# Hypogenic *versus* epigenic subterranean ecosystem: lessons from eastern Iberian Peninsula

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**Abstract:** Over the last 40 years, hypogenic karst/caves have become well known and hypogene speleogenesis has been used to explain the formation of some of the largest subterranean maze caves. These hypogenic systems involve confined aquifers with upwards flow, responsible for their karstification. Such spaces begun and could be remain isolated from the surface and the contiguous subterranean habitats, including the shallow ones. We studied the invertebrate fauna and the geology/speleogenesis of two recently opened caves from Eastern Iberian Peninsula, which clearly showed features of hypogenic origin. Their scarce faunistic composition, formed by non cave-adapted fauna, is similar to other hypogenic caves from Europe and North America, suggesting that there are restrictions for faunal colonization of the hypogenic subterranean ecosystems. We propose differentiating the hypogenic from the epigenic subterranean ecosystem based on the fact that the first one lacks fauna during its genesis. This new scenario may have consequences in the regional biodiversity patterns of troglobiont species.

**Keywords:** subterranean ecosystem; hypogene speleogenesis; epigenic hypogenic karst caves; troglobiont fauna; biodiversity patterns

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## INTRODUCTION

At the beginning of the last century, the Romanian biospeleologist Émile G. Racovitza, in his comprehensive monograph 'Essai sur les problèmes biospéologiques' (Racovitza, 1907), drew the attention to the extension of the subterranean domain, far beyond human accessibility and highlighted the connection between caves, small voids and the deeper soil layers through the fissure network. This network of interconnected spaces allows faunal migration directly across pits or sinks of water or through the shallow subterranean habitats SSHs (Culver & Pipan, 2009a, 2009b; for more details see Camacho, 1992). The SSHs ranges from the 'upper hypogean zone' (Uéno, 1987) or 'milieu souterrain superficial' (MSS) through to caves and other non-karstificables lithologies (Juberthie et al., 1980, 1981; Gers, 1998), including the recently proposed alluvial MSS (Ortuño et al., 2013). The SSHs include, among others, the

epikarst, a very superficial habitat under the surface of the karst in the infiltration zone (Bakalowizc, 2005), which is an ecotone between surface water and groundwater (Pipan, 2005); and the hypotelminorheic habitat (Meštrov, 1962; Culver & Pipan, 2009b), a persistent shallow subsurface of wet spots fed by subsurface water in a slight depression (Fig. 1). The aquatic compartment of the subterranean ecosystem extends through the deepest aquifers such as the Edwards Aquifer in Texas (USA) at 600 to 1000 meters deep, to the shallow interstitial habitats composed of water filled spaces between unconsolidated sediments (Culver & Pipan, 2009a). Among these subterranean compartments, the subterranean-adapted fauna can inhabit from the shallow habitats in the subsurface, through to the deepest known galleries at more than -2000 m and from the giant subterranean chambers to the smallest fissures (Sendra & Reboleira, 2012).

In the early 70's the discovery of the hypogenic karst, firstly studied in Europe and North America

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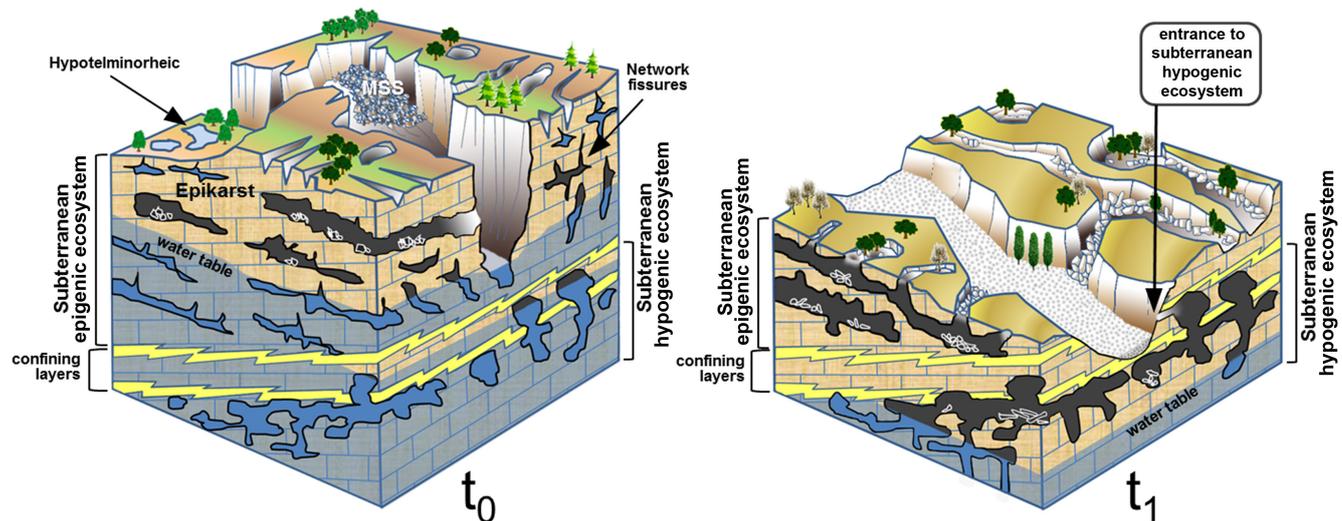
Fig. 1. Diagram of subterranean epigenic and hypogenic ecosystems: $t_0$ active phase and $t_1$ inactive phase with connection of epigenic and hypogenic ecosystems. SSH, Shallow Subterranean Habitats.

and the diffusion of hypogene speleogenesis, enabled the explanation of the formation of some of the largest subterranean maze systems around the world (Sebev, 1970; Müller & Sarvary, 1977; Bakalowicz et al., 1987; Takács-Bolner & Kraus, 1989; Davis et al., 1990; Klimchouk, 1990; Dublyansky, 1995). The formation of hypogenic karst/caves is explained as the result of three main genetic processes: i) Sulfidic emanations ($H_2S$) and their transformation into sulfuric acid, which would explain some of the largest subterranean maze systems, such as Carlsbad Caverns or Lechuguilla Cave in New Mexico, USA (see Davis et al., 1990; Palmer & Palmer, 2000; Jagnow et al., 2000); ii) A thermal origin, such as Jewel and Wind caves in South Dakota, USA (Bakalowicz et al., 1987), in some cases including thermal fluxes with high concentrations of $CO_2$, which is the case in the large subterranean network surrounding Buda in Hungary (Pál-Völgy, Szemló-Hegy, Castle caves, etc.) (Takács-Bolner & Kraus, 1989) and the huge underground chambers in the Rhodope Mountains of Bulgaria (Sebev, 1970; Müller & Sarvary, 1977; Dublyansky, 1995, 2000); iii) A deep dissolution of gypsum by upward flows under confinement conditions, as in the large caves of Optimisticheskaja, Ozernaja, Zolushka in the Podolia region in Ukraine (Klimchouk, 1990). Since 2000, hypogenic models have begun to be widely used and proposed in literature as a new type of karst genesis, quite distinct from the epigenic or classical karst/caves (see Klimchouk et al., 2000; Klimchouk & Ford, 2009 and several papers in a 2012 special issue of the Geomorphology journal).

Regardless of the speleogenetic processes, hypogenic karst/caves are characterized by several geomorphological features (though not always exclusive) and, especially, by being formed in confined aquifers and related to corrosive ascending fluxes: gases, acid solutions and/or thermalism. Often, those are fluxes of deep-water that locally interact with shallow water or local groundwater flow systems (Klimchouk, 2009). This new hypogenic concept allowed reconsideration of the genesis of certain previously known caves and karst systems whose origin had not been sufficiently understood yet. Thus,

Palmer (1991) estimated that the hypogenic cave systems account for only 10% of the studied cave systems, although they include some of the largest ones. Later, Klimchouk (2007) stated that hypogenic/confined karst systems are much more widespread and that this relatively small percentage is merely an exploration bias, due to their inherent lack of accessibility from the surface. For Molerio (2004), the epigenic karst is directly controlled through karst kinetics, while the hypogenic karst responds more to a mass balance. In the same way he considers that in the epigenic karst exchange occurs with subaerial processes (water movement and mixture) and dissolution capacity is enhanced (and sometimes decreased) in the direction of flow. On the contrary, in the hypogenic karst the exchange through subaerial processes would not virtually occur, except in distal areas and those areas connected to a phreatic aquifer where dissolution capacity is generally independent of flow.

Although the knowledge of the hypogenic karst/caves occurred relatively early, the biospeleological studies did not start until the 90's, after the discovery of a small number of sulfidic caves, many of them considered to have an hypogenetic origin. Some of them became extensively studied due to their interesting ecosystems, supported partly or totally by chemolithotrophic primary production (Sarbu, 1990, 1991; Engel et al., 2004a, 2004b; Cambell et al., 2006; Engel, 2007; Jones et al., 2008; Porter et al., 2009), in a similar way to deep-sea hydrothermal vents (Jannasch & Wirsen, 1979). The microorganisms of these caves depend on the oxidation of chemical compounds and if they are abundant enough, they may produce enough organic matter to support a community with large organisms such as arthropods (Sarbu et al., 1996).

A previous prospection of two caves from the Eastern Iberian Peninsula revealed both their possible hypogenetic origin due to their morphological features and a remarkable lack of cave adapted fauna. Those circumstances lead us to conduct a more exhaustive study of those two caves, studying their speleogenetic origin and monitoring their fauna. The lack of

subterranean adapted species in these studied caves, as also happens in many other hypogenic caves, leads us to propose a new insight on the colonization of the subterranean ecosystems. A discussion on the hypogenic features of Autopista and Far caves and their colonization by invertebrate terrestrial fauna is also provided.

## MATERIAL AND METHODS

### Study sites

The studied caves are included in the Prebaetic biospeleological district in Spain, according to Sendra et al. (2006), corresponding to the northeastern border of the Baetic Chain, near the Mediterranean Coast (Fig. 2), but far from the influence of the littoral and the Quaternary fluctuations of the sea level.

Autopista Cave (Real de Gandia, La Safor, Valencia, ETRS89, 30S X=7/42594 m, Y=43/15728 m) is located in the oriental border of Serra Falconera Mountain, a small karst area in the Eastern border of Serra Grossa hydrogeologic system (Pulido-Bosch, 1979). Several small entrances were opened during the construction of the AP7 highway in a vertical slope at more than 90 m a.s.l. This cave is a complex, anastomotic subterranean net, with more than 8 km of passages oriented SE-NW (Fig. 3), reaching the maximum depth of -82 m through a wide shaft of -40 m in the Alucine Pit (Grup Espeleològic Murta et al., 1987).
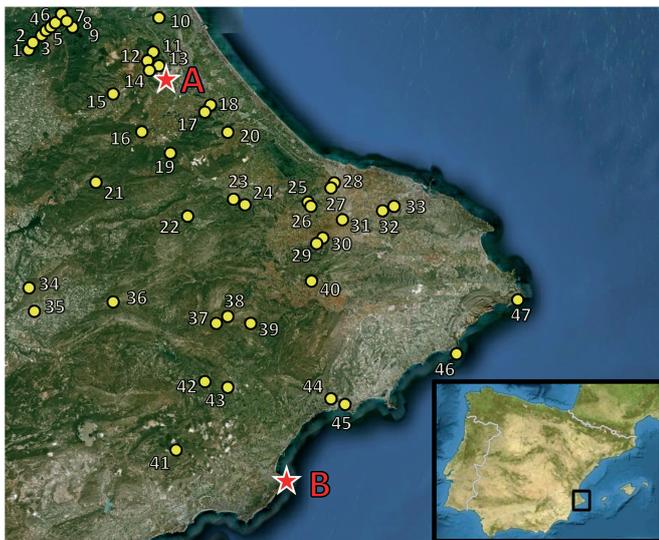


Fig. 2. A map with caves inhabited by cave-dwelling species of northeastern Prebaetic, and the locations for Autopista Cave (A) and Far Cave (B). List of caves: 1) Avenc de Quatretonda; 2) Cova de l'aigua; 3) Avenc de la Vinya Vella; 4) La Covota; 5) Cova de l'Aigua d'Engarbullers; 6) Avenc Pla dels Engarbullers; 7) Cova Fresca; 8) Cova del Perro; 9) Sima Sancho; 9) Cova dels Canellons; 10) Cova de l'Aigua; 11) Cova dels Emboscats; 12) Cova de les Maravelles; 13) Avenc del Real; 14) Cova de les Rotes Penades; 15) Cova de Soliganyes; 16) Cova de l'Angel; 17) Sima Blanca; 18) Avenc Lléngua de Sérvol; 19) Cova de l'Amuixic; 20) Cova Font dels Bassiets; 21) Cova del Rull; 22) Cova de la Mina de Luis Santonja; 23) Cova de Sant Joan; 24) Cova Bolumini; 25) Avenc de la Cigarra; 26) Cova Fosca; 27) Cova de la Pedrera; 28) L'Avenc; 29) Cova de les Calaveres; 30) Cova del Pouet; 31) Cova de la Punta de Benimaquia; 32) Cova de l'Andorial (probably destroyed); 33) Cova de Les Maravelles; 34) Cova de Barrina; 35) Avenc del Morro del Estepar; 36) Cova del Somo; 37) Avenc Gran i Petit del Frare; 38) Cova dels Morets; 39) Cova de les Meravelles; 40) Sima el Cremat; 41) Cova Massatava; 42) Cova de la Pinta Mister; 43) Mina del Capellá; 44) Cova dels colombs; 45) Cova dels Rats Penats; 46) Cova Gran.
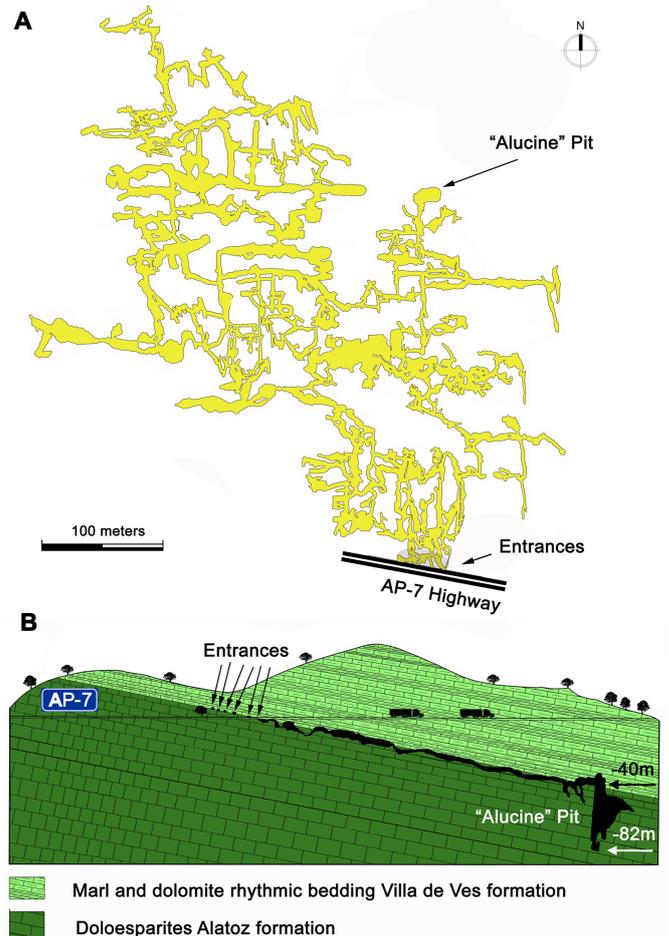




Fig. 3. Autopista Cave (Serra Falconera Mountain): A) Plan view of the cave, a hypogenic maze cave near the coast, with more than 8 km of passages; B) Outline of the geological scenario showing the main gallery between the entrances and the end Alucine Pit.

Far Cave (Alfás del Pi, La Marina Baixa, Alicante, ETRS89, 30S X=7/56426 m, Y=42/72590 m) is a labyrinthic network with about two kilometers of tunnels carved into the northeast slope of Serra Gelada Mountain, with a predominant E-W orientation (Fig. 4) and only accessible through one small size entrance located at 120 m a.s.l. (Speleo Club Covak Vila Joiosa, pers. comm.).

Both caves present some areas with constant water infiltration from the surface in some galleries or small pools. In Autopista Cave the water level rises periodically, flooding its deepest zone.

### Fieldwork

The Autopista Cave was monitored from 25th November 2011 to 10th June 2012, near the entrance and along the main galleries. The Far Cave was monitored during two years, from 24th June 2006 to 15th May 2008. A set of pitfall traps (6 cm in diameter and 7 cm in depth) was set in each cave, with a minimum separation among them of 100 meters. The traps were partially filled with 1.2-propanediol and cheese was used as bait. The pitfall sampling was supplemented by one hour of active search during each visit to the caves. One half liter of guano was processed for total extraction of fauna using Berlese (1905) method. Samples were sorted and each taxonomic group was identified.

In the Far Cave, temperature was measured using an Escort iLog Temperature Logger and in Autopista Cave
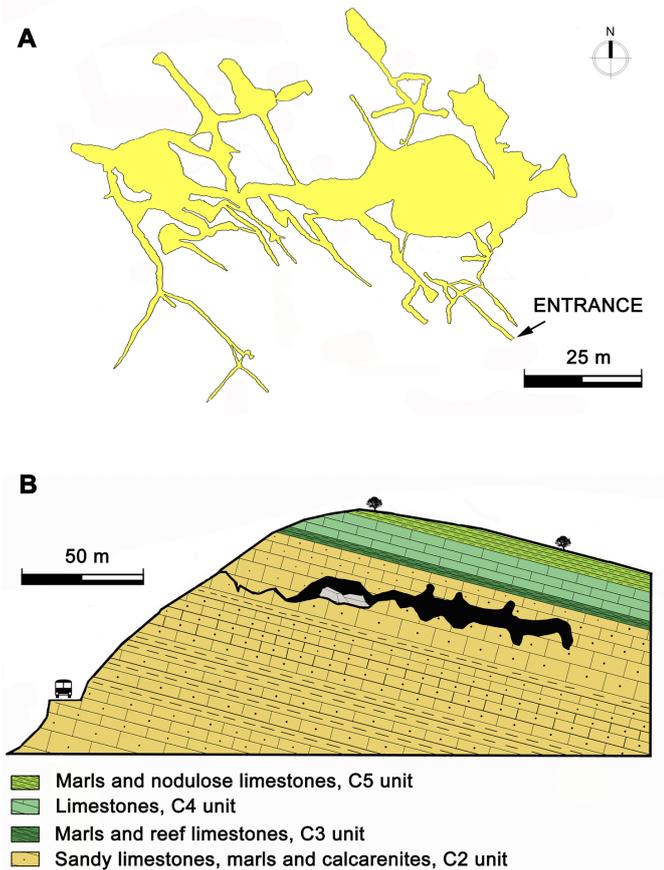
Fig. 4. Far Cave (Serra Gelada Mountain): A) Plan view of the cave, a hypogenic maze cave with >2 km of passages and chambers; B) Outline of the geological scenario showing the main gallery.

Fig. 5. A) Autopista Cave, showing the entrances opened due to the construction of the highway and also the contact between the marl and dolomite rhythmic bedding and the dolosparite in which the cave is developed; B) Far Cave, showing the slope with the entrance in the highest part of C2 unit and the contact between the calcarenitic limestone and the marl formation C3 unit as the confining layer.

with a Thermo-hygrometer Lufft (Hand Held Device E200) and the humidity of both caves with the latter device.

## RESULTS

### Geological features of studied caves

The Autopista Cave has developed, in its upper part, within the dolosparite of Alatoz Formation (Cenomanian), just above the contact with the marl and dolomites rhythmic bedding of Villa de Ves Formation (Cenomanian-Turonian), superimposed on it and acting as a confining layer (Figs. 3B, 5A). The dolosparite of Alatoz Formation is about 60 m thick and consists of massive layers of dolosparite (dolomite crystals of 100 to 200 µm), with more than 93% of carbonates. Villa de Ves Formation is over 90 m thick. Marls are especially abundant and dominant in the lower levels of the formation, observed in detail in some subsidences (collapses) of the ceiling (Figs. 6A & B). Its anastomotic network has developed mainly in a slope, defining the contact between the two formations mentioned above with a dip of about 15 to 20° NE. The geomorphology of the cavity is dominated by a maze of coalescing canals (maze cave), more or less circular and controlled by ascending corrosion forms, such as cupolas, feeders (Figs. 6D & E), rising wall channels and anastomotic pipes and tubes, occasionally alternating with areas of collapse, where the flat roof formed by the rhythmic bedding formation has collapsed, yielding small rooms with debris cones and detached parallelepiped

blocks (Figs. 6A & B), often hindering or obstructing the exploration of this subterranean network. The cave walls show some structures such as the boxwork formations through many sectors of the cave (Fig. 6F). The Alucine Pit is located in the lower section (Fig. 6C), which is considered a big feeder, the main upstream source of the currently known network. The geological structure and the regional hydrogeological framework show that the Autopista cave was formed within a dolomitic confined aquifer, located in the ascending or distal zone of the Hydrogeological Subsystem of Serra Grossa (Pulido-Bosch, 1979) and with hydrothermal traits. The current vadose position of the cave is consistent with the regional piezometric decline experienced by the aquifers in the area during the Quaternary.

The Far Cave is formed within a large monoclinal block of 7 km$^2$, with NE-SW direction and westward dip, forming part of the eastern flank of the coastal syncline of Villa Joiosa, according to geologic map of Spain n° 848 (Hernández et al., 2008). This syncline is occupied by the Quaternary Plain of Benidorm, which is a detrital aquifer disconnected from infra-adjacent limestone, due to the existence of Cretaceous marls, which are part of the syncline structure itself. The cave is basically a network of labyrinthine coalescent
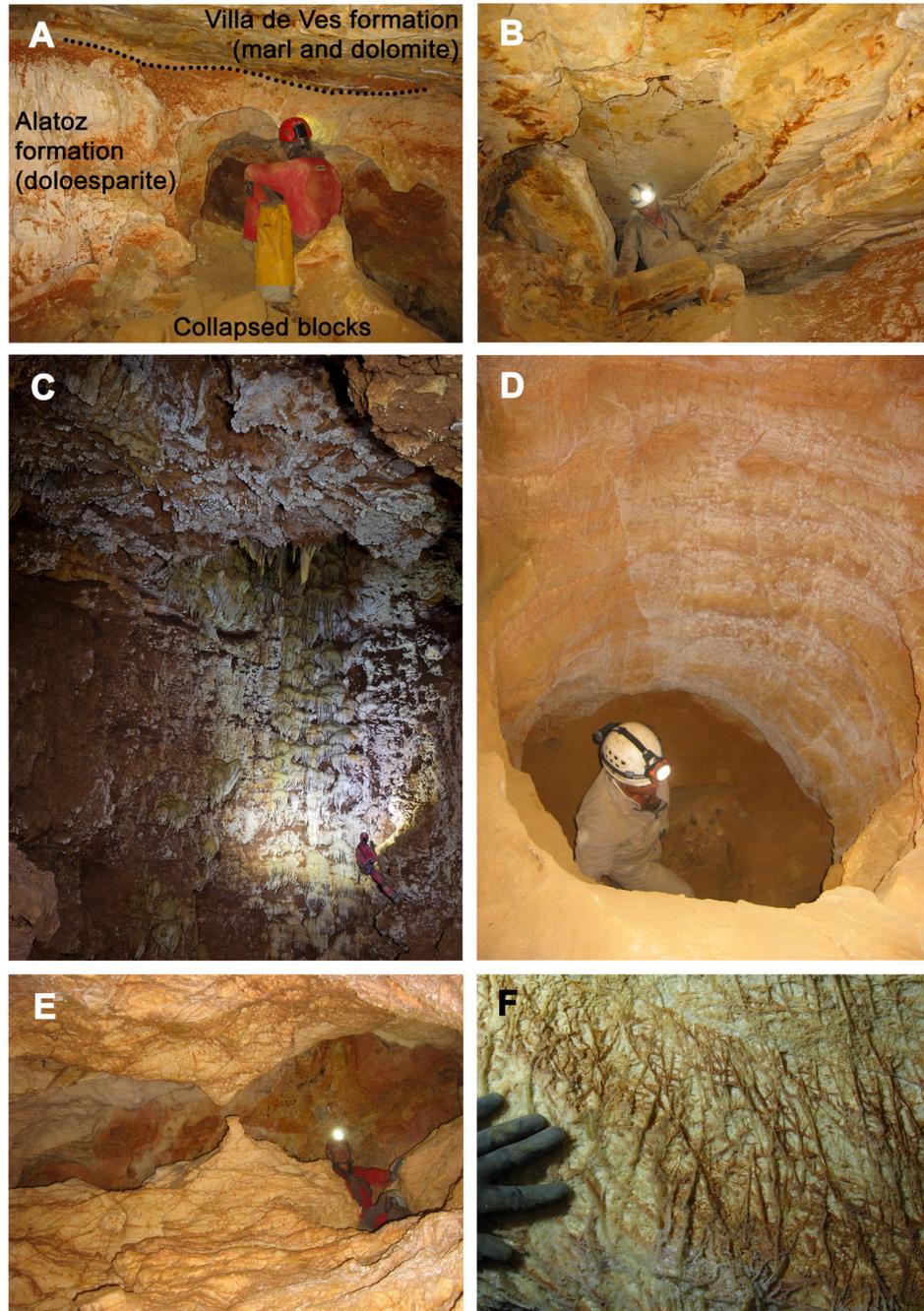
Fig. 6. Autopista Cave: A) Upper gallery showing the contact between the marl and dolomite rhythmic bedding and the dolosparite where the cave is excavated; B) Collapsed parallelepiped blocks from the ceiling of marl and dolomite rhythmic bedding; C) -40 meters Alucine Pit; D) Feeder near the entrances; E) Outlets connecting ceiling channels viewed from below; F) Boxwork formations.

ducts and often overlapping sections showing frequent spongework and vertical connections (Fig. 7A). It has a very irregular subhorizontal development, with small wells (feeders) and numerous rising domes (outlets) (Figs. 7B & D). Micropits and pockets are also usual on the surface of the cave walls (Figs. 7E & F). Inclined sectors are seen as a result of the dip of the strata. There are also flat roof chambers, which are sloping due to clastic processes occurring subsequent to forming the hypogenic cave, which may facilitate access to endogean fauna (Fig. 7C). It has developed within a calcarenitic limestone formation, frequently with oosparites and biomicrites of 25 m wide (upper Albian) and 30° NW dip. This calcarenitic limestone forms the higher part of C2 unit, a robust set, about 200 m of sandy limestone and marl (aquitard) and the ceiling has a marl formation (aquiclude) of about 4-8 m thick

correspondent to the C3 unit (Yébenes, 1996, 2004) (Figs. 4B, 5B). The cave presents the typical structure of a confined aquifer, currently semi dismantled by erosion and remarkably elevated – by neotectonic and/or eustatic processes, concerning its original saturation and confined initial genetic situation.

The subhorizontal development of the Far Cave suggests an old formation linked to the mixing zone and contact between a rising thermal flow (corrosive and gasified waters of confined aquifer) and the free and floating position of the water table in the upper part of this aquifer. This upward thermal flow would be tied to the artesian basin of the Vila Joiosa syncline, proceeding its water recharge from the extensive relief developed towards W and WNW from the mountains of Puig Campana, Aitana, and others. In addition to the rise of $CO_2$ linked to the deep aquifer and its possible thermalism, there is another corrosive
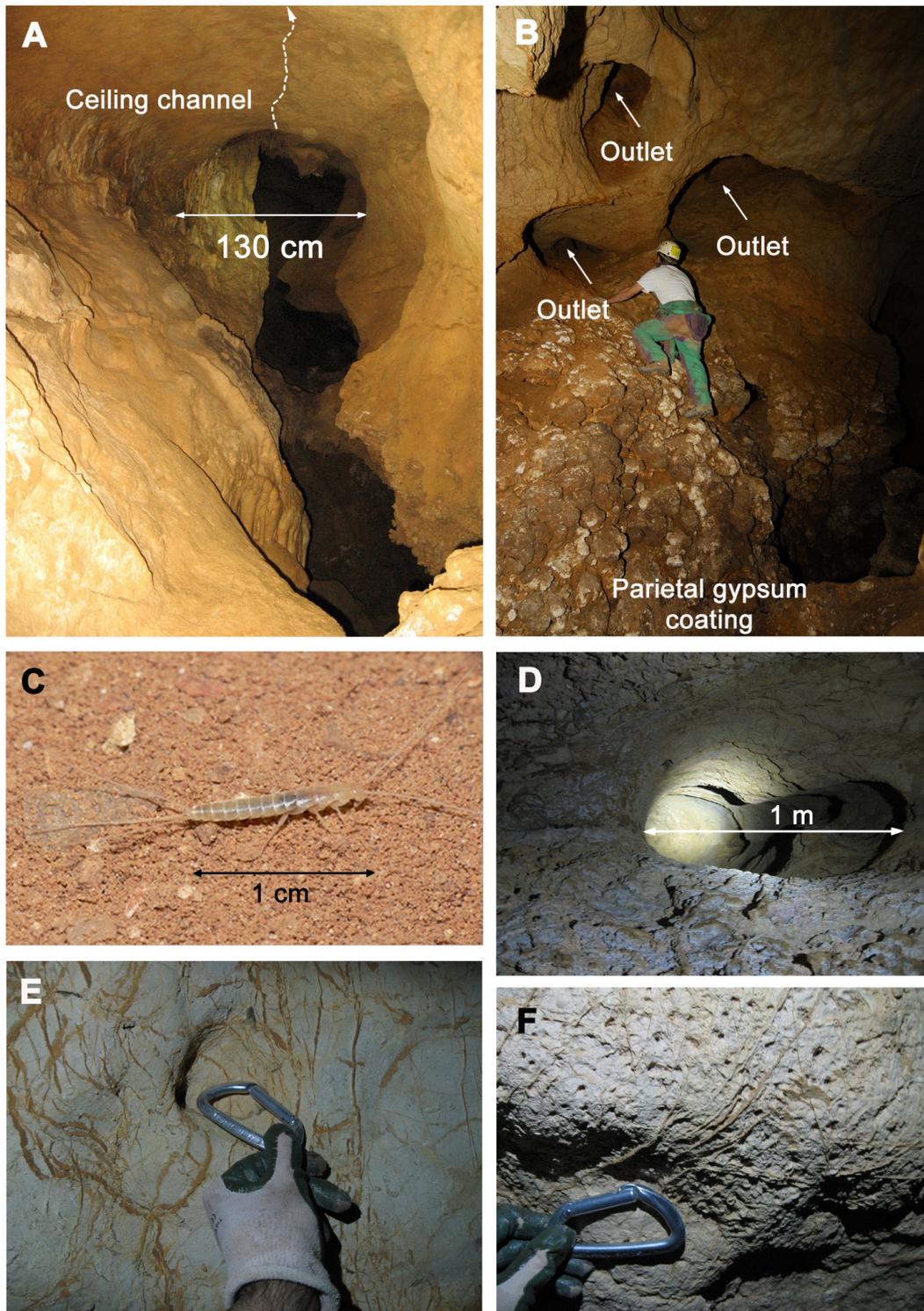
Fig. 7. Far Cave: A) Spongework gallery in the deep zone of the cave; B) Outlets in the deep zone, in a gallery with parietal gypsum coatings; C) Coletinia intermedia, a characteristic endogean frequent in the eastern chamber where roots from the surface penetrate; D) Outlet viewed from below; E) Ceiling pocket and ferruginous veins; F) Solutional micropits and ferruginous veins.

agent also involved in the hypogene speleogenesis of the cave, which may be the sulphuric acid resulting from oxidation of sulfide. This process is associated with the presence of ferric sulfide mineralization, which has been located within the host rock and, in the past, was the origin of iron ore holdings (Figs. 7E & F). Frequently ferruginous inclusions (pyrite or marcasite transformed in siderite or hematite) are observed on the walls (Figs. 7E & F). Evidence supporting the action of sulfuric acid in the speleogenesis is the presence of extensive parietal gypsum coatings, identified in several sectors of the cave (Fig. 7B).

## Habitats and cave communities

Due to the narrowness of both caves entrances, total darkness is reached within a few meters (Figs. 3, 4). Their mazes, horizontal in Far Cave and downward in Autopista Cave, have no appreciable airflow with the exception of some narrow passages between galleries at different levels. The air temperature ranges from 19.3 to 19.9°C in Autopista Cave and from 19.6 to 19.7°C in Far Cave, and relative humidity between 88.5% to 95.0% and 95 to 98%, respectively.

No strictly subterranean fauna, considered as troglobiont exhibiting troglobiomorphic adaptations,

was found in any of the two caves. At the entrance, the driest part of the Autopista Cave, where the relative humidity is constant and inferior to 90%, the presence of epigean fauna was recorded, such as the noctuid butterfly *Agrotis segetum*, the phorid and sciarid flies and occasionally harvestmen of the genus *Leiobunum* (Table 1). After the entrance there are abundant water pools on the floor, and the relative air humidity surpasses 90% and even 95% in the deepest galleries, where wet clay soils and small pools appear. The pitfalls located in the first 200 m have only captured epigean fauna such as sciarid flies and occasionally, the barkfly *Psyllipsocus ramburi*, being less frequent between 300-500 m and disappearing in its northwestern sector, after 500 m from the entrance (Table 1).

The Far Cave has a richer fauna community with several endogean, hygrophilous and lucifugous elements spread throughout the deep area of the cave. Near the entrance, in the narrow circular conducts, there are the typical elements of parietal fauna: the noctuid butterfly *A. segetum*, the harvestmen *Leiobunum,* the spider *Loxosceles rufescens*, and the tenebrionid beetle *Elenophorus collaris*, probably looking for shelter from the dry surface conditions. The access to the easternmost chamber is located in the deepest area, where the ceiling is near the surface and some roots of *Pistacia lentiscus* appear, creating a peculiar microhabitat that harbors endogean species, such as the nicoletiid silverfish *Coletinia intermedia*, recently described from this cave (Molero et al., 2013) (Fig. 7C), an unidentified species of geophilomorph centipede and a gnaphosid spider. In the eastern part of this chamber, there are guano accumulations up to two meters high (although bats were not detected during explorations), that support a diverse invertebrate fauna roughly linked to the existence of guano, among them: two species of diplurans, a japygid of *Japyx* genus and a projapygid of *Projapyx* genus, a non-troglomorphic *Pseudosinella springtail*, two species of isopods *Porcellio bolivari* and *Cristarmadillidium breuili* previously known from other caves of this area, as well as an epigean species of sciarid fly and a polydesmid millipede. In the deepest galleries only the non-troglomorphic springtails *Gisinurus malatestai,* a species of *Oncopodura* and a species of oribatid *Damaeidae* mite were found (Table 1).

## DISCUSSION

The karstification of hypogenic systems always involves confined aquifers and upwards flow. The hypogenic speleogenesis has different kinetics than epigenic karst since its origin lacks of surface connection. When it exists, it is always in the cessation of growth. Hypogenic karst/caves might not be the adequate name if we remember that the words "hypogenesis/hypogenic" have been used in relation to the geology of mineral deposits and endogen processes related to rising solutions and magmatic hydrothermalism. This is one of the reasons why Palmer (2011) does not share completely the concept of hypogenic karst/caves of authors such Klimchouk

& Ford (2009). For Palmer (2011) hypogenic caves are formed by upward flow of deep-seated water or by solution aggressiveness generated at great depth below the surface.

Although Autopista and Far caves were known for several decades (Grup Espeleològic Murta et al., 1987, Speleo Club Covak Vila Joiosa, pers. comm.), their hypogene speleogenetic origin has been now recognized for the first time. These two studied caves show obvious geomorphologic features of hypogenic origin. Both present reticular and maze developments typical of karstification in confined aquifers, where there is a confining layer acting as a roof and underneath an aquifer where speleogenesis occurs. Also they have many macro-morphological features due to hypogenic origin (Klimchouk et al., 2000; Klimchouk & Ford, 2009) caused by corrosive rising flows, such as feeders developed along networks, forming typical wells where corrosive ascent flow took place, the frequent outlets or blind chimneys developed in the roof of many conducts, micropits, pockets and in general the intersecting and anastomosed ductwork sometimes overlapped, forming floors intercommunicated by feeders. Considering these features we suggest defining a new natural model, easy to distinguish from the classical epigenic karst model, as it was often defined by authors such as Eraso (1973) with their classical features such as: scallops, vertical channels, pendants, potholes or detrital sediments.

In both studied caves, there was no connection between the subterranean hypogenic conduits and the surface during their genesis, yielding a subterranean space that prevents the input of fauna and organic nutrients (MOD or MOP) from the surface. This could be the explanation for the lack of true invertebrate troglobionts (and stygobionts) and the general scarcity of fauna (remarkably clear in Autopista Cave) in the studied hypogenic caves. Moreover, Autopista and Far caves are surrounded by non hypogenic caves inhabited by troglobiont fauna. Autopista Cave is carved in a small karst massif where there are many caves habited by troglobiont leiodid beetles and diplurans (Herrero-Borgoñón & González, 1993). Both Autopista and Far caves belong to the same karst region of the Eastern Prebaetic where at least 16 troglobiont species of arthropods are known (Zaragoza & Sendra, 1988; Domingo et al., 2007): spider (1 spp), pseudoscorpions (3 spp), diplurans (3 species) and leiodid beetles (3 spp) and carabid beetles (4 spp) (Fig. 2).

Thirty years have passed since the connection of Autopista Cave to the surface, as a result of the construction of the AP7 highway (Valencia-Alicante) in 1983, a short period of time for cave's faunal colonization. Its scarce invertebrate fauna may be the result of the active entrance of epigean species of flies and butterflies, favored by the organic inputs left by speleological activity, particulary the presence of opportunistic barkflies. The presence of vertebrates, the bat *Rhinolophus ferrumequinum* (Schreber, 1774) near one of the entrances, detected by Herrero-Borgoñón & González (1993), was not found during our study. Despite the high relative humidity (above 95%), constant temperature and the occasional water percolation in some narrow galleries

Table 1. Fauna of Autopista and Far caves, eastern Iberian Peninsula, Spain.

| Autopista Cave | | Entrance Zone | Deep Zone | | | |
|---|---|---|---|---|---|---|
| | | <100 m | 100-300 m | 300-500 m | 500-800 m | 800-1000 m |
| **Opiliones** | *Leiobunum* sp. C.L. Koch, 1839 | * | - | - | - | - |
| **Psocoptera** | *Psyllipsocus ramburi* Selys-Longchamps, 1872 | * | - | * | - | - |
| Lepidoptera | *Agrotis segetum* (Denis & Schiffermüller, 1775) | * | - | - | - | - |
| | sp. indet. | * | - | - | - | - |
| Diptera | Phoridae | * | - | - | - | - |
| | Sciaridae | * | * | * | - | - |

| Far Cave | | Entrance Zone | Deep Zone | | |
|---|---|---|---|---|---|
| | | < 50 m | 50-80 m endogean enviorenment | 50-80 m endogean enviorenment | 100 m deepest galleries |
| **Opiliones** | *Leiobunum* sp. | * | - | - | - |
| | *Scotolemon* sp. | - | * | - | - |
| **Araneae** | *Loxosceles rufescens* (Dufour, 1820) | * | - | - | - |
| | Gnaphosidae | - | - | - | - |
| **Acarina** | Oribatida Damaeidae | - | - | * | * |
| **Isopoda** | *Cristarmadillidium breuili* Vandel, 1954 | - | - | * | - |
| | *Porcellio bolivari* Dollfus, 1892 | - | * | * | - |
| **Diplopoda** | Polydesmida | - | * | * | - |
| **Chilopoda** | Geophilomorpha | - | - | * | - |
| **Collembola** | *Pseudosinella* Schaeffer, 1897 | - | - | * | - |
| | *Oncopodura* Carl & Lebedinsky, 1905 | - | - | - | * |
| | *Gisinurus malatestai* Dallai, 1970 | - | - | - | * |
| **Diplura** | *Japyx* Haliday, 1864 | - | - | * | - |
| | *Projapyx* Cook, 1899 | - | - | * | - |
| **Zygentoma** | *Coletinia intermedia* Molero, Bach & Gaju, 2013 | - | - | * | - |
| **Coleoptera** | *Elenophorus collaris* (Linnaeus, 1767) | * | - | - | - |
| **Lepidoptera** | *Agrotis segetum* | * | - | - | - |
| **Diptera** | Sciaridae | - | * | * | * |

(m) meters from the entrance

was not enough to facilitate the arrival of hygrophilous species that were present only at the entrance.

Far Cave is connected to the surface due to the progressive and rapid retreat of the slope during the Late Pleistocene. There are two facts that can serve as evidence of this erosion process: i) The location of the small entrance, which opens in a distal portion of the ductwork and ii) In the same sector of the cave, the presence of colluvial deposits and hardly any loose matrix (grèzes), denoting the retreat of the mountain slope.

Although Far Cave is about 120 m a.s.l., the hill descends steadily to the Mediterranean Sea and presents significant accumulations of sand deposits (rampant dunes) interdigitated with slope deposits (colluvial, usually with red matrix and sometimes crusted), indicating a relatively high position of an emerged wide sandy platform. Also striking is the possible existence of a tyrrhenian fossil beach, remnants of climbing dunes identified by Navarro et al. (1959) at 170 m a.s.l., on the southern slope of the mountain. These data help us to understand how the confined aquifer originated several hundred or a few thousand years ago, the dismantling of the slopes and the hydrothermal disconnection. The final result is a fossil cave isolated from the surface until relatively recent times. Despite the suitable ecological conditions of Far Cave (relative humidity close to 99%, constant temperature, presence of water in small pools, percolating water in several places within the cave and active movement of animals, especially bats), it has not been colonized by troglobiont species. However, this cave was colonized by guanophiles, endogean and hygrophilous species, facilitated by two factors: the input of bats and the temporary presence of guano, and the ease of access from the outside, particularly in the easternmost room, were roots coming from the surface are present. Noteworthy is the discovery of one species of Projapygidae family, a tropical dipluran previously

unknown in Europe, spread through Africa and South America, and whose presence has been detected before in guano accumulation (Paulian & Delamare-Deboutteville, 1948).

Both caves have poor communication with the surface, and thus they receive small contributions from the meteoric water that could bring organic matter, which may explain how only small populations of springtails and mites can exist in its deepest parts. Invertebrate colonization is still in its incipient phase. The recent connection to the surface of both caves and their isolation during the hypogenic formation seems to have impeded the colonization by geographically close troglobiont species, allowing only very recent colonization by non-specialized arthropods.

The lack of troglobiont fauna in Autopista and Far caves match with the fauna data in the literature of many hypogenetic caves. For example, the caves quoted in the introduction (some of them among the largest in the world), are almost without invertebrate fauna, in spite of their rich bacterial and fungi diversity (e.g., Lechuguilla Cave; Cunningham et al., 1995). The same situation is known from other caves that are longer than 200 km, such as the Jewel Cave in South Dakota (Olson, 1977) or Optimisticheskaja and Zolushka in Ukraine, where only microorganisms have been recorded (Andrejchuk & Klimchouk, 2001; Ridush, pers. comm.).

Nevertheless, not all sulfidic caves could be considered to have a hypogenetic origin. The karstification by sulfides does not always happen in hypogenic karst/caves, also in epigenic ones, especially when there is oxidation of pyrite or others sulfides. Eraso (1969) refers to 10 different speleogenetic processes in epigenic karst including sulphuric acid coming from oxidation of sulfurs. As such, we can consider some sulfidic caves as not truly or completely excavated in hypogenic conditions. This is the case with Ayyalon Cave (Israel) (Por et al., 2013), which does not have (or had) a confining layer and so its colonization from the surface was always possible. It is the same case for some Italian caves considered hypogenic such as the Buso della Rana Pisatella System (Tisato et al., 2012) and the well known Frasassi Caves (Italy) (Galdenzi & Sarbu, 2000; Sarbu et al., 2000). The Movile Cave (Romania) deserves special mention, given that it is an isolated ecosystem with a trophic web composed of 48 cave-dwelling invertebrates, 33 of them endemic to this system (Sarbu & Kane, 1995; Sarbu, 2000). This rich community of invertebrates colonized the cavity over extensive periods of time in several distinct episodes (Sarbu, 2000) when the cave was connected to the surface before being resealed again.

On several occasions some authors write about sulfidic caves making references to their poor communication with the surface and the subterranean shallow habitats (Forti et al., 2002; Engel, 2007) but without a general consideration of the scarcity of the fauna in hypogenic karst/caves.

From these observations, the reasoning would be as follows: all subterranean hypogenic confined karst/caves must lack fauna in their active phase due to isolation (Figs. 1 and 8, phase $t_0$), although they might contain a community of chemolithotrophic microorganisms, related or not to their speleogenesis processes.

Independently of the speleogenetic of the hypogenic karst/caves, the cessation of growth of the karst/caves and the drop of the piezometric level maintain this environment without fauna until a connection with the surface or to other subterranean habitats is established. Only then, fauna may colonize hypogenic karst/caves and the entry of food resources from the surface may also be established. However, the colonization becomes difficult in deep caves embedded in solid compact rocks that could prevent the interconnection with subterranean superficial well developed habitats, if they are present (Figs. 1 and 8, phase $t_1$).

## FINAL REMARKS

The classical definition of the subterranean ecosystem through bioespeleological literature, shown by Racovitza (1907), Juberthie (2000), or Culver and Pipan (2009a) may be summarized as a network of intercommunicated micro, meso and macro voids, filled or not with meteoric water, extending from the surface towards the subsurface, allowing the movement of fauna communities and nutrients mostly from the surface. Those spaces are in total darkness, with isothermal tendency, often close to saturated air humidity in the terrestrial compartment and generally low food resources. This allows the existence of troglobiont (and stygobiont) communities characterized by the absence of primary photosynthetic producers, with little presence of chemolithotrophic (except for the additional presence of sulfur or methane sources), and a more or less abundant animal community depending on the amount of nutrient input from the surface.

By considering the hypogenic karst/caves *sensu* Klimchouk & Ford (2009) and their lack of fauna, we suggest the concept of a singular hypogenic subterranean ecosystem separated from the classical or epigenic subterranean ecosystem. This hypogenic subterranean ecosystem should be defined as a network of micro, meso and macro subterranean spaces, which are excavated into karst rocks in confined conditions and thus isolated from the surface, resulting in semi-climatic-independence from the surface, a temperature slightly higher due to geothermal anomalies and without input of organic nutrients from the surface. This ecosystem may harbor an exclusive oligotrophic community of chemolitotrophic microorganisms that can be very abundant in sulfur-methane rich caves. Animal colonization only occurs once the confinement barrier with the surface or with other subterranean epigenic ecosystem is temporarily or definitively removed.

Hypogenic caves include some of the world's largest caves, often lacking fauna or accommodating a poor troglobiont community. Once the hypogenic karst/cave is opened to the surface, it might be colonized by faunal community in connection with other subterranean habitats better connected with the surface, or even by the passively carried by water or other animals (hydrochoria and zoochoria). In the case of sulfur-methane bacteria abundance, a rich faunal community can occur if the connection with
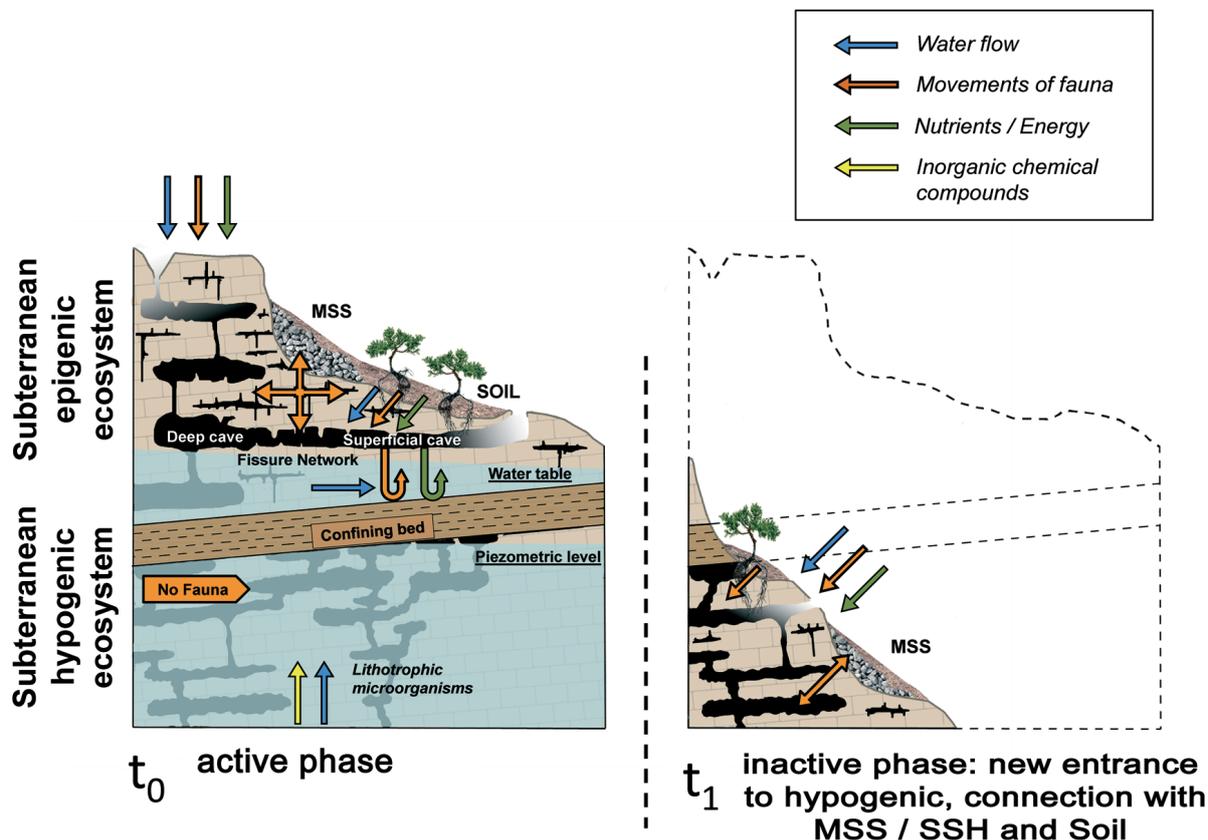
Fig. 8. Diagram of the flow of fauna, water and energy (in form of organic nutrients, or inorganic chemical compounds) in both epigenic and hypogenic subterranean ecosystems. $t_0$ active phase; $t_1$ inactive phase with the connection of hypogenic ecosystem with the surface, SSH and soil.

the epigenic subterranean ecosystem or the surface has been possible, for at least some period of time

The relation between the hypogenic karst/caves and their lack of troglobiont fauna may have relevant consequences on our knowledge of the biodiversity patterns of subterranean species. Such hypogenic karst/caves can explain the lack of troglobiont fauna in subterranean ecosystems with suitable environmental conditions, even when they are located within massifs rich in troglobiont species.

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