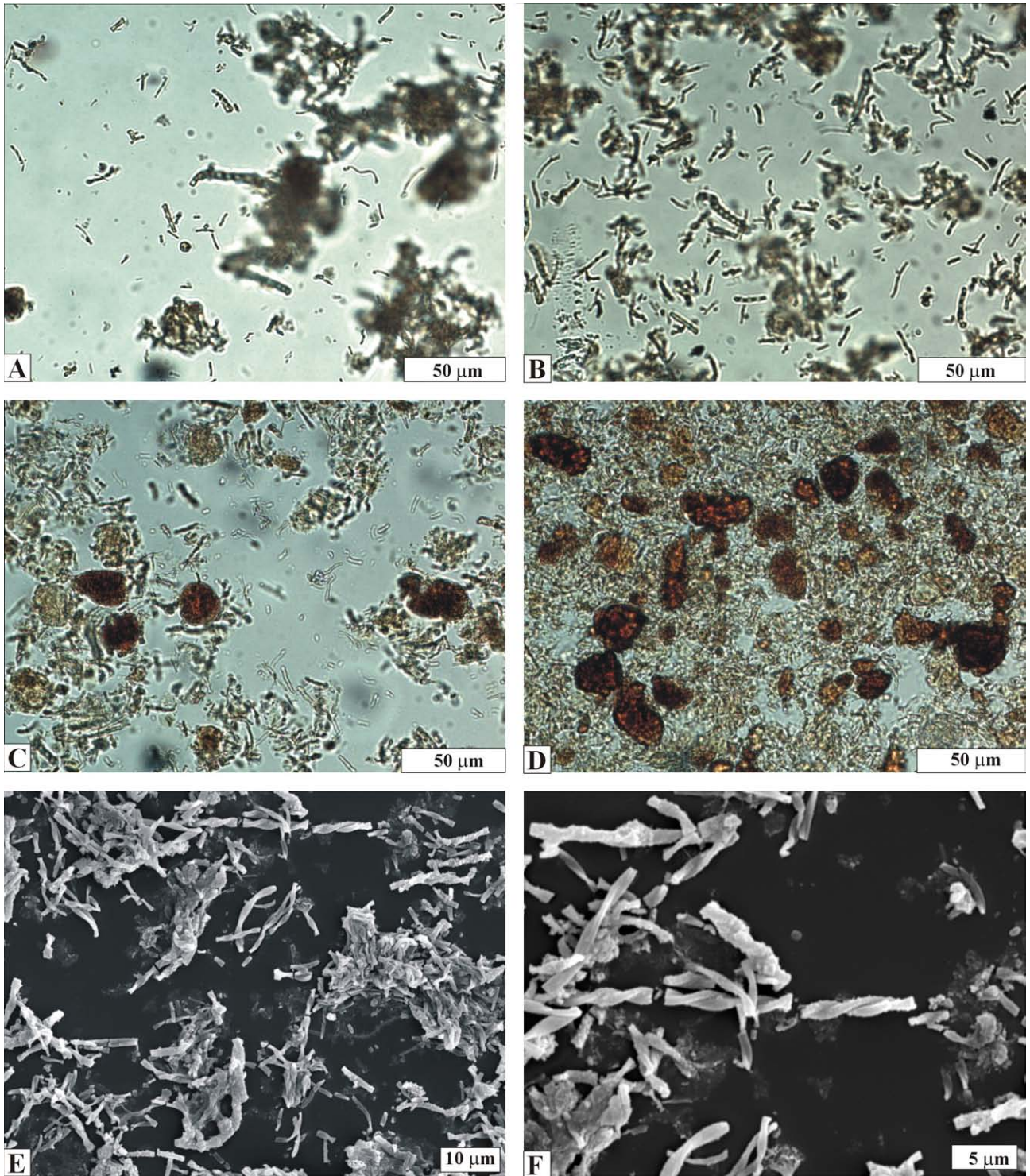


Fig. 101: Microphoto and SEM images of the "Barro Rojo" sample (Cueva Charles Brewer sector). A-B – Some enlarged photos reveal the presence of microbial cell strings similar to those in Fig. 100E). C-D – The main portions of this sample show a mixture of lateritic red globules and short, thin greenish filaments. E-F – SEM view of the greenish filaments. The filaments have the appearance of twisted tubes, similar to the stalks in *Gallionella ferruginea* Fe-bacteria.

Many of the speleothems observed in the Charles Brewer and Ojos de Cristal cave systems appear to contain or be associated with several forms of organisms. These range from various metazoan species, including spiders and insects which can be observed directly with the eye, to various other morphological types of

microorganisms. These latter types span from multicellular formations such as filamentous bacteria to single coccoid or rod-like cells which may or may not be aggregated. Their precise role is not currently understood, especially whether they contribute to speleothem formation, and if so, do they play an active role, or

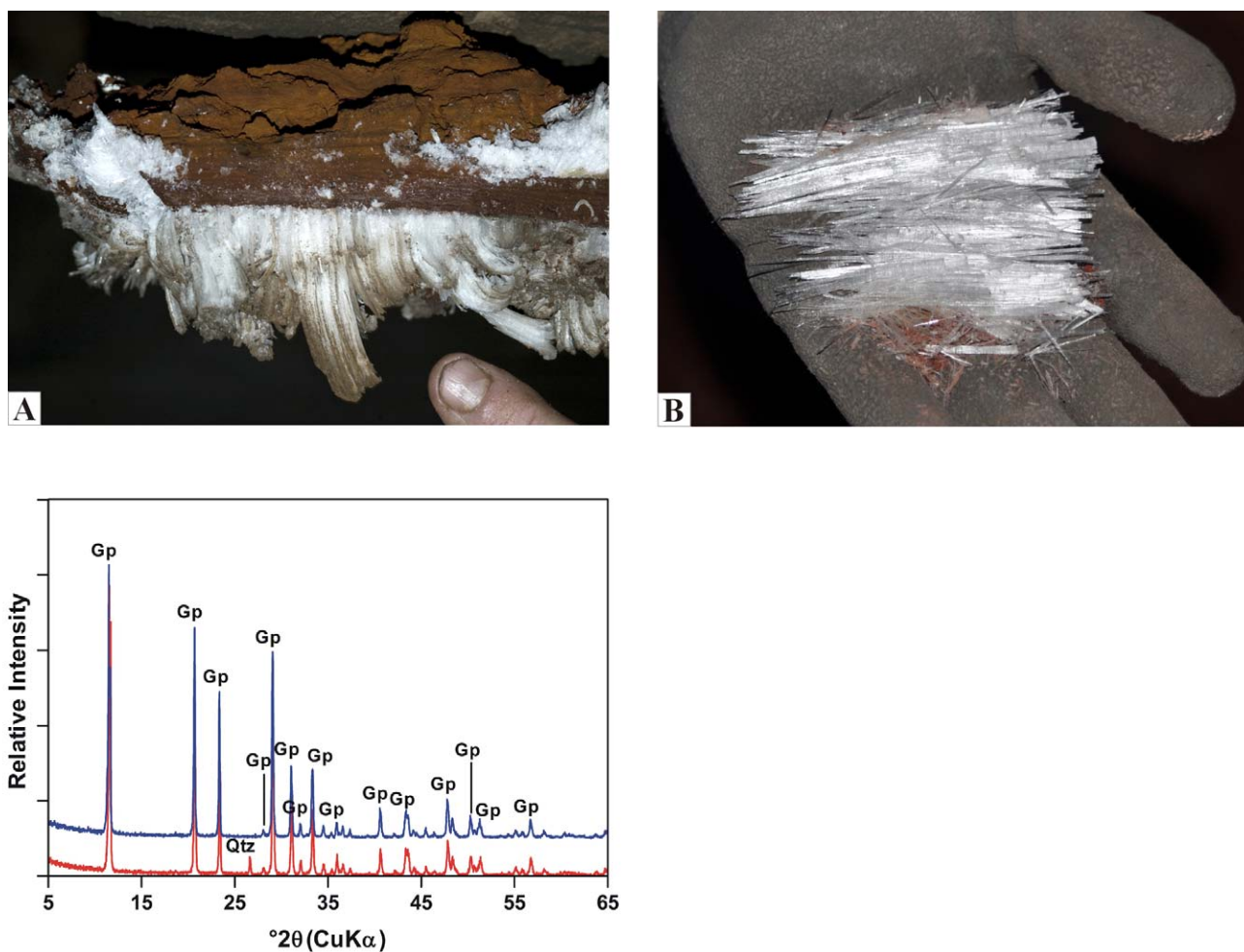


Fig. 102: A-B – Gypsum aggregates from the Cueva Charles Brewer sector. The gypsum needles are approximately 10-12 mm long. C – X-ray powder diffraction patterns of the fibrous to earthy aggregates composed of gypsum. Quartz was detected in significantly lower quantities.

they are only coincidentally associated with the speleothems? Irrespective of this, many speleothems in the Charles Brewer and Ojos de Cristal cave systems have recently been termed “biospeleothems”, due to the unusually high number of organisms in or around them (see the section 2.7.3.). Interestingly, similar observations and speculations have been made about at least some of the siliceous speleothems observed in other parts of the world. Some of those studies have clearly 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 concerning their microbial composition. Unfortunately, the few performed studies have used various approaches, so it is difficult to make systematic comparisons or to currently draw any indisputable general conclusions about the geobiology of siliceous speleothems.

The first microbiological study of opal speleothems in sandstone caves was performed on those in caves on Sarisariñama (Cueva de los Guácharos – Kunicka-Goldfinger, 1982). Here, only classical methods were applied to the organisms which could be cultured. However, although approximately only 1 % of all bacteria in the environment are culturable and only limited information was available from these classical methods, several interesting

results were obtained. The four types of physiological groups involved were; i) heterotrophic bacteria such as *Arthrobacter*, *Corynebacterium*, *Bacillus* and *Pseudomonas*; ii) nitrogen-fixing species including the *Azotobacter*; iii) cellulolytic species such as *Cytophaga*; and iv) autotrophic bacteria including nitrifying species and the sulfur oxidizing species *Thiobacillus ferrooxidans*. Although no in situ studies were performed to confirm the function and explore the extent of the various physiological processes, the results in this study do at least support the indication that the main trophic mode of life of Cueva de los Guácharos microbial communities appears to be adapted to decaying bat and bird excrements and fruit remnants from their diets. However, these results cannot be used to explore further detailed hypotheses about their potential role in cave speleogenesis.

Several studies have also reported different types of phototrophic organisms, such as diatomaceans and cyanobacteria, in certain types of siliceous speleothems and opal sinter deposits in hot springs and geysers (Jones et al., 2001b; Konhauser et al., 2001, 2003) in other parts of the world. These occurred, for example, in caves of Japan and USA, where speleothems were located close to the cave entrance (Kashima et al., 1987; Kashima and Ogawa, 1995).

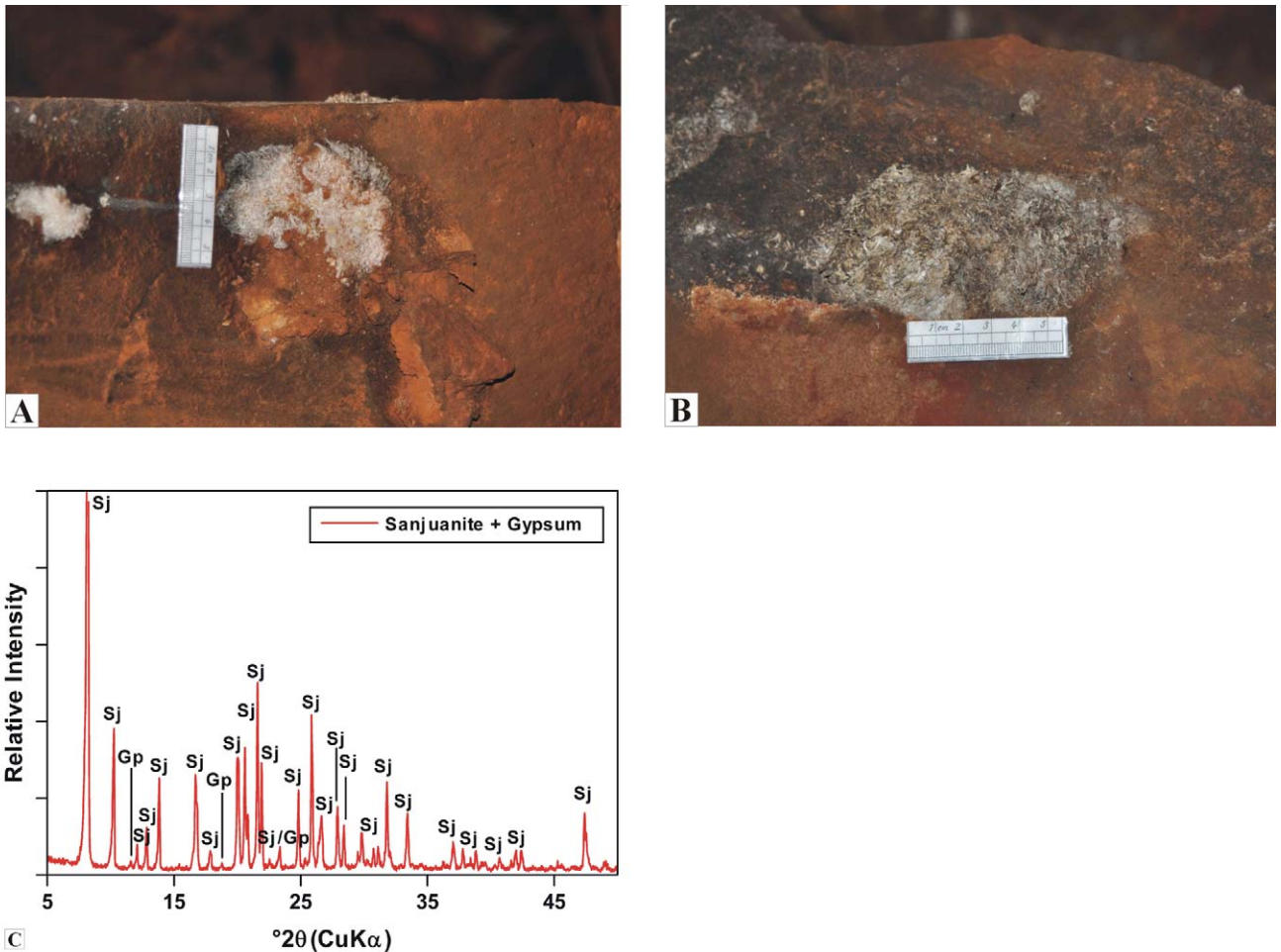


Fig. 103: A-B – Sanjuanite aggregates from the Cueva Colibrí sector. C – X-ray powder diffraction pattern of a sanjuanite sample. In addition to sanjuanite, gypsum was also detected in the mineralogical composition of the white earthy and fibrous aggregates.

The most recent study employing modern molecular methods on siliceous speleothems in the Ojos de Cristal Cave System on Roraima (called there Roraima Sur Cave) was performed by Giarrizo et al. (2009). A large range of different types of 16S rRNA gene sequences affiliated to various bacteria groups were examined in this study. Although the function of some of these groups is unknown, there were also the following groups which showed affiliation to bacterial groups with known function, such as hydrogen and methane oxidizing bacteria (*Methylocella*, *Methylosinus* and *Methylocystis*), different bacterial species involved in the nitrogen cycle, heterotrophs which degrade complex organic substrates such as *Rhodospseudomon*, iron oxidizing bacteria (*Rhodomyrobium*), anoxygenic phototrophic species including *Oscillochloris* and also the neustonic species including *Nevskia*, which trap compounds such as ammonia directly from the air. Although more detailed studies are needed to explore the function and activity of the various groups detected so far, it is obvious that bacteria involved in the nitrogen cycle form one of the most important parts of the ecosystem, since nitrogen is an essential element for all organisms. The bacteria involved in the nitrogen cycle in the Ojos de Cristal Cave System involve both nitrogen fixing bacteria (*Rhizobiales*) and different types of

nitrogen oxidizing bacteria (ammonia, nitrate and nitrite oxidizers, including representatives of *Planctomycetales*). Although this indicates that the ecosystem there is extremely complex, none of the currently detected microbial groups can be assigned with certainty to any direct involvement in silicate speleogenesis or the speleothem-forming process.

Our microbiological research has focused mainly on different types of microscopical analysis enabling elucidation of detailed morphological characteristics within and between some of the various speleothems described in the Charles Brewer and Ojos de Cristal cave systems. This process provided initial insight into the overall morphological diversities in the various speleothems. While the benefit of thorough microscopical analysis lies in obtaining detailed morphological structure, a major disadvantage is that only limited information can be obtained with regard to identity, function and activity. Morphology is an ambiguous indicator of biogenicity, even in these filamentous morphotypes (Ruiz et al., 2002; Hofmann et al., 2008). Despite this, our microscopical studies have proven to be most valuable for systematic comparison of the different types of speleothems from both the Venezuelan caves, and also in samples containing similar structures from other parts of the world. Several different

types of conjecturable information has been brought to light which will hopefully stimulate future research in geobiology, palaeontology and also astrobiology.

Several different morphotypes have been detected thus far in various types of siliceous speleothems. A very obvious feature in many of these speleothems is their different types of filamentous morphotypes. Some of these most likely represent either fungi or spider webs, as was mentioned in various sections, including 2.7.3. Others could possibly represent filamentous microbes, which played a past or currently sustained role similar to that of the filamentous bacteria in different types of stromatolites microbial mats (Golubic, 1976^a). Interestingly, Hofmann et al. (2008) recently reported that filamentous bacteria seem to be a rather common phenomenon in fossilized samples from various types of terrestrial/karst environments in different parts of the world. Although it is difficult to provide clear evidence for either biogenic or non-biogenic origin of these filamentous structures, several parameters similar to those in our studies indicate that at least some of those filamentous structures may have been formed by biogenic filament encrustation.

Characteristics of the filamentous microbes forming the central columnar stromatolite in Charles Brewer Cave System speleothems remain uncertain. However, based simply on morphological criteria, they bear resemblance to heterotrophic sulfide-oxidizing bacteria such as *Beggiatoa*, iron oxidizing bacteria and also to phototrophic filamentous cyanobacteria. All these possibilities are realistic as these species are often encountered in microbial mats and even in different types of stromatolites and other speleothem types in caves which date from the earliest evolutionary life on Earth (Hofmann et al., 2008). It is impossible to precisely determine these species based solely on morphological criteria, especially when they have been obliterated by silicified remnants and casts (Jones et al., 2001^b; Konhauser et al., 2003; Konhauser, 2007). Nevertheless, the opportunity to explore the similarities and differences to investigated species in similar systems is quite beneficial. Astonishingly, certain associations can be made to other microbial species. Simple septate tubes found in columnar stromatolites resemble *Phormidium* or other representatives of the Oscillatoriales order (Golubic, 1976^b: p. 135), and double-walled tubes, which are most likely sheathed, resemble either *Cyanostylon* (see Golubic, 1976^a: pl.I, fig. 5), or *Entophysalis* from the order *Chroococcales* (Golubic, 1976^b: p.117). The diagonal septae in the filament casts (Fig. 90D) indicate the possibility that the filament could be twisted, as is typical in iron-oxidizing bacteria such as *Gallionella*. A more detailed identification is not possible because only a few morphological features were discernable in currently produced microscopical preparations. In this regard, Castenholtz (2001) stated that approximately 37 different characteristics are required for cyanobacteria optimal identification.

The morphology of microbes forming the peloidal zones of the examined speleothems from these cave systems is less ambiguous, because here they bear many features indicative of nostocalean cyanobacteria.

The presence of phototrophic species such as cyanobacteria in these caves is not as surprising as one would expect. Several studies have already described cyanobacteria such as *Geitleria*



Fig. 104: Fine spray and aerosol droplets from waterfalls, which are normally visible only under flash light. Cueva Charles Brewer sector.

calcareo, *Scytonema julianum* and *Nostoc* in both illuminated and pitch-black zones in caves, as well as in other dark ecosystems (Friedman, 1955; Bourrelly and Depuy, 1973; Vinogradova et al., 1998). Furthermore, cyanobacterial species such as *Nostoc*, *Fisherella* and *Calothrix* can easily adapt to a heterotrophic life-style (as recorded in Whitton, 1987) and some cyanobacterial species are even light sensitive (Vincent and Roy, 1993; Quesada and Vincent, 1997). These have to protect themselves from light by either producing protective pigments in extracellular sheaths (e.g. *Lyngbya estuarii* produces scytonemine – Kylin, 1937), or else by digging deeper into the substrate, such as endolithic boring cyanobacteria *Hormathonema* and *Hyella* (Golubic, 1976^a). Cyanobacteria's nitrogen fixing ability is most relevant in the normally nitrogen-poor environment of dark caves. *Nostoc* is also easily adaptable to a heterotrophic life-style, and is a common endobiont in lichens and higher plants (Hoek et al., 1995). In addition to photosynthesis, it can also adapt to nitrate fixation. In symbiosis with higher plants, *Nostoc* provides them with nitrogen (Graham & Wilcox, 2000). Only a few heterocysts were detected in our research and this suggests that the cyanobacteria may have grown in a nitrogen-rich environment and were not nutrient stressed. However, further analysis using methods, such as molecular screening, are required to verify if these structures are indeed cyanobacteria.

The restricted number of microbial morphotypes mentioned above indicates that the diversity of microbes participating in speleothems construction is much poorer than that on the top of Chimantá Massif, especially regarding cyanobacteria (Ahti, 1992). The *Nostoc*-like microbes which form the peloidal stromatolites are not necessarily solely accumulations of cyanobacteria, because the peloids in which the *Nostoc*-like filaments are concentrated are too regular in size and too regularly arranged to consist only of a random accumulation of *Nostoc* spheres. While there appears to be a higher-level order than just isolated microbial colonies, it cannot be excluded that *Nostoc* may simply be symbiotic there with other organisms such as fungi (for comparison see Schüßler et al., 1994, 2007).

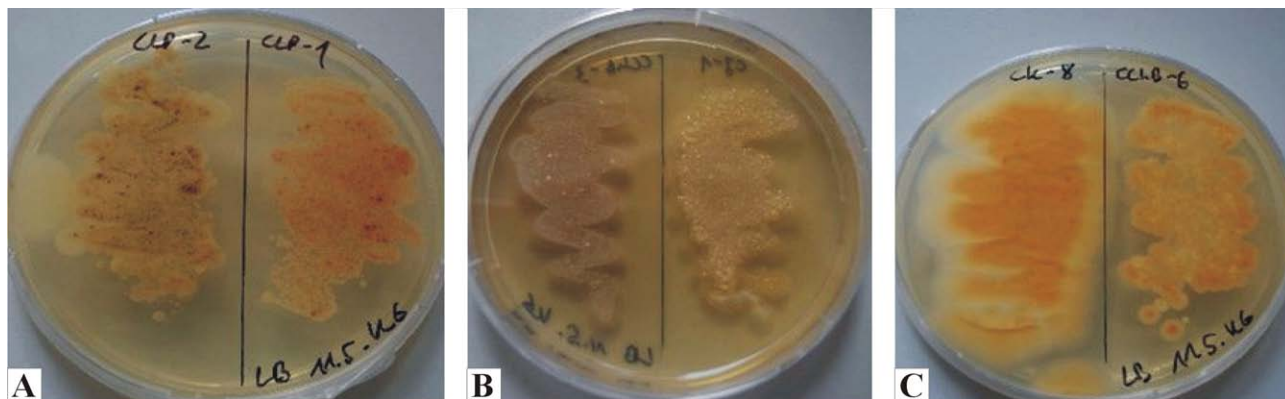


Fig. 105: Examples of agar plates containing different bacterial morphotypes from different types of bio-speleothems. The photos show the early stage of an ongoing isolation procedure made directly from the biospeleothems. See further explanations in Tab. 6. A – Isolates from the biospeleothems CLP1 and CLP2. B – Isolates from the biospeleothems CChB1 and CJ1. C – Isolates from the biospeleothems CK8 and CChB-6.

One obvious remaining enigma is the phenomenon of the biologically mediated silica precipitation which occurs on the microbial-like filaments while the surrounding rock remains intact. Although it has several times been proposed in literature that cyanobacteria protect themselves from excess silica encrustation by thickening their sheaths (see Konhauser, 2007: p. 186), our observations indicate that their presence actually promotes this silicification. Silicification in the examined Venezuelan arenitic caves takes place under normal temperature conditions, and this contrasts with the silicification conditions of the microbial assemblages observed in hot springs (Jones et al., 2001^b), and also in experiments by Oehler (1976), where he simulated encrustation of cyanobacteria under high-temperature conditions. Although our observations indicate biological mediation of silicification, it is not yet clear whether this silicification is caused by microbial metabolism or by products from their decay.

We are therefore currently employing various molecular biological, cultivation and activity targeted methods (e.g. microcalorimetry – Braissant et al., 2010) to pursue this question. So far, it is clear that: i) different bacterial and fungi species can be isolated from the speleothems (unpublished data – Fig. 105, Tab. 6); ii) different amounts of nucleic acids can be isolated from various speleothems (Tab. 7); and iii) that the diversity resulting from molecular analysis is considerably higher than that gleaned from standard microscopic analysis presented in earlier sections (unpublished results, Lee and Aubrecht). The difficulty now lies in assigning a possible role to this microbial diversity. This is very important in distinguishing between past and present speleothem-forming encrusted microbes and the non-speleothem-forming microbes which possibly played an indirect role in overall speleogenesis by providing nitrogen for the speleothem-forming bacteria. Alternatively, some microbes may just have been temporary contaminants.

At the moment, it is a great challenge to prove current microbial activity by molecular based methods, such as mRNA, which target clear indicators of microbial activity. Part of this problem can be assigned either to low microbial numbers and activity and/or to the field conditions which were unable to assist optimal sampling for such analysis. Fortunately, there

are other methods, including microcalorimetry, which can explore *in situ* activities directly. Initial attempts to employ this method on six various speleothems from various regions of the Venezuelan caves clearly demonstrated that at least some of the speleothems show significant microbial activity, while others do not (unpublished results; Braissant et al., 2010). This could indicate that the role of microorganisms in speleothem development differs in different types of speleothems. It is apparent that a broad holistic scientific approach is necessary to explore the validity of the hypothesis that microorganisms are involved in silicification of speleothems in these Venezuelan caves. Such an holistic approach may distinguish; i) obligate microbiota associated with the speleothems from other microbiota with different functions, irrespective of whether or not they are contaminants; and ii) past and present microbial processes. The ultimate proof of microorganism impact on silicification lies in retrieving actual isolates where this impact can be illustrated *in vitro* in the laboratory, in a similar manner to those calcite precipitating isolates retrieved from stalactites in carbonate caves (see e.g. Baskar et al., 2006; Lee et al., 2012).

2.7.5.4. Cobweb stalactites.

Siliceous speleothems most likely formed by spider thread encrustation have, to our knowledge, never previously been reported in the literature, although spiders and insects have often been sighted in many types of caves (Lee et al., 2012). Spiders are especially ubiquitous in the Charles Brewer Cave System because many insect species are there, either autochthonous or introduced by the river flowing from the surface. Although spider threads primarily served as a supporting framework during speleothem growth, their presence has been recorded not only in “cobweb stalactites” but also in numerous other speleothems, such as “dolls”, “guácimos” and “black corals”. This phenomenon is highlighted in SEM photos, and especially in Figure 87E.

Tab. 6: Table showing preliminary results from ongoing isolation attempts of bacteria and fungi from 11 different biospeleothems, on agar plates with two different types of media (nutrient rich LB and nutrient poor R2A).

Source of biospeleothem	Abbreviation	R2A agar medium	LB agar medium
Chimantá Tepui, Cueva Charles Brewer, Galería Adina	CChB1	Various bacteria colonies, mould/fungi	Various bacteria colonies
Chimantá Tepui, Cueva Charles Brewer, Cascada de Moravia	CChB2	Various bacteria colonies, mould/fungi	Various bacteria colonies, mould/fungi
Chimantá Tepui, Cueva Charles Brewer, Pared de los 100 Colores, inicial white microbial encrustations on the sandstone wall, at the end of the “Pared de los 100 colores”, on the right side of the corridor	CChB3	No growth	No growth
Chimantá Tepui, Cueva Charles Brewer, Pared de los 100 Colores, outermost part of the soft white champignons	CChB6	No growth	No growth
Chimantá Tepui, Cueva Charles Brewer, Pared de los 100 Colores, on the ledge on the right side of corridor, black mud (red on the surface) covered by white, yellowish and copper-red filamentous and “lichen-like” aggregates, surface sample of aggregates-rich parts	CChB9	Various bacteria colonies	Various bacteria colonies
Chimantá Tepui, Cueva Juliana, 50 m from the cave entrance. White encrustations on the ceiling, partly hard (yellow parts), white soft parts. White parts covered by filamentous and “lichen-like” aggregates (up to 5-6 mm)	CJ1	Some bacteria colonies, mould/fungi	Some bacteria colonies, mould/fungi
Chimantá Tepui, Cueva Colibrí, colonnade behind the triple junction some 300 m from the entrance	CK8	Some bacteria colonies, mould/fungi	Some bacteria colonies, mould/fungi
Chimantá Tepui, Cueva Colibrí, before waterfall on the triple junction, on the left side of the corridor	CK9	Various bacteria colonies, mould/fungi	Various bacteria colonies
Roraima Tepui, Cueva de los Pémones, large corridor 100 m W from the cave entrance Pokemon 3	CLP1	Various bacteria colonies, mould/fungi	Various bacteria colonies
Roraima Tepui, Cueva de los Pémones, at the end of the large corridor with Venezuelan sign L6	CLP2	Various bacteria colonies, mould/fungi	Various bacteria colonies
Roraima Tepui, Cueva de los Pémones, the same place as CLP2	CLP3	Various bacteria colonies, mould/fungi	Various bacteria colonies

2.8. CONCLUSIONS

1. Speleological, geological, geomorphological and hydrogeochemical research was performed in the two largest sandstone cave systems in the world – the Charles Brewer Cave System (17.8 km) in the Churí Tepui and Ojos de Cristal Cave System (16.14 km) in Mt. Roraima. Unlike most of the previously explored sandstone cave systems in Venezuela, these consist of subhorizontal caves. The Charles Brewer Cave System consists predominantly of large, mature cave spaces. However, several younger, smaller caves were located at deeper levels. The age of this system is apparent from the numerous collapses which resulted in recent discontinuity of the previously well-interconnected system. Meanwhile, the Ojos de Cristal Cave System is a complex labyrinth of younger, smaller caves which remain relatively well-interconnected due to their younger evolutionary stage.

2. The research revealed that quartz dissolution did not play a

substantial role in the formation of these cave systems. Erosion of non-cemented layers and lateritization of arkosic arenites with dissolution of feldspars and micas proved to be more important, while any quartz dissolution noted played only a minor role. This is quite apparent in the lack of dissolutional features on the quartz grains. Although water condensed on the cave walls proved to be the main quartz-dissolving agent, it could not have been a trigger for cave-formation because it appeared only after the cave space was created.

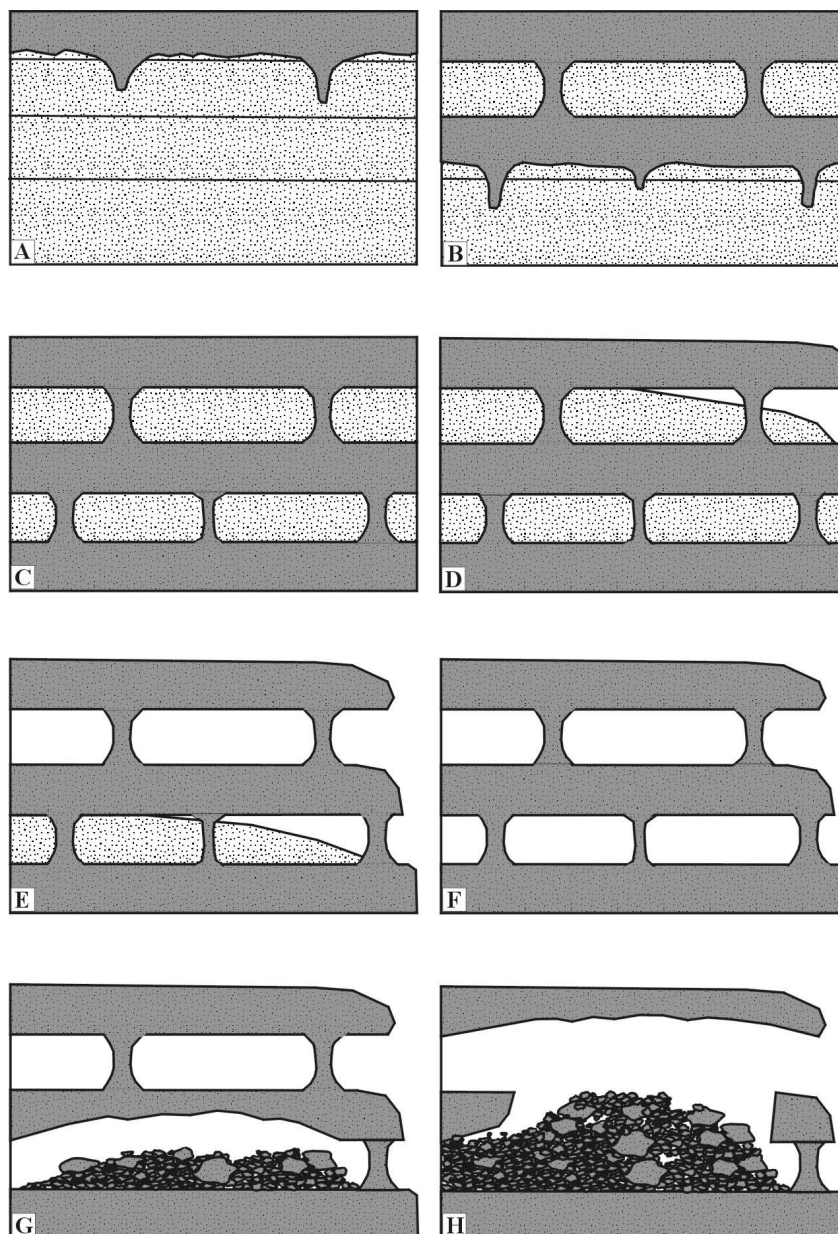
3. Softer beds in which the caves were initially formed showed a lack of cementation, or only kaolinite cementation, while the hard overlying and underlying beds and the “finger-flow” pillars are cemented by opal and quartz. These “finger-flow” pillars which penetrate the non-cemented arenite beds and ceilings and bottoms of the initial caves are smooth, free from irregularities, and they supply further evidence of the contrasting differences in cementation.

Tab. 7: Table showing preliminary results from ongoing nucleic acid extraction attempts from six different biospeleothems.

Source of biospeleothem	Abbreviation	DNA-concentration ($\mu\text{g}/\mu\text{l}$)
Chimantá Tepui, Cueva Charles Brewer, Galería Adina	CChB1	116.22
Chimantá Tepui, Cueva Charles Brewer, Cascada de Moravia	CChB2	0.31
Chimantá Tepui, Cueva Charles Brewer, Pared de los 100 Colores	CChB6	1.63
Chimantá Tepui, Cueva Colibrí, colonnade behind the triple junction some 300 m from the entrance	CK8	72.18
Roraima Tepui, Cueva de los Pémones, large corridor 100 m W from the cave entrance Pokemon 3	CLP1	123.18
Roraima Tepui, Cueva de los Pémones, at the end of the large corridor with Venezuelan sign L6	CLP2	16.36

- The important role of lateritization in speleogenesis is evident from vast quantities of the lateritic red mud (“Barro Rojo”) in these caves. This lateritization affects the arenites of Matauí Formation which contain considerable amounts of feldspars, micas and clay minerals. In addition to creating cave spaces, lateritization is the main source of SiO_2 for the large opal speleothems which occur in the caves. Lateritization here represents a dissolution process that is volumetrically important and it may even be considered a trigger for speleogenesis. The arenitic caves in these Venezuelan tepuis can therefore be regarded as karst phenomena.
- The following speleogenetic model can be inferred from the obtained results (Fig. 106): Stage 1 – the descending, SiO_2 -bearing diagenetic solutions caused complete lithification of some beds, whereas other beds with more coarse-grained arenites were only penetrated by narrow channels through which fluids flowed to completely fill some of the lower beds. This resulted in contrasting diagenesis, where most beds turned to sandstone and quartzite while parts of other beds remained intact. Stage 2 – hard, isolated beds were broken, and the flowing water which penetrated the poorly lithified beds signalled initial erosion. Lateritization then began in aluminosilicate-rich beds with the subsequent emptying of spaces by winnowing sand and other products of lateritization. The empty spaces were then supported solely by “finger-flow” pillars. Stage 3 – empty spaces collapsed further, thus creating larger caves, and superior propagation of these collapses created large collapse depressions on the surface.
- Flexible sandstone – itacolomite which was found in both examined cave systems possesses unique flexibility due to very thin spaces between the arenitic grains. Although the origin of these spaces requires clarification, quartz dissolution was observed in the itacolomite samples, and this is dissimilar to occurrences in other arenitic specimens.
- A new theory concerning the origin of tepuis is presented in this volume. According to this theory, tepuis originated in places where there was an intensive descending fluid flow, most likely emanating from surface water reservoirs, such as rivers or lakes. This continuous flow carried SiO_2 from the lateritized surface beds. Thus, the underlying part of the Roraima Supergroup was impregnated with SiO_2 and strongly lithified. These indurated parts of the formation remained as tepuis, while the remainder of the formation was removed by erosion. The softness of the underlying, non-lithified sediment below the tepuis causes undercutting of their margins thus maintaining steep walls. Speleogenesis in the tepuis was a process which most likely began at a later stage, with initial incision of the valleys followed by erosion. The recent “Barro Rojo” represents a new lateritic product, and it has nothing in common with the ancient silicification of the Matauí Formation.
- The vast majority of speleothems in the examined cave systems are siliceous, ranging from opal-A to micro-crystalline quartz. Speleothems from gypsum and sanjuanite were documented in some other places, and the laterite “Barro Rojo” is a further form of speleothem. Some of the siliceous speleothems have inorganic origin; they precipitated from water solutions by evaporation. These mainly include flowstones and stalactites, with the latter occasionally formed by encrustation of spider threads hanging from ceilings, thus forming the unique speleothems called “telerañas”. However, the vast majority of siliceous speleothems are microbialites, where initial microbial mats are encrusted by silica, leaving the surrounding rock intact. This procedure indicates that these microbes actively mediate silica precipitation and they are not just passive components of the speleothems. Although these microbial speleothems have many shapes and forms, their anatomy reveals they contain the following two main forms of microbialites; (1) columnar stromatolites, consisting of erect filamentous microbes; and (2) peloidal stromatolites, where the peloids are composed of short-filamentous microbes. Although the

Fig. 106: Schematic overview of the speleogenesis in the arenites of the Roraima Supergroup. Grey – well-lithified arenites, pale – poorly lithified arenites (cavities formed by lateritization are omitted). A-B – The gradual diagenesis of arenites caused by descending silica-bearing fluids (Stage 1). C – Two poorly-lithified horizons superimposed on each other. D-E – Flowing water penetrated the vertical cleft (on the right side) causing gradual winnowing of the poorly lithified sediment (Stage 2). F – Two horizons remained empty (two superimposed initial caves), with lithified pillars offering the only support against collapse. G-H – Gradual collapse of both floors, forming a large cave (Stage 3).



nature of these microbes is not yet fully understood, work on unravelling their mysteries still continues. Biological identification based on enrichment, molecular microscopy using fluorescence in situ hybridization and DNA analysis is currently underway. While this work is still in progress, only morphological criteria are available for their current identification, and these may not prove completely reliable. The morphology of both these microbe types bears some resemblance to cyanobacteria. For example, microbes similar to the Oscillatoriales order of cyanobacteria resemble columnal stromatolitic forms. In addition, other filamentous

microbes, including the *Beggiatoa* sulphur bacteria and the *Gallionella* iron oxidizing bacteria cannot yet be excluded. It appears likely that different types of filamentous bacteria are associated with different types of biospeleothems, and this depends on the surrounding geochemical conditions. For example, *Gallionella*-like filaments are ubiquitous in “Barro Rojo”. The peloidal microbialites are formed by filamentous microbes reminiscent of *Nostoc*-type cyanobacteria but eventual symbiosis with fungi species is not excluded.

3. Faunistic investigations of the Pantepui biogeographical region

“Islands in time” is a term introduced by Brewer-Carías (1974) to describe the isolation of the plants and animals inhabiting the remote summits of those peculiar mountains with a table shape in the Venezuelan Guyana. These mountains are known as tepuis (tepui in singular), a derived term of the indigenous language Pemón (tepü), which in fact means “mountain”. The unusual shape of most of them, with their vertical cliffs that make them virtually inaccessible, their apparently plain summits from the distance, and their isolation of the rest of tropical lowlands, took the novelist sir Arthur Conan Doyle to represent his acclaimed novel “The Lost World” in the scenario offered by one of the most famous tepuis, Roraima.

The ecological community of the tepuis summits is considered a distinct and discontinuous biogeographical province called Pantepui (Mayr & Phelps, 1967). The Pantepui includes about 50 mountains (topographic islands) with elevations ranging from 1,500 to 3,000 m a.s.l. They cover an area of about 5,000 km² and their surface area ranges between 0.2 and 1,096 km² (Berry et al., 1995; McDiarmid & Donnelly, 2005). The region is known for its extraordinary diversity and high level of endemism, which is, above all, remarkable at the isolated summits of the sandstone mesas (Huber, 2005; Rull, 2005; McDiarmid & Donnelly, 2005). In this chapter we tried to summarize the results of faunistic investigations of three different animal groups: land snails, aquatic insects, and amphibians and reptiles in the Pantepui.

3.1. THE PANTEPUI MALACOFUNA: LAND SNAILS OF CHURÍ TEPUI AND OTHER TEPUIS IN SOUTHERN VENEZUELA AND ADJACENT AREAS

3.1.1. Introduction

Land snails (Mollusca, Gastropoda) have been proposed as good model organisms for the study of complex ecosystems. They are renowned for their limited dispersal abilities, they can be easily collected and most of them can be identified on the basis of their shells. Land snails are also an important factor in the food web and are vulnerable to predation by other animals or their shell is used as a calcium source. However, tropical acidic soils are known to support only sparse land snail populations (Schilthuizen, 2011). Although the Neotropical land snail fauna is generally well-known, the Pantepui area (sensu Huber, 1995) is less-studied; this is the assemblage of sandstone table mountains in Venezuelan Guyana and in adjacent Brazil and Guyana. According to Huber (1995), the term Pantepui defines the area above 1,500 m elevation, but some authors include all the intervening lowlands as well. In this chapter we use Pantepui as comprising both the highlands and uplands (sensu Huber, 1988), but we treat all the land snail species reported from southern Venezuela and adjacent areas in Brazil. Currently, there is a total of 21 identified species (Tab. 8), 19 of which are endemic to the area. In addition, it is noteworthy that the identity of some reported species remains obscure at this time. This particularly refers to a juvenile *Plekocheilus* species (family Amphibulimidae) from near Santa Elena de Uairén (Breure, 2009), and a *Happiella* species (family Systrophiiidae) from Macizo del Chimantá (Haas, 1955). These species have been reported both from the highlands (*Happiella*) and lower elevations (*Plekocheilus*), and are a token of the relatively unexplored malacofauna of this region. Incidentally, both were collected by botanists (O. Huber, J.A. Steyermark respectively), and this illustrates a more generalized pattern: there is generally a paucity of data, with all known snails being collected by non-malacologists, such as botanists and herpetologists. The expeditions to Cerro de la Neblina (Brewer-Carías, 1988) and Churí Tepui (Brewer-Carías & Audy, 2010), however, are exceptions with also special interest for malacology. The aim of this chapter is to review all known species from this area, to provide additional anatomical and distributional data for Orthalicoidea, and to present preliminary cladistic and phylogenetic analyses for *Plekocheilus* species.

Tab. 8: Taxonomy of land snails reported from southern Venezuela and from adjacent areas in Brazil, arranged according to tepui massifs. Abbreviations: CH, Chimantá; DU, Duida-Marahuaka; GU, Guaiquinima; MA, Maigualida; NE, Neblina; RO, Roraima; YA, Yapacaná. Altitudinal distribution following Huber (1988): *, lowland; **, upland; *, highland. References: [1] Breure, 2009; [2] Breure & Schlögl, 2010; [3] Borrero & Breure (2011); [4] Simone, 2010; [5] Thompson, 2008. Notes: ¹The assignment of the genus *Plekocheilus* to the family Amphibulimidae now follows Breure et al., 2010. ²*Plekocheilus (Eurytus) coloratus* (Nyst, 1845), reported by Breure (2009: 39), is a different but as yet unidentified species. ³A single worn shell was tentatively identified as this species, hitherto only known from Colombia.**

Clade Stylommatophora
 Superfamily Clausilioidea Gray, 1855
 Family Clausiliidae Gray, 1855
 Genus *Columbinia* Polinski, 1924
Columbinia (C.) exul Thompson, 2008; NE; ***, [5]
 Superfamily Orthalicoidae Albers, 1860
 Family Amphibulimidae P. Fischer, 1873
¹Genus *Plekocheilus* Guilding, 1828
Plekocheilus (P.) linterae (Sowerby, 1890); RO; ***, [1]
Plekocheilus (P.) alticola Haas, 1955; CH; ***, [1]
Plekocheilus (P.) vlceki Breure & Schlögl, 2010; CH; ***, [2]
²Subgenus *Eurytus* Albers, 1850
³*Plekocheilus (Eurytus) plectostylus* (Pfeiffer, 1848); MA; ***, [3]
Plekocheilus (Eurytus) gibber (Oberwimmer, 1931); DU; ***, [1]
Plekocheilus (Eurytus) fusitorsus (Oberwimmer, 1931); DU; GU; ***, ***, ***, [1]
Plekocheilus (Eurytus) juliani Haas, 1955; CH; ***, [1]
Plekocheilus (Eurytus) mundiperditi Haas, 1955; CH; ***, [1]
Plekocheilus (Eurytus) tatei Haas, 1955; DU; ***, [1]
Plekocheilus (Eurytus) sophia Breure, 2009; RO; ***, [1]
Plekocheilus (Eurytus) tepuiensis Breure, 2009; YA; **, [1]
Plekocheilus (Eurytus) huberi Breure, 2009; NE; ***, [1]
Plekocheilus (Eurytus) nebulosus Breure, 2009; NE; ***, [1]
Plekocheilus (Eurytus) breweri Breure & Schlögl, 2010; CH; ***, [2]
 Subgenus *Eudolichotis* Pilsbry, 1896
Plekocheilus (Eudolichotis) sinuatus (Albers, 1854); *, [1]
 Family Bulimulidae Tryon, 1867
 Genus *Drymaeus* Albers, 1850
Drymaeus (D.) steyermarki (Haas, 1955); CH; ***, [1]
Drymaeus (D.) extraneus (Haas, 1955); CH; **, ***, [1]
Drymaeus (D.) yapacanensis Breure & Eskens, 1981; YA; **, [1]
Drymaeus (D.) rex Breure, 2009; NE; *, **, ***, [1]
 Superfamily Helicoidea Rafinesque, 1815
 Genus *Olympus* Simone, 2010
Olympus nimbus Simone, 2010; NE; *, [4]

Tab. 9: Key to families and genera of the Pantepui gastropods.

1 Shell sinistral ... Clausiliidae, *Columbinia exul*
 – Shell dextral ... 2
 2 (1) Shell depressed, height/diameter ratio < 1.0 ... Pleurodontidae, *Olympus nimbus*
 – Shell elongate, height/diameter ratio > 1.0 ... 3
 3 (2) Protoconch granulate ... Amphibulimidae, *Plekocheilus*
 Protoconch with a grating sculpture of equally strong spiral riblets and axial striae ... Bulimulidae, *Drymaeus*

Tab. 10: Key to *Plekocheilus* species which occur in the uplands and highlands of Venezuelan Guyana.

1 Sculpture on last whorl malleated ... 2
 – Sculpture on last whorl consisting of fine granules, spirally arranged “puckered” bands, or horizontal threads which are partly anastomosing ... 4
 2 (1) Malleation weakly developed over a sculpture of axial riblets broken by spiral lines into oblong granules; shell spindle-shaped; Roraima ... *P. linterae*
 – Malleation strongly developed; Macizo del Chimantá ... 3
 3 (2) Shell up to 31 mm, uniform (dark-)yellowish to chestnut-brown colour; Churí Tepui ... *P. vlceki*
 – Shell up to 44 mm, coloured with reddish-brown zig-zag streaks; Toronó Tepui ... *P. alticola*
 4 (1) Sculpture consisting of horizontal treads, partly anastomosing ... 5
 – Sculpture consisting of fine granules, or spirally arranged “puckered” bands ... 6
 5 (4) Shell up to 44 mm, colour uniform reddish-brown, suture descending in front; Yuruaní Tepui ... *P. sophia*
 – Shell up to 62.5 mm, colour (dark-)brownish with irregularly spaced darker coloured spots, suture slightly ascending in front; Neblina ... *P. nebulosus*
 6 (4) Sculpture consisting of granules ... 9
 – Sculpture consisting of spirally arranged “puckered” bands ... 7
 7 (6) Shell up to 52 mm, colour yellowish- to (light) chestnut-brown, with descending oblique, partly zig-zag stripes of reddish- to blackish-brown ... 8
 – Shell up to 47 mm, colour (dark) brown with darker brown to blackish dots dispersed; northern part of Macizo del Chimantá ... *P. mundiperditi*
 8 (7) Shell up to 42 mm, last whorl relatively swollen, suture regularly descending in front; Churí Tepui ... *P. breweri*
 – Shell height 46-52 mm, last whorl relatively flat, suture deeply descending in front; Macizo del Chimantá ... *P. juliani*
 8 (6) Shell larger than 40 mm ... 9
 – Shell smaller than 40 mm; Yapacaná-tepui ... *P. tepuiensis*
 9 (8) Shell larger than 48 mm, colour with irregular dots or with descending, brown streaks ... 10
 – Shell up to 48 mm, colour light chestnut brown with a regular pattern of descending, oblique, narrow reddish-brown stripes; Neblina ... *P. huberi*
 10 Colour pattern with dispersed dots, forming a few short, irregular streaks; aperture narrow and oblique; Cerro Marahuaka ... *P. gibber*
 Colour pattern with descending, brown streaks ... 11
 11 (10) Colour pattern with dark-brown to blackish streaks, paralleled with yellow ones, suture slightly ascending in front; Río Padamo; Guaiquinima ... *P. fusitorsus*
 – Colour pattern with dark-brown streaks only, suture not ascending nor descending in front ... *P. tatei*

Tab. 11: Key to the species of *Drymaeus* of Venezuelan Guyana.

1 Shell relatively large (up to 40.7 mm) with prominent last whorl, colour pattern varied; Neblina ... <i>D. rex</i>
Shell relatively smaller (up to 32 mm) ... 2
2 (1) Peristome well expanded, colour pattern with axial bands, which may be partly forked above; Yapacaná Tepui ... <i>D. yapacanensis</i>
– Peristome narrowly expanded, colour pattern uniform or with spiral bands ... 3
3 (2) Shell with straight sides, aperture relatively large; Apacará Tepui ... <i>D. steyermarki</i>
– Shell with slightly convex sides, last whorl somewhat swollen, aperture relatively smaller; Abacapá Tepui, Apacará Tepui ... <i>D. extraneus</i>

3.1.2. Material and methods

The following abbreviations are used to refer to depositories of material: AMNH, American Museum of Natural History, New York, U.S.A.; INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil; MLSC, Museo de Historia Natural 'La Salle', Caracas, Venezuela; MZSP, Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil; NHM, Natural History Museum, London, U.K.; RMNH, Naturalis Biodiversity Centre (formerly

Rijksmuseum van Natuurlijke Historie), Leiden, the Netherlands; SNMSZ, Slovak National Museum, Bratislava, Slovakia; UF, Florida State Museum of Natural History, Gainesville, U.S.A.

Mandibulae and radulae were studied under a Cambridge-II (*Plekocheilus mundiperditi* and *Drymaeus steyermarki*) and JEOL JSM-6480LV Scanning Electron Microscope (all other species). Morphological analyses were performed with a cladistic parsimony analysis using a 'traditional search' in the program TNT (Goloboff et al., 2008). The five characters used were coded as multistate and treated as unordered (Tab. 12). Preliminary phylogenetic molecular analyses were performed using *Plekocheilus* taxa, from both the Pantepui area and the Andean and West Indies regions. These analyses were carried out using partial cytochrome c oxidase subunit 1 (CO1) sequences. DNA was extracted from the foot of the snails with a DNEasy kit (Qiagen, Inc.) following the manufacturer's protocol for animal tissues; gene fragments were amplified in 25 µl reactions. Fragments of mitochondrial cytochrome oxidase 1 (CO1) were amplified using primers HCO2198 and LCO1490 (Folmer et al., 1994). Most reactions consisted of 2.5 µl of Qiagen PCR buffer, 0.5 µl of 10 mM dNTP, 1 µl each of forward and reverse 10 mM primers, 0.25 µl Taq DNA Polymerase (Qiagen Inc.), 1 µl of template DNA, and water to 25 µl. Reaction conditions included an initial

Tab. 12: *Plekocheilus* species arranged according to shell morphology: shell shape (0 = sides slightly convex/aperture relatively small, 1 = sides straight/aperture relatively large, 2 = sides hardly convex/aperture relatively wide); suture (0 = normal or slightly ascending in front, 1 = descending in front); columella (0 = no columellar fold, 1 = weak fold, 2 = strong fold); colour pattern (0 = dots, 1 = axial zig-zag streaks, 2 = obliquely descending streaks); sculpture (0 = malleation, 1 = granulation, 2 = 'puckered' bands, 3 = horizontal threads).

	Shell shape	Suture	Columella	Colour	Sculpture
<i>alticola</i>	0	0	2	2	0
<i>breweri</i>	2	1	1	1	2
<i>fusitorsus</i>	2	0	1	1	1
<i>gibber</i>	1	0	2	2	1
<i>huberi</i>	1	0	0	2	1
<i>juliani</i>	1	1	0	2	1
<i>linterae</i>	0	1	2	2	0
<i>mundiperditi</i>	2	1	1	0	2
<i>nebulosus</i>	2	1	1	0	3
<i>sophiae</i>	2	1	0	0	3
<i>tatei</i>	2	0	1	2	1
<i>tepuiensis</i>	2	0	1	2	1
<i>vlceki</i>	0	0	1	2	0

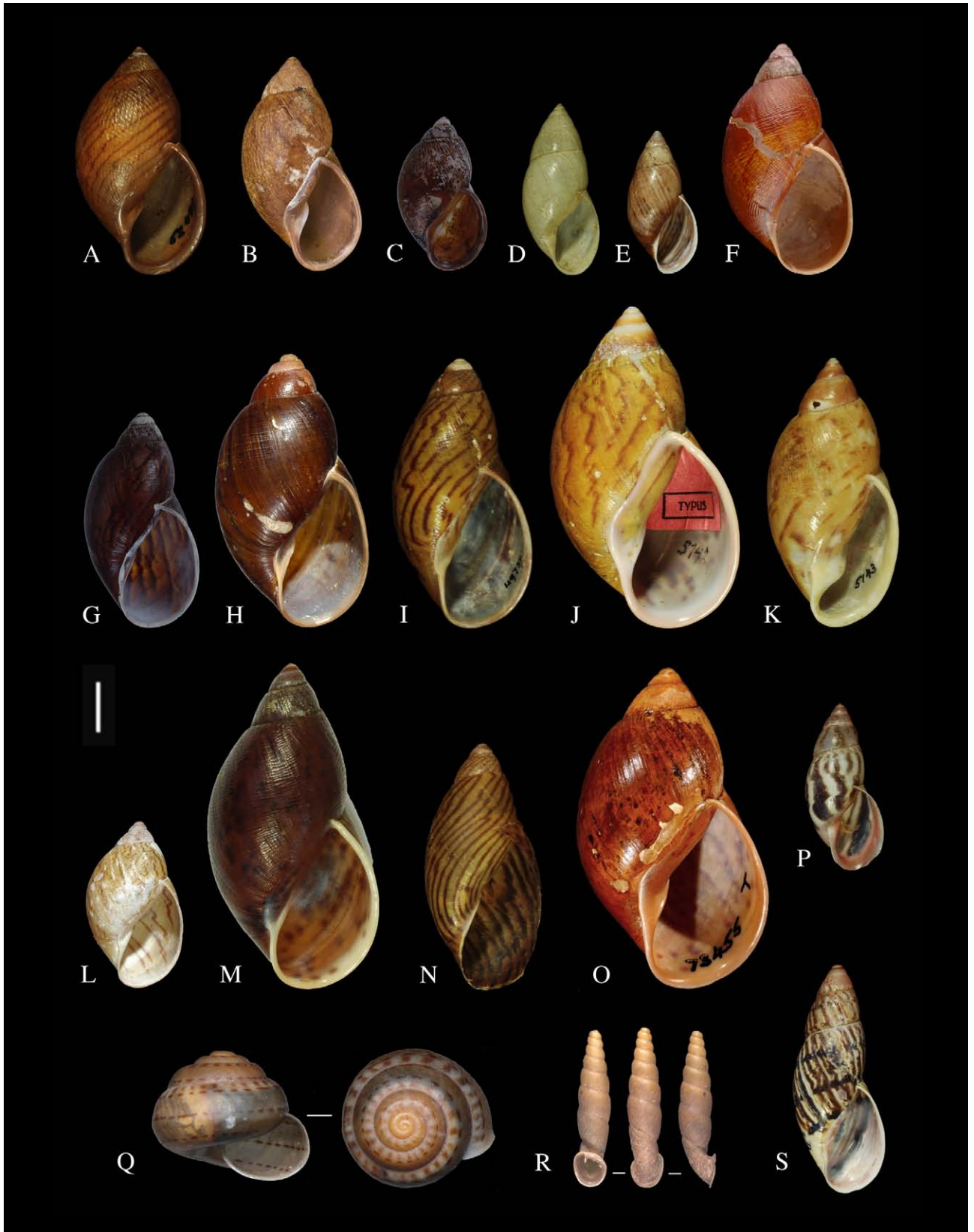


Fig. 107: Shells from the Pantepui area. A – *Plekocheilus alticola* Haas, 1955. B – *P. lintera* (Sowerby, 1890). C – *P. vlceki* Breure & Schlögl, 2010. D – *Drymaeus extraneus* (Haas, 1955). E – *D. steyermarki* (Haas, 1955). F – *P. sophiae* Breure, 2009. G – *P. breweri* Breure & Schlögl, 2010. H – *P. mundiperditi* Haas, 1955. I – *P. juliani* Haas, 1955. J – *P. fusitorsus* (Oberwimmer, 1931). K – *P. gibber* (Oberwimmer, 1931). L – *P. tepuiensis* Breure, 2009. M – *P. nebulosus* Breure, 2009. N – *P. huberi* Breure, 2009. O – *P. tatei* Haas, 1955. P – *D. yapacanensis* Breure & Eskens, 1981. Q – *Olympus nimbus* Simone, 2010. R – *Columbinia exul* Thompson, 2008. S – *D. rex* Breure, 2009. The scale line equals 2 cm (Q), 1.25 cm (R), 1 cm (all other figures).

denaturation step at 94 °C for 3 min, followed by 40–45 cycles of 94 °C for 15 s and annealing at 50 °C (COI) for 30 s and 72 °C for 40 s. PCR products were purified, and then sequenced under BigDye terminator cycling conditions, purified by ethanol precipitation and run on an Applied Biosystems 3730xl sequencer by Macrogen. All sequences were checked for contamination using a Blast search. Phylogenetic molecular analyses were performed using PhyML in Geneious 5.3.4 (Drummond et al., 2010; Guindon & Gascuel, 2003), using 500 bootstrap replicates, the Chi2-based aLRT parametric (Anisimova & Gascuel 2006) and an aLRT non-parametric branch support based on a Shimodaira-Hasegawa-like procedure (see benchmarks on <http://www.atgc-montpellier.fr/phyml/benchmarks/index.php?ben=sp>). Molecular analyses were achieved with the most appropriate model of sequence evolution (GTR+Gamma+Inv) selected by jModeltest 0.1.1 (Posada, 2008), and phylogenetic network analysis was completed using SplitsTree 4.11.3 (Huson & Bryant, 2006), with a NeighborNet drawn using K2P distance method, followed by a bootstrap of 1000 replicates. The closely related (Breure et al., 2010) taxa *Gaeotis nigrolineata*, *G. flavolineata* and *Pellicula appendiculata* were utilized as the outgroup.

3.1.3. Land snails in a hostile habitat

Snails use sources of calcium for the formation of their shells during growth. In the Pantepui area, limestone is not available due to the sandstone substrate; the only calcium sources appear to be the uptake of calcium from plants (Van Bruggen, pers. commun.) and the leaching of mineral from the sandstone rocks. Although no studies have been carried out on shell formation in these habitats, it can be safely assumed that both the geology of the area and the acidity of the habitat offer a challenge for land snails during their growth. This may partly explain their low abundance. As far as current data allows a conclusion, the occurrence of snails is concentrated on or near the summits of the tepuis. Huber (1988) has made a distinction between highlands (> 1,500 m), uplands (500–1,500 m) and lowlands (< 500 m). From the 21 species reported in this area, 14 are known to inhabit only the highlands; two are only from the uplands and one species has a broad altitudinal distribution (Tab. 8).

Ecologically, with the exception of *Olympos nimbus*, which is ground-dwelling, all species have been observed in low shrubs or tree-like vegetation (notably *Brocchinia* and *Bonnetia* forests with trees up to 3 m high). In a Principal Component Analysis (PCA) of different factors related to snail distribution, it appears that endemic plant species play an important role in the primary PCA factor of habitat diversity (Breure, 2009: tab. 5). Local endemic plant species have mainly been recorded from the slopes and summits of individual tepuis, with the highest numbers recorded at Cerro de la Neblina, Macizo del Chimantá, Cerro Duida and Cerro Sipapo (Berry et al., 1995; Huber, 1988). Among these plant endemics, *Bonnetia* species are worth mentioning since several endemic snails appear to be associated with them. It is noteworthy that *Plekocheilus* species in the Pantepui area often occur in paramoid scrub (Breure, 2009; Huber, 1988; Huber, 1995: pl. 37), a habitat which they share with certain Andean species groups in the same genus.

3.1.4. Systematics

All known land snails from the Pantepui region are Stylommatophora, with the majority classified in the superfamily Orthalicoidea. For a key to families, genera, and species, see Tables 9–11. The species are summarized below; see Thompson (2008), Breure (2009), Simone (2010), and Breure & Schlögl (2010) for more details, especially on the anatomy (data on radulae and mandibulae is presented below for Orthalicoidea species). The species are treated according to the different regions in the Pantepui area relevant to this paper; Berry et al. (1995) distinguished Eastern (herein Roraima, Yuruani, and Macizo del Chimantá), Central, Western, and Southern Pantepui regions.

3.1.4.1. Species of Macizo del Chimantá

Seven identified land snail species occur on the various tepuis which form part of Macizo del Chimantá. These are;

Plekocheilus (P.) alticola Haas, 1955 (Fig. 107A)

Description: The shell is up to 44.3 mm, 1.75 times longer than wide, elongate-ovate, last whorl relatively slender, dark-brown coloured with oblique reddish-brown stripes, sculptured with malleation and a distinct columellar fold visible in the aperture.

Distribution. The sole locality known is Toronó Tepui, where this type material was collected on the slopes bordering Caño Mojado, 2,250 m. Type material in FMNH (S2442, holotype).

Remarks. Breure & Schlögl (2010) expressed doubts on the subspecific status of *Plekocheilus fulminans alticola* and *P. f. lintera* (Sowerby, 1890).

Diagnosis: After having studied the type of *P. fulminans* (Nyst, 1845) in the Brussels collection (Breure, 2011), these two taxa are treated herein as separate species.

Plekocheilus (P.) vlceki Breure & Schlögl, 2010 (Figs. 107C, 108L–M)

Description: The shell is up to 30.9 mm, 1.75 times longer than wide, with an almost uniform (dark-) yellowish to chestnut-brown colour, a finely malleated sculpture crossed by spiral lines on the last whorl and a marked columellar fold. Its colour is yellowish-beige.

Radula. Rows are slightly V-shaped, the outermost lateromarginals curved distally; radula formula C/1 + LM 60/2 (teeth type C-6, LM-10, LM-11; see Breure, 1978, 1979). The central teeth are monocuspid, triangular, first lateral teeth acute, with weakly developed ectocones, the next 16 lateromarginals bicuspid, with rather blunt spatula-shaped mesocones and more acute, ovate ectocones. The outer 44 lateromarginals bicuspid, shifted, with rather blunt spatula-shaped mesocones and blunt deltoid ectocones, which may be bifid in the outermost teeth.

Genitalia. See Breure & Schlögl (2010: fig. 4A).

Ecology. Found on the floor of a canyon covered with a dense *Bonnetia* forest and low vegetation. The snails occurred in *Brocchinia tatei* (Bromeliaceae) at the time of collecting.

Distribution. Known only from Churí Tepui, Sima Colibrí, 2,100 m. Type material in MZSP, RMNH (114233, holotype), and UF.

Remarks. The central teeth of the radula are without the slight protuberances at base reported for *P. (Eurytus)* species and the first lateral teeth are more acute than the second and beyond. This pattern has also been observed in *P. (P.) aurissileni* (Born, 1780), type species of the genus, and a number of other *Plekocheilus* species (Breure, 1978). The mesocones of the first lateral in *P. vlceki* are, however, more developed than those in the group just mentioned, and resemble those of *P. (Eurytus)* species from Pantepui.

Plekocheilus (Eurytus) juliani Haas, 1955 (Fig. 107I)

Description: The shell is up to 54.2 mm, twice as long as wide, elongate-ovate, colour pattern consisting of obliquely descending dark-brown to blackish stripes on a brown background which is darker on the last whorl. Sculpture consisting of short, oblong granules arranged in spiral rows.

Ecology. Steyermark collected the species in *Bonnetia* forest.

Distribution. It occurs on Macizo del Chimantá: summit of Apacará Tepui, 2,100 m; northwest part of summit of Abácapa Tepui; Auyán Tepui, 1,970 m. Specimens tentatively referred to this species have been found on Churí Tepui, 2,130 m. Type material in FMNH (49737, holotype).

Plekocheilus (Eurytus) mundiperditi Haas, 1955 (Figs. 107H, 108F–I, 108O)

Description: The shell is up to 55.3 mm, 1.8 times longer than wide, elongate-ovate, last whorl somewhat swollen and saccate, colour pattern with blackish to dark-brown dots on a (dark-) brown background. Sculptured with puckered spiral bands of oblong granules divided by narrow, smooth areas.

Mandibula. Bow-shaped, central part consisting of three fused plates with 14 lateral plates on each side, tapering towards the end.

Radula. Data additional to Breure (1978). Rows straight; radula formula, one monocuspid central tooth (C/1) and 59 bicuspid lateromarginals (formula: C/1 + LM 59/2; teeth types C-6, LM-10, LM-11, see Breure 1978). The central teeth are monocuspid, with triangular to ovate mesocones and weakly developed protuberances. The first 15 lateromarginals bicuspid, with rather blunt spatula-shaped mesocones and more acute, ovate ectocones. The outer 44 lateromarginals bicuspid, shifted, with rather blunt spatula-shaped mesocones and blunt deltoid ectocones, which may be bifid in the outermost teeth.

Ecology. Found in herbaceous vegetation and in *Bonnetia* forest.

Distribution. Widely distributed on Macizo del Chimantá: Apacará Tepui, 2,150 m; Aparamán Tepui, 2,120 m; Toronó Tepui, bordering valley of Caño Mojado, 2,250 m; Murey Tepui, 2,300 m. Type material in FMNH (52436, holotype).

Plekocheilus (Eurytus) breweri Breure & Schlögl, 2010 (Figs. 107G, 108R)

Description: The shell is up to 41.7 mm, 1.8 times longer than wide, colour pattern with oblique stripes of reddish – to blackish-brown, often with a yellowish ‘shadow’ besides the stripes on the last whorl. Sculptured with spiral, puckered bands of oblong granules. Its colour is dark-grey to blackish.

Mandibula. Bow-shaped, central part consisting of three fused plates, 12 lateral plates on each side, tapering towards the end.

Radula. Row straight; radula formula C/1 + LM 52/2 (C-6, 20 lateromarginals C-10, 32 lateromarginals C-11); similar to *P. mundiperditi*.

Genitalia. See Breure & Schlögl (2010: fig. 4B–F).

Ecology. Collected in stands of *Brocchinia hecetioides*, up to 1 m high, and in *Brocchinia tatei*. See Breure & Schlögl (2010) for more details and discussion of the relationship between snails and carnivorous plants in the area.

Distribution. Churí Tepui; both on the summit plateau (2,400 m) and in the canyon Sima Colibrí (2,285 m). Type material in MLSC, MZSP, RMNH (114235, holotype), SNMSZ and UF.

Drymaeus (D.) steyermarki (Haas, 1955) (Figs. 107E, 108A–E)

Description: The shell is 27.3 mm, 2.1 times longer than wide, colour whitish to brownish with irregular axial, small streaks of chestnut-brown. White lip, with a very faint pinkish border lining the inside of the aperture.

Radula. Data additional to Breure & Eskens (1981). Rows slightly curved; radula formula C/1 + LM 53/3 (C-8, LM-12). Central teeth monocuspid, with relatively small, acute triangular mesocones. The lateromarginals are tricuspid, shifted, with rather blunt ovate mesocones, acute elongate-ovate endocones and acute, deltoid ectocones, which may be bifid in the outermost teeth.

Distribution. A single known specimen, collected on plateau below the summit of Apacará Tepui, 1,800 m. Type material in FMNH (49735, holotype).

Drymaeus (D.) extraneus (Haas, 1955) (Fig. 107D)

Description: The shell is up to 32 mm, 2.2 times longer than wide, uniform whitish or with spiral colour bands of reddish-brown, side slightly convex.

Mandibula. See Breure & Eskens (1981: fig. 340).

Radula. Formula C/3 + LM 90/3 (C-12, LM-18). See Breure & Eskens (1981: tab. 4).

Distribution. Summit of Apacará Tepui, 2,100 m, and along the trail from Río Tirica to the lower summit camp, 1,800 m; west side of Abacará Tepui, 1,189 m. One adult and two juvenile specimens known. Type material in FMNH (49736, holotype).

3.1.4.2. Species from other tepui areas

3.1.4.2.1. Eastern Pantepui region

Eastern Pantepui region has only partly been explored in terms of its malacofauna. Only two tepuis, Roraima Tepui and Yuruaní Tepui are currently known to have (endemic) snail species.

Plekocheilus (P.) linterae (Sowerby, 1890) (Fig. 107B)

Description: The shell is up to 43 mm, 1.8 times longer than wide, elongate-ovate, with a relatively slender last whorl, some irregular, undulating axial reddish-brown stripes may be present, sculptured with axial riblets broken into oblong granules by spiral, incised lines on the last whorl.

Distribution. Known from Roraima Tepui, 2,400 m. Type material in NHM (1889.4.25.1, holotype).

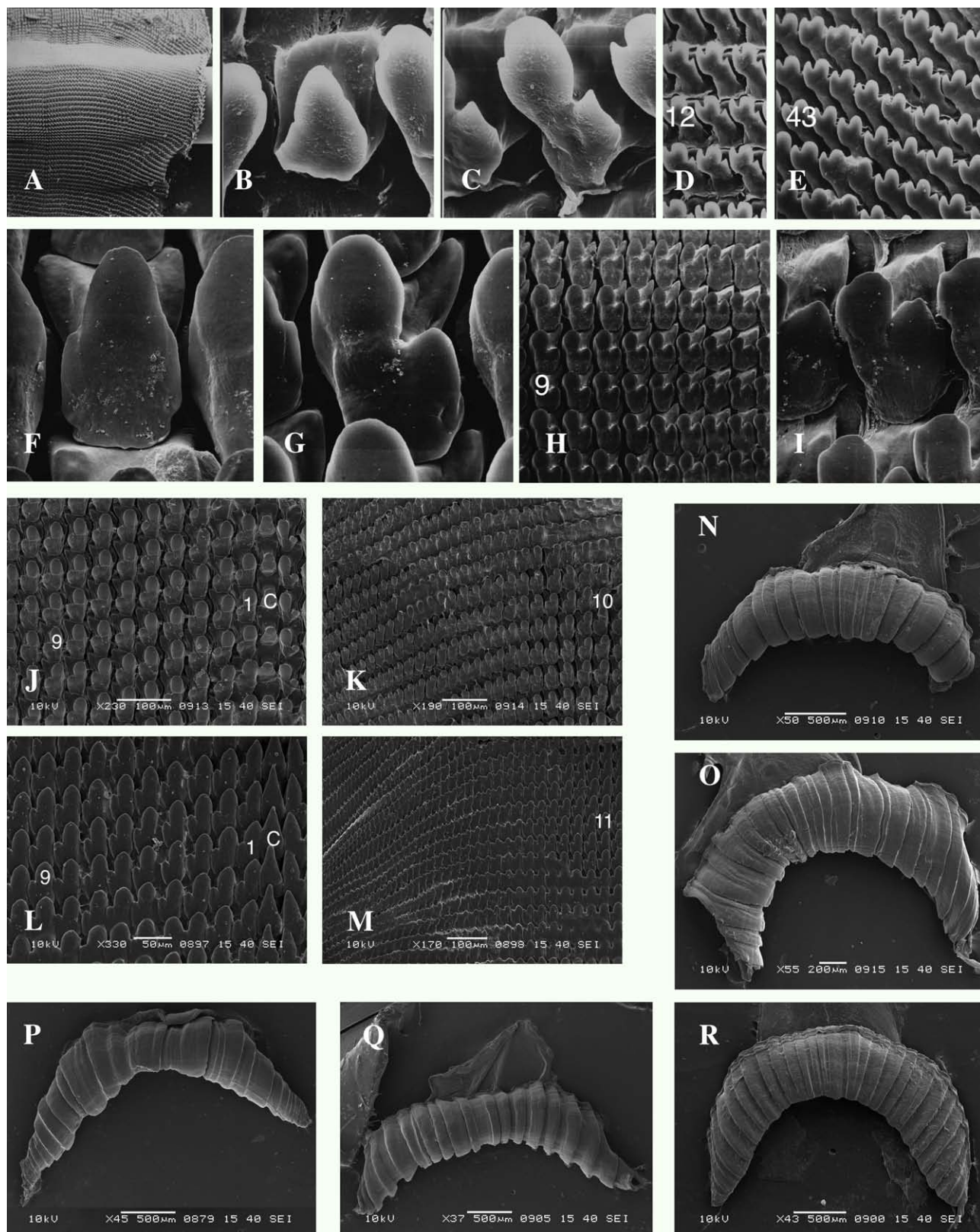


Fig. 108: Scanning electron microscope photographs. Radulae. A–E – *Drymaeus steyermarki* (Haas, 1955); A – overview of radula, x120; B – central teeth, x2300; C – lateromarginal 2, x1150; D – lateromarginals 12–14, x570; E – lateromarginals 43–49, x570. F–I – *Plekocheilus mundiperditi* Haas, 1955; F – central teeth, x1200; G – lateromarginal 2, x1250; H – lateromarginals 9–16, x240; I – lateromarginal 22, x1200. J–K – *P. nebulosus* Breure, 2009; J – central and lateromarginals 1–9; K – lateromarginals 10–34. L–M – *P. vlceki* Breure & Schlögl, 2010; L – central and lateromarginals 1–9; M – lateromarginals 11–45. Mandibulae. N – *P. nebulosus* Breure, 2009. O – *P. mundiperditi* Haas, 1955. P – *P. huberi* Breure, 2009. Q – *P. tatei* Haas, 1955. R – *P. breweri* Breure & Schlögl, 2010.

Plekocheilus (Eurytus) sophiae Breure, 2009 (Fig. 107F)

Description. The shell is 44 mm, 1.9 times longer than wide, elongate-ovate, last whorl rather convex, surface shining, sculptured with horizontal treads, partly anastomosing. Its colour is light brownish, with grey tentacles.

Genitalia. See Breure (1978: fig. 2 [as *P. blainvilleanus linterae*]).

Distribution. Described from a single shell in the UF collection (holotype 24413). In December 2010, a living specimen was observed at the type locality, Yuruaní Tepui, 2,300 m (Ph. Kok, pers. commun.).

3.1.4.2.2. Central Pantepui region

In this region, snail species have been recorded only from Cerro Guaiquinima, Cerro Marahuaka and Cerro Duida.

Plekocheilus (Eurytus) fusitorsus (Oberwimmer, 1931) (Fig. 107J)

Description: The shell is up to 63.3 mm, 1.7 times longer than wide, colour (yellowish-)brown with darker, undulating stripes which are bordered by a yellowish 'shadow' on the last whorl, sculptured with fine granulation, aperture ovate, relatively wide.

Distribution. "Río Padamo" (type locality); Cerro Guaiquinima. Type material in SMF (5142, holotype).

Plekocheilus (Eurytus) gibber (Oberwimmer, 1931) (Fig. 107K)

Description: The shell is 55.3 mm, twice as long as wide, colour yellowish, turning reddish-brown on the upper whorls, with irregular dots and short, narrow undulating lines of the same colour on the last whorl, sculptured with fine granulation, aperture ear-shaped with a distinct columellar fold.

Distribution. Known only from the holotype, collected on Cerro Marahuaka, 2,170 m (SMF 5143).

Plekocheilus (Eurytus) tatei Haas, 1955 (Figs. 107O, 108Q)

Description: The shell is up to 62 mm, 1.9 times longer than wide, colour brownish, lighter on the upper whorls, the last whorl with dark brown, oblique, slightly zig-zag stripes, sculptured with very fine granulation. Aperture ovate, relatively wide, with a weak columellar fold. Its colour is dark-brown.

Mandibula. Bow-shaped, central part consisting of three fused plates, eight lateral plates on each side, tapering towards the end.

Radula. Rows slightly V-shaped; radula formula C/1 + LM 42/2 (C-6, 14 lateromarginals C-10, 28 lateromarginals C-11); similar to *P. mundiperditi*.

Genitalia. See Breure (2009: fig. 2A).

Distribution. Cerro Duida. Type material in AMNH (73455, holotype) and FMNH.

Plekocheilus (Eurytus) tepuiensis Breure, 2009 (Fig. 107L)

Description: The shell is 35 mm, 1.7 times longer than wide, pale yellowish-brown with obliquely descending zig-zag streaks; surface hardly shining, with spiral lines of dot-like granules on the last whorl.

Distribution. Known only from the holotype in RMNH (112031), collected at 800 m elevation on Yapacaná Tepui.

Drymaeus (D.) yapacanensis Breure & Eskens, 1981 (Fig. 107P)

Description: The shell is up to 31.2 mm, 2.2 times longer than wide, colour pink to yellowish, with axial reddish-brown streaks,

which may be forked above but are broader below. Aperture with a slightly expanded peristome, pink inside.

Mandibula. See Breure & Eskens (1981: fig. 343).

Radula. See Breure & Eskens (1981: pl. 3, figs 5–6).

Genitalia. See Breure & Eskens (1981: fig. 159).

Distribution. Endemic to Yapacaná Tepui; recorded from 1,300 m elevation. Type material in RMNH (55331, holotype).

Plekocheilus (Eudolichotis) sinuatus (Albers, 1854)

Remarks: A single shell was found in the lowland northwest of Yapacaná Tepui (Breure, 2009: p. 39, fig. 6K).

3.1.4.2.3. Western Pantepui region

This region is virtually unknown for malacofauna.

Plekocheilus (Eurytus) cf. plectostylus (Pfeiffer, 1848)

Remarks: One weathered specimen, tentatively referred to this species is reported by Borrero & Breure (2011) from Cerro Guanay at the eastern tributary of Río Parguaza. This is approximately 05° 51' N 066° 18' W. The shell was found in tepui scrub at about 1,700 m, in the central-southern summit section of the meseta (O. Huber, pers. commun.).

3.1.4.2.4. Southern Pantepui region

Snails have only been collected on the Cerro de la Neblina, which is partly in Venezuela and partly on Brazilian territory.

Columbinia exul Thompson, 2008 (Fig. 107R)

Description: The shell is slender, up to 24 mm, 4.5 times longer than wide, colour brownish, lighter at the blunt apex which is minutely granulate, teleoconch sculptured with fine, straight thread-like riblets, last whorl relatively short. Aperture ovate, approximately as wide as shell, projecting forward on a short neck, the palatal plica are at a relatively low position.

Anatomy. See Thompson (2008).

Ecology. Collected in a dense, broadleaf rainforest 4–5 m above ground level on a dead tree-trunk.

Distribution. Venezuela, Edo. Amazonas, Cerro de la Neblina, valley north of Pico Phelps, at 1,200–1,400 m elevation. Type material in MLSC, SMF and UF (48631, holotype).

Plekocheilus (Eurytus) huberi Breure, 2009 (Fig. 107N)

Description: The shell is up to 47.9 mm, twice as long as wide, thin, with light chestnut-brown colouring and descending, narrow reddish-brown 'lightning' stripes; an almost lustreless surface, very finely granulated on the last whorl.

Mandibula. Bow-shaped, central part consisting of three fused plates, ten lateral plates on each side, tapering towards the end.

Radula. Rows slightly V-shaped; radula formula C/1 + LM 44/2 (C-6, 17 lateromarginals C-10, 27 lateromarginals C-11); similar to *P. mundiperditi*.

Genitalia. See Breure (2009: fig. 2B–D).

Ecology. Found in a cloud forest in bromeliads.

Distribution. Venezuela, Edo. Amazonas, Cerro de la Neblina, at the Brazilian-Venezuelan border and near Pico Maguire; at 1,800–2,000 m elevation. Type material in RMNH and UF (284764, holotype).

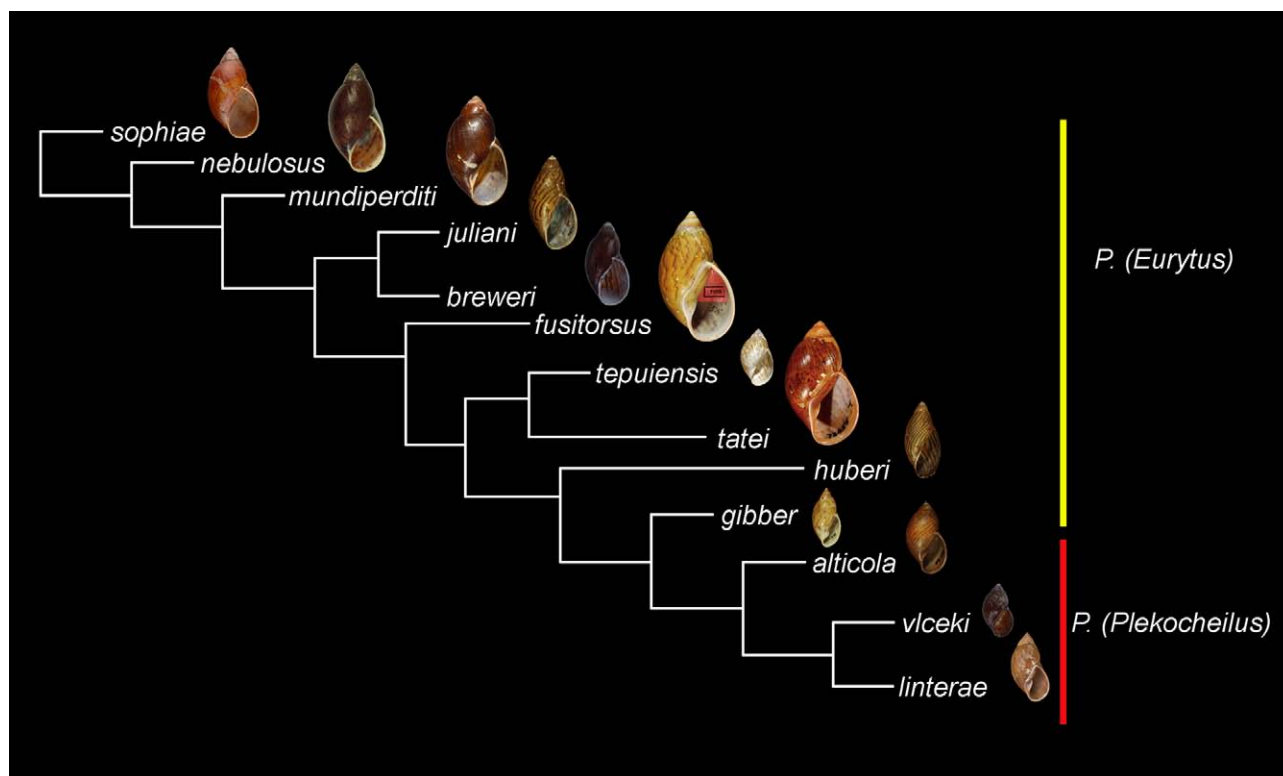


Fig. 109: Parsimonious tree of Pantepui *Plekocheilus* species, based on the characters given in Tab. 12, using traditional search with equal weights in TNT.

Plekocheilus (Eurytus) nebulosus Breure, 2009 (Figs. 107M, 108J–K)

Description; The shell is up to 62.5 mm, twice as long as wide, sculptured on the last whorl with horizontal threads of various length, often anastomosing; with darker spots on uniform brownish background colouring; aperture decidedly descending in front, peristome somewhat thickened and reflexed.

Mandibula. Bow-shaped, central part consisting of three fused plates, nine lateral plates on each side, tapering towards the end.

Radula. Rows slightly V-shaped; radula formula C/1 + LM 42/2 (C-6, 16 lateromarginals C-10, 26 lateromarginals C-11); similar to *P. mundiperditi*.

Genitalia. See Breure (2009: fig. 2E–F).

Ecology. Found in bromeliad scrub forest of *Bonnetia maguireorum*, 2–3 m high.

Distribution. Venezuela, Edo. Amazonas, Cerro de la Neblina, various localities near Pico Phelps and Pico Maguire; at 1,800–2,100 m elevation. Type material in RMNH and UF (284723, holotype). New records: Brazil, Edo. Amazonas, Pico de la Neblina, Igarapé Café, V. Py-Daniel & U. Barbosa leg., 28.ix.1990 (INPA 1502a/1); ibidem, Pico de la Neblina, Cumbre do Pico, 3,014 m, V. Py-Daniel & U. Barbosa, 2.x.1990 (INPA 1517/2).

Drymaeus rex Breure, 2009 (Fig. 107S)

Description: The shell is up to 40.7 mm, 2.2 times longer than wide, with a white line below the suture and typically with three interrupted spiral colour bands of chestnut – to blackish brown, crossing weaker axial streaks of a less intense colour. Aperture with a white, slightly expanded lip, bordered pink inside.

Genitalia. See Breure (2009: fig. 7).

Ecology. Found in *Brocchinia* plants.

Distribution. Venezuela, Edo. Amazonas, Cerro de la Neblina and various localities near Pico Phelps and Pico Maguire; typically at elevations of 1,800–2,100 m, but recorded as low as 200 m on the northwestern side of Cerro de la Neblina. Types in RMNH and UF (284726, holotype).

New record: Brazil, Edo. Amazonas, Pico de la Neblina, Igarapé Café, V. Py-Daniel & U. Barbosa leg., 28.ix.1990 (INPA 1502b/1)

Olympus nimbus Simone, 2010 (Fig. 107Q)

Description: The shell is up to 15 mm wide with a height/width ratio of 0.9, spire dome-shaped and relatively well developed, sculptured with a regular mosaic of uniformly spaced nodules, each row intercalated with neighbouring rows, with about 4–5 spiral rows on the penultimate whorl and the last whorl is smooth; colour beige, with three spiral, narrow bands split into spots which are fairly uniformly and equidistantly distributed. Aperture semicircular, compressed by penultimate whorl; umbilicus very narrow.

Anatomy. See Simone (2010).

Distribution. Brazil, Edo. Amazonas, São Gabriel da Cachoeira, Cachoeira do Tucano, at 100 m elevation. Type material in MZSP (87151, holotype).

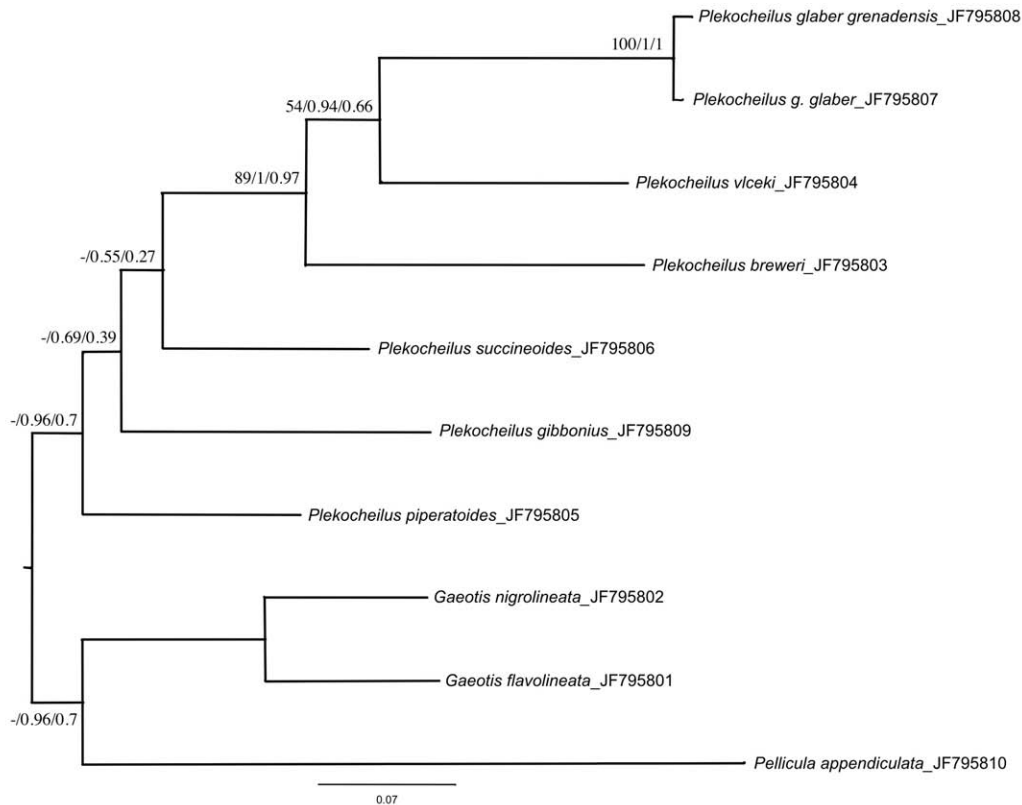


Fig. 110: Maximum likelihood tree of *Plekocheilus* species, based on CO1 sequences (GenBank accession numbers mentioned behind the taxon names); Chi2-based parameter respectively SH-like Approximate Likelihood-Ratio Test values are presented as node values. Scale bar in substitutions per site.

3.1.5. Morphological and phylogenetic analyses

Morphological analysis divided the *Plekocheilus* species into different sub-groups, based on several characteristics of their external shell morphology (Tab. 12). They were then analysed under parsimony using TNT. The results in Figure 109 show that (1) *Plekocheilus* (*P.*) species are more derived than *P. (Eurytus)* species; and (2) with the sole exception of *P. nebulosus*, the species occurring on the western tepuis are more derived than those on the eastern ones.

Phylogenetic analyses of CO1 sequences were performed only on *Plekocheilus* species. These comprised seven taxa; two from Pantepui, three from Colombian and Venezuelan Andes and two from the West Indies (Fig. 110). The maximum likelihood analyses resulted in a tree (log-likelihood – 3987.16), where the three Andean species are basally placed. The support values are, however, relatively low (bootstrap < 50 / Chi2 0.94 / SH 0.66). The Pantepui/West Indian taxa appear as a well-supported group (89 / 1 / 0.97), in which the two Pantepui taxa are more basal. A network analysis of this molecular data indicates a reticulate pattern (Fig. 111); however, internal nodes in split graphs are not necessarily equivalent to those in a bifurcating tree and hence reticulation in these graphs may only be seen as an indicator of phylogenetic complexity rather than diagnostic of specific evolutionary events (Winkworth et al., 2005; Huson & Bryant, 2006). Although the limited taxon sampling does not allow further conclusions, the

grouping of the Pantepui taxa corroborates the results of the morphological analysis. Additional analyses with other species from this genus should clarify the intra-generic relationships.

3.1.6. Discussion

Shell morphology was the prime characteristic used to divide *Plekocheilus* into sub-genera. All sub-genera occur in the Pantepui region, with the exception of the Andean *P. (Aeropictus)*, but the highland species all belong to *P. (Plekocheilus)* and *P. (Eurytus)*. A more in-depth analysis of the patterns, found among different *Plekocheilus* taxa, reveals that groupings based on external shell morphologies do not always coincide (Breure, unpublished data). Moreover, there are some taxa showing characteristics that may be attributed to two different subgenera (Borrero & Breure, 2011). The anatomical work done for this study generally corroborates the data by Breure (1978), showing that two groups may be distinguished by their radula structure. However, the radula of *P. vlceki* shows that the differences between the two groups may be more transitional than previously thought (Breure, 1978). The overall conclusion related to Pantepui *Plekocheilus* taxa is that there appears to be insufficient available data to test any biogeographical hypothesis. At the same time, it is notable that the complexity indicated in the phylogenetic network analysis in Figure 111 is reflected in the morphological data.

In addition, the limited data on *Drymaeus* taxa does not warrant conclusions at this time. However, it is interesting that a

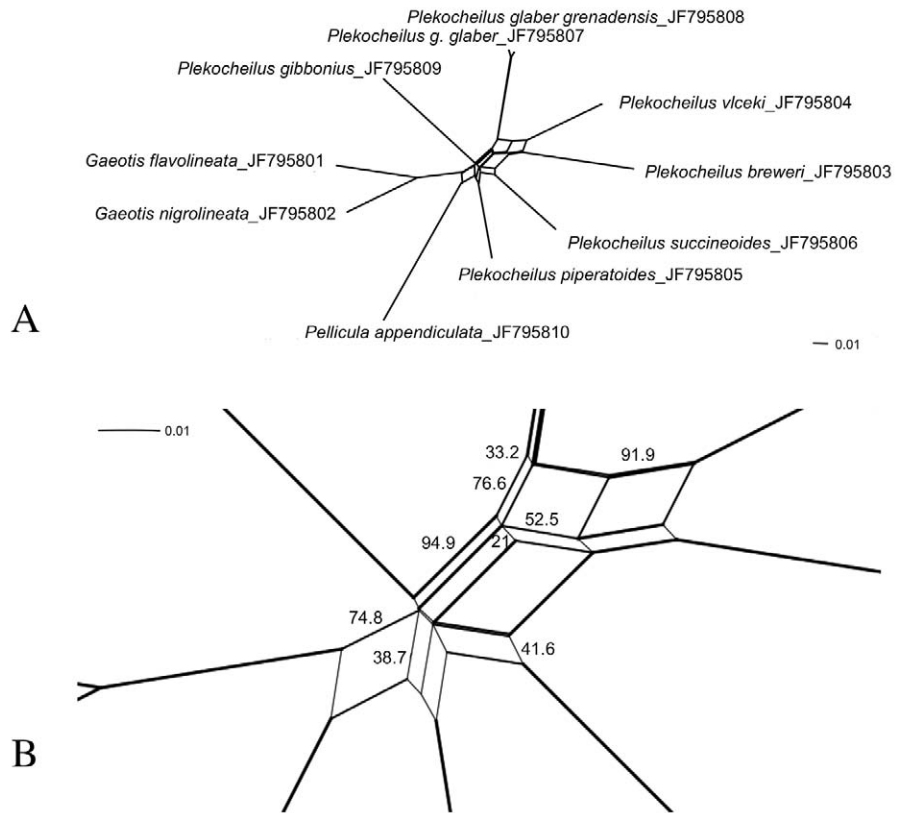


Fig. 111: A split tree inferred from the same sequences as in the previous figure, showing the relationships between the different lineages (A); bootstrap percentages of the reticulate central pattern, with 95% confidence values shown in bold lines (B).

preliminary phylogenetic analysis shows that *D. rex* appears quite basal in the tree of analyzed *Drymaeus* taxa (Breure, unpublished data). No anatomical or molecular data is available for the only non-Orthalicoid highland taxon, *Columbinia exul*, to be able to ascertain its relationships within the Clausiliidae.

When we restrict ourselves to the ‘true’ Pantepui species [excluding lowland species such as *Olympus nimbus* and *Plekocheilus (Eudolichotis) sinuatus*], the biodiversity of the land snails is strikingly large compared to the general situation in Venezuela (Fig. 112). The total summit area of the tepuis is 12,290 km² (Huber, 1995: p. 61), and this is just 1.4 % of the area of Venezuela. This figure includes tepuis where no snails are known,

and when this area is restricted to the tepuis mentioned in this paper (4,060 km²), it amounts to 0.05% of the Venezuelan territory. The number of land snails on the tepuis, however, accounts for 15% of the known Venezuelan malacofauna (Fig. 112D; see also Martínez, 2003). It must be noted that the Venezuelan terrestrial malacofauna is relatively poorly known and appears not to be very biodiverse (Breure & Mogollón, 2010: fig. 1). Comparing orthalicoid and other species in the Pantepui area, the relative dominance of the former group is apparent (Fig. 112B vs. 112C). Given the specific acidic habitats found in the Pantepui highlands, the relatively high biodiversity of snails in this still under-explored area is quite remarkable. However, it

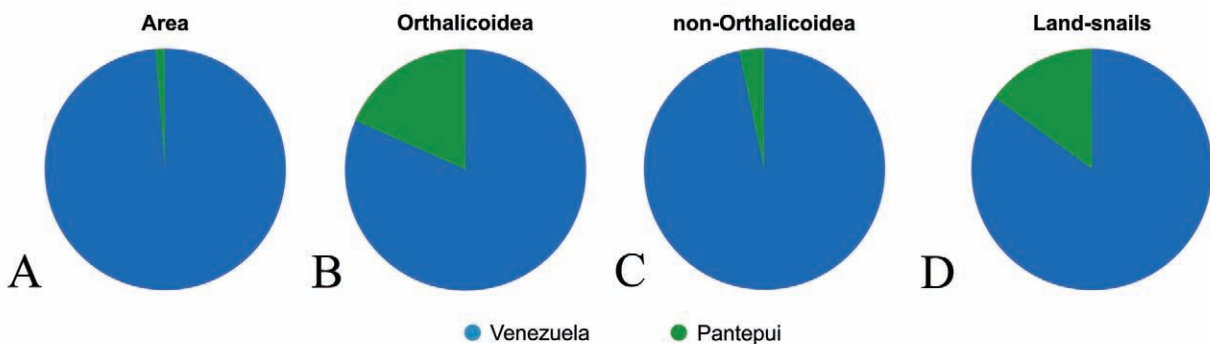


Fig. 112: Pantepui versus Venezuela as a whole. A – Area (Pantepui area equals total summit area of tepuis, cf. Huber, 1995). B – Total number of Orthalicoidea species (this study). C – Total number of non-Orthalicoid land snails (adapted from Martínez, 2003). D – Total number of land snails.

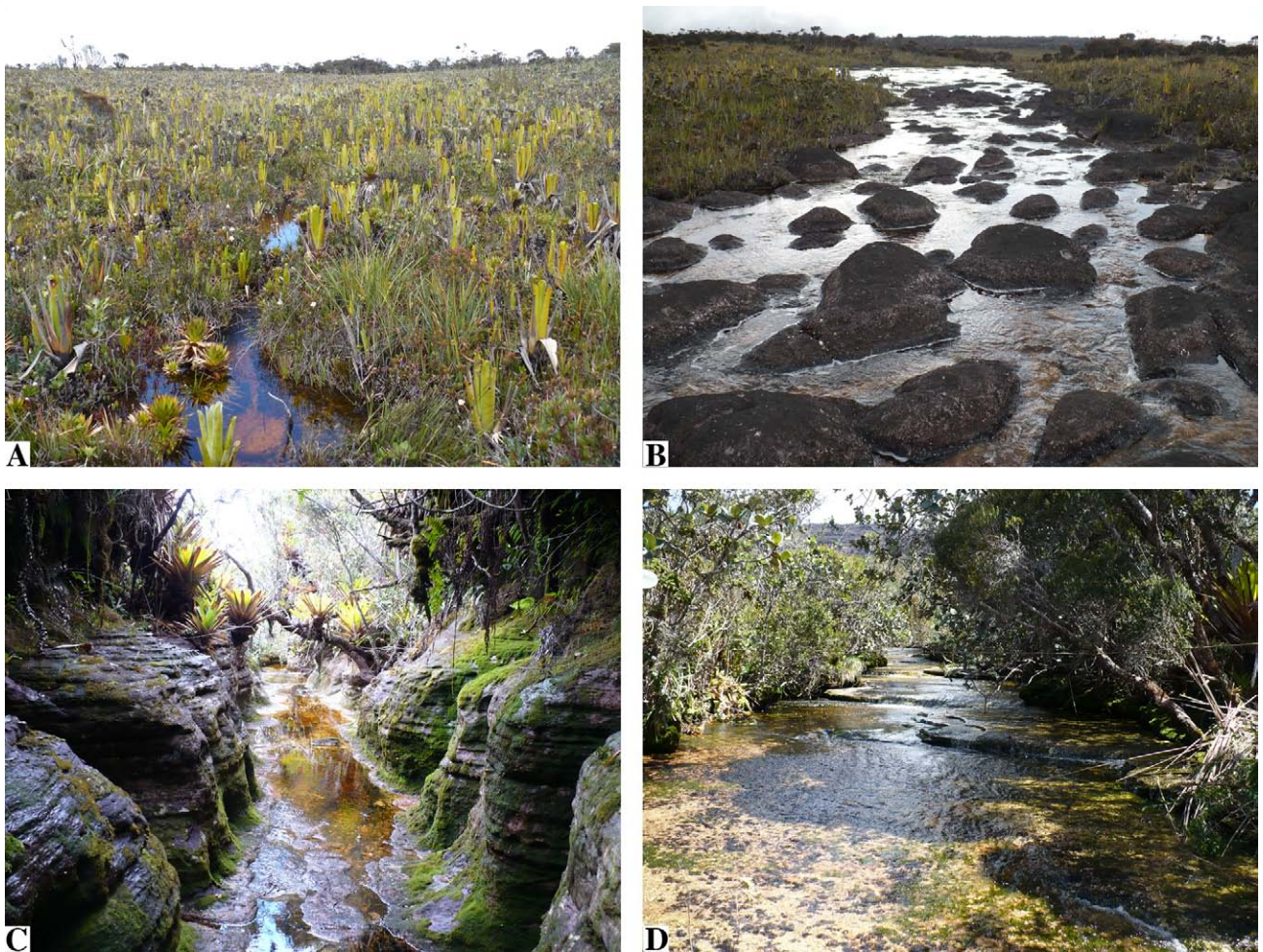


Fig. 113: Aquatic habitats on Churí Tepui: A – Helocrene springs of Western River (C10). B – Middle reaches of Western River (C9). C – Quebrada Lila (C1), typical spring stream with bedrock bottom. D – Río Olinka (C5) with bedrock bottom.

must be noted that while Orthalicoidea are relatively large species that non-malacologists can easily find, it is fully expected that the relative importance of other groups will increase when the area is better explored by malacologists.

3.2. MAJOR GROUPS OF AQUATIC INSECTS OF PANTEPUI

3.2.1. Introduction

Aquatic fauna of the Guyana region follows the general pattern of the high level of endemism on the summits of tepuis (Spangler & Faitoute, 1991; Čiampor & Kodada, 1999; Issa & Jaffe, 1999; Kodada & Jäch, 1999; De Marmels, 2007; Derka et al., 2009; Maier & Spangler, 2011; Nieto & Derka, 2011). The summits bear different types of aquatic habitats, from phytotelmata and temporary pools in bare rocks to large wetland meadows and medium sized rivers. Black water streams with bedrock bottoms, cascades and waterfalls and long and deep pools are the most common types of running waters (Fig. 114A–C). The total absence of a hyporheic environment is also a typical attribute of

Pantepui streams (Figs. 113B–D, 114A,C,E). Another important factor is the very low water retention capacity of watersheds, which is responsible for wide discharge fluctuations (Derka, pers. observation). Moreover, these streams are also extremely oligotrophic and low in minerals (conductivity usually ranges between 10 and 20 $\mu\text{S}\cdot\text{cm}^{-1}$). They are acidic ($\text{pH}=3.5\text{--}5.5$) and they can contain high concentrations of organic compounds leached from vegetation (Lánczos et al., 2007; Aubrecht et al., 2011). The streams flow through the quartzite caves at Churí Tepui and Mt. Roraima (e.g. Šmída et al., 2008^a). But even at the most visited and explored tepuis of Mt. Roraima, Auyán Tepui or tepuis in Chimantá Massif, aquatic insects were insufficiently studied. In addition, important components of aquatic ecosystems such as algae have been studied only during the last decade (Fučíková & Kaštovský, 2009; Kaštovský et al., 2011). Entire insect orders were practically unknown from the plateaus. For example, although mayflies are a common part of the stream ecosystems (Derka et al., 2012), the first mayfly records from Chimantá Massif and Mt. Roraima have been published only recently (Derka et al., 2009). This is also true for stoneflies, previously unknown in the Pantepui Province (Derka et al., 2010). Records of other aquatic insect groups have now been published;

including Orthoptera (Issa & Jaffe, 1999; Derka & Fedor, 2010), Heteroptera (Spangler, 1986), Trichoptera (for a review see Derka & Zamora-Muñoz, 2012), Coleoptera (Spangler, 1981, 1985; Spangler & Faitoute, 1991; Čiampor & Kodada, 1999; Kodada & Jäch, 1999; Maier & Spangler, 2011; Kodada et al., 2012), Diptera (Barrera et al., 1989; Harbach & Navarro, 1996). One of the best studied groups is the order Odonata, thanks to numerous articles by the Venezuelan specialist Jurg Carl De Marmels (e.g. De Marmels, 1983, 1985, 1988, 1990, 1992, 1994, 1999, 2007). Odonata is considered to be the first group of aquatic insects described from the tops of Mt. Roraima and Mt. Duida (Needham, 1933; Needham & Fischer, 1940; Klots 1944). The study of Cerro de la Neblina organized by Charles Brewer-Carías (Brewer-Carías, 1988) was a great contribution to investigation of aquatic fauna, and is responsible for the majority of information on Pantepui fauna. Although Cerro de la Neblina is not a typical tepui with a flat summit isolated by sheer cliffs, it has similar geological and climatic conditions to the other tepuis (Brewer-Carías, 1988), and therefore, specimens sampled above 1,500 m a.s.l. should be attributed to the Pantepui Province. Numerous new taxa from there have been described from the material of aquatic insects collected during various expeditions. These descriptions were published by Spangler (1985, 1986), Savage (1987), Flint et al. (1987), Holzenthal (1988), Schmid (1989), Johanson & Holzenthal (2004), Hamilton & Holzenthal (2005) and Maier & Spangler (2011).

Although Venezuelan cave fauna comprises more than 500 species, only three aquatic insect orders have been reported from Venezuelan caves to date; (1) Hemiptera, genera *Microvelia*, *Rhagovelia* (fam. Veliidae) and *Brachymetra* (fam. Gerridae); (2) Diptera from the families Tipulidae, Psychodidae and Chironomidae; and (3) Coleoptera from the families Dytiscidae, Hydrophilidae, Dryopidae and Elmidae (Galán & Herrera, 2006; Kodada et al., 2012). Since the majority of biospeleological research has been carried out in karst systems, there is almost a complete lack of information available from the recently discovered quartzite caves (e.g. Vignoli & Kovayik, 2003). The first data on aquatic insects from the Venezuelan quartzite caves was published by Charles Brewer-Carías (in Šmída et al., 2005^b). This included the unique record of mayflies in a stream in the recently discovered Cueva Charles Brewer. The author mentioned “one species of *Ephemera* flying in dimness near where the river emerges from the cave”. Obviously, this was not a member of the genus *Ephemera*, but some different unidentified mayfly, which Derka et al. (2009) later identified as an undescribed member of the genus *Massartella*. Derka et al. (2009, 2010) reported mayflies (Ephemeroptera) and stoneflies (Plecoptera) from Cueva Charles Brewer and from other caves at Churí Tepui. These articles and the above mentioned report of Brewer-Carías in Šmída et al., (2005^b) are considered to be the first reports of mayflies and stoneflies in Venezuelan caves. Orthoptera is a terrestrial insect order found there with representatives of the Gryllidae, Palangopsidae and Rhaphidiophoridae families, as reported by Galán & Herrera (2006). Although this last group was often seen during our explorations in the Churí Tepui and Mt. Roraima caves, the collected material remains unidentified. The same is true for other aquatic invertebrates, e.g. *Turbellaria*

(Fig. 115F). Issa & Jaffe (1999) described a new genus *Hydrolutos* comprising four species from four tepuis, unique within orthopterans, having a plastron-like structure on the pleuro-sternal area of their thorax and abdomen. Derka & Fedor (2010) described a further species, *Hydrolutos breweri* (Anostostomatidae), from Cueva Charles Brewer. Recently, new still unidentified material was collected in Cueva del Tigre in the vicinity of Santa Elena de Uairén (Derka, unpublished data).

Aquatic fauna of the Pantepui caves and spring streams is mostly composed of cold stenotherms, intolerant to elevated temperatures. Meanwhile, the fauna found in larger shallow streams (Figs. 113B,D, 114A–C), in wetlands with stagnant water (Figs. 113A, 114D) and in the temporary pools on tepuis' plateaus is assumed to be adapted to high diurnal thermal fluctuations. Research herein contributes to the knowledge of the Pantepui aquatic fauna, with special attention paid to the inhabitants of cave and spring streams. Study focuses on mayflies, stoneflies, caddisflies, beetles of the Elmidae family and orthopterans from the genus *Hydrolutos*, and also reviews assembled information concerning Pantepui Ephemeroptera, Plecoptera and Trichoptera. Previously, this information was scattered throughout different articles, especially in the case of Trichoptera (Derka & Zamora-Muñoz, 2012).

3.2.2. Material and methods

Qualitative samples were taken by a 0.5 mm mesh kick net and by individual collection from stones and woody debris. Winged adults were collected by entomological net, individually collected from foam accumulations in streams, and also by light trapping. Some mayfly nymphs were reared to subimagos and adults during our field work. Collected material was fixed in 97% ethanol. Morphological characters were studied and photographed under stereomicroscopes and microscopes. The material was identified using works of Domínguez et al. (2006) for mayflies, Stark et al. (2009) for stoneflies and Angrisano & Sganga (2009^a) for caddisflies. Additional articles regarding particular taxonomical groups used for material identification are cited in the relevant sections.

Electric conductivity (EC) and pH values were measured in the field using the WTW pH/Cond 340i SET field device. Stream variables, including their mean width, depth, bottom substrate and water temperature were measured at each sampling locality.

3.2.3. Sampling area and localities

A total of 24 localities were sampled at Churí Tepui, Mt. Roraima and Auyán Tepui. Localities R1, R5, R6, A1 and A2 (see below) were not situated directly on the Mt. Roraima and Auyán Tepui plateaus, but on the tepuis slopes at altitudes above 1,500 m a.s.l., which is the low altitudinal limit for the Pantepui (Berry et al., 1995). Therefore, all the following localities belong to the Pantepui Province. Auyán Tepui is the largest of the sampled tepuis, with a total surface area of 700 km². It is the lowest one, with sampling localities situated between 1,700 and 1,851 m a.s.l. The next biggest is Churí Tepui with a summit area of 47.5 km² and altitudes 2,100 to 2,400 m a.s.l. Churí Tepui is one of the 12 tepuis forming the Chimantá Massif, which has a total summit

area of 623 km² and the slope area of 915 km² (McDiarmid & Donnelly, 2005). Mt. Roraima is the smallest and the highest one with a summit area of approximately 36 km² and altitudes from 2,700 to 2,800 m a.s.l.

Sampling localities at Churí Tepui (C), Mt. Roraima (R) and Auyán Tepui (A) were:

(C1) Quebrada Lila (Fig. 113C) – a stream on the plateau above Cueva Charles Brewer, Churí Tepui plateau, 26. I. 2009, altitude 2,250 m a.s.l., N 05° 14' 57.6" W 62° 01' 36.5", pH = 4.35, EC = 14 µS.cm⁻¹, T = 14 °C, depth 0.02 – 1.5 m, width 1 – 3 m. This is a cascade stream shaded by surrounding forest. It has a bedrock bottom with occasional deposition of gravel and stones, and submerged tree roots and mosses.

(C2) Cueva Charles Brewer – Churí Tepui plateau, 15. I. 2009, altitude ca 2,200 m a.s.l., pH = 4.58, EC = 9 µS.cm⁻¹, T = 14 °C, depth 0.02 – 1.5 m. This stream has a bedrock bottom with scattered deposition of gravel and stones.

(C3) Spring streams below Cueva Charles Brewer – Churí Tepui plateau, 17. I. 2009, altitude ca 2,200 m a.s.l., pH = 4.5, EC = 9 µS.cm⁻¹, T = 13.6 °C. This has a bedrock bottom with occasional deposition of gravel and stones in some places.

(C4) The stream above Pozo Capuchino – Churí Tepui plateau, 15. I. 2009, altitude ca 2,200 m a.s.l., T = 15 °C, depth up to 1.8 m, width 2 – 6 m. It has a bedrock bottom with deposition of sand, woody debris, and with submerged roots.

(C5) Río Olinka (Fig. 113D) – a stream over the waterfall above Cueva Juliana, 28. I. 2009, Churí Tepui plateau, altitude 2,115 m a.s.l., N 05° 14' 40.9" W 62° 02' 05.5", pH = 4.48, EC = 9 µS.cm⁻¹, T = 17 °C, depth up to 1 m, mostly up to 0.2 m, river bed width 10 – 15 m. This has a bedrock bottom with occasional deposition of gravel and stones and patches of moss. This stream has wide and frequent discharge fluctuations. Its bed is almost entirely dry during low discharge periods and water is then restricted to transverse crevices and pools connected to almost arid streams.

(C6) Cueva Juliana – Churí Tepui, 23. I. 2009, altitude 2,300 m a.s.l., pH = 4.38, EC = 18 µS.cm⁻¹, T = 14.3 °C, depth up to 0.5 m, width = 0.3 – 1 m. This shallow stream flows inside the cave, and it has a bedrock bottom with some sand accumulations and stones.

(C7) Spring stream below the waterfall at Río Olinka emanating from Cueva Juliana – Churí Tepui, 20. I. 2009, altitude ca 2,100 m a.s.l., T = 14.3 °C, depth 0.01 – 0.3 m, width 0.3 – 1 m. This has a bedrock bottom with some coarse gravel deposits, mosses and roots.

(C8) Río Rojo – Churí Tepui, 20. I. 2009, altitude ca 2,100 m a.s.l., pH = 3.3, EC = 25 µS.cm⁻¹, T = 17.5 °C, depth up to 1.5 m, mostly up to 0.2 m, river bed width 1 – 4 m. This has a sandy bed with tree roots, woody debris and stones.

(C9) Middle reach of the Western River (Fig. 113B) – Churí Tepui plateau, 24. I. 2009, altitude 2,399 m a.s.l., N 05° 15' 39.8" W 62° 00' 44.0", pH = 4.56, EC = 11 µS.cm⁻¹, T = 22.4 °C, depth up to 1.5 m, mostly up to 0.1 m, width 0.1 – 1.5 m. This reach has a bedrock bottom, and it forms pools with small deposits of gravel and stones and submerged tree roots.

(C10) Springs of the Western River (Fig. 113A) – Churí Tepui plateau, 23. I. 2009, altitude ca 2,400 m a.s.l., pH = 3.75

– 4.58, EC = 2 – 17 µS.cm⁻¹, T = 16.8 – 17.6 °C, depth 0.1 – 0.7 m, width 0.2 – 1.5 m. These consist of pools in a wetland meadow connected by small rapids, and they possess an abundance of cyanobacteria and macrophyta, and also occasional stones.

(C11) Pools in wetlands in the northern part of Churí Tepui – Churí Tepui plateau, 22. I. 2009, altitude 2,438 m a.s.l., N 05° 16' 12.6" W 62° 00' 58.8", pH = 2.7, EC = 46 µS.cm⁻¹, T = 27.8 °C, depth up to 0.3 m. This is a peat-swamp meadow with carnivorous plants, and there are abundant cyanobacteria in these scattered pools.

(C12) Cueva Colibrí – Churí Tepui, 26. I. 2009, altitude ca 2,300 m a.s.l. This is a shallow stream flowing inside the cave, with a bedrock bottom and some accumulations of sand and stones. Although there is no further available data, this is considered similar to C2 and C6.

(R1) Tuná Deuta – This is a spring stream below the south-western wall of Mt. Roraima at "La Rampa", 4. II. 2009, altitude 2,346 m a.s.l., N 05° 09' 58.0" W 60° 46' 72.4", pH = 4.76, EC = 19 µS.cm⁻¹, T = 14.1 °C. The stream emanates through a small waterfall in the Mt. Roraima wall. The stream bottom is covered with boulders, stones and moss, and it is surrounded by a cloud forest.

(R2) Tuná Damú – Mt. Roraima plateau, 6. II. 2009, altitude 2,700 m a.s.l., N 5° 10' 17.34" W 60° 45' 37.74", T = 16.8 °C, pH = 5.05, depth 0.05 – 0.5 m, width 1m. The stream flows through a small cave below the path to Punto Triple, and its bed is covered with stones and quartz crystals.

(R3) Cueva de los Pémones – Mt. Roraima plateau, 4. II. 2009, altitude ca 2,700 m a.s.l., T = 12 °C, pH = 4.78, depth up to 0.5 m, width 0.3 – 3 m. Stream flows inside the cave, and it has a bedrock bottom with accumulations of sand, gravel and stones.

(R4) Spring stream in a crevice close to Tuná Damú – Mt. Roraima plateau, 7. II. 2009, altitude ca 2,700 m a.s.l., T = 14.3 °C, depth to 0.3 m, width 0.5 – 1 m. This has a stony bottom.

(R5) The spring stream at "La Rampa" on Mt. Roraima, approximately 100 metres below the plateau – Mt. Roraima massif, 7. II. 2009, altitude ca 2,600 m a.s.l., T = 13.1 °C, depth up to 0.3 m, width up to 1 m. The stream also has a rocky bottom.

(R6) Stream above the Mt. Roraima Base Camp – 7. II. 2009, altitude 1,840 m a.s.l., T = 16 °C, width 2 m, depth up to 0.8 m. This stream is entirely shaded by a dense cloud forest. Stream bed comprises stones and boulders, and there are sand accumulations in its pools.

(A1) Tuná Terciopelo – a stream ca 20 min below El Peñón Camp, Auyán Tepui, 7. I. 2010, altitude 1,733 m a.s.l., N 5° 44' 23.3" W 62° 32' 18.5", T = 16.5 °C. This is a montane stream in a cloud forest, with its bottom covered by stones and gravel.

(A2) Quebrada El Peñón in El Peñón Camp – Auyán Tepui, 7. I. 2010, altitude 1,832 m a.s.l., N 5° 44' 40.4" W 62° 32' 29.7", T = 14.6 °C, width 2-5 m. This is also a montane stream in a cloud forest and it has a bedrock bottom. Its pools have gravel and leaf accumulations and also submerged tree roots.

(A3) Springs of Río Churún (Fig. 114A) – Auyán Tepui plateau, 8. I. 2010, altitude 1,851 m a.s.l., N 5° 46' 15.1" W 62° 32' 7.9", T = 25.4 °C, width = 15 – 20 m. This is restricted to a small stream during low water discharges, while the rest of the bed is just an arid bedrock bottom.



Fig. 114: Aquatic habitats on Auyán Tepuí (A-C) and Mt. Roraima (D-E): A – Upper reaches of Río Churún (A3). B – Río Churún (A6), long and deep pools. C – Río Churún (A5) in very dry period. D – Wetlands on Mt. Roraima plateau, biotop of *Odonata* (Anisoptera) nymphs. E – Typical small stream on Mt. Roraima plateau.

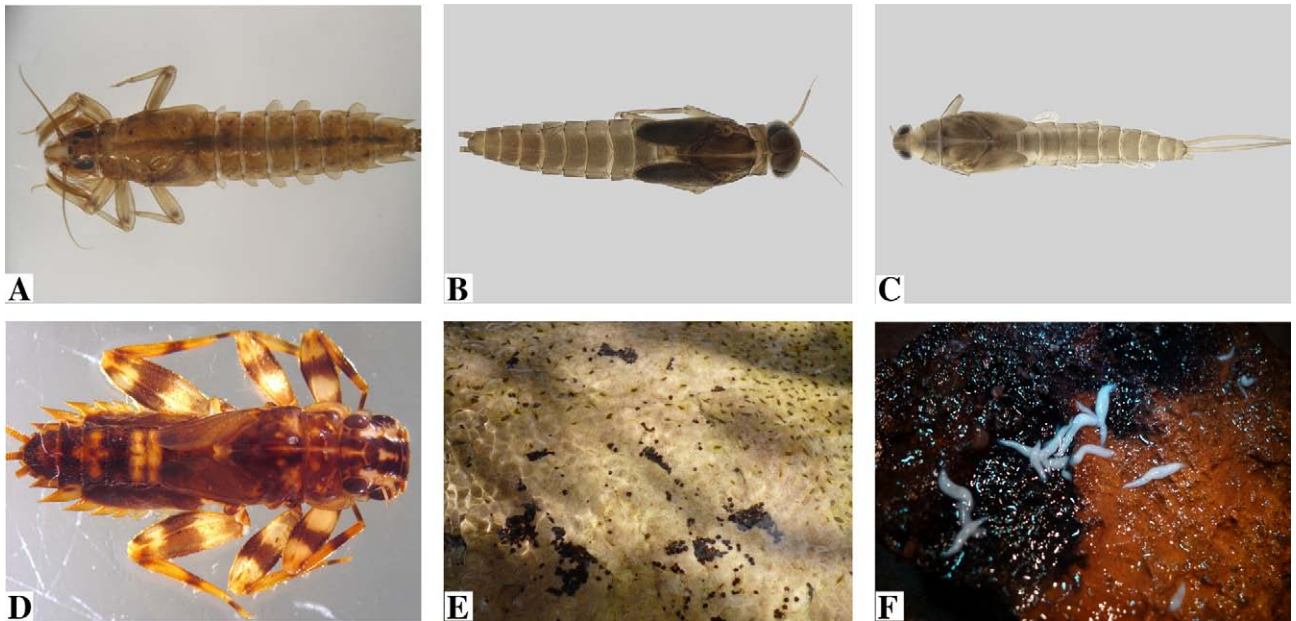


Fig. 115: A – Nymph of *Fittkauneria adusta* (Ephemeroptera, Oligoneuriidae). B – Nymph of *Parakari auyanensis* (Ephemeroptera, Baetidae). C – Nymph of *Parakari churiensis* (Ephemeroptera, Baetidae). D – Nymph of *Massartella hirsuta* (Ephemeroptera, Leptophlebiidae). E – Larvae of *Helicopsyche* sp. (Trichoptera, Helicopsychidae) in their natural environment, Río Olinka, Churí Tepui. F – Unidentified aquatic *Turbellaria* from Cueva Charles Brewer sector.

(A4) **Río Oso in El Oso Camp** – Auyán Tepui plateau, 9. I. 2010, altitude 1,733 m a.s.l., N 5° 47' 1.4" W 62° 32' 12.5", T = 14.9 °C, width 2 – 4 m. It has a bedrock bottom, it is surrounded by tepui forest, and it forms numerous pools with stones, woody debris and tree roots.

(A5) **Río Churún ca 30 minute walk above El Oso Camp** (Fig. 114C) – Auyán Tepui plateau, 10. I. 2010, altitude ca 1,740 m a.s.l., T = 21.1 °C, width 18 – 20 m. Again, this has a bedrock bottom, and it is almost entirely dry during low water discharges. It is restricted to pools and transverse crevices connected to a rather small stream.

(A6) **Río Churún close to El Lecho Camp** (Fig. 114B) – Auyán Tepui plateau, 10. I. 2010, N 5° 49' 34.6" W 62° 32' 27.9", altitude 1,730 m a.s.l., T = 19.7 °C, width 6 – 15 m, depth up to 2 m. This is a montane river with long, deep pools and bedrock riffles. The pools have bedrock and sandy bottoms, covered with a lot of woody debris.

3.2.4. Ephemeroptera

3.2.4.1. Introduction

The order Ephemeroptera is a small, almost cosmopolitan group of hemimetabolous insects. It comprises more than 3,000 described extant species in 42 families and more than 400 genera (Barber-James et al., 2008). Ephemeroptera is the oldest extant order of winged insects with fossils dating to the Carboniferous and Permian periods (Barber-James et al., 2008). They are unique among insects, as they have two winged stages, subimago and imago. Most of the mayfly life is spent in water in the immature stages of nymphs. The length of nymphal development varies from a few months to more than two years, depending on the species and environmental conditions (Barber-James et al., 2008).

The nymphs feed on algae and detritus, with only a few species being predators; and non-feeding adults depend on nymphal reserves. They live for only a few hours or days, long enough to fulfil mating, oviposition and dispersal functions. Nymphs play an important role in processing organic matter in aquatic ecosystems, and they provide a vital food source for fish, and for predaceous aquatic organisms including insects. Winged stages serve as prey for birds, bats, insects and spiders. Their highest generic diversity is in the Neotropics, with correspondingly high species diversity (Barber-James et al., 2008). South America has a unique mayfly biota comprising 14 families, over 100 genera and more than 450 species, with high endemism at different taxonomic levels (Domínguez et al., 2006). Precise knowledge of Venezuelan mayfly fauna is very limited; only 33 species representing 20 genera and six families have currently been reported (Chacón et al., 2009). This low number reflects the history of collection rather than the actual taxa richness. Recently, various new taxa have been reported and/or described (Derka et al., 2009; Chacón et al., 2010; Molineri et al., 2011; Nieto et al., 2011; Nieto & Derka, 2011, 2012). The majority of these new finds came from Gran Sabana region. Derka et al. (2009) described the new species *Massartella hirsuta* (Leptophlebiidae) (Fig. 115D) and reported the occurrence of two *Massartella* species from Mt. Roraima and Churí Tepui which have not currently been described. Molineri et al. (2011) described two new species; the *Caenis tepuinensis* (Caenidae) and the *Macunahyphes pemonensis* (Leptohyphidae), and reported for the first time in Venezuela *Coryphorus aquilus* Peters, 1981, *Amanahyphes saguassu* Salles & Molineri, 2006 and *Tricorythopsis yucupe* Dias, Salles & Ferreira, 2008. Nieto et al. (2011) reported 4 genera (*Cryptonympha*, *Harpagobaetis*, *Spiritiops* and *Zelusia*), and 9 species found for the first time in Venezuela. These findings doubled the recorded number

of species and genera of Baetidae in Venezuela. However, the knowledge of mayflies from the Pantepui Province still remains very limited. Published records are mainly based on sampling from already mentioned expeditions to Cerro de la Neblina. Some records and species descriptions are from localities below the Pantepui low altitudinal limit. These include the description of *Miroculis nebulosus* (Savage, 1987), two new *Farrodes* species (Domínguez et al., 1996), and also records of *Miroculis fittkaui* (Savage, 1987) and *Hagenulopsis minuta* (Peters & Domínguez, 2001). The following three species were reported or described from localities over 1,500 m a.s.l.: *Miroculis bicoloratus* (Savage, 1987), *Hagenulopsis minuta* (Peters & Domínguez, 2001) and *Fittkauneria carina* (Pescador & Edmunds, 1994). Derka (2002) described *Massartella devani* from a stream on Mt. Roraima plateau and Nieto & Derka (2011) published a new Baetidae genus *Parakari* with two species endemic to Churí Tepui and Auyán Tepui. In addition, Nieto & Derka (2012) described new *Spiritiops* species in streams on the Churí and Auyán tepuis and Mt. Roraima. Thus, the number of mayfly species known from the Pantepui now totals seven, and Derka et al. (2012) have summarized all the published results, together with the first author's own research on Pantepui mayflies.

3.2.4.2. Results and discussion

Although mayfly nymphs are a common component of the aquatic communities in the Churí and Auyán tepuis plateau streams, they are rarely found on the Mt. Roraima plateau. Representatives of the Baetidae and Leptophlebiidae families were discovered on the tepuis plateaus, and *Fittkauneria adusta* nymphs from the family Oligoneuriidae were found in a stream on Auyán Tepui. Facts concerning the distribution of these taxa in the study area and supplementary ecological information is presented (explanatory note: N – nymph).

Family Baetidae Leach, 1815

The family Baetidae has almost cosmopolitan distribution and it currently includes almost 100 genera worldwide. In South America, this family now encompasses 28 genera and more than 130 species (Nieto, 2010; Nieto & Derka, 2011; Salles et al., 2010). Most genera were described in the last decade of the 20th century, with *Parakari* being the last genus described from this region (Nieto & Derka, 2011). The Baetidae nymphs inhabit a variety of lotic and lentic habitats with sandy, rocky or organic substrates. There are representatives of 7 genera found on the tepuis' plateaus.

Genus *Baetodes* Needham and Murphy, 1924

The genus, including more than 40 species, is recognized in North, Central and South America (Nieto et al., 2011). Of these, 27 species are described from South America, making it one of the most species rich genera in the Neotropics (Domínguez et al., 2006; Salles & Polegatto, 2008; De Souza et al., 2011). Four species are known from Venezuela (Nieto et al., 2011). Although the nymphs are very abundant in streams on Auyán Tepui plateau, especially in sections with a strong current, they were absent on Churí Tepui and Mt. Roraima plateaus.

Material examined: *Baetodes* sp.: A2 – 2N, A4 – 6N, A5 – 239N, A6 – 175N, R6 – 18N.

Genus *Callibaetis* Eaton, 1881

This genus has a distribution from North America to Argentina. In South America, 16 species are recognized from adults, especially female imagos, but associated nymphs were found in only 8 cases (Nieto, 2008; Cruz et al., 2009). Blanco-Belmonte et al. (2009) reported this genus from Orinoco and Caura rivers. Nymphs occur in different habitats, generally with lentic waters. These were found in pools in streams on both Churí Tepui and Auyán Tepui, and constituted unique but abundant mayfly representatives in pools in peat-swamp meadows on Churí Tepui.

Material examined: *Callibaetis* sp.: C1 – 1N, C3 – 1♀ subimago, C9 – 3N, C10 – 36N, C11 – 7N, A6 – 53N.

Genus *Camelobaetidius* Demoulin, 1966

This genus is widely distributed in North, Central and South America, with 29 species in the latter area (Boldrini & Salles, 2009). Five species have been recorded in Venezuela (Nieto et al., 2011), and nymphs from this genus are easily recognizable by spatulate tarsal claws with a fan-shaped row of denticles. This is a unique characteristic among Neotropical mayflies.

Material examined: *Camelobaetidius* sp.: A4 – 7N, A6 – 5N.

Genus *Cloeodes* Traver, 1938

Cloeodes enjoys a widespread pantropical distribution in South, Central and North America, in Africa, Madagascar, Southeast Asia and Australia. Seventeen species have been reported from South America (Nieto & Richard, 2008), with one of these in Venezuela (Nieto & Emmerich, 2011; Salles & Cavalcante do Nascimento, 2009).

Material examined: *Cloeodes* sp.: C1 – 5N, 1♂, 1♀; A1 – 1N; A2 – 1N; A3 – 94N; A4 – 7N; A6 – 4N; R6 – 2N.

Genus *Parakari* Nieto & Derka, 2011

Nieto & Derka (2011) described this genus from material collected on Churí Tepui and Auyán Tepui plateaus (Figs. 115B–C, 116A). The only other recorded material was *P. auyanensis*, found in the stream below Salto Angel which is the highest waterfall on Earth, cascading 979 m from Auyán Tepui plateau. Recently, Derka (unpubl.) found *Parakari* nymphs in the stream at Roraima foothills and at locality R6. Nymphs have habitats ranging from spring streams to larger mountain rivers, and they were discovered in a stream inside Cueva Charles Brewer. They apparently tolerate a wide range of temperatures, from oligostenothermal cave streams possessing a stable temperature around 14 °C to wide and shallow streams with high diurnal thermal fluctuations.

Material examined: *Parakari churiensis*: C1 – 91N, 3♂♂, 12♀♀, 11♂♂ subimagos, 3♀♀ subimagos; C2 – 167N, 1♂, 8♂♂ subimagos, 10♀♀ subimagos; C3 – 1N, 1♂, 3♀♀, 7♂♂ subimagos, 7♀♀ subimagos; C4 – 52N; C5 – 1N; C6 – 3N; C7 – 15N; C10 – 1N; *Parakari auyanensis*: A1 – 5N, A2 – 14N, A4 – 21N, A5 – 17N, A6 – 31N.

Genus *Spiritiops* Lugo-Ortiz & McCafferty, 1998

This monotypical genus was described from nymphs, before Salles & Nieto (2008) described the adult from Brazil. *S. silvudus* was reported from Brazil, Colombia, Surinam and French Guiana (Domínguez et al., 2006), and more recently, Nieto et al.

(2011) found these nymphs in streams in Gran Sabana region of Venezuela. One undescribed species was also found in streams at all three tepuis, and it was described by Nieto & Derka (2012). Nymphs inhabit a wide range of streams but they prefer habitats with strong currents, even in waterfall cascade zones.

Material examined: *Spiritiops tepuiensis*: A1 – 18N; A2 – 23N; A3 – 6N; A4 – 236N, 1♀ subimago; A5 – 35N; A6 – 124N; R1 – 6N; R5 – 6N; R6 – 86N; C1 – 22N, 15♀♀; C3 – 1♀ subimago, 1♂ subimago; C4 – 70N; C5 – 39N, 1♀; C6 – 8N; C7 – 9N; C9 – 5N.

Family Leptohlebiidae Banks, 1900

This is the most diverse mayfly family in the Neotropics. It includes approximately 40 genera and more than 150 species from South America, all belonging to the subfamily Atalophlebiinae (Domínguez et al., 2006). In Venezuela, 19 species have been reported from 8 genera (Chacón et al., 2009; Derka et al., 2009). More recently, Blanco-Belmonte et al. (2009) added 4 genera and one undescribed genus.

Genus Hagenulopsis Ulmer, 1920

Eight species of this dipterous genus are currently recognized, with five of them from South America (Domínguez et al., 2009). However, only *H. minuta* is known from Venezuela (Chacón et al., 2009). Peters & Domínguez (2001) redescribed this species, and they reported nymphs and male adults from the 140 m a.s.l. Cerro de la Neblina base camp, and also a male adult from 1,800 m a.s.l.

Material examined: *Hagenulopsis* sp.: C1 – 1♂, 1♀, 1♂ subimago; C2 – 1N; C4 – 1N; C8 – 7N; R6 – 3N; A4 – 1N.

Genus Massartella Lestage, 1924

This genus is known from 5 described species, 2 of which live in Brazil and 3 in Venezuela (Derka et al., 2009). One undescribed species was also reported from north-eastern Argentina (Pescador & Peters, 1990). Derka (2002) described *M. devani* from Mt. Roraima (R1). Later, this species was found in other streams at Roraima foothills. Material collected on Mt. Roraima plateau and at locality R5 is from an undescribed species. *Massartella* nymphs and adults collected at different localities of Churí Tepui belong to a further undescribed species (Fig. 116C). This species was often sampled at the entrance of Cueva Charles Brewer (Boca de Mamut). Numerous remnants of adults were seen in spider webs deep in Cueva Charles Brewer, where they were compelled to fly in absolute darkness. Nymphs were also collected in other caves on Churí Tepui. Another undescribed species was sampled at Auyán Tepui and also in a stream below Salto Ángel. In the Pantepui, these *Massartella* nymphs exclusively inhabit the cold stenothermal streams with temperatures ranging from 14 to 18 °C. They prefer pools in streams where they can hide underneath rocks and stones. Female subimagos (Fig. 116C) were observed flying before sunset.

Material examined: *Massartella devani*: R1 – 12N, R6 – 1N; *Massartella* sp.1: R2 – 52N; R3 – 5N; R4 – 6N; R5 – 9N; *Massartella* sp.2: C1 – 18N, 7♀♀; C2 – 25N, 2♂♂, 8♀♀, 1♂ subimago, 3♀♀ subimagos; C3 – 3N, 1♀, 2♂♂ subimagos, 2♀♀ subimagos; C4 – 2N; C5 – 1N; C6 – 23N; C7 – 10N; C12 – 70N;

Massartella sp.3: A1 – 13N; A2 – 27N; A3 – 3N, 1♂ subimago; A4 – 30N, 1♀ subimago; A5 – 7N; A6 – 4N.

Genus Miroculis Edmunds, 1963

The genus *Miroculis* currently has 15 described species in a distribution area which ranges from northeastern Argentina to Trinidad (Domínguez, 2007; Peters et al., 2008; Salles & Lima, 2011). Three species have been recorded in Venezuela (Savage, 1987). *M. nebulosus* Savage, 1987 and *M. fittkaui* Savage & Peters, 1983 were collected at the Cerro de la Neblina base camp at 145 m. a.s.l. Meanwhile, Peters et al. (2008) recorded *M. nebulosus* in Serranía de Chiribiquete in Colombian Amazonia which belongs to the Guyana Shield. Savage (1987) also described Pantepui species *M. bicoloratus* from Camp II at Cerro de la Neblina (ca 2,100 m a.s.l.). The material collected on both Churí and Auyán tepuis is similar to *M. bicoloratus*, but it belongs to a different undescribed species.

Material examined: *Miroculis* sp.1: C1 – 9N, 2♂♂, 2♂♂ subimago, 2♀♀ subimagos; C2 – 1N; C10 – 2N; *Miroculis* sp.2: A5 – 23N, 3♀♀; *Miroculis* sp.3: R6 – 3N.

Family Oligoneuriidae Ulmer, 1914

Among 6 genera of the family documented from the South America, the genus *Fittkauneria* is the only one known from Venezuela.

Genus Fittkauneria Pescador & Edmunds, 1994

Two species are known from this genus; (1) *F. adusta* Pescador & Edmunds, 1994 is described from southeastern Venezuela and northern Brazil, and it is relatively common in small streams in Gran Sabana region (Fig. 115A). Although it was not recorded on tepuis plateaus, it has been sampled above 1,800 m a.s.l.; and (2) *F. carina* Pescador & Edmunds, 1994 was sampled in various streams at Cerro de la Neblina at altitudes ranging from 750 to 1,820 m a.s.l. (Pescador & Edmunds, 1994). Both these species can therefore be attributed to Pantepui Province.

Material examined: *Fittkauneria adusta*: A1 – 4N, R6 – 1N.

3.2.5. Plecoptera

3.2.5.1. Introduction

Plecoptera, is a small order of hemimetabolous insects with about 3,500 described extant species in 16 families with 286 genera (Fochetti & Tierno de Figueroa, 2008). Stonefly adults have two pairs of large membranous wings which are sometimes reduced or absent, and almost equal-sized fore and hind wings which fold horizontally over and around the abdomen when they are at rest. The nymphs resemble adults, possessing a closed tracheal system with or without filamentous gills. Plecoptera nymphs are aquatic and they live mainly in cold, well-oxygenated running waters, although some species can also be found in lakes. However, the increasing number of stoneflies described from the tropics and their high rate of endemism modifies the common belief that Plecoptera are cold-water specialists, and suggest that the actual hot spots of Plecoptera biodiversity are tropical areas (Fochetti & Tierno de Figueroa, 2008). The main factors responsible for their high endemic rate are the ecological requirements of nymphs,

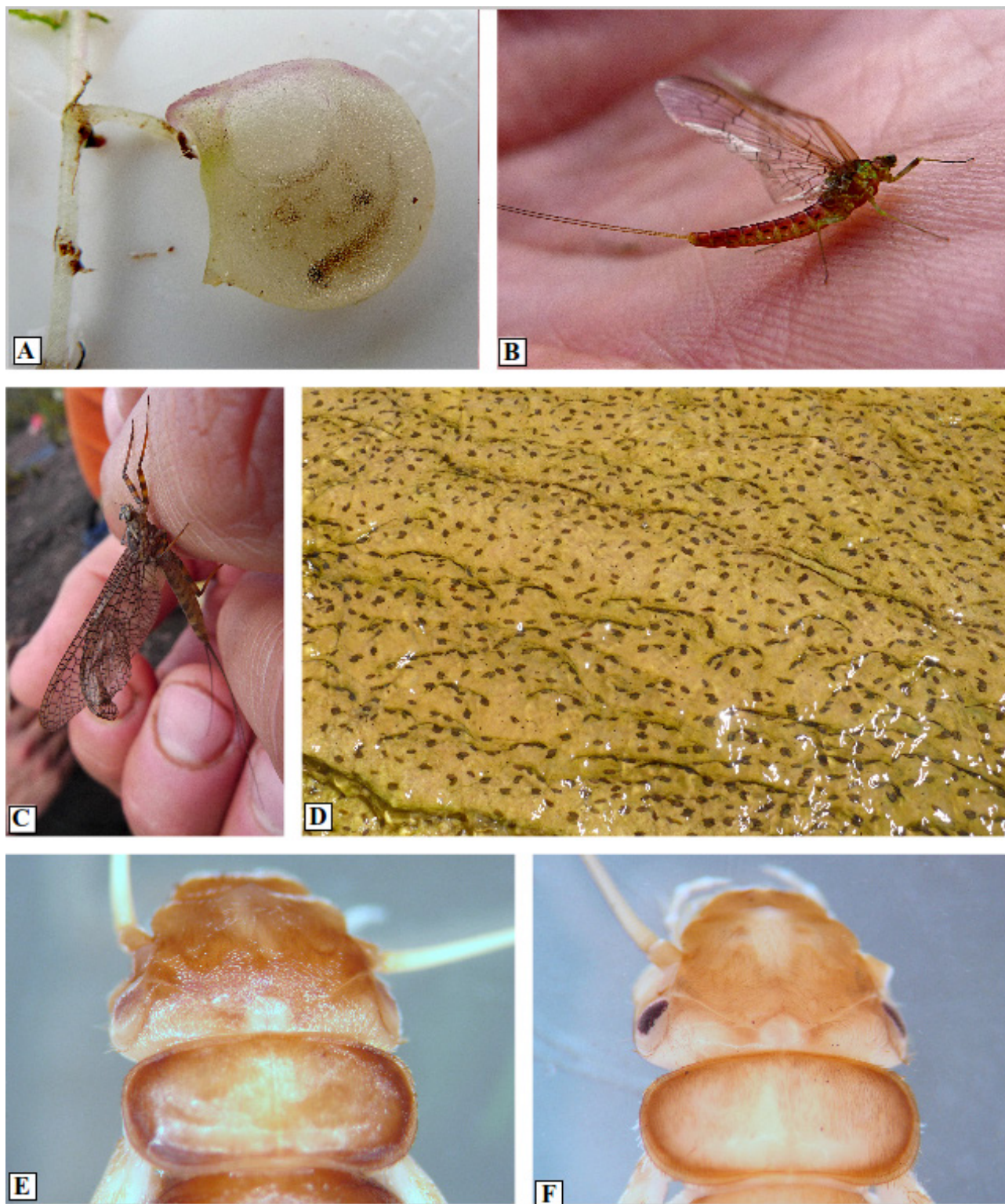


Fig. 116: A – Nymph of *Parakari churiensis* (Ephemeroptera, Baetidae) in a trap of *Utricularia humboldti*, Churí Tepui. B – Female imago of *Spiritiops tepuiensis* (Ephemeroptera, Baetidae) from Churí Tepui. C – Female subimago of an undescribed species of *Massartella* (Ephemeroptera, Leptophlebiidae) from Churí Tepui. D – Pupae of *Zumatrichia* sp. (Trichoptera, Hydroptilidae), Churí Tepui. E – F – Nymph of *Kempnyia* (Plecoptera, Perlidae) from Cueva Colibrí (Charles Brewer Cave System) with reduced ocelli and partial depigmentation of the compound eyes.

and adults' reduced flight capacity. Their life cycle lasts one or more years, but there are also bi- or tri-voltine species. These nymphs represent a very important component of stream ecosystems in terms of biomass and diversity of ecological roles. They feed on detritus, periphyton, aquatic invertebrates and small vertebrates as collectors, scrapers, shredders and predators. Adults live for days or weeks and their diet can include pollen, lichens and cyanobacteria, although the adults of the largest species do not seem to feed. Females lay their eggs on water (Fochetti & Tierno de Figueroa, 2008). The currently recognized stonefly fauna of South America, comprising approximately 380 species, is poor and it does not represent their actual diversity (Fochetti & Tierno de Figueroa, 2008; Stark et al., 2009). Only these three Plecoptera genera have been recorded in Venezuela: *Anacroneturia*, *Macrogynoplax* and *Enderleina* (Derka et al., 2010), and they all belong to the Perlidae family. This family accounts for ten Neotropical genera (Stark, 2001; Hamada & Marques Couceiro, 2003; Stark et al., 2009). Although Plecoptera were previously unknown in Pantepui, the following data from tepuis has now been published; (1) from Mt. Roraima; *Enderleina preclara* by Jewett (1960); and (2) from Pico de la Neblina; *Enderleina flinti* and *E. yano* by Stark (1989), *Macrogynoplax neblina* and *M. spangleri* by Stark & Zwick (1989), and *Anacroneturia blanca*, *A. cruzi*, *A. baniva*, *A. pequeña*, *A. menuda*, *A. vistosa*, *A. shamataria* and *A. pinza* by Stark (1995). However, since all this material was collected at foothills it cannot be attributed to the Pantepui Province. Recently, Derka et al. (2010) published the first records of stoneflies from Pantepui. They found nymphs from the genera *Macrogynoplax* and *Kempnyia* at Churí Tepui, and the *Kempnyia* nymphs in the Tuná Deuta stream on Mt. Roraima. It was the first record of the genus *Kempnyia* in Venezuela. Derka et al. (2010) observed the total absence of ocelli in one *Kempnyia* nymph with different degrees of ocelli reduction, and partial compound eyes depigmentation in others (Fig. 116E, F). These were especially noted in nymphs from Cueva Colibrí on Churí Tepui, where these characteristics were attributed to their cavernous habitat. Stonefly findings from Churí Tepui and Mt. Roraima published by Derka et al. (2010) are reviewed herein, together with new data from Auyán Tepui. Comments on distribution of these taxa in the study area and ecological information are given below (explanatory note: N – nymph).

3.2.5.2. Results and Discussion

One highlight here is total absence of the most common and most widely distributed Neotropical genus *Anacroneturia* from streams on Mt. Roraima and Churí Tepui summits. Also, it is only recently that *Anacroneturia* nymphs were recorded on Auyán Tepui. Stoneflies were collected almost exclusively in caves and oligostenothermal spring streams originating in the caves. Although *Anacroneturia* nymphs were found in medium sized rivers, they were always hidden in shaded and cooler habitats below the river banks. It is quite surprising that no stonefly nymphs were recorded on the Mt. Roraima plateau, because the waters at these higher altitudes were the coldest, and would have provided suitable habitats for them. Poor macroinvertebrate communities and therefore the lack of suitable prey is probably the reason of absence of stonefly nymphs in streams on Mt. Roraima plateau.

Genus *Anacroneturia* Klapálek, 1909

This is the most diversified and widely distributed genus of the Neotropical Perlidae, reaching to the Nearctic Region. It has more than 300 species distributed from the SW of the USA to northern Argentina (Stark et al., 2009). Specific recognition of these nymphs is very difficult, and in many cases it is impossible because so few of them have been described.

Material examined: A2 – 13 N, 1♂ imago, 1♀ imago, A5 – 14N; A6 – 12N.

Genus *Macrogynoplax* Enderlein, 1909

With 14 described species, this genus is distributed in Brazil, Guyana, Peru, Surinam, Venezuela and also Colombia (Froehlich, 1984; Stark, 1996; Stark & Zwick, 1989; Ribeiro-Ferreira & Froehlich, 1999; Bispo et al., 2005; and Ferreira Ribeiro & Rafael, 2007). Identification of nymphs at the species level is not possible at the moment.

Material examined: C2 – 1♀ imago and its exuvia, C6 – 2N, C7 – 2N, A1 – 3N, A2 – 1N.

Genus *Enderleina* Jewett, 1960

This genus is distributed in northern Brazil and Venezuela (Stark et al., 2009). Five species have currently been described: *E. preclara* Jewett, 1960, *E. flinti* Stark, 1989, *E. yano* Stark, 1989, *E. bonita* Stark, 1989 and *E. froehlichii* Ribeiro-Ferreira, 1995. The three latter species were described from individuals collected in Venezuela (Stark, 1989; Ferreira Ribeiro & Rafael, 2005; Stark et al., 2009). The type locality of *E. preclara* is Brazilian part of Mt. Roraima, at altitudes around 2,100 m a.s.l., so their presence is also expected in Venezuela. It is impossible to identify *Enderleina* nymphs at the species level with current knowledge, and although this genus was not collected, we expect it to inhabit the Pantepui Province.

Genus *Kempnyia* Klapálek, 1914

This genus includes 35 species, and it was previously known only from Brazil (Stark et al., 2009; Froehlich, 2011^{a,b}) until Derka et al. (2010) published the first records of the genus in Venezuela. The nymphs are oligostenothermal insects, mainly inhabiting mountain streams (Froehlich, 1981), but identification at the species level is not yet possible.

Material examined: A2 – 1N, C2 – 1N, C7 – 2N, C12 – 2N, R1 – 3N.

3.2.6. Trichoptera

3.2.6.1. Introduction

The order Trichoptera (caddisflies) comprises a group of holometabolous insects closely related to the Lepidoptera. It includes more than 13,000 extant species within 45 families and approximately 600 genera (Holzenthal et al., 2007; de Moor & Ivanov, 2008). The adults are moth-like terrestrial insects with wings covered by hairs, not scales as in Lepidoptera. The adult Trichoptera ranges in size from minute with a wing span of less than 3 mm to large with a wing span approaching 100 mm (de Moor & Ivanov, 2008). Larvae are best known for the transportable cases and fixed shelters that many, but not all,

species construct. Similar to Lepidoptera, Trichoptera larvae spin silk which they use for constructing their retreats and larval cases. Silk has enabled Trichoptera larvae to develop numerous morphological adaptations for their ecological diversity and the success of this order. Larvae and pupae are important components of food webs in the rivers, lakes and streams which they inhabit (Wiggins, 2004; Holzenthal et al., 2007; de Moor & Ivanov, 2008).

Approximately 2,100 species from 148 genera have been reported in the Neotropics, and 69% of the (sub-) genera are endemic (de Moor & Ivanov, 2008). According to Johanson & Holzenthal (2004), the Venezuelan Trichoptera fauna has almost 240 described species, of which 90% are in the following 6 families: Helicopsychidae (14 spp.), Hydrobiosidae (20 spp.), Hydroptilidae (49 spp.), Hydropsychidae (57 spp.), Leptoceridae (27 spp.), and the Philopotamidae (46 spp.). Records and species descriptions of the Venezuelan caddisflies are scattered throughout 40 publications (Holzenthal & Cressa, 2002), with most of these based on material collected and described by O. S. Flint Jr. (cited in Flint et al., 1999). Since the frequency of new species in some regions of the Neotropics can reach 75% of all collected species, the recorded Venezuelan Trichoptera fauna certainly underestimates the actual number of species, which could reach well over 500 (Holzenthal & Cressa, 2002). Records of Trichoptera in Pantepui are mainly based on material collected on the Cerro de la Neblina expeditions of the 1980's (Flint et al., 1987; Flint, 1998; Holzenthal, 1988; Schmid, 1989; Blahnik, 1997; Johanson & Holzenthal, 2004; Hamilton & Holzenthal, 2005; Chamorro & Holzenthal, 2010). Species findings and descriptions have also been published from four other tepuis: Mt. Roraima (Ross & King, 1952; Holzenthal, 1986), Auyán Tepui (Flint et al., 1987), Ptari Tepui (Schmid, 1989) and Mt. Duida (Flint et al., 1987). A total of 23 species from 8 genera and 6 families have currently been published from Pantepui (Derka & Zamora-Muñoz, 2012).

The highest number of species were located in Cerro de la Neblina – 16 spp. from 7 genera and 6 families (Derka & Zamora-Muñoz, 2012): Helicopsychidae: *Helicopsyche* (*Feropsyche*) *succinta* Johanson & Holzenthal, 2004; *H. (Feropsyche) laneblina* Johanson & Holzenthal, 2004; Hydrobiosidae: *Atopsyche ayacucho* Schmid, 1989; *A. ayahuaca* Schmid, 1989; *A. chimuru* Schmid, 1989; *A. chinchacamac* Schmid, 1989; *A. huallaripa* Schmid, 1989; Hydropsychidae: *Leptonema neblinense* Flint, McAlpine & Ross, 1987; *L. amazonense* Flint, 1978; Leptoceridae: *Triplectides tepui* Holzenthal, 1988; Polycentropodidae: *Polycentropus neblinensis* Hamilton & Holzenthal, 2005; *Polyplectropus amazonicus* Chamorro & Holzenthal, 2010; *P. flintorum* Chamorro & Holzenthal, 2010; Philopotamidae: *Chimarra (Curgia) ensifera* Flint, 1998; *Ch. (Curgia) medioloba* Flint, 1971; and *Chimarra (Chimarrita) neblina* Blahnik, 1997.

Three species from 2 genera and 2 families have been reported from Mt. Roraima (Derka & Zamora-Muñoz, 2012): Hydrobiosidae: *Atopsyche iana* Mosely, 1949; *A. hamata* Ross & King, 1952; and Leptoceridae: *Notalina roraima* Holzenthal, 1986.

Two Hydrobiosidae species are known from Ptari Tepui (Derka & Zamora-Muñoz, 2012): *Atopsyche atahuallpa* Schmid, 1989, and *A. calahuaya* Schmid, 1989. Also, one Hydropsychidae

species was found on Auyán Tepui: *Leptonema guayanense* Flint, McAlpine & Ross, 1987 and another one on Mt. Duida: *Leptonema ramosum* Flint, McAlpine & Ross, 1987. In addition to these, the genus *Austrotinodes* Schmid, 1955 from the family Ecnomidae, with trans-Antarctic distribution from Australia to the Neotropics (Thomson & Holzenthal, 2010), was described by Flint & Denning (1989) from Cerro de la Neblina. They have described *A. fuscomarginatus* at 760 m a.s.l. and *A. neblinensis* at 140 m a.s.l., and although this genus has not been located in the Pantepui, its occurrence there is quite likely.

3.2.6.2. Results and Discussion

The Calamoceratidae, Hydroptilidae, Odontoceridae and Sericostomatidae families have been recorded for the first time in the Pantepui, together with the following nine genera: *Phylloicus* (Calamoceratidae), *Blepharopus*, *Macrostemum* (Hydropsychidae), *Orthotrichia*, *Oxyethira*, *Zumatrichia* (Hydroptilidae), *Oecetis*, *Nectopsyche* (Leptoceridae) and also the unidentified genus of Sericostomatidae (*Notidobiella?*). However, the genus *Polyplectropus* from Cerro de la Neblina was not recorded in the Pantepui.

The lowest genera richness was found in Mt. Roraima, where there were only 4 genera from 4 families recorded. Similar genera richness was observed on Churi Tepui, with 8 families and 13 genera, and Auyán Tepui with 9 families and 13 genera. Odontoceridae and Philopotamidae were absent on Churi Tepui, while Calamoceratidae and Sericostomatidae were lacking at Auyán Tepui. Comments on the distribution of these taxa in the study area and notes on the diagnostic features of some of them follow (explanatory notes: L – larva, P – pupa).

Family Calamoceratidae Ulmer, 1906

This is a cosmopolitan family with approximately 175 described species in 8 genera (Holzenthal et al., 2007). Adults are more diurnal in their activity than most Trichoptera (Flint et al., 1999). The larvae are large caddisflies, ranging in length up to 25 mm, and they have different ways of constructing their portable tubes. For example, *Phylloicus* has quadrate panels of leaves or bark fastened together at lateral seams, thus forming a flattened cylinder (Wiggins, 2004). Meanwhile, the Neotropical species' larvae inhabit tranquil backwater areas of streams and rivers where they feed on detritus (Flint et al., 1999). Two genera are recorded from Venezuela: *Banyallarga* Navás, 1916 which is limited to the Andes (Prather, 2004), and *Phylloicus* Müller, 1880 in the Guyana region (Prather, 2003). The omnivorous larvae of *Banyallarga* mainly build their tubular cases from mineral fragments combined with other materials, while detritivorous larvae of *Phylloicus* have flat cases composed of leaves (Flint et al., 1999).

Genus *Phylloicus* Müller, 1880

This is a Neotropical genus of 57 extant species, with several species extending their range to the southwestern United States (Prather, 2003; Moreira Santos & Nessimian, 2010; Quinteiro et al., 2011). Prather (2003) reviewed this genus, describing 4 new species at Cerro de la Neblina, located between 140 and 760 m a.s.l.: *P. amazonas*, *P. cordatus*, *P. elektoros* and *P. passulatus*.

Although this author reported *P. fenestratus* Flint, 1974 at 1,250 m a.s.l., no specimens have been collected above 1,500 m a.s.l.

Material examined: *Phylloicus* sp. C2 – 1♀.

Family Helicopsychoidea Ulmer, 1906

The snail-case caddisflies (Fig. 115E) of this cosmopolitan family comprise 250 species; the Neotropics alone host almost 100 species (Flint et al., 1999; Holzenthal et al., 2007; Johanson & Holzenthal, 2010), while mainland South American fauna includes 41 species (Johanson & Malm, 2006). The larvae of the genus build remarkable helical, sand-grain cases so similar to snail-shells that early workers described these insects as molluscs. All helicopsychid larvae feed as scrapers on periphyton and other organic matter on exposed rock surfaces (Fig. 115E). They inhabit different environments, from springs to lowland rivers and wave-washed shores of lakes and thermal springs, but they can also occur in hyporheic zones (Wiggins, 2004). All American Helicopsychoidea are from the *Helicopsyche* genus, and are divided into two subgenera: *Helicopsyche* (*Feropsyche*) Johanson, 2002 and *Helicopsyche* (*Cochliopsyche*) Müller, 1885. *Feropsyche* has 86 described species (Johanson, 2002; Johanson & Holzenthal, 2004, 2010), and it is the largest subgenus, while *Cochliopsyche* comprises 16 species (Johanson, 2003).

Genus *Helicopsyche* von Siebold, 1856

There are 24 *Helicopsyche* species known from Venezuela (Johanson & Holzenthal, 2004). Four species were sampled at Cerro de la Neblina: *Helicopsyche* (*Feropsyche*) *neblinensis* and *H. (Feropsyche) linabena* were collected at altitudes of 140 – 760 m a.s.l., while *H. (Feropsyche) succinta* and *H. (Feropsyche) laneblina* were collected exclusively at 1,690 – 1,950 m a.s.l., and thus these are true Pantepui species. *Cochliopsyche* subgenus, however, was not noted in the Pantepui (Johanson, 2003).

Material examined: *Helicopsyche* form 1: C1 – 2L, C2 – 10L, C7 – 15L, A2 – 24L, R2 – 20L, R4 – 30L, R5 – 28L, 2P; *Helicopsyche* form 2: C1 – 4L, C4 – 12L, 10 empty cases, C5 – 25L, P, C7 – 1L, A4 – 80L; *Helicopsyche* form 3: C2 – 20 empty cases, A1 – 30L, A2 – 1L, A4 – 13L, A5 – 54L, A6 – 70L; *Helicopsyche* (*Feropsyche*) sp. nov. 1: R2 – 2♂♂; *Helicopsyche* (*Feropsyche*) sp. nov. 2: A2 – 5♂♂, 1♀; *Helicopsyche* (*Feropsyche*) sp. nov. 3: C4 – 11♂♂, 1♀; *Helicopsyche* (*Feropsyche*) sp. nov. 4: A4 – 2♂♂; C5 – 38♂♂, 7♀♀.

Family Hydrobiosidae Ulmer, 1905

Hydrobiosidae represent the Gondwanaland equivalent of Rhyacophilidae, and these are restricted to Neotropical and Australasian biogeographic regions. Only a few species in each region have distribution extending into Oriental, Palearctic, or Nearctic regions (Holzenthal & Cressa, 2002; Holzenthal et al., 2007). Schmid (1989), who reviewed the world fauna, considered that there are approximately 50 recognized genera, and most generic diversity is concentrated in either the Chilean subregion of the Neotropics or in the Australasian region. There are 168 species in 22 (23) genera described from the Neotropics, and while all but 2 are endemic to the Chilean subregion (Flint et al., 1999; de Moor & Ivanov, 2008), only the genus *Atopsyche* occurs in Venezuela (Holzenthal & Cressa, 2002). Larvae do not

possess cases, and they live as predators restricted to running waters (Wiggins, 2004).

Genus *Atopsyche* Banks, 1905

The genus *Atopsyche*, contains more than 120 species, and it is the largest genus of the family. It is widespread in the Neotropics, except for the Chilean subregion, and it extends north to Central America, Mexico and the southwestern United States (Holzenthal et al., 2007). In Venezuela, the majority of the 23 known species are largely restricted to the higher elevations of the Andes or the Guyana Highlands (Schmid, 1989; Holzenthal & Cressa, 2002). The first known Pantepui species was *Atopsyche iana* Mosely, 1949 described from Guyana and the Brazilian parts of Mt. Roraima plateau (Ross & King, 1952). Still the same year, these authors also published description of *A. hamata* from this area. The following 7 Pantepui species from Venezuelan Guyana were described by Schmid (1989): *A. atahuallpa* and *A. calahuaya* (Ptari Tepui at 1,800 m a.s.l.); *A. ayacucho*, *A. ayahuaca*, *A. chimuru*, *A. chinchamac* and *A. huallaripa*, above 2,000 m a.s.l. at Cerro de la Neblina.

Material examined: *Atopsyche* spp.: C1 – 25L, 1♀; C2 – 3P, C3 – 2L, C4 – 3L, C5 – 7L, C6 – 2L, C7 – 4L, C8 – 2L, C9 – 7L, 3P, C10 – 2L, C11 – 3L, R2 – 8L, R3 – 6L, 2P, A1 – 3L, A4 – 7L, A5 – 5L, A6 – 9L; *Atopsyche* sp. nov. 1: A2 – 2♂♂, A4 – 16♂♂, 2♀♀, *Atopsyche* sp. nov. 2: A2 – 1♂; *Atopsyche* sp. nov. 3: C2 – 1♂, 2♀♀, 2♀P, 1♂P.

Family Hydropsychidae Curtis, 1839

The Hydropsychidae family has approximately 1,500 described species. It is the third largest family in the order Trichoptera and the most diverse of the net-spinning annulipalpans (Holzenthal et al., 2007). Hydropsychids' nets are attached to rocks in flowing waters and are used to capture detritus or microorganisms from stream. Hydropsychid larvae are often quite abundant and important filter-feeders in streams (Wiggins, 2004). The following eight genera are recorded in Venezuela: *Blepharopus* Kolenati, 1859; *Centromacronema* Ulmer, 1905; *Leptonema* Guérin, 1843; *Macronema* Pictet, 1836; *Macrostemum* Kolenati, 1859; *Plectromacronema* Ulmer, 1906; *Smicridea* McLachlan, 1871; and *Synoestropsis* Ulmer, 1905 (Flint et al., 1999). In addition to these, *Smicridea caligata* Flint, 1974 was reported from Kanarakuni in the Jaua Jidí-Sarisariñama Massif foothills at 450 m a.s.l., and *S. marlieri* Flint, 1978 was found in Puerto Ayacucho (Flint, 1978). Finally, four *Leptonema* species have been published from the Pantepui Province (Flint et al., 1987).

Genus *Blepharopus* Kolenati, 1859

This is a monotypical genus. *B. diaphanous* Kolenati, 1859 is known from Argentina, Brazil and Venezuela (Flint et al., 1999), and larva and pupae of this species were described by Flint & Wallace (1980).

Material examined: *Blepharopus* sp.: A6 – 2L.

Our sampled early-instar larvae clearly differ from the known species.

Genus *Leptonema* Guérin, 1843

The genus *Leptonema* contains more than 125 species, largely

in the Neotropics, but also in Africa, Madagascar and south-western United States (Holzenthal et al., 2007). More than 100 species are widespread in the Neotropics (Flint et al., 1987, 1999; Flint, 2008), and the following 4 species were recorded at the Pantepui: *L. guayanense* Flint, McAlpine & Ross, 1987 from Río Churún on Auyán Tepui, and *L. ramosum* Flint, McAlpine & Ross, 1987, sampled in 1929 during Tate's expedition at Mt. Duida. Neither of these species is endemic in the Pantepui Province, and both have large distribution areas: *L. guayanense* was sampled in Kanarakuni (450 m a.s.l.) and also in the foothills of Jaua Jidí-Sarisariñama Massif and Mt. Roraima and Auyán Tepui (Flint et al., 1987), while *L. ramosum* was recorded at La Escalera (Piedra de la Virgen), Salto Pará at Río Caura and Kanarakuni (Flint et al., 1987). Meanwhile, the remaining two species were recorded in the Pantepui Province at Cerro de la Neblina: *L. neblinense* Flint, McAlpine & Ross, 1987 sampled from 1,690 to 1,850 m a.s.l., and *L. amazonense* Flint, 1978 sampled from 140 to 1,820 m a.s.l. (Flint et al., 1987). At least these further 12 *Leptonema* species have been recorded in Venezuelan Guyana. The following five of these were sampled and/or described at Cerro de la Neblina from 140 to 760 m a.s.l.; (1) *Leptonema davisi* Flint, McAlpine & Ross, 1987; (2) *L. sparsum* Ulmer, 1905; (3) *L. irroratum* Flint, 1974; (4) *L. aterrimum* Mosely, 1933; and (5) *L. viridianum* Navás, 1916. In addition, (6) *L. lacuniferum* Flint, 1978 was sampled in Bolívar State at La Escalera at 1,100 m a.s.l.; and (7 and 8) *L. hirsutum* Flint, 1974 and *L. spinulum* Flint, McAlpine & Ross, 1987 are known from Kanarakuni (450 m a.s.l.) but they have larger distribution areas. (9) *L. aspersum* Ulmer, 1905; (10) *L. sancticaroli* Flint, McAlpine & Ross, 1987; and (11) *L. gadzux* Flint, McAlpine & Ross, 1987 are known from San Carlos de Río Negro, while (12) *L. albovirens* Walker, 1852 is widespread in South America (Flint et al., 1987).

Material examined: *Leptonema* sp.: A1 – 2L, A2 – 20L, A6 – 2L.

Genus *Macrostemum* Kolenati, 1859

Although this is a widely spread genus in North and South America, Africa, and Asia, it was previously unknown in the Pantepui (Flint et al., 1999). The immature stages of the genus are rheophilous, therefore living in or on solid substrate (Flint et al., 1999). This genus has not yet been found in the Pantepui.

Material examined: *M. erichsoni* Banks, 1920: C1 – 2♂♂, 1♀.

Family Hydroptilidae Stephens, 1836

This family is commonly referred to as microcaddisflies, because it has the smallest body size in this order, with adults ranging between only 1.5 and 5 mm. It is, however, the largest in species diversity with about 2,000 species on every habitable continent and on many remote islands (Holzenthal et al., 2007). It currently includes 28 genera and 290 species in South America (Angrisano & Sganga, 2009^b). The larvae are highly diverse in form, habitat, and feeding behaviour. Most build cases of silk or sand, while some construct flat, fixed shelters and others are free-living until pupation (Wiggins, 2004). At least 18 genera have been recorded in Venezuela (Flint & Harris, 1992; Flint et al., 1999; Harris & Flint, 2002; Harris et al., 2002^{a-c}; Wasmund & Holzenthal, 2007), but no data has been published from the Pantepui. Finds related

to the Pantepui reported from Cerro de la Neblina at 140 m a.s.l. were; (1) *Neotrichia colmillosa* Harris, 1990; (2) *N. cuernuda* Harris, 1990 (Harris, 1990); (3) *N. cayada* Harris & Davenport, 1992 (Harris & Davenport, 1992); (4) *Alisotrichia neblina* Harris & Flint, 2002 (Harris & Flint, 2002); and (5) *Taraxitrichia amazonensis* Flint & Harris, 1992 (Flint & Harris, 1992). In addition, Wasmund & Holzenthal (2007) also described *Rhyacopsyche otarosa* from Cerro de la Neblina at 760 m a.s.l. and representatives of genera *Flintiella* Angrisano, 1995 and *Orinocotrichia* Harris, Flint & Holzenthal, 2002 are recorded from Río Cataniapo and San Carlos de Río Negro, with *Oxyethira* Eaton, 1873 from the Bolívar State (Flint et al., 1999; Harris et al., 2002^{a,b}). Although three genera were clearly identified, some material requires more detailed study: C2 – 1♂, C4 – 1♀; A2 – 1♂, A4 – 2♂♂.

Genus *Orthotrichia* Eaton, 1873

Orthotrichia is a large genus with world-wide distribution. In the Neotropics, this genus has been reported from the Antilles, Panama, Ecuador and Peru (Flint et al., 1999).

Material examined: *Orthotrichia* sp.: A2 – 25L, A4 – 3L, 3♂♂, 3♀♀.

Genus *Oxyethira* Eaton, 1873

Oxyethira is a very large genus with world-wide distribution. Their larvae are well known because they build distinctive flask-shaped silken cases (Wiggins, 1996).

Material examined: *Oxyethira* sp.: C9 – 40L, C10 – 7L, R2 – 4L.

Genus *Zumatrichia* Mosely, 1937

Larvae of *Zumatrichia* are indistinguishable from *Abtrichia* Mosely, 1939 (Angrisano & Sganga, 2009^a). However, *Abtrichia* is a small genus reported in southern Brazil, Uruguay and Argentina, while *Zumatrichia* is a fairly large genus, which occurs from the United States through Central America and Lesser Antilles to northern areas of South America, including Venezuela (Flint et al., 1999). Therefore, the collected larval material here is most likely from the genus *Zumatrichia* (Fig. 116D).

Material examined: *Zumatrichia* sp.: C5 – 20L, 15P; A2 – 25L, 7P.

Family Leptoceridae Leach, 1815

The Leptoceridae, or long-horned caddisflies, are recognized by their long, narrow forewings and very long, filiform antennae. They comprise one of the largest families in the order, with about 1,800 described species (Holzenthal et al., 2007). The larvae are found in a wide variety of habitats, including large and small rivers, cascades, and even in semiterrestrial habitats in both lowland and highland areas (Flint et al., 1999). They construct a wide diversity of cases, perhaps the most diverse in the order. Cases are fundamentally tubular, but can be made entirely of silk secretions, of plant debris arranged spirally or laid transversely, or of large leaf fragments, which then form flattened cases (Wiggins, 2004). Larvae feed as leaf detritus shredders, periphyton scrapers, predators, and they even feed on freshwater sponges. Fifteen genera have been reported in South America, with seven of these endemic to the Neotropics (Flint et al., 1999;

Holzenthal et al., 2007). The genera *Achoropsyche* Holzenthal, 1984; *Atanatolica* Mosely, 1936; *Grumichella* Müller, 1879; *Nectopsyche* 1879; *Notalina* Mosely, 1936; *Oecetis* McLachlan, 1877; and *Triplectides* Kolenati, 1859 have been recorded in Venezuela (Flint et al., 1999). While *Notalina* and *Triplectides* genera had previously been reported in the Pantepui (Holzenthal, 1986, 1988), *Oecetis* and *Nectopsyche* are recorded for the first time.

Genus *Notalina* Mosely, 1936

This genus has a trans-Antarctic distribution between Australia and the Neotropics (Holzenthal et al., 2007). In South America, it comprises 10 described species placed in the subgenus *Neonotalina*. The genus is subdivided into two species groups; the *braziliana* and the *roraima* (Holzenthal, 1986; Calor, 2008; Calor et al., 2006). Calor & Froehlich (2008) described the immature stages. The only record of the genus from the Pantepui was one *N. roraima* Holzenthal, 1986 male described from the Mt. Roraima plateau (Holzenthal, 1986).

Material examined: *Notalina* sp.: C2 – 6L, 1♂, A2 – 4L, R3 – 1L; *N. roraima*: R2 – 3♂♂.

Genus *Triplectides* Kolenati, 1859

Similar to *Notalina*, the genus *Triplectides* has a trans-Antarctic distribution between Australia and the Neotropics, with species occurring in New Caledonia, India, Southeast Asia and Japan (Holzenthal et al., 2007). More than 70 species are known, and 14 of these were recorded in South America (Holzenthal, 1988; Dumas & Nessimian, 2010). Holzenthal (1988) described *T. nevadus* from San Carlos de Río Negro and *T. neblinus* and *T. neotropicus* from Cerro de la Neblina, at 140 and 760 m a.s.l. He also described *T. tepui* from Cerro de la Neblina (1,250 – 2,100 m a.s.l.) which is the only Pantepui representative of the genus. This species has also been recorded at 1,600 m a.s.l. in Río Teuanen, north of Kavanayén in the Bolívar State.

Material examined: *Triplectides* sp.: C4 – 34L, C8 – 4L, A2 – 1L, A4 – 5L.

Genus *Oecetis* McLachlan, 1877

This is a cosmopolitan genus of more than 200 described species, with 22 known from South America (Rueda Martín et al., 2011). Two widely distributed species *O. excisa* Ulmer, 1907 and *O. punctipennis* Ulmer, 1905 were sampled in Cerro de la Neblina at 140 m a.s.l. (Rueda Martín et al., 2011).

Material examined: *Oecetis* sp.: C4 – 2L, A6 – 1L.

Genus *Nectopsyche* Müller, 1879

The New World genus *Nectopsyche* has approximately 57 described species, with 48 known from South America and 10 from Venezuela (Flint et al., 1999). *N. multilineata* Flint, 1983 was collected in Caroní River (Flint, 1983).

Material examined: *Nectopsyche* sp.: C1 – 1♂, 1♀.

Species identification was impossible because specimens were leached in ethanol and wing colour patterns are necessary for species-level classification.

Family Odontoceridae Wallengren, 1891

This small family contains approximately 115 extant species

in both the Old World and the New World (Holzenthal et al., 2007). Three genera occur in the Neotropics (Flint et al., 1999). Larvae live in springs and small to medium-sized streams and rivers, and some are associated with waterfalls. Their cases are made of sand grains or larger mineral fragments and are very resistant to crushing. The larvae themselves are omnivorous, feeding on detritus, vascular plants, moss, algae and aquatic arthropods (Wiggins, 2004).

Genus *Marilia* Müller, 1880

The genus *Marilia* is worldwide distributed, with 53 extant species (Dumas & Nessimian, 2009), with its greatest diversity in the Neotropics; 33 species occur in South America and one in Venezuela (Flint et al., 1999; Dumas & Nessimian, 2009). Until our own data, no previous record was reported from the Pantepui.

Material examined: *Marilia* sp.: A1 – 2L, A2 – 2L, 3♂♂, 1♀; A3 – 5L, A4 – 35L, 1♂; A5 – 7L, A6 – 85L.

Family Philopotamidae Stephens, 1829

This is a cosmopolitan family with approximately 1,000 described species. Three of the five genera recorded in South America are known in Venezuela: *Chimarra* Stephens, 1829; *Chimarrhodella* Lestage, 1925; and also *Wormaldia* McLachlan, 1865 (Flint et al., 1999; Holzenthal et al., 2007). Larvae construct elongate tubular nets which are usually attached to the underside of rocks, and spin an extremely fine mesh inside the coarse outer supporting meshwork. Larvae feed on detritus and microorganisms filtered from water passing through the net (Wiggins, 2004). Three species of the genus *Chimarra* have been reported from the Pantepui (Blahnik, 1997; Flint, 1998).

Genus *Chimarra* Stephens, 1829

This cosmopolitan genus is one of the largest genera in the order Trichoptera. It includes approximately 570 described species, and many more which have not been described (Holzenthal et al., 2007). Flint (1998) revised the subgenus *Curgia* and described and reported from the Pantepui two species: *Ch. (Curgia) ensifera* Flint, 1998, and *Ch. (Curgia) medioloba* Flint, 1971. Besides their Pantepui localities at Cerro de la Neblina 1,690 and 1,850 m a.s.l., both species have also been reported at 140 m a.s.l. Two additional species from the subgenus are known at 140 m a.s.l. at Cerro de la Neblina, and 2 species at La Escalera in the Bolívar State (Flint, 1998). Blahnik (1997) defined the new subgenus *Chimarrita*, and also described the Pantepui species *Ch. (Chimarrita) neblina* Blahnik, 1997 at Cerro de la Neblina (1,820 m a.s.l.). He reported and/or described two more species from the subgenus at lower altitudes at Cerro de la Neblina, and also two species from Tobogán de la Selva near Puerto Ayacucho. Blahnik (2002) defined the further new subgenus *Otarrha* and reported three species from Cerro de la Neblina at 140 m a.s.l.

Material examined: *Chimarra* sp.: A2 – 1♂.

Family Polycentropodidae Ulmer, 1903

This is a large and diverse cosmopolitan family containing approximately 650 species in 26 genera (Holzenthal et al., 2007). The larvae are found in most types of waters, although

they are virtually absent from small, cold spring streams (Flint et al., 1999). Larvae construct a variety of nets, either as a larval silken retreat or as a capture net (Wiggins, 2004). Although most species are predators, they also ingest plant detritus (Flint et al., 1999). Six genera occur in South America, four of which have been recorded in Venezuela (Flint et al., 1999; Hamilton & Holzenthal, 2005). The widely distributed species *Cyrtellus fraternus* (Banks, 1905) is the only representative of the genus *Cyrtellus* Banks, 1913 known from Venezuela. One species from the *Polycentropus* genus and two *Polyplectropus* species have recently been described in the Pantepui at Cerro de la Neblina (Hamilton & Holzenthal, 2005; Chamorro & Holzenthal, 2010). According to authors Chamorro & Holzenthal (2010), 12 species have been recorded in Venezuela, 2 of these from Cerro de la Neblina in the Pantepui: *Polyplectropus amazonicus* (1,820 m a.s.l.) and *P. flintorum* (1,450 – 2,100 m a.s.l.). Two additional *Polyplectropus* species were described by Chamorro & Holzenthal (2010) from lower altitudes at Cerro de la Neblina: *P. guyanae* at 140 m a.s.l. and *P. maculatus* between 140 and 760 m a.s.l. Finally, *Polycentropus beccus* from Puerto Ayacucho region was described by Hamilton & Holzenthal (2005).

Genus *Polycentropus* Curtis, 1835

This is a cosmopolitan genus of more than 170 species (Holzenthal et al., 2007), with 102 species recognized in the Neotropics (Hamilton & Holzenthal, 2011). There are 5 species known in Venezuela (Flint et al., 1999; Hamilton & Holzenthal, 2011). Here, one species, *P. neblinensis* Hamilton & Holzenthal, 2005 was described at 1,690 – 2,100 m a.s.l. at Cerro de la Neblina in the Pantepui.

Material examined: *Polycentropus* sp.: C1 – 15L, C2 – 12L, C4 – 10L, 1♂, C8 – 1L, C9 – 13L, C10 – 3L, A2 – 1L, A4 – 2L, A6 – 7L.

Family Sericostomatidae Stephens, 1836

This family contains 19 genera and approximately 100 species. In South America, four genera were considered endemic to southern Chile and adjacent Argentina, and a further genus with the single species *Grumicha grumicha* (Vallot, 1855) was considered endemic to southern and southeastern Brazil and adjacent Argentina (Flint et al., 1999; Holzenthal et al., 2007). However, Holzenthal & Blahník (2010) described the new species named *Notidobiella amazoniana* from Ecuador and Amazonian Brazil. These authors suggest that recent dispersal of the genus to northern tropical South America from Patagonia was followed by its subsequent diversification. This constitutes the first record of this family in the Guyana region, and the northernmost record in South America.

Material examined: Sericostomatidae indet: C7 – 1L, C5 – 4L.

3.2.7. Orthoptera

3.2.7.1. Introduction

Orthoptera are hemimetabolous insects and although these are not normally considered to be aquatic insects, some members are some-how linked to freshwater habitats, mainly through relationship with an aquatic plant host. Species which cannot develop without freshwater, especially for egg-laying and nymph

development are considered to be primary inhabitants of freshwater biota (Amédégnato & Devriese, 2008). The freshwater Orthoptera community is mainly represented by Acridomorpha, Acridoidea. Among Ensifera, the predaceous Ensifera katydid genus *Phlugis* specialises on nymphs of aquatic grasshoppers in South America (Amédégnato & Devriese, 2008). The South American *Hydrolutos* species are medium-sized flightless anostomatids known from Venezuelan tepuis. As a typical almost fully southern hemispheric group of orthopterans, Anostomatidae are believed to owe their distribution to the split of Gondwanaland (Fleming, 1979; Gibbs, 2006). The genus *Hydrolutos* Issa & Jaffe, 1999 (Orthoptera: Anostomatidae: Lutosinae) had the 4 species: *H. auyan*, *H. chimantea*, *H. roraimae* and *H. aracamuni*, described from four different tepuis in southeastern Venezuela (Issa & Jaffe, 1999). Derka & Fedor (2010) described the new species *Hydrolutos breweri* from Cueva Charles Brewer, and Derka & Fedor (2012) contributed an additional description of the female of this species. All these appear unique and unusual in their aquatic ecology, and their existence in this environment is enabled by a plastron-like structure on the pleuro-sternal area of the thorax and abdomen, which is generally unique in orthopterans. The external morphology is highly conserved in all species of this genus, as reported in the original description of *Hydrolutos* by Issa & Jaffe (1999). In body length, the species ranges between 38 – 54 mm in males and 38 – 62 mm in females, with the latter tending to be slightly larger than the males. All members of genus *Hydrolutos* have brown colouring and they are apterous and nocturnal.

3.2.7.2. Results and Discussion

Charles Brewer-Carias reported the occurrence of many 10 to 12 cm long individuals of the genus *Hydrolutos* in his eponymous newly discovered gigantic cave on Churí Tepui on the Chimantá Massif, that submerged underneath the water in case of danger (Šmída et al., 2005^a). Derka & Fedor (2010) described the new species, *Hydrolutos breweri* (Fig. 117A, B) from this Cueva Charles Brewer. Male genitals of the genus *Hydrolutos* were figured and described for the first time. Like other members of the genus, *H. breweri* inhabits aquatic habitats, and many individuals were observed walking and swimming in the stream, and also walking outside the water at the floor and walls of this cave. Their powerful legs and tarsal claws enable them to cling tightly and also to move even against strong currents. Because of permanent darkness in this cave, individuals were active 24 hours a day, and not only nocturnally as in some members of this genus (Issa & Jaffe, 1999; Derka, pers. observ.). However, it can not be considered to be troglobiont because of the lack of the typical adaptations of eye reduction and colouring. Occurrence of this species can also be expected in other streams at Churí Tepui plateau outside Cueva Charles Brewer. We observed numerous individuals of *H. roraimae* in the cave systems of Mt. Roraima and *H. auyan* in the stream near the El Oso Camp site on Auyán Tepui. Digestive tract analysis of four specimens of *H. breweri* from Cueva Charles Brewer revealed plant and animal detritus, aquatic fungi hyphae and other animal remains identified as originating from Chironomidae larvae, mayflies and stoneflies. Therefore, these observed specimens did not feed on

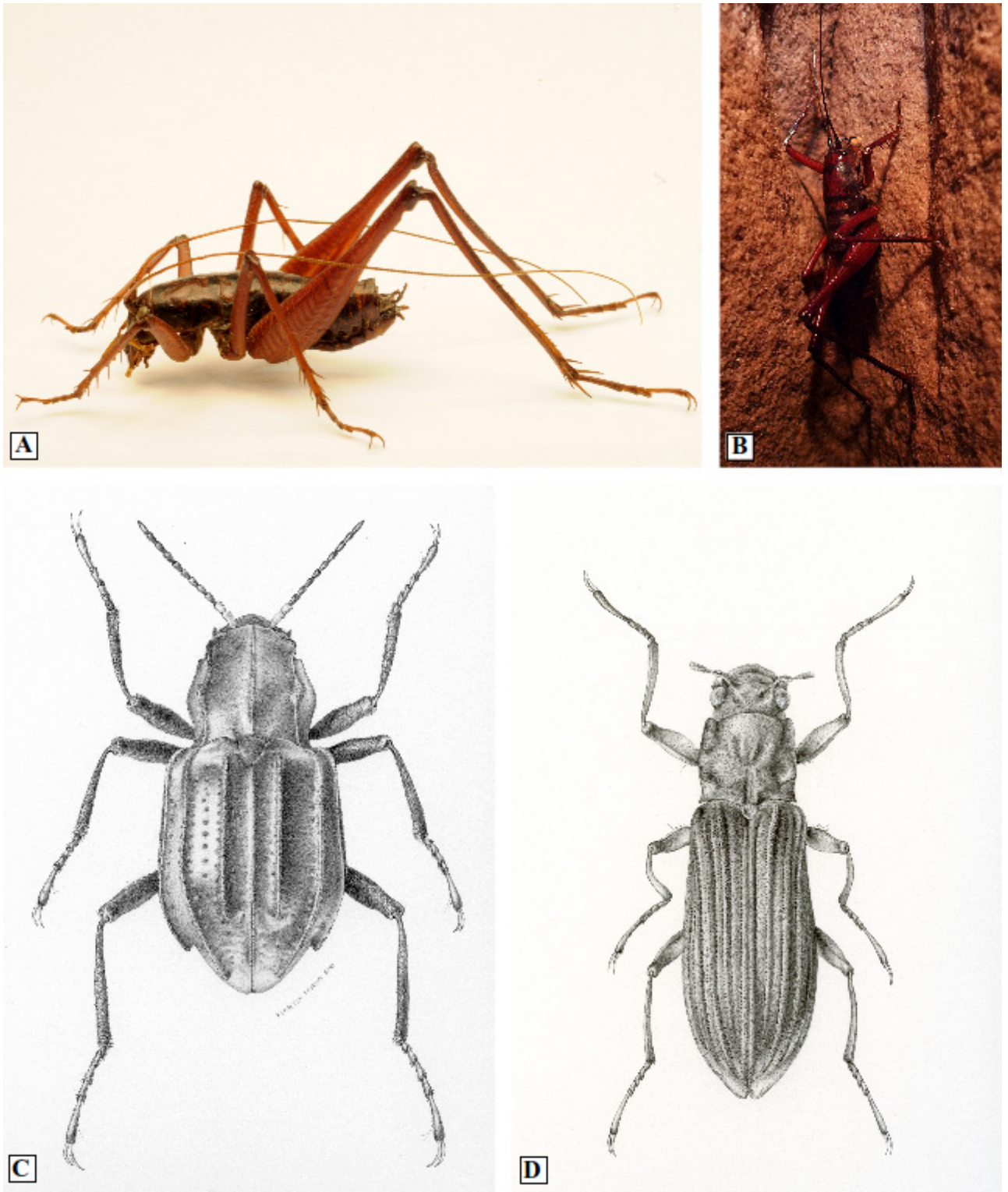


Fig. 117: A-B – *Hydrolutos breweri* from Cueva Charles Brewer. C – *Jolyelmis auyana* (Coleoptera, Elmidae) from Auyán Tepui. D – *Roraima carinata* (Coleoptera, Elmidae) from Mt. Roraima.

algae as Issa & Jaffe (1999) reported for other *Hydrolutos* species, instead they had changed their diet in this environment which lacked light and algae.

3.2.8. Coleoptera

3.2.8.1. Introduction

Beetles are holometabolous insects, normally with adecticous, exarate pupae. Adults are characterized by a strongly sclerotized body with forewings hardened into elytra, which serve to protect the more delicate hind wings and the dorsal surface of the hind two thoracic segments (pterothorax) and abdomen. Beetles have the largest number of species in the entire animal world, with 400,000 currently described (Jäch & Balke, 2008). Although the Coleoptera are one of the largest orders of “aquatic” animals containing approximately 18,000 aquatic species, this is a very small percentage and the majority are terrestrial. According to Jäch & Balke (2008) approximately 12,600 (70%) were described prior to October 2005. About 30 beetle families have aquatic representatives, and in 25 families at least 50% of the species can be considered truly aquatic (Jäch & Balke, 2008). The following six families are thought to include 1,000 or more aquatic species: Dytiscidae (3,908 described species/5,000 estimated), Hydraenidae (1,380/2,500), Hydrophilidae (1,800/2,320), Elmidae (1,330/1,850), Scirtidae (900/1,700) and Gyrinidae (750/1,000). The Neotropical region is home for 2,510 known species and 3,900 estimated species (Jäch & Balke, 2008).

Our study focused on the family Elmidae. This family has approximately 1,330 species in 146 genera (Kodada & Jäch, 2005). Two subfamilies are currently recognized: Larainae (26 genera, 130 species), and Elminae (120 genera, 1,200 species). Adults and larvae of all the species are considered aquatic, many Larainae species adults are often encountered below or a little above the water line, and also in spray zones of waterfalls and cascades. Of all the larger water beetle families, only the elmids appear to be exclusively confined to running water. Although the Neotropical region has approximately 360 described Elmidae species, it still remains inadequately explored (Jäch & Balke, 2008).

3.2.8.2. Results and Discussion

A few genera of Elmidae have been found at the studied tepuis, and three of these are identified: *Roraima* Kodada & Jäch, 1999, *Jolyelmis* Spangler & Faitoute, 1991, and *Gyrelmis* Hinton, 1940.

Subfamily Larainae LeConte, 1861

Larainae represent a small subfamily, which occurs in all major regions of the world. The Palearctic, Nearctic, Neotropic and Afrotropical faunas are reasonably well known, in contrast to those in Oriental and Australian regions. The species diversity appears highest in Afrotropical and Neotropic regions (Kodada & Jäch, 2005). Eleven genera have been reported in the Neotropics (Kodada & Jäch, 1999, Maier & Spangler, 2011). Adults are always associated with running waters. Most species can be regarded as true water beetles, and although many species can fly readily and rapidly when disturbed, their larvae are considered to be strictly aquatic.

Genus *Roraima* Kodada & Jäch, 1999

The genus *Roraima* can be easily distinguished from all other known Larainae genera by the shape of the pronotum, elytral carinae and by the unique forking and fusion of the medial field veins of the hind wing (Kodada & Jäch, 1999). *Roraima carinata* (Fig. 117D) was described from R1. One *Roraima* species, which is yet to be described, was found in the streams at Churí Tepui and also at the entrance of Cueva Charles Brewer, while the second was found in Auyán Tepui streams.

Material examined: *Roraima carinata*: R1 – 2♂♂, 2♀♀; *Roraima* sp. 1: C1 – 4 adults, 4 larvae; C2 – 14 adults, 10 larvae; C5 – 3 adults, 4 larvae; C9 – 4 adults, 1 larva; *Roraima* sp. 2: A2 – 5 adults, 2 larvae; A4 – 7 adults, 10 larvae; A5 – 6 adults, 7 larvae.

Subfamily Elminae Curtis, 1830

The subfamily Elminae currently includes 119 genera with approximately 1,200 recognized species (Kodada & Jäch, 2005). All Elminae species are regarded as true water beetles and there are no terrestrial or riparian representatives in this subfamily. Larvae are considered strictly aquatic, adults live exclusively in running water, which includes both hygropteretic habitats and subterranean streams, and they are seen quite rarely in wave-washed lake shores. Their preferred habitats are rapidly flowing reaches of streams and rivers, and especially shallow riffles and rapids. In these streams and rivers, they are found on stony substrates of varying grain size, including rocks, boulders, gravel and sand, as well as on dead wood, dead leaf accumulations and vegetation. Elminae exhibit several obvious morphological adaptations to their unusual habitat: the cuticle is very strongly sclerotized and the head is retractable into the prothorax to minimize injury when dislodged in the strong current; the legs are long and their claws are very large so that this strength enables them to cling firmly to substrates. Adults do not need to come to the surface to breathe, because they possess an incompressible gas gill or microplastron incorporating a very thin layer of air held by a dense coating of hydrofuge structures, which can replace oxygen through diffusion of dissolved oxygen from the surrounding water, thus functioning as a physical gill (Kodada & Jäch, 2005).

Genus *Jolyelmis* Spangler & Faitoute, 1991

The genus *Jolyelmis* Spangler & Faitoute (1991) comprises one of the numerous South American elmid genera. It was established on the single, very distinctive species of *Jolyelmis auyana* Spangler & Faitoute, 1991, which was collected from a cascade on Auyán Tepui. The most striking characteristics of the type species, *Jolyelmis auyana*, are three distinct longitudinal carinae on the pronotum and each elytron and also carinae on the metasternum and the first ventrite (Spangler & Faitoute, 1991). Two additional species, *J. derkai* Čiampor & Kodada, 1999, and *J. reitmaieri* Čiampor & Kodada, 1999, were discovered in a few small samples from streams crossing the footpath to Mount Roraima. In contrast to the type species, longitudinal carinae on these species are much less pronounced and less distinctive (Čiampor & Kodada, 1999). Representatives of four species have been collected: *Jolyelmis auyana* was collected in Auyán Tepui (Fig. 117C); individuals of *J. reitmaieri* were found in Cueva de los Pémones; while the new *Jolyelmis* species specimens came

from various streams on Churí Tepui plateau and the entrance to Cueva Charles Brewer. These were defined as *J. spangleri* by Kodada et al. (2012), who also described the larva of *J. spangleri* and *J. reitmaieri*.

Material examined: *J. derkai*: R1 – 5♂♂; *J. reitmaieri*: R1 – 11♂♂, 9♀♀; *J. spangleri*: C1 – 3♂♂, C2 – 4♂♂, C4 – 1♀, C7 – 12♂, 7♀♀, C9 – 1♀, 1 unsexed specimen. *J. auyana*: A2 – 3 adults, 2 larvae; A4 – 4 adults, 7 larvae; A5 – 8 adults, 1 larva.

Genus *Gyrelmis* Hinton, 1940

There are twelve Neotropical species currently recognized (Kodada & Jäch, 2005). Representative of one, probably undescribed species was collected at Churí Tepui.

Material examined: *Gyrelmis* sp.: C1 – 1♂, 1♀

3.3. HERPETOFAUNA OF THE “LOST WORLD”

3.3.1. Introduction

Tepuis result from the erosion of a once extensive plain that was part of Gondwana, comprising South America, Africa and Antarctica. Their impressive appearance resembles islands towering from their surrounds of pluvial forest and herbaceous savannas, and they are often surrounded by clouds. In terms of evolutionary history, their isolation transforms the higher tepuis into isolated ecosystems with high speciation and endemism. The life that evolved in each tepui is unique, although some genera, and very occasionally, some species are shared with other tepuis. With regard to herpetofauna, each genus possesses one or more endemic species in each tepui. The herpetofauna of the tepuis is impoverished compared with its surrounding, which include endemics of the Guyana Shield with Amazon elements of wide distribution.

In this part, we examine only a minimum selection of species inhabiting the summits of selected tepuis all over 1,000 m (Tab. 13). There are some lower tepuis ranging from 650 m to 1,500 m a.s.l., but these generally have forested summits with few endemic elements. It is considered that endemic species exist only on the higher tepuis at 2,000 to 3,000 m a.s.l., without the possibility of existing elsewhere. Species above 1,000 m altitude are only considered here because Autana is a low tepui with 1,450 m summit, and fauna changes significantly between its base and its summit. In all other respects, the higher tepuis in Bolívar State are usually treated differently with highland fauna above 1,500 m being considered different to those below (see MacCulloch et al. 2007). While the eastern tepuis contain common lowland species to 1,000 m, only tepui summits of at least 2,000 m are considered here; with the single exception of Autana.

3.3.2. History of herpetological collections in the “Lost World”

Expeditions to these remote sandstone tables, and especially their summits, are logistically difficult, expensive, and therefore scarce. Early explorations began at the end of the 19th century, in 1894 and 1898, when E. Im Thurn and H. Perkins, and then

F.V. McConnell and J.J. Quelch, ascended Roraima and collected botanical specimens. Some reptile and amphibian samples collected on the slopes and summit went to the British Museum, where they were described by Georges Boulenger (1900). Thus, the first described tepui species originated from the slopes and summit of Roraima. These were: *Oreophrynella macconelli*, *O. quelchii*, *Otophryne robusta*, *Riolama leucosticta* (Fig. 121F), *Neusticurus rudis* and *Pristimantis marmoratus*. Although Roraima is the most visited tepui, only two species of herps have been described since 1900, *Anomaloglossus praderioi* and *A. roraima*, although we know at least one additional species of *Pristimantis* that is being described (McDiarmid & Donnelly, 2005; C. Barrio-Amorós, in prep.).

The first specimens from the Auyán Tepui were collected during the Phelps Expedition with the American Museum of Natural History (AMNH) in 1937-38 (Roze, 1958^a; Myers, 1997; Myers & Donnelly, 2008), and these latter authors also presented data from AMNH collections.

The Chimantá Massif was explored for the first time by the Museum of Natural History of Chicago in 1955. The expedition led by botanist Julian Steyermark was able to access this massif only by foot. Roze (1958^b) reported on herpetofauna, describing several new species. Gorzula (1992) presented results from years of collecting. In our three recent expeditions, we have now been able to observe a significant portion of the herpetofauna inhabiting it.

The only existing herpetological reports on Autana are, the description of *Stefania breweri* (Barrio-Amorós & Fuentes, 2003; personal data), and the report of the presence of *Cercosaura phelpsorum* by Fuentez & Rivas (2000).

Modern explorations of these tepuis began in the 1960s, when helicopters were used for the first time to reach the otherwise inaccessible summits. Charles Brewer-Carías, the Michelangeli brothers, Otto Huber and a few other scientists are responsible for revealing some of the mysteries of the “Lost World” to the academic community, especially regarding its biota. However, the most fruitful herpetological collector in the tepui area has certainly been Stefan Gorzula, who used EDELCA helicopters in the 1980s to explore a great part of the sandstone summits of Bolívar and Amazonas states (Gorzula & Señaris, 1999). Other herpetologists who have published their collections from Venezuelan tepuis are; José Ayarzagüena, Celsa Señaris, Charles Myers, Maureen Donnelly, Roy McDiarmid, Philippe Kok and the authors of this part of the volume. The following five tepuis are described as examples: Autana, Auyán, Chimantá, Roraima and Sarisariñama (Tab. 13).

3.3.3. Results

3.3.3.1. Cerro Autana

The Autana sacred mountain has a peculiar shape (Fig. 118A). Due to its unique “tree stump” form, it has been worshipped from remote times by the Piaroa natives as the tree of life. The Piaroa and the Hiwi call it “Wahari-Kuawai” and “Caliebirri-nae” respectively (Brewer-Carías, 1972, 1976^a). This small tepui is located 90 km to the South of Puerto Ayacucho in the Amazonas State. It is composed of pink sandstone and runs south to

Tab. 13: Composition of the tepui herpetofauna treated in the text. It remains extremely complicated to formulate a list which includes all species inhabiting different altitudes. The inferior limit for Autana and Sarisariñama is 1,000 m. a.s.l. For Auyán, Chimantá and Roraima we consider the inferior limit at 1,500 m. a.s.l.

	Auyán	Chimantá	Autana	Roraima	Sarisariñama
Amphibians					
<i>Oreophrynella cryptica</i>	+				
<i>O. macconelli</i>				+	
<i>O. quelchii</i>				+	
<i>Rhaebo guttatus</i>		+			
<i>Rhinella granulosa</i>		+			
<i>Centrolene gorzulai</i>	+				
<i>Hyalinobatrachium mesai</i>					+
<i>H. cappellei</i>	+			+	
<i>H. taylori</i>	+				
<i>Anomaloglossus rufulus</i>		+			
<i>A. moffetti</i>					+
<i>A. praderioi</i>				+	
<i>A. roraima</i>				+	
<i>A. tepuyensis</i>	+				
<i>Dendrobates leucomelas</i>					+
<i>Stefania breweri</i>			+		
<i>S. ginesi</i>		+			
<i>S. riae</i>					+
<i>S. roraimae</i>				+	
<i>S. schuberti</i>	+				
<i>Hypsiboas aff. crepitans</i>		+			
<i>H. jimenezi</i>	+	+			
<i>H. roraima</i>	+			+	
<i>H. sibleszi</i>	+	+		+	
<i>H. tepuianus</i>	+				+
<i>Myersiohyala kanaima</i>				+	
<i>Osteocephalus taurinus</i>					+
<i>Tepuihyla edelcae</i>	+	+			
<i>T. warreni</i>				+	
<i>Ceuthomantis duellmani</i>					+
<i>Pristimantis auricarens</i>	+				
<i>P. marmoratus</i>	+			+	
<i>P. sarisarinama</i>					+
<i>P. muchimuk</i>		+			
<i>Pristimantis</i> sp. 1				+	
<i>Leptodactylus cf. lithonaetes</i>			+		
<i>L. longirostris</i>	+	+			
<i>L. rugosus</i>	+				
<i>L. sabanensis</i>		+			

	Auyán	Chimantá	Autana	Roraima	Sarisariñama
<i>Pseudopaludicola</i> sp.				+	
<i>Otophryne robusta</i>	+			+	
<i>O. steyermarki</i>		+		+	
Reptiles					
<i>Gonatodes superciliaris</i>					+
<i>Norops carlostoddi</i>		+			
<i>N. chrysolepis</i>	+			+	
<i>N. ewi</i>	+	+			
<i>N. ortonii</i>					+
<i>Plica</i> aff. <i>plica</i>			+		
<i>Tropidurus bogerti</i>	+				
<i>T. hispidus</i>	+				
<i>Tropiduridae</i> sp.					+
<i>Mabuya nigropunctata</i>				+	+
<i>Anadia mcdiarmidi</i>		+			
<i>Euspondylus auyanensis</i>	+				
<i>Arthosaura montigena</i>	+				
<i>A. tyleri</i>					+
<i>A. versteegii</i>	+				
<i>Arthosaura</i> sp.		+			
<i>Cercosaura phelpsorum</i>			+		+
<i>Neusticurus rudis</i>	+	+		+	+
<i>N. tatei</i>					+
<i>N. racenisi</i>	+				
<i>Riolama leucosticta</i>				+	
<i>Epictia albifrons</i>	+		+		
<i>Anilius scytale</i> "phelpsorum"	+				
<i>Atractus guerreroi</i>	+				
<i>A. steyermarki</i>		+			
<i>Chironius fuscus</i>	+				+
<i>Erythrolampus aesculapii</i>	+				
<i>Leptodeira annulata</i>	+	+			
<i>Mastigodryas boddaerti</i>	+				
<i>Liophis ingeri</i>		+			
<i>L. lineatus</i>	+				
<i>L. torrenicola</i>					+
<i>L. trebbai</i>	+	+			
<i>L. reginae</i> aff. <i>semilineata</i>			+		
<i>Pseustes poecilonotus</i>					+
<i>Thamnodynastes chimanta</i>		+			
<i>Bothriopsis taeniata</i>		+		+	

	Auyán	Chimantá	Autana	Roraima	Sarisariñama
<i>Bothrops atrox</i>	+				+
<i>Crotalus durissus ruruima</i>				+	
Known total	35	23	6	21	20

north for approximately 2.5 km², culminating in its northern tower at 1,450 m. a.s.l. It is located at 04° 52' N, 67° 27' W. The Autana appears to be the remainder of the Sipapo-Cuao Massif which borders it, and geologically, it is part of the Roraima Supergroup (Colvée, 1972, 1973). The vegetation at its summit is composed of a tepui grassy meadow, and the bushes there contain the dominant *Kunhardtia rhodanta* and *Brocchinia hechtoides* plants. The predominant temperature range at the summit is between 18° and 24° C.

Few scientific expeditions have been carried out on the summit, and most of these have been by TV crews, as witnessed in the famous 1973 documentary by Félix Rodríguez de la Fuente for TVE (Spanish Television). Another expedition was carried out by the Radio Caracas TeleVision for its "Expedition" series, and this episode was called "Autana, the tree of life". However, it was Brewer-Carías's 1971 exploration expedition, with its mapping of the sandstone cave crossing the north tower of Autana, that have made Autana famous and created excitement throughout the scientific community. In his first expedition in February 1971, Carlos Julio Naranjo collected a tree-frog that was described 32 years later, and eponymously named *Stefania breweri* after Brewer. However, its morphological description remains the only thing known about this species, because there was only a single specimen, and despite all efforts it has never been sighted since (Barrio-Amorós & Fuentes, 2003).

It is interesting to note that Félix Rodríguez de la Fuente's 1973 film mentioned some specimens to be identified by the Spanish naturalist Dr. Javier Castroviejo. Although such identification was never performed, that documentary did highlight a specimen similar to the one collected later in 2000, and identified by Oswaldo Fuentes as *Leptodactylus cf. lithonaetes*.

The only exhaustive scientific expedition to the Autana summit forms part of a work that is still in preparation, and this is based on the study of herpetofauna collections from the Cuao-Sipapo Massif, including Sipapo, Cuao, Autana and Lago Leopoldo or "Paraka-Wachoi" Lake. These collections were carried out in Lago Leopoldo and the Autana summit by Oswaldo Fuentes-Ramos (OFR), after the invitation of Charles Brewer-Carías in 2000. This expedition also included investigations in the Cuao-Sipapo Massif lowland areas and the Autana surrounds made by OFR and Cesar Barrio-Amorós (CLBA), together with Santiago Castroviejo and Fernando Rojas.

Since only the material collected by OFR at the summit of the Autana is of interest in this present work, the following specimens collected during that April 2000 expedition are recorded here; (1) *Leptodactylus lithonaetes* Heyer, 1995. Only several males observed, darker than in surrounding lowlands, under small stones, active near small pools; (2) *Stefania breweri*, despite an extensive day and night search, the only known endemic Autana

frog, *Stefania breweri*, was not found; (3) *Plica* aff. *plica* (Linnaeus, 1758) collected on a rock on the southern side (the species is a common element in pluvial forests throughout the entire Amazon); and (4) *Cercosaura phelpsorum* (Lancini, 1968) sitting sunbathing one morning at the base of a *Brocchinia hechtoides* on the edge of a cliff (Fuentes & Rivas, 2000). This was its first sighting outside its typical locality of Cerro Yaví (Myers & Donnelly, 1996). Taxonomic controversy currently remains concerning the small tepui lizards *Cercosaura goeletti* and *C. phelpsorum*, and this will most likely continue until new specimens from several tepuis are collected and their DNA analyzed. Two snakes were also collected on Autana's summit: *Liophis reginae* aff. *semilineata* with dark colouration and *Epictia albifrons*, collected under a small rock on the edge of the Cerro Autana.

3.3.3.2. Auyán Tepui

Auyán Tepui, located at 05° 55' N, 62° 32' W, is without doubt the tepui which has attracted the most attention throughout the scientific world (Fig. 118B, C). It covers 715 km², and reaches 2,450 m. a.s.l. in height, and despite being the most studied tepui, the complexity and diversity of its flora and fauna ensures that decades will pass before its herpetofauna is completely identified and understood. This tepui is also renowned for the information contained in Myers & Donnelly (2008) whose work remains an excellent reference for details of its macro and microhabitats, and also for its herpetofauna. The history of the interest in Auyán Tepui begins with Jimmy Angel's romantic and exaggerated histories and the bold efforts to find a fabulous mine of gold at its summit. In his aerial exploration, Angel glimpsed the highest waterfall in the world, and named it eponymously. When Angel's plane accidentally landed on the tepui summit in 1936, Gustavo Heny, Miguel Delgado and the Angel couple discovered that the only way to descend the tepui was exactly the same that remains used today, on foot. The first specimens from there were collected during the AMNH and William Phelps expedition in 1937 – 1938. In 1956, a Universidad Central de Venezuela expedition collected further specimens and also installed a Simón Bolívar statue which remains clearly visible on the summit. Roze (1958^a) described *Tropidurus bogerti* (Fig. 119A) present on the summit and *Neusticurus racenisi* and *Liophis trebbai* on the slopes. Frogs known to inhabit the tepui summit are; *Oreophrynella cryptica*, *Stefania shuberti*, *Tepuihyala edelcae*, (Fig. 119F) *Hypsiboas jimenezi*, *H. roraima*, *Centrolene gorzulae* (Fig. 120B), *Hyalinobatrachium cappellei*, *Pristimantis auricarens*, *P. marmoratus* (Fig. 119C), *Leptodactylus rugosus* (Fig. 119D), and *Anomaloglossus tepuyensis* (Fig. 119B). Barrio-Amorós et al. (2011) considered the recently described frog *Hypsiboas angelicus* Myers & Donnelly 2008 to be synonymous with *H. roraima*. The CLBA visit in 2007 provided precise species data

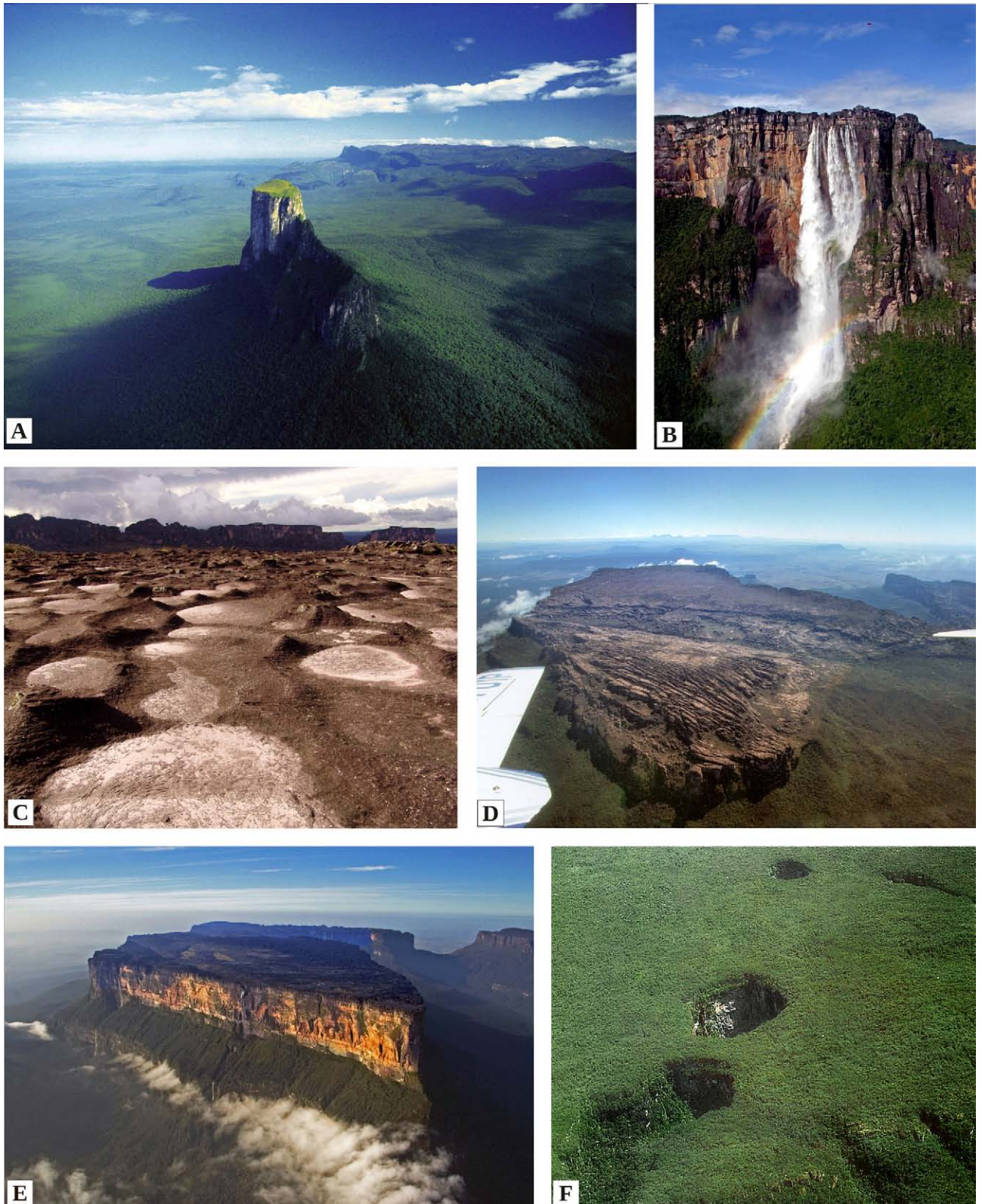


Fig. 118: A – Cerro Autana (in front) and Sipapo Massif (in the background). B – The Salto Angel on Auyán Tepui. C – Surface of the meseta on Auyán Tepui. D – The aerial view of Churí Tepui from the west (Chimantá Massif). E – The aerial view of Roraima from the north. F – Sinkholes (Simas) on Sarisariñama.

on *Anomaloglossus tepuyensis*, which commonly inhabits rapid creeks with small waterfalls. Since this species is not as agile as other small dendrobatids, they were relatively easy to capture, and Myers & Donnelly (2008) reported a wide variety of patterns amongst them. Several *Pristimantis* were found in the forested southern slope, and these proved quite difficult to identify. They were initially considered to be *P. pulvinatus* by Myers & Donnelly (2008), but a recent work on tepui terraranans by CLBA revealed that they are *P. marmoratus* which inhabit the slopes of several tepuis in the Guyana Shield. CLBA party searched the summit, looking especially for the rare species *Oreophrynella cryptica* and *Euspondylus auyanensis*, but he was unsuccessful in this pursuit.

There was only the one abundant endemic species, *Tropidurus bogerti*, sighted during the day, and this was extremely difficult to capture because it is a very rapid mover and quickly disappears under heavy slabs. In addition, common species such as *Tepuihyla edelcae* (Fig. 119F) and *Stefania shuberti* could also be seen beneath rocks. Moreover, we herein report *Norops eewi*, previously Chimantá endemic, from Auyán (Fig. 119E), waiting for a comprehensive taxonomic solution.

3.3.3.3 Chimantá Massif

Chimantá is a huge massif consisting of 12 different tepuis, all connected and biologically related. It is located between 05° 05'–05° 23' N, and 61° 54'–62° 15' W. Chimantá has been one of the most explored tepui massifs in all ambits of the natural history (Huber, 1992; Gorzula, 1992). However, this extensive exploration presents no obstacle to discovering further astonishing findings. These have already included the largest sandstone cave on the planet and the complex system that accompanies it (Brewer-Carías & Audy, 2011). Although its herpetofauna is well characterized, as reported by Roze (1958^b), Gorzula (1988, 1992), Williams et al. (1996) and Barrio-Amorós et al. (2010), unknown species may still exist. For example, CLBA has heard two anuran calls at the summit of Chimantá which do not correspond to any well-known species. The summit of Chimantá is enormous at 1,470 km² and it is divided into 12 tepuis. It hides valleys, canyons and the most complex system of sandstone caves in the world (Fig. 118D). It is clear that so far we have uncovered only the very surface of its mysteries. The three common anuran species located on the summit of this massif are; (1) *Stefania ginesi*, which doesn't call and is quite easily found under rocks or slabs (Fig. 120C); (2) *Tepuihyla edelcae*, which calls around ephemeral pools after dark, and hides under slabs and inside the tubes of bromeliad *Brochinnia hechtiioides* during the day (Fig. 120F); and (3) *Anomaloglossus rufulus* (Fig. 121B), which is an agile frog which calls during the day following rain, and inhabits shady areas in deep canyons and *Bonnetia* forests. In spite of this last species's abundance and its easily heard calls throughout the entire massif, it is extremely difficult to locate and capture (Gorzula, 1988, 1992; and personal observation). Barrio-Amorós & Santos (2011) re-described this species and assigned it to the correct genus, which has progressed from the original *Dendrobates* to *Epipedobates* and to *Allobates*, and is now correctly recognized as *Anomaloglossus*. Although a presence of *Otophryne steyermarki* has been reported at Chimantá summit, unfortunately this anuran has never been heard or seen during

our explorations. The most recently described species *Pristimantis muchimuk* (Fig. 120A) is also extremely rare, and only one specimen has ever been reported (Barrio-Amorós et al., 2010). It was surprising that we could not locate some highly expected Pantepui species in Chimantá, including *Oreophrynella* and especially some glass frogs, since there are at least three species of these frogs inhabiting neighbouring tepuis such as Auyán.

The reptile most frequently found at the summit is *Anadia mcdiarmidi* (ex *breweri* sensu Kok & Rivas, 2011; Fig. 121A) which resides under slabs. *Norops eewi* has also been reported (but see Myers and Donnelly 2008 for its nomenclatural history) and *Norops carlostoddi* (Williams et al., 1996). The last taxon is apparently endemic on Chimantá. One *Arthrosaura* is mentioned by Gorzula (1992) as undescribed, but this description is currently in the process of clarification by Philippe Kok and CLBA (Fig. 120D). Five snakes have been reported from the summit of the massif. The following two are apparently endemics, *Atractus steyermarki* and *Thamnodynastes chimanta* (Fig. 121C), while a third one, *Bothriopsis taeniata lichenosa*, is also possibly endemic but its relationships require further study. The remaining two occurring species *Liophis trebbau* and *Leptodeira annulata* are more broadly distributed.

The Chimantá slopes have not been extensively explored, and it is almost certain that they contain a more varied herpetofauna. Only the following few species have currently been recognized there: *Dendrobates leucomelas*, *Hypsiboas* aff. *crepitans*, *H. jimenezii*, *H. sibleszi*, *Hyalinobatrachium cappellei*, *H. taylori*, *Vitreorana helena*, *Leptodactylus* aff. *sabanensis*, *Rhaebo gutatus*, *Rhinella* cf. *humboldti*, *Norops auratus*, *Neusticurus rudis* (Fig. 120E), and *Dipsas catesbyi*.

3.3.3.4. Roraima

Since Roraima is more frequently visited by tourists and scientists because of its easier accessibility by foot, it is surprising that so few studies of its herpetofauna have been made. As previously mentioned, the earliest species to be described from any tepui were from Roraima. Boulenger (1900) named four species from the slopes and two from the summit. Duellman & Hoogmoed (1984, 1992) described the following three species of frogs on the north hillside in Guyana based on collections by Adrian Warren (Warren, 1973): *Stefania roraimae*, *Hypsiboas roraima* (Fig. 121D) and *Tepuihyla warreni*. Surprisingly, *S. roraimae* and *T. warreni* have never been officially reported from Venezuela. Barrio-Amorós et al. (2011) commented on the distribution of *H. roraima*. La Marca (1996) described two dendrobatids from the slopes of Roraima: *Anomaloglossus praderioi* and *A. roraima*, while MacCulloch et al. (2007) provide an excellent account of the Roraima herpetofauna.

Roraima is a paradigmatic tepui, possibly the best known, and lies between three countries, Brazil, Guyana and Venezuela at 05° 12' N, 60° 44' W. The summit of Roraima, with a maximum altitude of 2,810 m and a surface of 34 km², is small compared to that of other bigger tepuis (Autana is the only smaller one covered in this work). The slopes of Roraima are covered with a cloudy forest and countless streams. Typical Guyanese herpetofauna species exist there, including *Hypsiboas sibleszi*, *Hyalinobatrachium cappellei*, *Anomaloglossus praderioi*, *Otophryne*



Fig. 119: Species on Auyán Tepui. A – *Tropicurus bogerti*. B – *Anomaloglossus tepuyensis*. C – *Pristimantis marmoratus*. D – *Leptodactylus rugosus*. E – *Norops eewi*. F – *Tepuihyla edelcae*.

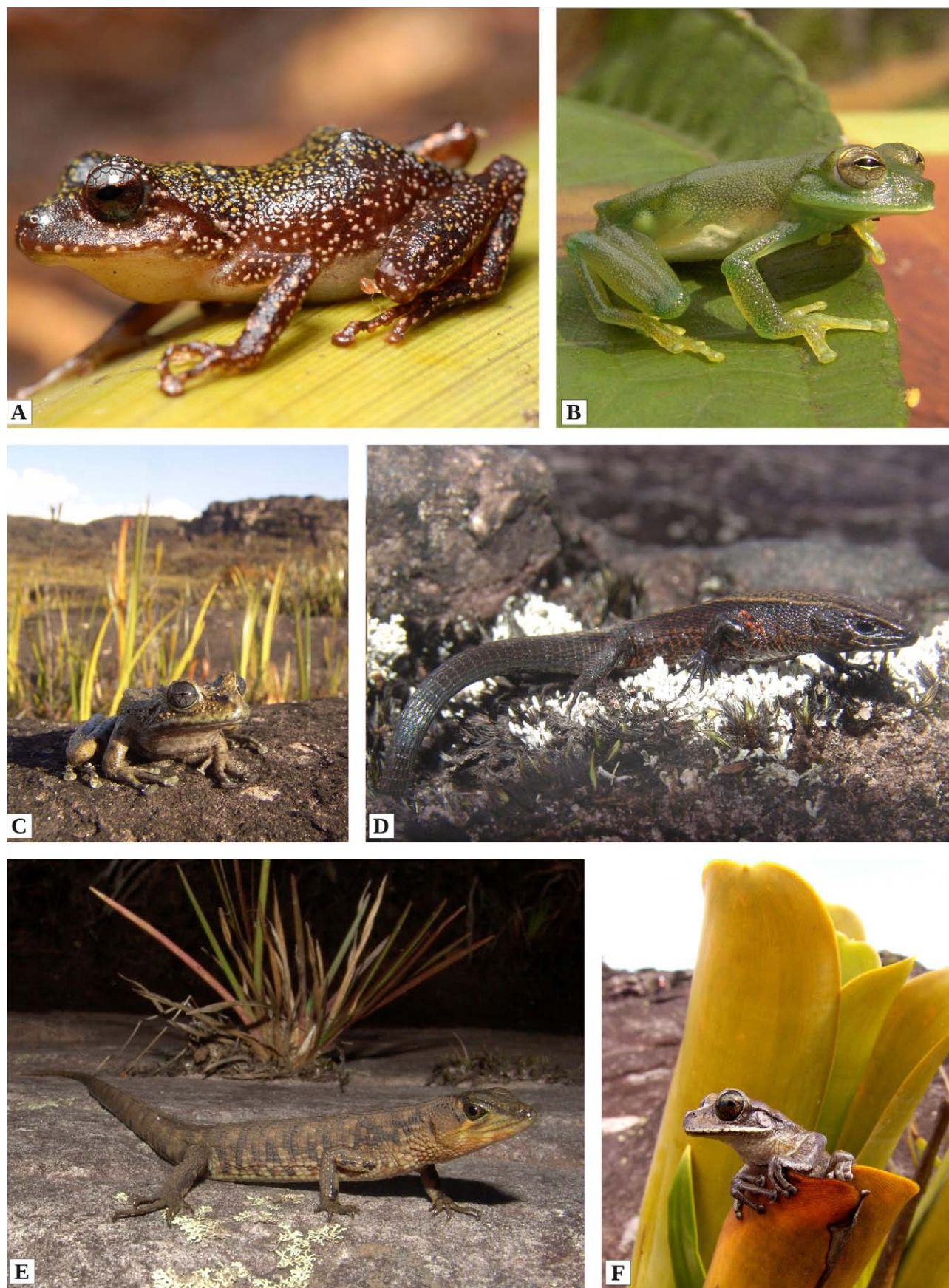


Fig. 120: Species on Auyán and Churí Tepui: A – *Pristimantis muchimuk* (Churí Tepui), B – *Centrolene gorzulai* (Auyán), C – *Stefania ginesi* (Churí Tepui), D – *Arthrosaura* sp. (Churí Tepui), E – *Neusticurus rudis* (Churí Tepui), F – *Tepuihyla edelcae* (Churí Tepui).



Fig. 121: Species on Churí Tepui, Roraima and Sarisariñama: A – *Anadia mcdiarmidi* (Churí Tepui). B – *Anomaloglossus rufulus* (Churí Tepui). C – *Thamnodynastes chimanta* (Churí Tepui). D – *Hypsiboas roraima* (Roraima). E – *Stefania riae* (Sarisariñama). F – *Riolama leucosticta* (Roraima).

robusta, *O. steyermarki*, *Neusticurus rudis* and *Bothriopsis taeniata*. However, it is on the summit where one of the most astonishing species in the “Lost World” exists. This is the Roraima’s rough toad, *Oreophrynella quelchii*. Still abundant in the whole summit of Roraima, it is a terrestrial species with a small body, almost entirely black except for yellow ventral parts. It is not certain if this ventral colouration serves as defence the way yellow and black colouring does in other amphibians because *Oreophrynella quelchii* is best known for its defensive strategy of curling into a ball and rolling downhill to escape danger; other summit *Oreophrynella*, including *O. nigra* from Kukenán and Yuruani tepuis have also been observed to use this defensive technique. A further species of *Oreophrynella*, *O. macconelli*, exists in the base of the same tepui, and it possibly extended throughout the uplands towards Guyana. This is a rare arboreal species from the Bufonidae family. In addition, a very rarely seen species of *Pristimantis* is found on the summit (Barrio-Amorós & McDiarmid, in prep.), and this is certainly similar to both *P. yuruaniensis*, described recently from the summit of Yuruani Tepui by Rödder & Jungfer (2007), and *P. aureoventris* from Wei-Assipu Tepui (Kok et al., 2011).

3.3.3.5. Sarisariñama

Sarisariñama is an immense tepui with maximum altitude of 2,100 m a.s.l. (Steyermark & Maguire, 1972), or 2,350 m a.s.l. (according to McDiarmid & Donnelly, 2005). However, a large part of the summit surface lies at a lower altitude. Its location is 04° 30' N, 64° 14' W, with its summit area of 546 km² and a slope area measuring 286 km².

The western part of Sarisariñama was originally considered part of a larger complex known as Jaua, but now both Jaua and Sarisariñama are recognized as separate tepuis. Sarisariñama was initially visited by William Phelps and Julian Steyermark in a helicopter, and the first herpetological specimen, *Euspondylus phelpsi*, was caught at that time (Lancini, 1968). This species, however, is currently named *Cercosaura phelpsorum*.

While flying over Sarisariñama in 1968, Charles Brewer-Carías observed some immense sinkholes (simas). He lost a lot of sleep wondering about these phenomena before he organized a large expedition in 1974, inviting a variety of scientists to join him. These included the botanist Julian Steyermark, and two couples, the Phelps who were ornithologist and the orquideologist Dunstervilles. They were also accompanied by the Uruguayan herpetologist Braulio Orejas-Miranda who worked for the United States National Museum, Smithsonian Institute (USNM). Regrettably, no herpetology specimens were collected from the sinkholes and no herpetological report resulted from this expedition. However, based on specimens recovered from other parts of Sarisariñama during the expedition, a new species, *Stefania riae*, was described by Duellman & Hoogmoed (1984) (Fig. 121E). All other specimens from this expedition remain unstudied at the USNM.

Four other expeditions exploring the Sarisariñama simas aroused scientific interest. One in 1976 was again led by Brewer, where he acted as guide for a group of Japanese shooting a documentary film, and a further one was organized in 1976 by Polish and Venezuelan speleologists (Zawidzki et al., 1976).

In 1988, an RCTV crew accompanied scientists from the University Simón Bolívar to film a documentary on the tepui and its exploration. Led by Omar Linares, they filmed and collected herps which were later studied by Barrio-Amorós & Brewer-Carías (2008).

The most recent scientific expedition occurred in March 2002, when Brewer-Carías again organized an expedition for Japanese TV NHK. This proved to be the most important systematic collection in Sarisariñama, with 34 species reported. These included the following five completely new ones; *Anomaloglossus moffetti*, *Hyalinobatrachium mesai*, *Hypsiboas tepuianus* (Fig. 122B, D), *Pristimantis sarisarinama* (Fig. 122C), and *Gonatodes superciliaris* (Barrio-Amorós & Brewer-Carías, 2008). *Ceuthomantis duellmani* described by Barrio-Amorós (2010) remains the most recent species published from Sarisariñama (Fig. 122A).

Table 13 presents species from these five tepuis recorded above the altitudinal limit of 1,000 m.

As colophon, during his 2004 overflight of Aprada Tepui which lies between Auyán Tepui and Chimantá, Charles Brewer landed with three helicopters in an impressive cave in the wall of the tepui. This cave was subsequently immortalized as Cueva de El Fantasma (Fig. 13). In the few minutes that he and his companions remained inside this immense 200 metre high cave, they were able to catch frogs jumping in a puddle created by the cave’s waterfall. These specimens were given to CLBA, who called them *Colostethus* (= now *Anomaloglossus*) *breweri* in honor to the collector (Barrio-Amorós, 2006).

3.4. CONCLUSIONS OF THE FAUNISTIC INVESTIGATIONS IN THE PANTEPUI

“The Lost World” or the “Islands in time” are popular terms used for the mostly inaccessible tops of the tepuis. The tepuis can also be called “Sky islands”, the term used for montane regions isolated from one another by intervening valleys with drastically different environmental conditions (Schultheis et al., 2012). Due to the inaccessibility of the tops of the tepuis, zoologists are still filling large gaps in a sparse mozaic of mostly unknown fauna. This is especially true for invertebrates. Despite the fact that our zoological research was only an appendix to the speleological and geological research, it has brought valuable results. In this monograph we summarize and review the results from this and previously investigated land snails, selected groups of aquatic insects and herpetofauna.

Our investigations have enabled description of two new land snails from Churi Tepui; *Plekocheilus* (*P.*) *vlceki* and *Plekocheilus* (*Eurytus*) *breweri* (Breure & Schlögl, 2010). The research into aquatic insects has also proven especially fruitful. The short list of three mayfly species previously recognized from the Pantepui has been substantially enlarged. Additionally, the six genera of mayflies (*Baetodes*, *Callibaetis*, *Camelobaetidius*, *Cloedes*, *Spiritiops* and *Parakari*) from the family Baetidae and *Massartella* from the Leptophlebiidae have been reported for the first time (Derka, 2002; Derka et al., 2009, 2012), one of them, *Parakari*, is the newly described genus (Niето & Derka, 2011). Moreover, four new species (*Massartella devani*, *Spiritiops tepuiensis*,

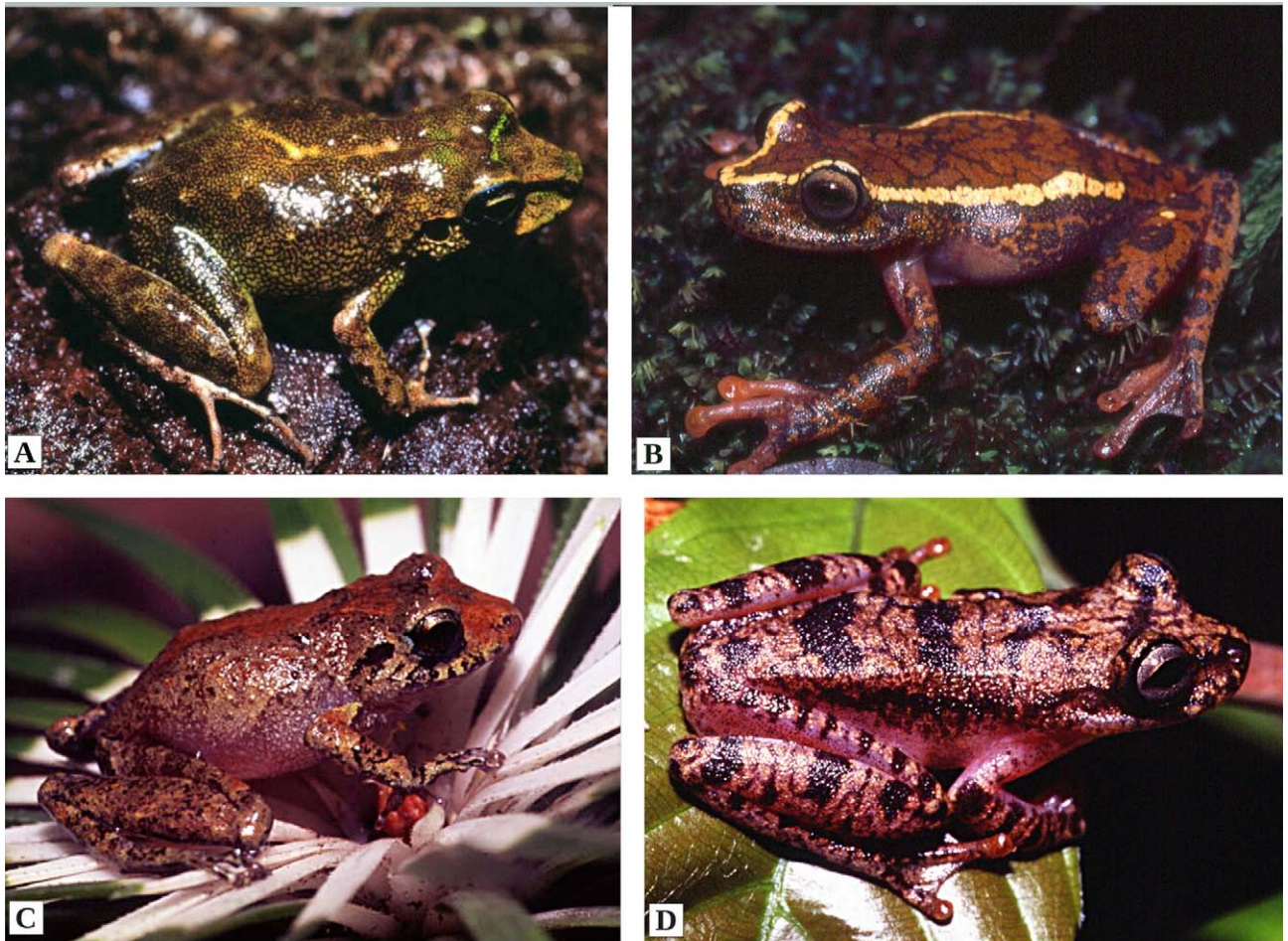


Fig. 122: Species on Sarisariñama: A – *Ceuthomantis duellmani*. B – *Hybsiboas tepuianus* (female holotype). C – *Pristimantis sarisarinama*. D – *Hybsiboas tepuianus* (male holotype).

Parakari auyanensis and *P. churiensis*) have been described (Derka, 2002; Nieto & Derka, 2011, 2012), and the species *Fittkauneria adusta* (Oligoneuriidae) was reported for the first time from the Pantepui. Other potentially new species from the genera *Mas-sartella*, *Miroculis* and *Hagenulopsis* remain in our collections for their formal description and publication.

The entire order Plecoptera, represented by three genera *Macrogynoplax*, *Anacroneuria* and *Kempnyia*, has been reported from the Pantepui for the first time. Unfortunately, the collected nymphal material does not allow more precise identification and/or new species description.

The same is partly true for Trichoptera, where the four families of Calamoceratidae, Hydroptilidae, Odontoceridae and Sericostomatidae, together with the following nine genera, were recorded in the Pantepui for the first time: *Phylloicus* (Calamoceratidae), *Blepharopus*, *Macrostemum* (Hydroptilidae), *Orthotrichia*, *Oxyethira*, *Zumatrichia* (Hydroptilidae), *Oecetis*, *Nectopsyche* (Leptoceridae) and an unidentified genus from Sericostomatidae (Derka & Zamora-Muñoz, 2012). New species from various genera have also been collected, and their details will soon be published.

We found a new species of unique aquatic orthopteran inhabiting Cueva Charles Brewer which Derka & Fedor (2010)

have already described as the new species *Hydrolutos breweri*, and Derka & Fedor (2012) published the description of a female from this species. It attracted the attention of the scientific community, and it was the Biofresh Cabinet Freshwater Curiosity in the September issue (<http://cabinetoffreshwatercuriosities.com>). Despite absence of typical troglomorphic adaptations in colouring and reduction of the eyes, this cave-dwelling species was observed walking and swimming in the stream of Cueva Charles Brewer in Churí Tepui plateau. Recent investigations in the Gran Sabana region and in Puerto Ayacucho region revealed the presence of the genus *Hydrolutos* in lowlands below the Pantepui (Derka, unpublished data). Although it is considered an endemic of the Pantepui, and it is widespread in streams in the Guyana highlands and lowlands, it remains quite impervious to standard entomological and hydrobiological sampling methodology. Its elusiveness is aided by its nocturnal habits and photophobia, and resultant affinity to caves, cavities and other dark well-hidden places which are difficult to access.

Coleoptera from the family Elmidae were commonly sampled in the Pantepui streams. The genus *Roraima* was discovered and the species *Roraima carinata* described by Kodada & Jäch (1999) from the Tuná Deuta spring stream on Roraima slope. One undescribed *Roraima* species was sampled in the entrance of

Cueva Charles Brewer and in various streams at Churí Tepui, and a second one in streams at Auyán Tepui. Two *Jolyelmis* species, *J. derkai* Čiampor & Kodada and *J. reitmaieri* Čiampor & Kodada, were discovered in a few small samples from the same stream as the *Roraima carinata*. Individuals of *J. reitmaieri* were found in Cueva de los Pémones and individuals of the new *Jolyelmis* species were found in various streams on Churí Tepui plateau, including those at the entrance of Cueva Charles Brewer. These were described as *J. spangleri* by Kodada et al. (2012).

Finally, we reviewed and published our own data on herpetofauna of Autana, Auyán, Chimantá, Roraima and Sarisariña-ma. The most recently described was the species *Pristimantis muchimuk* which was discovered on a speleological investigation of Churí Tepui (Barrio-Amorós et al., 2010).

“The Lost World”, although no longer so “lost”, continues to fascinate all its explorers. Despite having dedicated their whole lives to its exploration, many scientists consider that they have only scratched the surface of its wondrous mysteries. We are certain that there are many more creatures awaiting discovery, and we are excited by the expectation of imminent expansion of the sparse knowledge of Pantepui fauna which currently exists. Meanwhile, the investigations reported herein hopefully contribute to better understanding of the origin and evolution of Pantepui fauna, and lead to effective protection of all evolutionary treasures inhabiting the “Lost World”.

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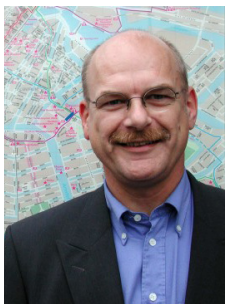
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