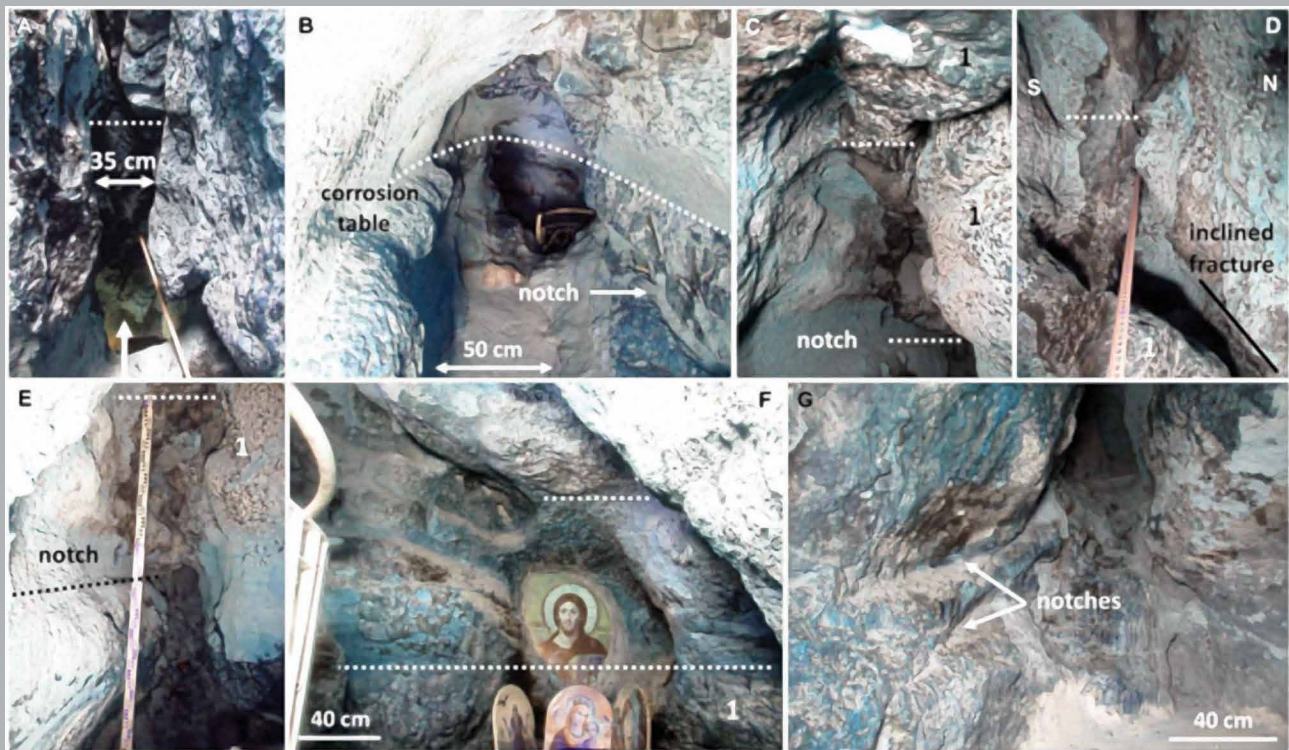


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Front Cover: Saint Anthony Cave. See Fahim in this issue.

SAINT ANTHONY CAVE: MORPHOLOGY, GENESIS, AND AGE OF ONE OF THE OLDEST RELIGIOUS SHRINES, SOUTHERN GALALA PLATEAU, EASTERN DESERT, EGYPT

Wafaa Khalaf Fahim¹

Abstract

Saint Anthony Cave is an important cultural, religious, and historic site; it was home of Saint Anthony, one of the earliest Christian monks (ca. 251–356 AD). The cave is located in a *tectonically*-complex karst area developed in partially dolomitic, sandy limestones of latest Paleocene age. Saint Anthony Cave had been described as a phreatic cave in previous research, but the cave lacked a detailed map and its speleogenesis was unclear. New data show the cave is a multi-phased uplifted cave formed primarily under *phreatic* conditions, with later modification by rising water levels. *Deep sources* of dissolutionally aggressive solutions likely have been involved. Speleogenesis likely began in Oligocene time associated with the Gulf of Suez Rift evolution and has been erosionally dissected. New, detailed mapping using ArcGIS shows the cave has an area of 22.13 m² with a length and depth of 17.10 m and 5.33 m, respectively. The cave consists of a northwest–southeast oriented, steeply inclined, fracture controlled, upper-level entrance passage connected to an east–west oriented, fracture controlled, lower-level room with a vertical drop of 2.46 m. Dissolution pockets, cupola-like features, ceiling bell holes, notches, and corrosion tables are present in the cave. Subaerial and subaqueous speleothems moderately decorated the cave with likely Egyptian calcite alabaster. Based on field investigation, regional volcanic and tectonic history, paleoclimates, and other background information, we identify four distinct speleogenetic phases: First, during the late Oligocene, volcanic and extensional tectonic activities fractured the rocks, generated deep-seated acids, and enhanced the rising deep thermal water. Dissolution by other mechanisms such as carbonic/sulfuric acid and mixing dissolution were prevalent. In the early Miocene (Burdigalian), the cave was uplifted. Second, in the late Miocene (about 7.5 Ma), subaerial speleothems were being deposited in the cave under humid climate conditions. Third, post-Miocene, the cave enlarged and modified at and above the water level by likely warm, sulfuric water. Fourth, water levels dropped and speleothems were deposited again during later humid climate conditions.

INTRODUCTION

The presence of dissolution caves is well documented in arid to hyper-arid regions (e.g., Ford and Williams, 2007, and references therein). These caves are mostly inactive relict features, and many have been modified and overprinted by later processes such as dissolution, deposition, and tectonic uplift, obscuring their origin.

Some studies attribute these caves to epigene speleogenesis, where carbonic acid derived from the surface caused speleogenesis (Ford and Williams, 2007). Other caves have no apparent genetic relationship to surface recharge and have certain characteristics suggesting hypogenic speleogenesis.

Hypogenic speleogenesis can result from dissolution mechanisms such as: (1) deep-seated acidic solutions (CO₂/H₂S), (2) cooling thermal water, (3) mixing of waters of contrasting chemistry, such as where deep water mixes with near-surface water or along a freshwater-saltwater contact, (4) sulfuric acid, where H₂S-bearing water interacts with oxygenated shallower water near or above the water table. The last mechanism can take place if both waters are saturated with calcite, but that requires a closed system. H₂S can also be produced by local oxidation of iron sulfides such as pyrite. (Myroie and Carew, 1990; Palmer, 1991; Palmer, 2007; Dublyansky, 2013; Klimchouk, 2019).

Hypogenic speleogenesis is well documented in arid to hyperarid localities around the world (e.g., Klimchouk et al., 2017). In Egypt, caves that have the characteristics of hypogene caves have been documented in the Southern Galala Plateau (Fahim, 2019). Flank margin caves formed in a freshwater-saltwater contact zone have been documented along the Matruh coast in northwest Egypt (Fahim, 2015).

A BRIEF HISTORY OF SAINT ANTHONY CAVE

Saint Anthony Cave is an important cultural, historic, and religious site. The cave is named after the monk, Saint Anthony the Great, also known as Saint Anthony of Egypt (ca. 251–356 AD). He is considered the first Christian monk and is an important figure among the Desert Fathers and to all of later Christian monasticism.

The cave was the dwelling place of Saint Anthony between approximately 312 and 356 AD. He chose the cave because it was a sanctuary and because of the persistent springs that helped him live in solitude far away from civilization to pursue ascetic ideals. Since his death, Saint Anthony Cave has served as a place for veneration and prayer

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for pilgrims and for visitors from all over the world. A detailed account of the history of the life of Saint Anthony can be found in Rubenson (2016).

Previous Work

The Southern Galala Plateau is also called “El-Galala El-Qibliya” and is located at the northeastern portion of the Eastern Desert of Egypt. The plateau lies at the western shoulder of the Gulf of Suez Rift, a northern extension of Red Sea. Topographically, the plateau is very rugged with a maximum elevation of 1480 m. It is characterized by dry valley (wadi) systems with autogenic recharge (Fig. 1A–C).

The Southern Galala Plateau is tectonically and geologically complex with *highly fractured* carbonate rocks that have surface karst landforms and caves.

Little prior work has been done on caves in the area (Goodman et al., 1992; Hobbs and Goodman, 1995; Halliday, 2000; Halliday, 2001; Halliday, 2003), and there have been few studies of their genesis and ages. A small dissolution cave was located inside the Church of Saint Paul Monastery, but human modification has obscured its location (Lyster, 1999).

Recently work by Fahim (2019) has shown that the Southern Galala Plateau contains a complex and diverse assemblage of karst landforms including karren, caves, residual carbonate hills, dolines, and pocket valleys. This study also discovered and described other karstic caves in the plateau.

The most impressive, newly-discovered cave in the Southern Galala Plateau is Al-Jarf Cave located in the eastern side of the plateau in Wadi Al-Jarf (Al-Jarf Al-Qibli). Al-Jarf Cave is developed in limestone and dolomitic limestone of early Eocene age. The cave is fracture controlled, multilevel, and multi-phased, and it has an area of 1208 m². The cave is at least Oligocene in age. The cave is polygenetic, formed primarily under phreatic and water table settings, likely influenced by deep fluids. Al-Jarf Cave shows 16 types and subtypes of subaerial and subaqueous speleothems with different morphologies, such as stalagmites up to 2.75 m high and 2.10 m in diameter, stalactites, draperies, flowstone, helictites, spar, small raft cones, and others. Deflected stalactites and oriented coralloids are also present. Calcite, gypsum, anhydrite, halite, and other minerals have been identified (Fahim, 2019).

Dissolution caves are present in the northern side of the Southern Galala Plateau and also in the flanks of the wadis. Most have the characteristics of phreatic, water table, epigene caves. Dissolution pockets are the most common features in the caves. Some of the caves contain speleothems. Um Hamada Cave is one of the largest and inaccessible caves and consists of a single large room 1454 m² in area. Some small caves at about 500 m MSL in the northern cliff of the plateau west of the Saint Anthony Monastery are filled with secondary deposits of spar and Egyptian calcite alabaster (see discussion section) (Fahim, 2019).

In the Saint Anthony Monastery, there are some karstic caves, but their origins have been obscured by modification for use as dwellings for monks. Most of the known caves in the area are relict and inactive. In different expeditions, we have discovered other new caves at Wadi Al-Jarf, and condensation-corrosion processes caused by rising vapors are active in one of them (Fahim, 2022). There are extraordinarily unusual, active, large tufa stalactites with a maximum length of about 6 m in Wadi Kharaza, probably fed from active, unopened caves (Fig. 1C).

Saint Anthony Cave was given a brief and useful description by Halliday (2000; 2001; 2003). Halliday gave the dimensions (length, width, height) of the cave but did not map it. Halliday suggested that the cave was formed phreatically

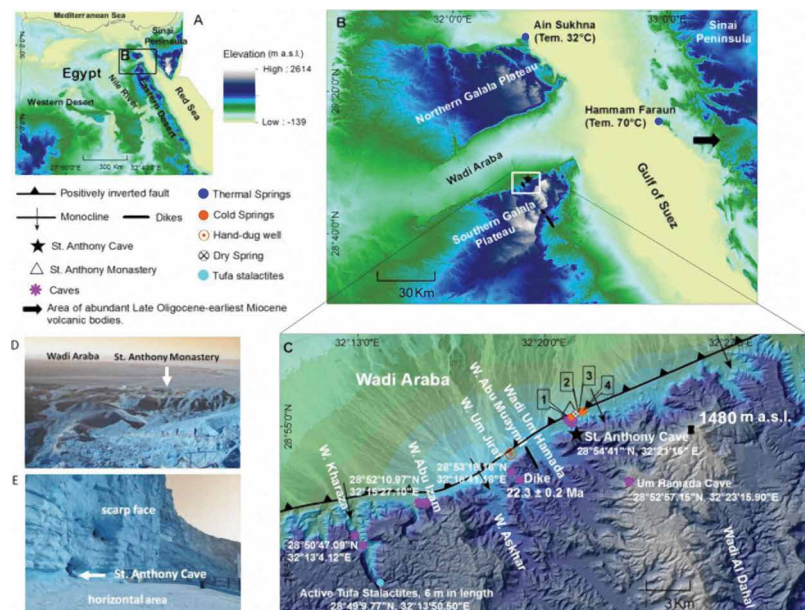


Figure 1. (A) ASTER 90 m-resolution digital elevation model of Egypt. (B) ASTER 90 m resolution digital elevation model showing the location of the Northern and Southern Galala Plateaus. (C) Shaded-relief image of the digital elevation model of the area of Saint Anthony Cave. The inverted fault and the monocline are added according Schütz (1994) and Moustafa and Khalil (1995), respectively. The data and the locations of the volcanic bodies are from Klitzsch et al. (1987), Patton et al. (1994), and Bosworth et al. (2015). Temperatures of the thermal waters are from Sturchio et al. (1996). Numerals 1-4 show springs discussed in the text. Caves are from Fahim (2019). Coordinates for the caves and the tufa stalactites were added according the current study. (D) View of the Saint Anthony Monastery and Wadi Araba near the site of the cave (note people for scale). (E) View in front of Saint Anthony Cave and the nearby area surrounding (note the barrel in the right side of the photo for scale).

along joints and appeared to be a fossil outflow route. A floor of flowstone, possibly Egyptian alabaster, is located at the cave entrance. There are small phreatic features near the cave. Halliday compared the study area to the North Rim of the Grand Canyon in the USA, where the karstification began in middle Eocene time. Fahim (2019) provided a simple map of the cave and confirmed that the cave had formed at or below the water table.

The aim of this work was to survey the cave and produce a detailed map and to describe the cave morphology in detail, including small dissolution features, and speleothems. This information was used in concert with previous studies on karst development, regional geology, volcanics and tectonics, paleoclimates, and the geologic and hydrologic history of Wadi Araba to determine the physical, structural, and chemical controls on speleogenesis as well as the speleogenetic phases and their relative timing.

LOCATION, CLIMATIC, AND GEOLOGIC SETTING

Saint Anthony Cave (latitude 28°54'41" N, longitude 32°21'16" E, 800 m MSL) opens within the northern cliff of the Southern Galala Plateau (Fig. 1A–C). The cave is currently accessed from the entrance gate of the Saint Anthony Monastery by a 1.5 km walk to a stairway consisting of about 1,400 steps. This stair leads to an unroofed, semi-artificial, horizontal area, 101 m² in area, located in front of the cave and overlooking Wadi Araba and the monastery (Fig. 1D–E).

Proximal to the cave, the scarp face is vertical to overhanging and is highly fractured with joints and normal faults. The scarp face has a corrosion surface with a variety of dissolution features such as small phreatic cavities, hollows with spongework textures, honeycomb-like features, and shallow, flat-roofed notches at localized areas on different levels. Mineral-filled fractures have been observed with some displaying small scalenohedral calcite crystals with different colors. Below the cave, there is a gorge undermined with terraces at different elevations. There are karstified, collapsed rock blocks on the sloped area near the cave. Springs emerge at the foot of the cliff inside the Saint Anthony Monastery.

Climate data for 24 years (1991–2014) was obtained from the Bir Arida meteorological station, located in Wadi Araba at 300 m MSL. The annual average maximum air temperature averaged 29.29 °C over the past 24 years, with individual years ranging between 28.49 °C and 31.35 °C. The annual average minimum air temperature averaged 13.82 °C, ranging between 12.57 °C and 15.20 °C. The annual average daily air temperature averaged 23.36 °C, ranging between 22.13 °C and 24.80 °C. The average daily air temperature ranged between 10.9 °C and 22.4 °C in winter and averaged between 27.4 °C and 33.5 °C in summer.

The highest average monthly maximum temperature was 37.27 °C in July, while the lowest average monthly minimum temperature was 5.16 °C in January. The total amount of annual rainfall ranged between 0 and 14.3 mm. The inland area of the Southern Galala Plateau and Wadi Araba is classified as extremely arid (hyper-arid) punctuated by sudden catastrophic *torrents*.

Saint Anthony Cave developed within partially-dolomitic, sandy limestone (10%–20% quartz) of the Southern Galala Formation (Jochen Kuss, University of Bremen, personal communication, 2021), of late Paleocene-early Eocene age. This formation dips gently to the southeast and has highly fractured and weathered beds and calcite veins (Abdallah et al., 1970). This formation reaches a thickness of about 250 m (Scheibner et al., 2001) (Fig. 2).

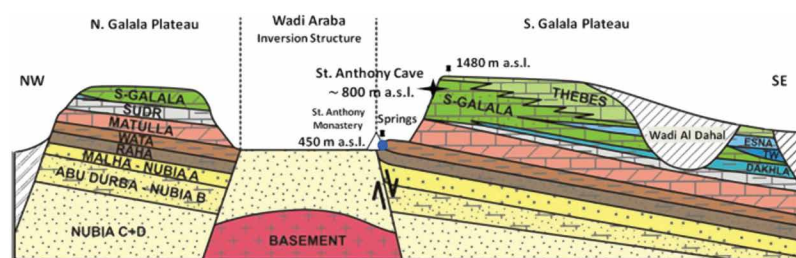


Figure 2. Geological cross-section of the North and South Galala Plateaus separated by Wadi Araba. Nubia C+D (sandstones), Nubia B (sandstones with shales/claystone, dolomites, and subordinate limestones), and Nubia A (sandstones occasionally shales/claystone) are Paleozoic to Early Cretaceous in age. The Raha, Wata, and Matulla Formations (a mixed facies sequence, containing marls, shales/claystone, sandstones, dolomites, and limestones) are Late Cretaceous in age. The uppermost Cretaceous rocks are represented by the Sudr Formation (chalk, chalky limestones). Paleocene and Eocene rocks are represented by S-Galala and Thebes Formations (sandy limestones, dolomitic limestones, limestones with marl intercalations, partly conglomeratic). Other formations in blue are marls and shales (Moustafa and Khalil, 2017; Moustafa and Khalil, 2020; Scheibner et al., 2001). The site of the cave is added according to the current study. The elevation points according to the GPS measurements and a topographic map at a scale of 1:50,000. The figure is adapted from Höntzsch et al. (2011).

SPRINGS

There are inactive and active springs and both hand dug and drilled wells in the study area, and most are located in Wadi Araba. Most of the springs are unconfined, but some are confined, and groundwater generally appears to be controlled by structural features (i.e., faults and folds), lithology, and topography (Aggour, 1990).

The water is brackish. Total dissolved solids range from 1.344 g L⁻¹ to 2.822 g L⁻¹, temperature ranges from 13 °C to 28.3 °C, and pH ranges from 6.9 to 8.5. The water type is mostly CI (407–1,098 mg L⁻¹), SO₄ (200–848 mg L⁻¹), HCO₃ (129–405 mg L⁻¹), and isotopic measurements suggest meteoric recharge (Wannous et al., 2021; Khalil et al., 2021).

Four brackish springs emerge 340–354 m below Saint Anthony Cave in the Saint Anthony Monastery. They are (1) Saint Anthony, (2)

Maryam (Aladra), (3) Smar, and (4) Agathon Springs (Fig. 1C). The latter two springs have the highest SO_4 values recorded in the area. The Saint Anthony and Maryam Spring waters flow through active karst spring caves. They are fracture controlled and developed in upper Cretaceous carbonate rocks (Aggour, 1990). Currently, the springs below Saint Anthony Cave have low discharge volumes of about $5 \text{ m}^3 \text{ d}^{-1}$, except the spring of Saint Anthony has a constant discharge of about $100 \text{ m}^3 \text{ d}^{-1}$, which it has had since the 1st century AD, as documented by the monks.

The water chemistries of the springs of Saint Anthony and Maryam (Aladra) in February 2018 were brackish (1465 and 1547 mg L^{-1} dissolved salts, respectively) with a pH of 7.3 and 7.8, respectively. Their water types were Cl (407 and 437 mg L^{-1} , respectively)– SO_4 (314 and 349 mg L^{-1} , respectively)– HCO_3 (279 and 255 mg L^{-1} , respectively), and their temperatures were 24°C and 17°C , respectively (Wannous et al., 2021). In January 2016, the water chemistry of the Saint Anthony spring was brackish (1335 mg L^{-1} dissolved salts) with a pH 7.3 and a water type of Cl (450 mg L^{-1}), HCO_3 (305 mg L^{-1}), SO_4 (180 mg L^{-1}) (Saint Anthony Monastery, unpublished data, 2016).

Based on the field investigation and the information from the monks, Saint Anthony Spring Cave (latitude $28^\circ 55' 22.98'' \text{ N}$, longitude $32^\circ 21' 1.31'' \text{ E}$) consists of a narrow entrance, less than 1 m wide and high. This entrance leads to a passage about 0.50 m wide, 0.80 m high, and 0.30 m depth below the water level that extends about 8 m to where the

water emerges from rocks (Fig. 3A). Maryam (Aladra) Spring Cave (latitude $28^\circ 55' 24.79'' \text{ N}$, $32^\circ 21' 5.41'' \text{ E}$) consists of an entrance room that measures about $4 \text{ m} \times 3 \text{ m}$, with a height of about 3 m above the water level and a depth of about 1 m below the water level. This room connects upstream to a narrow passage about 1 m wide (Fig. 3B).

Our personal observations show that the Saint Anthony spring cave has a corrosion table slightly higher than the water level of the spring. The Maryam (Aladra) Spring Cave shows corrosion tables, nearly flat ceiling pendants, a small

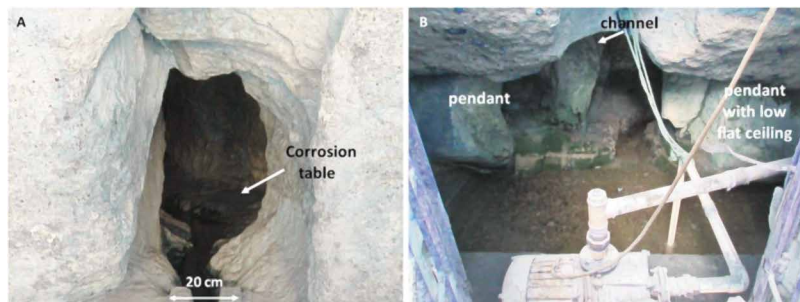


Figure 3. Active karst spring caves, Saint Anthony (A) and Maryam (Aladra) (B), at the Saint Anthony Monastery.

smooth curving channel on the wall, with likely secondary gypsum. These features are common in sulfuric acid caves (e.g., Audra et al., 2009) and suggest that sulfuric acid may have been involved in the formation of Saint Anthony and Maryam Spring Caves.

REGIONAL TECTONIC HISTORY AND AREA BACKGROUND

Late Cretaceous to early Paleocene pulses of tectonic deformation across the study area produced the asymmetrical plunging anticline of Wadi Araba with nearly vertical beds at the Saint Anthony Monastery (Moustafa and Khalil, 1995). There is a debate about whether or not Wadi Araba is the expression of a fault-propagation fold (Moustafa, 2020) with a deep-rooted fault present at the northern cliff of the Southern Galala Plateau that separates Wadi Araba from the plateau (Schütz, 1994). From the late Paleocene to the middle Eocene, the area was under marine conditions (Said, 1962), and the upper Paleocene/lower Eocene rocks in which Saint Anthony Cave has formed were deposited.

There are no deposits dating from the late Eocene until the Miocene present in the Southern Galala Plateau and until the Pleistocene present in Wadi Araba (e.g., Klitzsch et al., 1987). However, sediments dating from these periods were recorded at the eastern side of the Gulf of Suez Rift directly opposite the study area. There, late Eocene marine deposits are recorded by the shallow marine Tanka Formation (Hume et al., 1920; Abul-Nasr and Thunell, 1987). The deposition of the Tanka Formation in the study area is a matter of debate; most workers have suggested that it was deposited and later eroded. In the middle Oligocene, a global major eustatic sea level drop occurred (Haq, 1987). The study area was exposed to erosion before the Gulf of Suez Rift was initiated, and the erosion was not more than a few hundred meters (Garfunkel, 1988).

From possibly the middle Oligocene or late Oligocene to the early Miocene, the Gulf of Suez Rift began to open at sea level (e.g., Robson, 1971; Garfunkel and Bartov, 1977; Patton et al., 1994; Bosworth and McClay, 2001; Moustafa and Khalil, 2020). Continental conditions are recorded in the first syn-rift formation called “Abu Zenima” (Hantar, 1965), which was deposited under arid and semi-arid climate conditions (Jackson et al., 2006). Volcanic activity that preceded the rift phase was recorded and assigned a variety of ages. The oldest exposed late Cenozoic volcanic basaltic dike in the Gulf of Suez area has been dated at $25.7 \pm 1.7 \text{ Ma}$ in the Southern Gabel Ataqa (Bosworth and McClay, 2001), north of the study area.

Non-marine conditions were followed by shallow marine conditions at the 2nd syn-rift formation called “Nukhul” (Egyptian General Petroleum Corporation, 1964). The Nukhul Formation recorded slow subsidence rates of the rift and

it is early Miocene (Aquitanian-early Burdigalian or early Burdigalian) in age (e.g., Evans, 1990; Bosworth and McClay, 2001).

The margins of the Gulf of Suez Rift and the plateau have been uplifted, but the timing of the uplift is unclear. Omar et al. (1989) used apatite fission track analysis on the rocks of the western margin of the Gulf of Suez rift and concluded that the beginning of uplift in the area was at 22 ± 1 Ma.

In the early Miocene (Burdigalian), uplift of the margins of the Gulf of Suez Rift accelerated and was accompanied by subsidence of the Gulf of Suez Rift. This persisted until about 17 Ma (mid-Clysmic event); then the uplift and subsidence decelerated (Garfunkel and Bartov, 1977; Moretti and Colletta, 1987; Steckler et al., 1988; Evans, 1988; Richardson and Arthur, 1988; Jarrige et al., 1990; Patton et al., 1994; Bosworth and McClay, 2001; Moustafa and Khalil, 2020). Open and deep-marine conditions were recorded in the central parts of the Gulf of Suez Rift Basin during deposition of the *Burdigalian-middle Langhian* Rudeis Formation (Egyptian General Petroleum Corporation, 1964). In the Southern Galala Plateau, the syn-rift formations are recorded at the eastern margin of the plateau and unconformably overlay the middle Eocene rocks (Egyptian Mineral Resources Authority, 2005).

METHODS

Although Saint Anthony Cave is relatively small, large numbers of visitors made it difficult to conduct detailed fieldwork in one day. Different one-day trips were carried out from August 2015 to August 2021. The fieldwork was performed using measurements, observation, and information from monks living in the monastery.

We surveyed the cave in detail on June 15 and August 3, 2021, using a compass and clinometer with 0.5° of accuracy, a laser range finder, and tape.

Because the cave opening is in a steep scarp face, approximate coordinates and altitude of the cave were determined based on the GPS measurements integrated with a 1:50,000-scale topographic map. Cave minerals were identified in the field based on observations and on the use of hydrochloric acid.

Cave mapping was conducted using the methods outlined in Chabert and Watson (1981) and Dasher (1994). Cave survey data processing was performed using ArcGIS 10.3. Cave symbols used in the cave map are based on National Speleological Society standard map symbols by Hedges et al. (1979), as well as the caves style symbols in ArcMap, and suggested symbols.

RESULTS

Cave Morphology

Saint Anthony Cave consists of an upper-level passage, 4.43 m^2 , leading to a lower-level room, 17.70 m^2 . The cave has a total area of 22.13 m^2 , volume of 44 m^3 , length of 17.10 m , and depth of 5.33 m . The cave entrance is a horizontal, fracture-controlled opening. It is $2.22\text{--}2.70 \text{ m}$ high and $0.68\text{--}1.25 \text{ m}$ wide (Figs. 4, 5(A)). The cave entrance was very narrow but has been artificially widened by the monks of the monastery.

Immediately outside the cave entrance, the floor takes the shape of the conduit and extends outward for 5.20 m . The sides of this conduit-like passage are the side faces of a deep notch. Small, relict speleothem deposits are present on

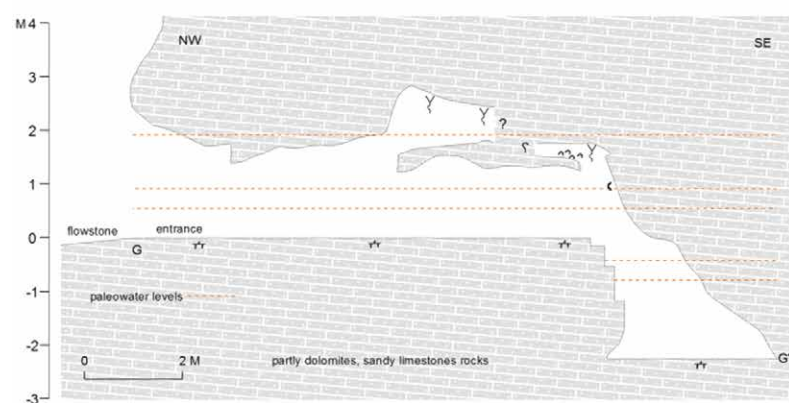
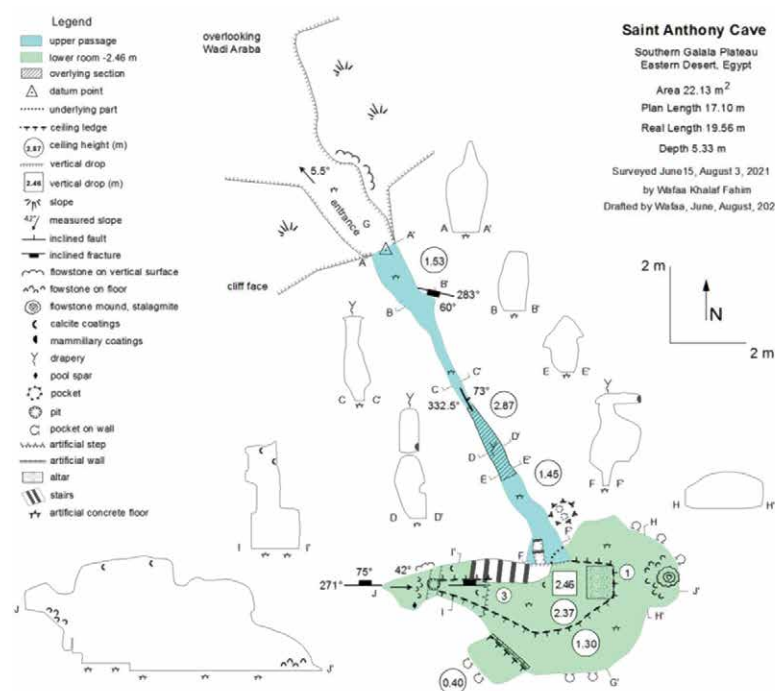


Figure 4. Map of Saint Anthony Cave showing a plan view, cross sections, and longitudinal profile. The yellow section is the entrance passage, and the green section is the terminal room. (The floor steps are artificial.)

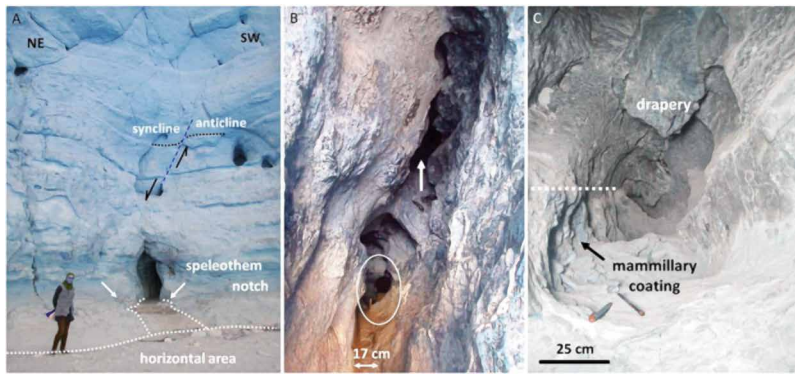


Figure 5. (A) Front view of the entrance of Saint Anthony Cave in the year 2015 showing speleothems (*white arrows*), a normal fault (*dashed red line*), and faces of a notch (*dashed white lines*). (B) Cave passage illuminated by morning daylight (looking inward) showing a person for scale (*white circle*), a vertical metal stair railing (*white, west of the person*), and the overlying section shown in Fig. 5C (*white arrow*). (C) Overlying sub-horizontal section showing a paleowater level (*dashed white line*).

parallel fracture occurred during the opening of the Gulf of Suez Rift at Oligocene-Miocene time (Moustafa and Khalil, 2020).

The entrance passage is nearly straight, steeply inclined at the start, and very narrow with irregular cross sections (Fig. 5B). The passage ranges from 0.17 to 1.00 m wide and from 1.35 to 2.87 m high. The passage varies in height along its entire length. The width of the passage also varies inversely with passage height, i.e., the narrow parts are higher and the wide parts are lower.

The cave passage ends at the terminal room. Near the junction between the entrance passage and the terminal room, the main fracture along the passage gradually changes orientation to another steeply-inclined fracture oriented N 89° W (271°) that dips to the north at 75° and that runs along the western side of the room. It is not clear whether this fracture is a fault or a joint, but the trend of this fracture is similar to the orientation of the transverse or cross faults (N 50°–75° E). The transverse faults were active during the opening of the Gulf of Suez Rift and developed through the reactivation of pre-existing basement fractures (Patton et al., 1994; Moustafa and Khalil, 2020). The passage drops 2.46 m into the terminal room. The terminal room is 7.76 m long and ranges from less than 1 m to 4 m wide and from less than 1 m to 3 m high with irregular cross sections.

Meso- and Micromorphological Features

The most significant feature of Saint Anthony Cave is an upward branch of the upper-level entrance passage. This branch has formed along the same fracture as the main passage and is associated with the highest and narrowest part of it. This overlying section is 0.50 m wide and penetrates 2.10 m sub-horizontally toward the inner parts of the cave and apparently ends just out of sight. Inside this feature, there are niche-like features (convection-related features) at the same level, but their origin is not clear (Fig. 5C). This overlying section may be a small sub-horizontal passage or a modified fracture-controlled chimney, and it may represent the early or the later dissolutional phase of the cave development.

Almost all the features of the floor of the cave are obscured by concrete and in some places the lower parts of the cave wall as well. There are other structures that have been built in the terminal room, obscuring some of the natural features. But 0.90 m before the inner termination of the passage, it contains a fissure in its floor. Along this downward-narrowing floor, there are three small stairs with a total vertical drop of 1.30 m connected to the stair of the terminal room. According to the monks of the monastery, these steps are artificial and overlie a deep floor fissure both there and at the middle section of the passage, but they sealed the fissure to protect the visitors (Fr. Ruwais Al Antony and Fr. Faltaos Al Antony, personal communications). The floor of the terminal room is flat, except the westernmost side. There, a sloped floor has terraces that cut into thick layers of flowstone. Other dissolution or precipitation features in the floor of the cave are unknown.

A cupola-like feature and a ceiling-bell hole are found at the junction between the upper-level entrance passage and the lower-level terminal room. Both of these features have formed near each other at slightly different levels (Fig. 6A–E). The cupola-like feature has formed along the entrance passage fracture. This feature is 0.60 m long, 0.40 m wide, and 0.25 m high. It is undermined and some parts of it are not directly observable. The cupola-like feature is decorated by mammillary coating, draperies, flowstone, and one small stalagmite on its floor. It is not clear whether the cupola-like feature dead-ends or connects to the overlying branch of the entrance passage.

the sides of the notch.

The cave entrance leads to a passage 9.35 m long (from the datum of the cave). This cave passage is controlled by a steeply-inclined fracture oriented 332.5° that dips northeast at 73°. There is no definite evidence that this fracture is a fault or a joint, but there is a steeply-inclined, normal fault through the heavily-weathered cliff face immediately above the cave entrance. This fault has about 10 cm displacement and has a dip and a strike similar to the fracture along the entrance passage.

The extension (if present) of this fault downward is not clear, but it may be the fracture that appears at the eastern side of the cave entrance. It is likely that the cave passage is fault controlled, at least in the higher, middle parts of it. The trend of the fracture of the cave passage is called “clysmic” or “rift parallel.” The rift-par-

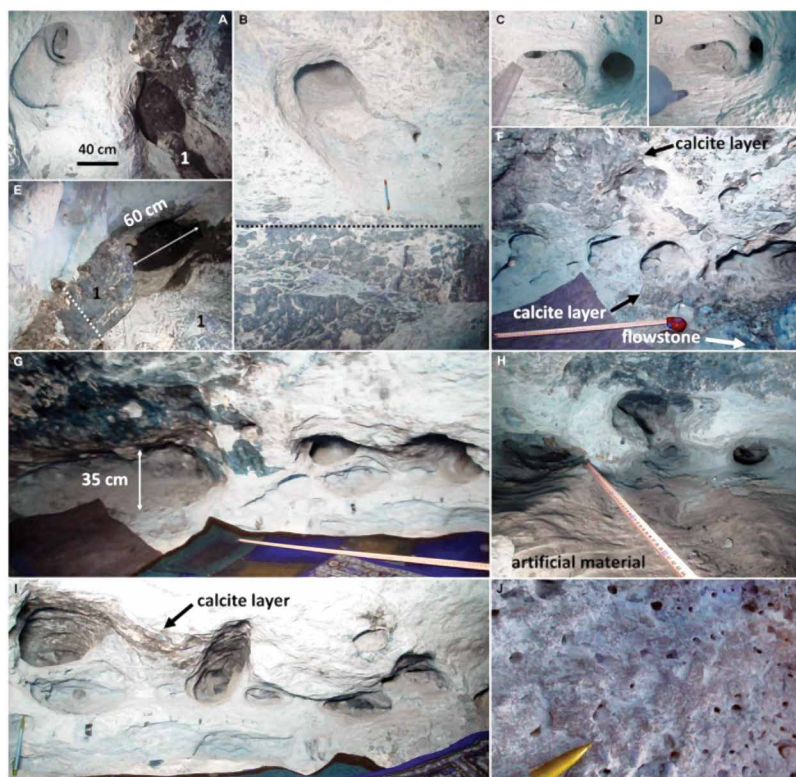


Figure 6. (A–E) Cupola-like feature and bell holes on the ceiling at the junction of the entrance passage and the terminal room. Figs. 6C and 6D are located inside the opening shown in Fig. 6B. In Figs. 6A and 6E, the numeral 1 refers to a thick calcite layer. In Figures 6B and 6E, the dashed lines show paleowater levels. (F–I) A series of dissolution pockets in the lower part of the southern wall of the terminal room. Fig. 6F is located at the northeast side of the terminal room. Fig. 6I is a close up view of the pocks in Fig. 6G. (J) Small hollows in the upper part of the wall of the passage.

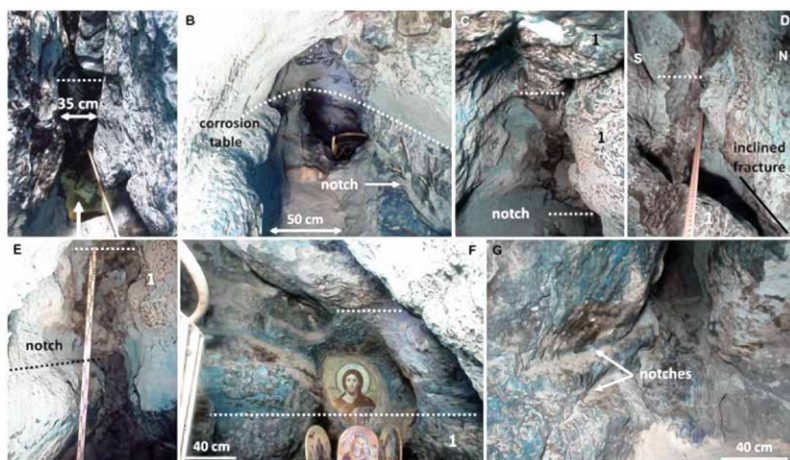


Figure 7. Paleowater levels (dashed lines). (A) Ceiling of the passage (white arrow points to the overlying section). (B) Back part of the entrance passage. (C) Upper part of the western side of the terminal room. (D) Ceiling of the westernmost side of the terminal room, looking upward. (E) Western side of the terminal room. (F) Hanging wall of the eastern side of the terminal room. (G) Lower part of the southwest side of the terminal room. The numeral 1 refers to a thick calcite layer with white weathering rinds.

The ceiling bell hole is formed along a minor, mineral-filled fracture above a paleowater level and reaches 0.90 m in height and 0.55 m in diameter. This feature branches inside into 2 small cylindrical holes, and one of them does not connect directly to the main hole. No deposits have been observed inside it.

Dissolution pockets are found in the cave's ceiling and walls. The wall dissolution pockets are concentrated in the lower parts of the southern and eastern sides of the terminal room. Some of them have formed along bedding planes. Others do not follow visible fractures and sometimes have a spongework texture or resemble replacement pockets (sulfuric acid-related pockets, usually small with a smooth inner surface, with replacement gypsum). They have no noticeable gypsum crusts. The bedding plane-controlled pockets are limited to the southern side of the terminal room. These are not connected, blind, and do not exceed 1 m deep. A few of them are connected to the floor of the terminal room and show very shallow channels on the floor. Small hollows with various shapes and sizes have also been observed throughout the cave (Fig. 6F–J). Remnants of wall pockets have also been found (Fig. 7F).

Former water level positions are present in the cave. There is a definite correlation between the elevation of one paleowater level inside the cave and a notch in the cliff face outside the cave. The relationships with other paleowater levels are difficult to examine. The paleowater levels can be seen as poorly developed notches, corrosion tables, paleowater lines, and flat ceilings (Fig. 7A–G). The paleowater levels were measured relative to a single datum located at the middle part of the entrance passage using a laser range finder.

In the entrance passage, 3 major paleowater levels are present at 2.10 m, 0.95 m, and 0.60 m above the datum. In the terminal room, there are 3 notable major paleowater levels. The 1st level at 0.55 m above the datum approximately corresponds to the 3rd paleowater level in the entrance passage. The other major levels are located in the terminal room at 0.45 m and 0.85 m below the datum. Very shallow notches have also been found in 2 lower parts of the wall of the terminal room.

Speleothems

Speleothems are secondary mineral deposits in caves. Saint Anthony Cave is currently moderately decorated with inactive speleothems, and most bedrock fractures have filled with minerals. Most of the speleothems are decomposed. Some are partially eroded, or visible only as remnant patches (Fig. 8A–B). Others have small

erately decorated with inactive speleothems, and most bedrock fractures have filled with minerals. Most of the speleothems are decomposed. Some are partially eroded, or visible only as remnant patches (Fig. 8A–B). Others have small

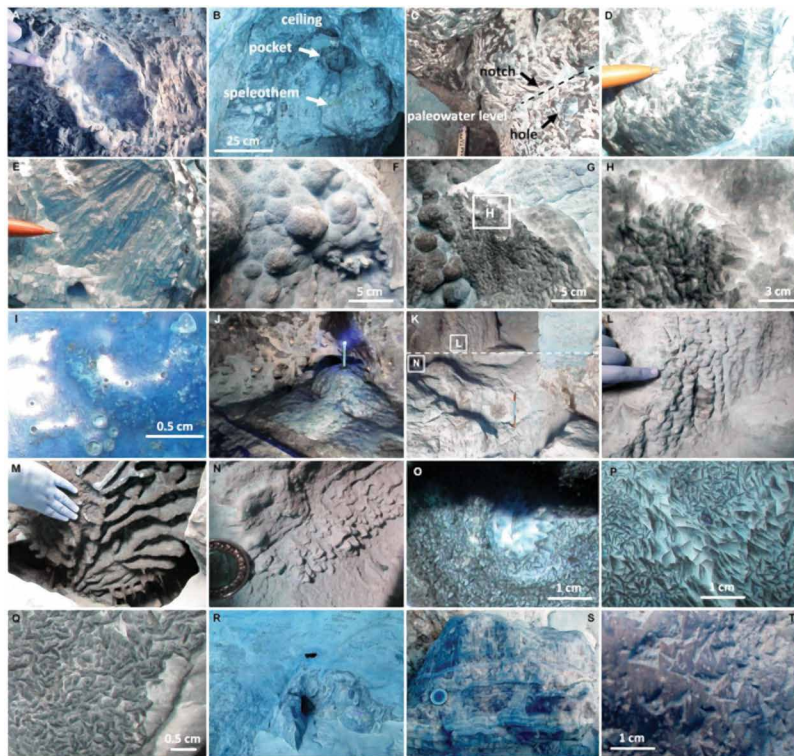


Figure 8. (A) Remnant of speleothem on the wall of the passage near the cave entrance. (B) Block of speleothem in the ceiling near the cave entrance. (C) Thick calcite layer on the wall of the northern side of the terminal room. (D) Internal structure of the thick calcite layer in the terminal room. (E) Columnar calcite crystals in a hanging wall in the terminal room, looking upward. (F) Mammillary coating in the overlying section of the entrance passage. (G) Mammillary coating at the cupola-like feature. (H) Close up view of the internal structure of the mammillary coating in Fig. 8G. (I) Thin flowstone with pits in the terminal room. (J) Flowstone on the floor at the easternmost side of the terminal room. (K) Waterfall flowstone at the westernmost side of the terminal room, showing a paleowater level (*dashed line*) and the location of Figs. 8L and 8N (*white boxes*). (L) Subaqueously-formed popcorn on the surface of the flowstone. (M) Draperies on the ceiling of the cupola-like feature. The black color is a fire-smoke pigment. (N) Pool spar. (O and P) Calcite crystals in the cupola-like feature. (Q) Modified crystals with vermicular texture on the surface of a speleothem in the cave passage. (R) Relict speleothem on the face of the notch outside the cave on the eastern side of the cave entrance. (S) Cross section of the speleothem that is shown in Fig. 8R looking downward. Coin is 2.5 cm in diameter. (T) Triangles of calcite crystals on the surface of the speleothem in Figs. 8R and 8S.

modified macro crystals, giving the surface a vermicular texture (Fig. 8Q).

A thin layer of calcite has been found in the lower parts of the eastern side of the terminal room. This layer has covered the low ceiling and parts of the wall, and it has lined most of the dissolution pockets (Fig. 6F–I).

Outside the current cave entrance, speleothems have only been found in two areas as flowstone deposits. The first deposit is located 1.35 m away from the cave entrance and east of it. It is present on the face of the notch and has covered an area of 1.5 m². A cross section of a part of this speleothem shows alternating, slightly wavy bands of whitish, creamy, and brownish calcite, totaling 21 cm. The surface is usually macrocrystalline and shows triangular crystals that are dark brown (Fig. 8R–T).

The 2nd flowstone deposit is located 1.5 m east of the first deposit. This speleothem lines an enlarged small fracture that dissects the floor of the notch. This deposit has colored-banded layers similar to the first deposit. Apparently, those speleothems were formed in an enlarged fracture and cavity and then were intersected by the later erosion (the notch) although they could be misinterpreted as having been deposited on the notch floor.

In 2015, there were speleothems on the western side of the cave entrance as well, but they were removed by human modification. No other speleothems have been found outside the cave.

DISCUSSION

holes or are coated by thin, white, weathering rinds composed of fine-grained calcite.

The speleothems in the cave are layers of calcite, mammillary coatings, flowstone, draperies, spar, and a few small stalactites. Nearly all speleothems are composed of calcite, sometimes with impurities.

The most notable speleothem in the cave is a thick layer of calcite in the upper and middle parts of the terminal room. The surface of this layer is very weathered and displays holes and white rinds. The surface is coarsely crystalline with distinct crystal faces, while its internal structure shows columnar crystals up to 6 cm in length (Fig. 8C–E).

Mammillary coatings have been observed in the overlying section of the entrance passage and in the inner wall of the cupola-like feature. The latter coating has columnar crystals a few centimeters thick and all the mammillaries have modified macrocrystalline surfaces (Figs. 5C, 8F–H).

The flowstone ranges from less than 1 mm to several centimeters thick. It can be clearly seen in the terminal room on the wall, on the terraced floor, and in the easternmost side as a sheet and small, stalagmite-like deposits. Some flowstone that is associated with the paleowater levels shows an irregular, crenulated surface with subaqueous calcite coralloids (Fig. 8I–L). The draperies are found in localized areas along the ceiling fractures and in the cupola-like feature (Fig. 8M). A few terminate with stalactites.

Spar lines a small pool at the western side of the terminal room and is adjacent to subaqueous popcorn. The spar is one centimeter or less in size (Fig. 8N). Macro crystals are also observed in the cave. They can be seen on the ceiling of the cupola-like feature and on the draperies inside, and they are adjacent to the mammillary coating (Fig. 8O–P). Some speleothems display

This study complements previous work and interpretation of the speleogenesis of Saint Anthony Cave as primarily phreatic. Our new results support that origin with new observations of paleowater-level dissolution features and at least four phases of cave development. The volcanic and tectonic background of the area suggests a high possibility of the contribution of deep fluids in the formation of the cave, supporting a hypogene origin (e.g., Klimchouk, 2007; Klimchouk, 2009; Palmer, 2007), at least in the earliest phase of development.

At a regional scale, Saint Anthony Cave is located within a cliff face adjacent to a deep-rooted fault and the steeply-inclined flank of an asymmetrical anticline. The bedrock containing the cave has been subject to extensional tectonics owing to its proximity to the western margin of the intracontinental Gulf of Suez Rift. Late Oligocene volcanic bodies are present in the vicinity of the cave (Fig. 1A–C). These settings and environments have been shown to be conducive to hypogene speleogenesis (Klimchouk, 2017).

There is no strong speleogenetic relationship between the cave and overlying or adjacent surface features. The strata overlying the cave are thick and mainly carbonates. The surface of the plateau directly above the cave (about 100 m above the cave entrance) has a hanging, dry, and small catchment area with autogenic recharge. Surface water flows from this catchment area in the direction of Wadi Araba, opposite the downward-gradient direction of the cave. Sinkholes, sinking streams, and shafts are absent. Floodwater-cave characteristics are not distinct (e.g., small waterfalls, few speleothems) (Palmer, 2007). Backflooding from Wadi Araba cannot be ruled out, but it did not initiate the speleogenesis, as discussed below.

Saint Anthony Cave is controlled by steeply-inclined fractures that are probably faults. The cave floor rises in the downstream direction of the cave. The cave varies in size and morphology with irregular cross-sections. The cave ends abruptly along fractures and bedding planes with blind terminations. Dissolution pockets, cupola-like features, ceiling bell holes, notches, corrosion tables, and flat ceilings are present in the cave. The floor of the entrance passage, in some parts, was originally a fissure extending downward, likely a feeder that transmitted water from depth and later partially choked by calcite deposits. This fissure has now been mostly filled and covered in concrete.

Remnants of the speleothems everywhere in the cave, especially at the cave entrance and immediately outside the cave, indicate that the cave extended beyond the current threshold. It was very decorated and opened after depositional conditions by cliff retreat. Paleowater level features superimposed on the subaerial speleothems suggest inundation following subaerial deposition.

The thick calcite layer is absent from the later-enlarged parts, and where it is present, it has been partially dissolved along distinct horizons. The interior columnar structure of this layer is similar to those in the mammillary coating found in the cupola-like feature. Additionally, nearly all the white-weathering rinds in the cave have been found on its surface except a few occurrences on bedrock walls.

White rinds form by dissolution in the presence of moisture and cave air rich in carbon dioxide, and this process is more effective if the cave air contains hydrogen sulfide (Palmer, 2007). It is clear the thick calcite layer is a relic of the earliest phase of the cave development. This calcite layer was likely deposited subaqueously and was modified by later events.

The depositional age of the well-defined mammillary coatings is difficult to determine. They may have formed early in the early cave's development and were preserved because of their protected positions or formed during a later phase of the cave development.

The depositional environment of the thin calcite layer located in the lower part of the eastern side of the terminal room is not clear. This layer has a coarse texture similar to a wall calcite layer located above the pool spar. This layer was likely deposited during later subaqueous conditions. Further work could be done to establish the age and depositional environment of the calcite.

The speleothems located immediately outside the cave show characteristics of the Egyptian calcite-alabaster as documented by Halliday (2003). Egyptian calcite-alabaster consists of thin straight to curved bands of creamy-white opaque calcite crystals alternating with thicker layers of brownish, translucent calcite crystals (Harrell et al., 2007). Egyptian alabaster has been observed in some caves in the northern cliff of the Southern Galala Plateau. These deposits are also known in the Northern and Southern Galala Plateaus (Abu Zeid and Mazhar, 1992). An isotopic study by Tourre (2000) estimated water temperature between 32 °C and 86 °C for the Egyptian calcite-alabaster from an ancient quarry in Wadi Araba and attributed it to the hydrothermal solution (Harrell et al., 2007). The triangular crystals on the surface of these deposits are parallel to the growth surface and probably formed later under subaqueous conditions.

Scalenohedral calcite crystals common to thermal deposits (Dublyansky, 2013) were observed inside the fracture outside the cave. These crystals are also present in the cave, but there is no direct evidence of their origin. Within the cave, smooth bedrock walls, ceiling bell holes, and niche-like features are located just above the paleowater levels. These features may indicate condensation-corrosion processes by convective airflow above thermal/warm water (e.g., Cigna and Forti, 1986; Audra et al., 2009).

Currently, the springs below the cave and in Wadi Araba have been classified as cold (e.g., Khalil et al., 2021;

Wannous et al., 2021), although the data of the latter study show a few springs with water temperatures 4 °C to 5 °C higher than the average annual air temperature in the area (23.36° C). Those latter few springs are considered slightly thermal or warm according to the 4 °C threshold of Schoeller (1962). Thermal springs are known in the surroundings of the Northern and Southern Galala Plateaus (Fig. 1A–C). The thermal paleowater was present in the past and likely contributed to the development of the cave.

No gypsum or anhydrite rocks are known in the northern side of the Southern Galala Plateau. No secondary gypsum has been observed inside Saint Anthony Cave although it may have been removed by later processes. Two springs below the cave have the highest sulfate values in the area. Features that suggest sulfuric acid speleogenesis (e.g., Audra et al., 2009), such as flat ceilings, corrosion tables, notches, pockets with spongework texture, and replacement-like pockets, are present in Saint Anthony Cave. While the remaining evidence is inconclusive, dissolution by sulfuric acid cannot be ruled out.

Wadi Araba and the Cave Evolution

Saint Anthony Cave overlooks Wadi Araba and is located at its eastern margin. The cave entrance opened by the retreat of the northern cliff of the plateau during the incision and widening of the wadi. The timing and the processes that formed the wadi may provide additional clues for the age and the speleogenetic phases of Saint Anthony Cave, as described below.

Wadi Araba extends from the west-southwest to the east-northeast for about 85 km with an area of about 2000 km². The wadi is characterized by the presence of residual hills, shallow channels, and large paleo-alluvial fans left by the smaller wadis that drained into it.

The Wadi Araba anticline has undergone erosion, exposing Carboniferous rock in the anticline core that has become overturned. It extends offshore into the Gulf of Suez Rift basin. Paleocene and Eocene rocks are absent in the offshore extension of the anticline (Moustafa and Khalil, 1995). Schütz (1994) assumed Miocene surface karst erosion of the Eocene units. In the basin adjacent to this extension, thick sands derived from the rocks of the Wadi Araba anticline are recorded in the Rudeis and Kareem Formations (post-Aquitainian) (Schütz, 1994).

Additionally, the sand isolith maps of the syn-rift formations at the *offshore extension* of the *Wadi Araba* anticline show a negligible volume of sands in the 2nd syn-rift Nukhul Formation and a large volume in the Rudeis and Kareem Formations (Peijs et al., 2012). These sands were derived from the erosion of the Wadi Araba anticline (Moustafa and Khalil, 2017). These studies suggest the strong erosion phase of the Wadi Araba anticline was post-Aquitainian, particularly in Burdigalian and Langhian times.

The youngest formation that is recorded in the highest altitude areas of the Southern Galala Plateau formed in the middle Eocene. Currently, the cave is located at about 800 m MSL. The maximum altitude of the plateau is 1480 m MSL and is covered by the middle Eocene rocks. Therefore, the rock hosting the cave was at least 680 m or more below the surface prior to the opening of the Gulf of Suez Rift.

Saint Anthony Cave has phreatic characteristics and was controlled by fractures having orientations similar to the rift-related fracture trends. The cliff face at the cave is dissected by normal faults dipping towards the Gulf of Suez Rift. The coincidence of these trends suggests it is likely that the cave fractures were related to rifting.

The timing of the primary erosion phase of the Wadi Araba anticline is synchronous with rapid uplift in Burdigalian time (e.g., Moustafa and Khalil, 2017). Uplift and valley incision would have likely lowered the water table. These were followed by an abrupt drop in global sea level in the late Miocene followed by sea level rise in the early Pliocene (Haq, 1987). The later immersion of the cave probably occurred post-Miocene. Therefore, the phreatic phase of the cave is no younger than Burdigalian or probably no older than the beginning of the opening of the Gulf of Suez Rift in Chattian time. We propose that the speleogenesis initiated with the onset of the rifting.

In the late Oligocene (early Chattian), the Gulf of Suez Rift began to open. Volcanism preceded the rifting and is recorded proximal to the study area by basaltic dikes, sills, and lava flows at the base of the syn-rift succession (e.g., Steen, 1984; Meneisy, 1990). A large dike of age 22.3 ± 0.2 Ma is also present 3 km west of the Saint Anthony Monastery at approximately 553 m MSL (Bosworth et al., 2015) (Fig. 1C).

Volcanism affected the chemical and thermal attributes of the groundwater and would have increased heat flux during that time, increasing groundwater temperature and also the CO₂ and H₂S content of the water (Klimchouk, 2017).

Extensional tectonics would have likely enhanced the upwelling of deep fluids (e.g., Sibson, 1996). The large anticline of Wadi Araba, the deep-rooted fault of the wadi, and related fractures would provide favorable flow paths for ascending deep groundwater.

Both CO₂ and H₂S are commonly present together in deep groundwater (Klimchouk, 2019). Accordingly, the speleogenesis began in the presence of CO₂/H₂S and thermal water. More than one dissolution mechanism could have operated either sequentially or simultaneously, such as CO₂/H₂S, cooling thermal water, mixing of high-CO₂ thermal water with low-CO₂ shallow water, and mixing of water of contrasting chemistry.

Saint Anthony Cave and other caves began to form, particularly in the area surrounding the deep-rooted fault. Dis-

solution would have also been concentrated within the carbonate rocks along the crest of the Wadi Araba anticline.

Until the earliest Burdigalian, there was little uplift of the rift shoulder (e.g., Garfunkel and Bartov, 1977; Bosworth and McClay, 2001; Moustafa and Khalil, 2020). In Burdigalian time the uplift rates of the rift shoulder increased, uplifting the study area to shallower hydrologic conditions. Under these conditions, dissolved CO₂ forms a separate phase, and calcite precipitation can occur (Dublyansky, 2013). The solutions eventually favored subaqueous calcite deposition. Then the cave was uplifted into a vadose setting (Table 1).

In the late Miocene (about 7.5 Ma), humid climatic conditions were prevalent in the Gulf of Suez Rift and the Red Sea

Table 1. The main phases of the development of the Saint Anthony Cave.

Phase	Time	Condition	Main Process
1	Possibly middle Oligocene to early Miocene (Burdigalian) (about 17 MYA)	Volcanism, extensional tectonic activity, deep-seated acids, deep-rooted fractures, thermal water	Dissolution and precipitation
2	Late Miocene (about 7.5 Ma)	Base level fall, humid climate conditions	Precipitation
3	Post-Miocene or early Pliocene	Base level rise	Dissolution and precipitation
4	Post-Miocene	Base level fall	Precipitation

areas (Griffin, 2002) with a *large drop in global sea level* in the Messinian time. During this time, the cave was characterized by the growth of subaerial speleothems.

Post-Miocene, particularly in the early Pliocene, global sea level rose (Haq, 1987) and reached up to 200 m MSL in combination with continued extensional tectonic activity in the southern part of the Gulf of Suez Rift area (Bosworth and McClay, 2001). The rising sea levels elevated the base level, and the cave was submerged. During upwelling/lowering the water level, dissolution processes occurred at and above the water level. During this 3rd phase, infiltrating meteoric water very likely was involved, and more than one dissolution mechanism was occurring. Back-flooding from Wadi Araba likely has also been involved.

This 3rd speleogenetic phase can clearly be seen in the paleowater levels features superimposed on the speleothems of previous phases (Fig. 7), although the notches in the cave could have formed from water oscillations. Other features such as the corrosion table, flat ceiling, pockets with spongework texture, and replacement-like pockets may reflect sulfuric acid dissolution during this phase.

The branching bell hole is located above a paleowater level at a later-enlarged part of the cave. These bell holes did not have speleothems, likely because they have formed along a mineral vein, supporting a later phase for their origin. The origin of dissolution niches is not clear, but they resemble convection niches features that form above the surface of thermal/warm ponds (Audra et al., 2009). There are well-preserved crystals, likely scalenohedral calcite crystals in the cupola-like feature and in the small pool. All these features may indicate that there was thermal/warm water in the cave during the 3rd phase.

The correlation between one paleowater level inside the cave, with a notch outside the cave, with and the absence of speleothems on the floor of the notch outside the cave, suggest that the cave was exposed to the surface at or slightly after the 3rd phase. This likely occurred during the latter filling phase of Wadi Araba. The cave appears to be a fossil overflow route as suggested by Halliday (2001) and was an active spring with likely sulfuric thermal/warm water.

When the water levels lowered, the cave dried out and was again characterized by speleothem deposition under wetter climatic conditions of later periods.

More than one dissolution mechanism such as mixing dissolution has likely been involved in the formation of the cave and the area in general. Dissolution was prominent in Oligocene-early Miocene time when volcanic activity was followed by extensional tectonics that provided deep fluids and deep-rooted fractures, and when the uplift rates of the area were slow. It is most likely that there are other caves near Saint Anthony Cave and in the area that have not yet opened to the surface.

CONCLUSION

A detailed map has been created of Saint Anthony Cave. The cave opens within the northern cliff face of the uplifted Southern Galala Plateau at about 800 m MSL. The cave is a steeply-inclined, fracture-controlled, isolated cave consisting of a very narrow entrance passage ending in a small, lower-level, terminal room. A small overlying section is present in the entrance passage. The cave has an irregular profile and cross sections and has characteristics of phreatic and water table caves. The cave has little relationship to the surface features and has opened by scarp retreat. This study identified four phases of cave development caused by different processes at different times:

1. An early phreatic phase, before uplifting (late Oligocene to early Miocene), when volcanic and tectonic activities

- fractured the rocks and provided deep acids and heat, enhancing dissolution by different mechanisms;
2. A speleothem depositional phase, after uplifting (late Miocene, about 7.5 Ma) during humid conditions;
3. A dissolution and depositional phase (early Pliocene/post-Miocene), when the base-level rose, flooding and enlarging the cave at and above the water level, and when sulfuric thermal/warm water likely was present; and
4. A speleothem depositional phase (post-Miocene) during humid climatic conditions of later periods.

Presently, Saint Anthony Cave is inactive and is exposed to dissolution by acidic moisture. Recent corrosion may be due to carbon dioxide emissions from candle smoke and other human activity. Therefore, we highly recommend replacing the candles with a clean light to preserve this important religious, cultural, and historic cave. We expect this research to be helpful for more advanced studies, such as isotopic analysis of the speleothems.

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CONSEQUENCES OF THE GLOBAL CLIMATE CRISIS ON THE CAVE BEETLE *DARLINGTONIA KENTUCKENSIS* VALENTINE BASED ON THERMAL TOLERANCE AND DEHYDRATION RESISTANCE

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Abstract

Rising temperatures and diminishing groundwater availability due to the current climate crisis are predicted to expose cave faunas in eastern North America to unprecedented environmental conditions that could prove detrimental to their unique ecosystems. Organisms that inhabit relatively stable environments like caves are known to develop narrow physiological tolerances. Cave habitats with their organisms are simple ecosystems whose homogeneity offers an ideal system for testing the ability of a highly specialized fauna to tolerate abiotic changes. We tested the capability of a cave-specialized beetle in the eastern United States, *Darlingtonia kentuckensis* Valentine, to withstand future climatic shifts in its environment. We exposed individuals to a range of relative humidities and temperatures for 10 days. The data strongly suggest that there is a temperature threshold for the survival of *D. kentuckensis*, but it is a higher thermal tolerance than would be expected in an environment that has not fluctuated in recent evolutionary time and suggests remnant physiological characteristics of ancestral epigean carabids. Decreasing the relative humidity in the environment resulted in a much more dramatic decline in survival, indicating highly evolved specialization for constant high-humidity environments. The narrow humidity threshold in which troglobionts can survive may be a much more apparent limiting factor than temperature in adapting to climatic shifts within a cave environment.

INTRODUCTION

Caves in eastern Kentucky formed through the dissolution of limestone within deposits that began accumulating when shallow seas covered much of this area during the Mississippian Period that began about 360 Ma (Kentucky Geological Survey, 2021; Grabowski, 2001). Karst landscapes, in which water travels underground through carbonate rock rather than in above-ground streams, account for 20–25 % of all ice-free land surface on earth (Ford and Williams, 2007). Karst ecosystems provide homes to organisms that are highly specialized for the extreme conditions within these habitats (Barr, 1969; Culver et al., 2009; Romero, 2009).

It has been commonplace to deem caves as dismal and depauperate ecosystems due to their lack of primary productivity, and a relatively limited amount of ecological research has been done within these environments (Romero, 2009). In reality, some cave ecosystems are teeming with a surprisingly large array of taxa that have often convergently evolved various traits to survive in the generally low-energy, lightless environment they inhabit (Soares and Niemiller, 2020; Romero, 2009). For example, 18 different families of Coleoptera (beetles) have been reported to have colonized caves in different regions around the world (Romero, 2009). In North America, three families of this order, the Carabidae, Leiodidae, and Staphylinidae (Pselaphidae), include true obligate cave dwellers (troglobionts) (Barr, 1968; Peck, 1998).

The south-central Kentucky karst system is among the top 10 most endangered karst systems in the world (Romero, 2009), and the interior plateau is home to among the largest assemblages of obligate cave fauna in North America (Christman et al., 2005; Lewis and Lewis, 2005; Niemiller and Zigler, 2013). Further, eastern North American cave ecosystems are home to 170 described trechine cave beetle species with some endemic to single caves, as well as several critically endangered species (Barr, 1979; Christman et al., 2005). North American cave beetles are extremely diverse, with over 250 species estimated in the genus *Pseudanophthalmus* alone (Peck, 1998).

Eastern North American cave trechines were once thought to have evolved during glacial-interglacial transitions of the Pleistocene that concluded by warming and drying as the Holocene began (Barr and Holsinger, 1985), but cave beetles likely evolved much earlier than the Quaternary. If similar to the evolution of cave trechines in the Pyrenees (Faille et al., 2010), the time of origin may be around 10 Ma, an age that is close to an unpublished estimate of 13 Ma made by one of the authors (Philips) for the eastern US clade. In contrast, the cave trechines and a clade of subterranean European leiodids (Ribera et al., 2010) may have first appeared as early as the late Eocene about 35 Ma (Faille et al., 2013). Regardless of age of origin, fauna adapted for an earlier cooler, wetter surface climate are believed to have utilized caves originally as refugia but eventually became specialized troglobionts confined to life in caves (Barr and Holsinger, 1985). Long appendages, conversion to winglessness, and reduction or elimination of functional eyes are all

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unique troglomorphisms that hinder or even prevent cave-specialized organisms from dispersing outside of their cave refuges (Hedin, 1997; Snowman et al., 2010; Cardoso et al., 2011a; Cardoso et al., 2011b; Romero, 2011; Yao et al., 2016). There has been only one record of a troglobitic *Pseudanophthalmus* beetle occurring outside of a cave, but this was after heavy rains presumably washed the individual out from its cave habitat (Barr and Peck, 1965).

Cave environments have a constant temperature year-round that usually reflects the average annual temperature of the region but can fluctuate depending on elevation and presence of water (Tuttle and Stevenson, 2011). Caves that support subterranean life also exhibit relative humidities that do not reflect the conditions outside the cave and are typically much higher, as evaporation rates are near-zero within a short distance inside the cave entrance (Barr and Holsinger, 1985; Tuttle and Stevenson, 2011).

Inhabitants of relatively constant environments such as caves are known to exhibit narrower physiological tolerances (Futuyma and Moreno, 1988). For example, several specialized hypogean arthropods are limited to either a constant or narrow range of subterranean environmental conditions in which they are found (Delay, 1978; Huey and Kingsolver, 1989; Lencioni et al., 2010; Bernabò et al., 2011; Novak et al., 2014; Rizzo et al., 2015). Further, the effects of changing climates have already been noted in cave arthropods. Populations of highly specialized troglobitic spiders in the western Alps are declining, and it is suggested that this is due to slight temperature changes in their cave environments (Mammola et al., 2018). Other cave-specialized arthropods, like troglobitic and troglophilic beetles in the Alps, appear to exhibit tolerance to slight temperature increases for a short period of time but only up to a certain threshold (Rizzo et al., 2015; Pallarés et al., 2019).

Cave systems in Kentucky and nearby states normally average around 12–13 °C and nearly 100 % relative humidity (Marsh, 1969; Perry, 2013). The consistency of the conditions inside any cave is due to the insulation and protection offered by the cave substrate from weather changes happening above ground. The impact of constant temperature and humidity on the tolerance range of cave organisms has been little researched, but it is vitally important to understand how climate change and anthropogenic activity will impact cave faunas in the future. While the climate in caves will not change as quickly as in above-ground habitats, it is predicted to shift due to rising temperatures and changing precipitation patterns (Badino, 2004); indeed, the eastern United States is expected to become both warmer and wetter (US EPA, 2016). While rainfall is expected to increase in Kentucky, it will be countered by rising evaporation rates. One prediction suggests that groundwater recharge is expected to decrease 2.5–5 % each year, and droughts are likely to be increasingly severe (US EPA, 2016). While cave conditions are considered relatively constant, there is a direct association between the external climate and the cave environment (Moore and Nicholas, 1964; Smithson, 1991; Badino, 2004; Badino, 2010; Covington and Perne, 2015).

Climate change remains an existential threat to global biodiversity. As a part of the web of life, cave habitats and their species are simple ecosystems whose homogeneity offers an ideal model system for testing the ability of specialized fauna to tolerate abiotic changes within ecosystems (Rizzo et al., 2015). In that light, research was conducted on the cave-specialized beetle, *Darlingtonia kentuckensis* (Valentine, 1952). A robust population enabled one of the most statistically significant studies to date on the tolerance of a troglóbiont to adverse (i.e., non-cave) conditions. Experiments were conducted by exposing individuals to both different relative humidities and temperatures to document their ability to survive. We hope this study improves our understanding of the ability of troglóbionts to withstand future climate changes within their cave habitats.

MATERIALS AND METHODS

Target Species, Collection, and Holding Conditions

Darlingtonia kentuckensis Valentine is one of the better-known cave beetle species that has a large range in eastern Kentucky. A relatively large-bodied (7.3–7.7 mm) trechine, this beetle can have considerable populations with a hundred or more individuals present on a single sand bank in a cave. Here they hunt for their main food source of cave cricket (*Hadenocetus* sp.) eggs. This cave beetle acts as a top terrestrial predator in much of the Mississippian karst hypogean habitats located in a nearly 200-square-mile area on the eastern flank of the Cincinnati arch karst system (Boyd et al., 2020).

Adult specimens were collected by hand in July 2021 in Wind Cave, Pulaski County, Kentucky. The specific location may be obtained through the Kentucky State Nature Preserves Commission. This cave has a notably large population of *Darlingtonia*. Teneral individuals (freshly emerged adults with untanned exoskeletons) were excluded to maintain physiological consistency between individuals. Temperature at the site of collection was 11.8–12.2 °C, and it had a relative humidity (RH) of 95 % (measured with a HOBO Pro Series data logger).

Specimens were transported to Western Kentucky University (Bowling Green, Kentucky) in a Styrofoam cooler under controlled temperature and humidity to minimize the amount of stress on the beetles. A wet paper towel was placed in each transport container to maintain humidity (>90 % RH), and cooler packs were used to maintain a temperature of approximately 12 °C. An Onset HOBO Pro Series data logger placed in the transport container confirmed

cave conditions were maintained during transport. Once in the lab, specimens were placed in plastic containers (15 cm × 15 cm) with a moist plaster of paris (DAP) layer (approximately 1 cm thick) and acclimatized in a humidity control chamber at 12 °C (Intellus environmental controller chamber, Percival Scientific) for two days prior to placement into different conditions. To avoid starvation stress, frozen *Drosophila* were provided *ad libitum* to each container during acclimatization and replenished throughout the experiment.

Dehydration Resistance

To estimate the tolerance to desiccation, survival was assessed at different relative humidities for seven days. Four Pyrex knob-top nonvacuum glass desiccators (approximately 30 cm × 30 cm, from Fisher Scientific) were placed inside a Percival Scientific Intellus environmental control chamber and the temperature was kept at constant cave temperature (12 °C) for all four treatments to avoid any thermal stress. Ratios of glycerol/water mixtures in the bottom of each humidity control chamber were used to achieve 50 %, 65 %, 80 %, and 100 % RH and were confirmed by Onset HOBO Pro Series data loggers. The chambers were allowed to stabilize for two days before specimens were introduced. A high-walled glass dish of specimens ($n = 10$) was placed on a shelf above the glycerol/water mixture within each chamber. Survival was checked every 12 hours, and beetles were recorded as dead (no movement when agitated with a brush) or alive (any kind of movement including when agitated with a brush).

Basal Heat Tolerance

Survival rates at different temperatures were used to estimate heat tolerance. Containers of beetles ($n = 18$ – 20) were placed into five treatments for 10 days at 12 °C, 16 °C, 20 °C, 24 °C, and 30 °C using Intellus environmental control chambers (12 °C and 20 °C) and VWR incubators (16 °C, 24 °C, and 30 °C). High humidity (>95 % RH) was maintained throughout the experiment by wetting paper towels within the container to avoid any desiccation stress. Survival was checked every 12 hours and was recorded as dead or alive as in the previous experiment.

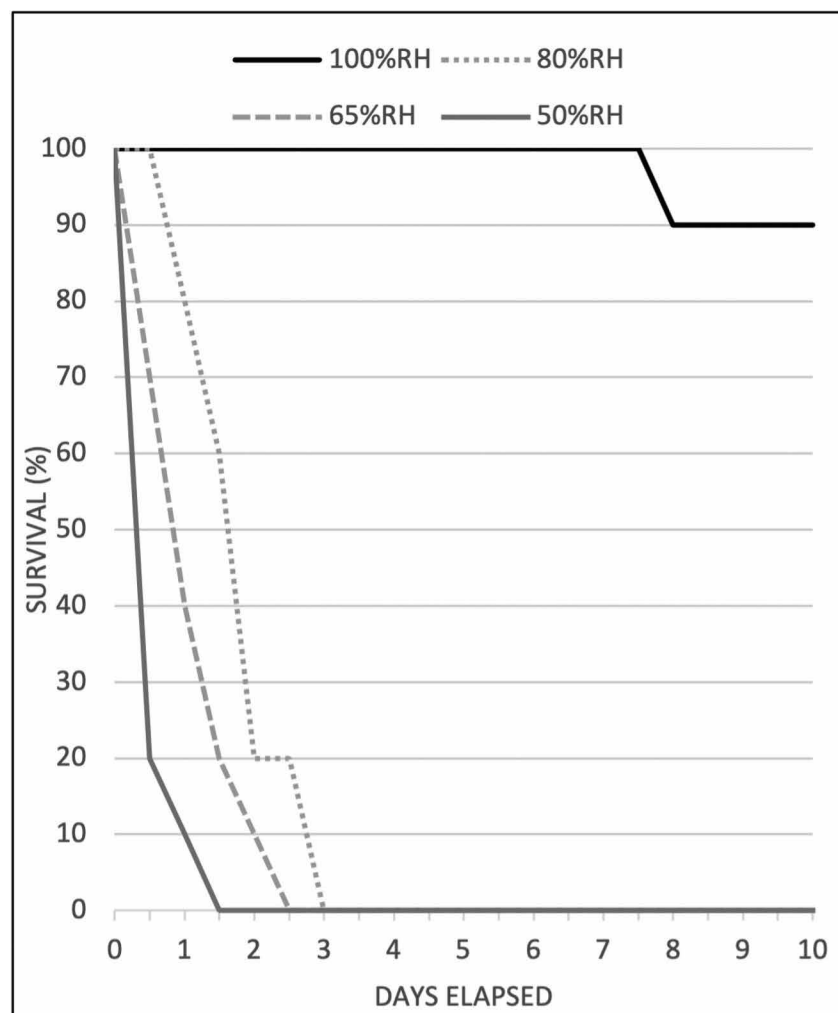


Figure 1. Percentage survival throughout the experiment at respective relative humidities.

Data Analysis

Non-parametric Kruskal-Wallis and Mann-Whitney U-tests were used to evaluate the difference in survival at various temperatures and humidities. These tests are ideal for testing if there is a significant difference between two or more groups of an independent variable with ordinal values (i.e., the different temperatures and humidities) that were used in this study. Multiple comparison tests were also conducted to detect significant differences between treatments. All statistical analysis was conducted using VASSARSTATS (vassarstats.net).

RESULTS

Dehydration Resistance

Beetles exposed to conditions drier than that of a cave environment (50 %, 65 %, and 80 % RH) did not survive longer than three days once in treatment (Fig. 1). The closer the humidity was to 100 %, the longer beetles survived (Fig. 2). A Kruskal-Wallis test indicated that the survival of *D. kentuckensis* differed significantly between normal cave conditions and the drier artificial conditions ($H(3) = 29.7$, $p < 0.0001$; Table 1). Additional pairwise Mann-Whitney U-tests indicated that survival in all 3 drier treatments differed significantly from the natural cave environment and from each other (Table 2).

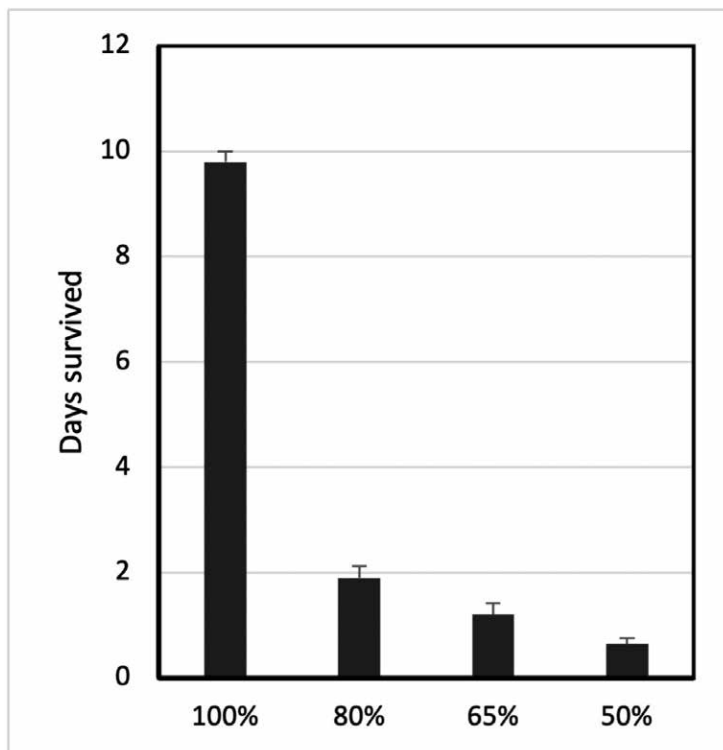


Figure 2. Average number of days *D. kentuckensis* survived at respective relative humidities. Error bars indicate standard error ($n = 10$).

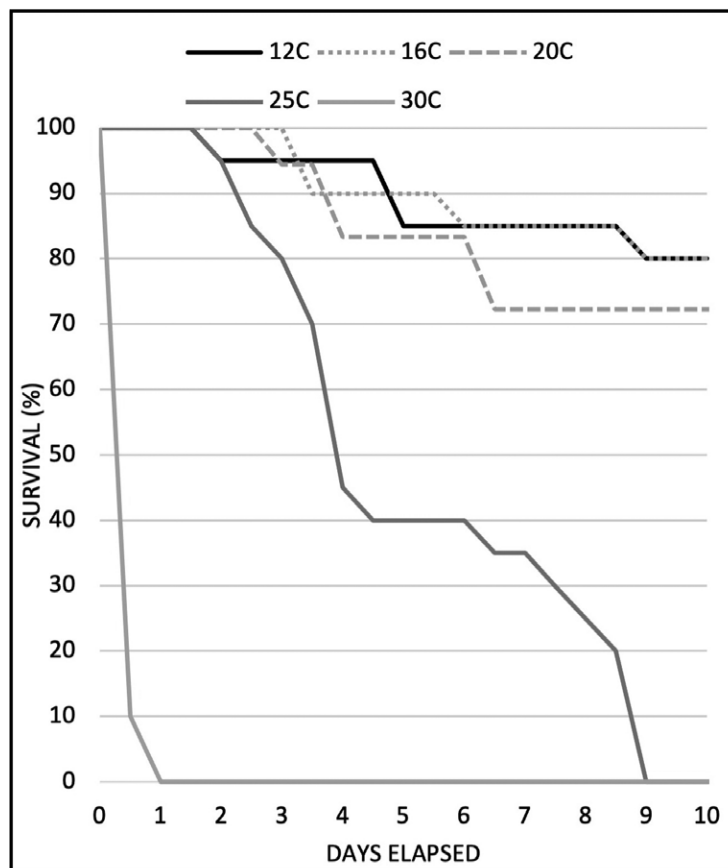


Figure 3. Percentage survival throughout the experiment at respective temperatures.

Basal Thermal Tolerance

Sample populations of *D. kentuckensis* were tolerant to higher temperatures for relatively long periods of time (Fig. 3), although beetles survived for less time when exposed to the highest temperatures (Fig. 4). A Kruskal-Wallis test indicated that there was a significant difference in *D. kentuckensis* survival when exposed to conditions warmer than their cave environment ($H(4) = 64.66$, $p < 0.0001$; Table 1).

Interestingly, the 12 °C, 16 °C, and 20 °C data did not differ significantly from one another when analyzed with pairwise Mann-Whitney *U*-tests. At the highest temperature of 30 °C, beetles did not survive more than 24 hours and their average survival time was significantly less than all of the other four temperatures tested ($p < 0.0001$, $n = 20$). At the next-highest temperature of 24 °C, the population ($n = 20$) survived for significantly less time than cave conditions ($p < 0.0001$), but survival was significantly higher than at 30 °C ($p < 0.0001$). The next two lowest temperatures, 20 °C and 16 °C, did not show any significant variation from survival under cave conditions (Table 3).

DISCUSSION

The physiological mechanisms behind tolerance to a great range of conditions are processes that are energetically costly and could have been selected against once confined to a stable environment (Krebs and Loeschcke, 1994; Monaghan et al., 2009; Tomanek, 2008). It is thought that the troglomorphic, ancestral fauna adapted to cooler, wetter conditions took refuge in caves, sinkholes, ravines, leaf litter, and deep soil to avoid desiccation when the surface environment dried and warmed (Barr, 1968; Boyd et al., 2020). Prolonged orthogenesis under relatively stable conditions in caves (and possibly in deep soil) resulted in the eventual shift from a troglomorphic to a troglomorphic species (Barr, 1968).

Thermal Tolerance

The climatic variability hypothesis (Stevens, 1989) states that species from more thermally stable environments should have much narrower thermal tolerance breadths and reduced acclimation capacity than species from more climatically variable environments. This higher sensitivity to thermal variability has been observed in both invertebrates and vertebrates found in environments that maintain stable temperatures (Di Lorenzo and Galassi, 2017; Feder, 1978; Somero, 2005; Tomanek, 2008; Shah et al., 2017; Markle and Kozak, 2018). In contrast, tolerance to a great range of temperatures in some species inhabiting stable environments have been observed, such as in troglomorphic leiodid beetles in Europe that have maintained a high level of thermal plasticity (Pallarés et al., 2020).

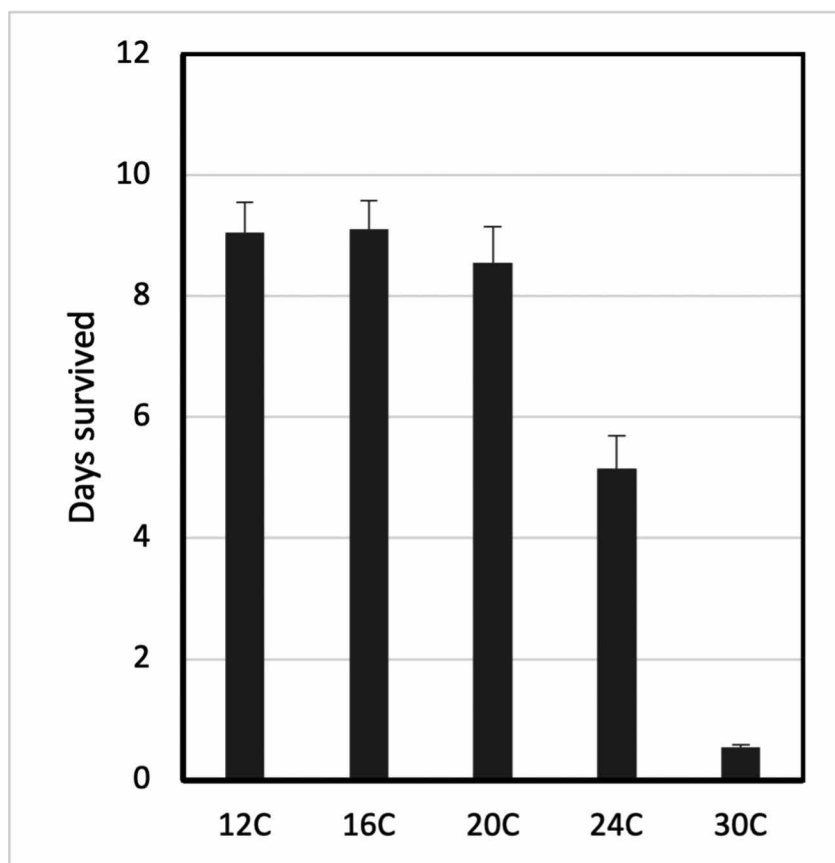


Figure 4. Average number of days *D. kentuckensis* survived in different temperatures. Error bars indicate standard error ($n = 18-20$).

Table 1. Results of Kruskal-Wallis *K*-tests to evaluate whether the population medians on temperature and relative humidity are statistically different across all levels.

Environmental Factor	Kruskal-Wallis <i>K</i>	d.f.	<i>p</i> -value
Temperature	64.66	4	<0.0001*
Relative Humidity	29.7	3	<0.0001*

Table 2. Respective *p*-values, U values, and z-values for pairwise Mann-Whitney U-tests comparing survival at different relative humidities ($n = 10$).

Treatment Comparison, %	z-value	U-value	<i>p</i> -value
100 vs 80	3.74	0	<0.0001*
100 vs 65	3.74	0	<0.0001*
100 vs. 50	3.74	0	<0.0001*
80 vs. 65	2.0	23	0.0228*
80 vs. 50	3.44	4	0.0003*
65 vs. 50	1.97	23.5	0.0244*

(Issartel et al., 2005; Mermillod-Blondin et al., 2013; Rizzo et al., 2015; Pallarés et al., 2019).

There were observable behavioral differences in populations with varied temperatures. At 12 °C, the beetles were notably active but did not seem to eat or tamper with

The thermal tolerance of *D. kentuckensis* was surprisingly broad. Beetle survival only began to decline significantly between 20 °C and 24 °C (Figs. 3 and 4), which is 7–11 °C higher than any temperature they or their ancestors presumably would have had to endure for several million years or more. The data suggest there is a temperature threshold of slightly higher than 20 °C for the survival of *D. kentuckensis*. Troglobitic and troglophilic coleopterans have exhibited similar temperature thresholds (20–25 °C) in cave systems around the world (Pallarés et al., 2019; Rizzo et al., 2015).

While the fauna found in thermally stable environments is expected to exhibit a relatively narrow thermal tolerance, this may be shaped by its evolutionary history. Lineages of troglobitic fauna that are believed to have colonized caves earlier in their evolutionary history are thought to correspond with higher thermal sensitivity. In contrast, fauna that has colonized caves more recently may still exhibit greater tolerances remnant of its phylogenetically closer generalist epigean ancestors (Pallarés et al., 2019). As the climate of eastern North America was highly variable during glacial-interglacial transitions and much less so via annual seasonal fluctuation, troglophilic ancestors may

have had wide temperature tolerance breadths which could still exist in their extant troglobitic descendants despite their now-stable environment

Table 3. Respective *p*-values, U-values, and z-values for pairwise Mann-Whitney U-tests comparing survival at different temperatures ($n = 18-20$).

Treatment Comparison, °C	z-value	U-value	<i>p</i> -value
12 vs. 16	0	200.5	0.50
12 vs. 20	-0.42	195	0.337
12 vs. 24	4.45	35	<0.0001*
12 vs. 30	5.40	0	<0.0001*
16 vs. 20	-0.39	194	0.3483
16 vs. 24	4.36	38.5	<0.0001*
16 vs. 30	5.40	0	<0.0001*
20 vs. 24	3.74	51.5	0.0001*
20 vs. 30	5.25	0	<0.0001*
24 vs. 30	5.40	0	<0.0001*

any dead beetles. In contrast, beetles in the 16 °C treatment were observed carrying pieces of beetle carcasses in their mandibles and likely scavenging, although predation cannot be rejected. No disarticulation of carcasses was observed in the three higher temperature regimes, but activity had notably increased. Large cave trechines have very low metabolisms that allow them to sustain themselves for weeks on a single meal (Griffith and Poulson, 1993). A single egg can satiate an adult *Neaphaenops* (a taxon native to central Kentucky and morphologically similar to the study species) for more than two weeks in normal cave conditions (Smith, 1986). It is possible that sustained exposure at a higher temperature caused a rise in metabolism, resulting in a strong need to replenish energy stores via feeding. This shift in metabolism could significantly impact long-term survival in *D. kentuckensis* and other troglobionts that have highly specialized physiologies adapted to a decreased, erratic food supply in most caves (Barr, 1968).

Dehydration Resistance

The results from exposing populations of *D. kentuckensis* to lower-than-normal relative humidities were dramatic and suggest highly evolved specialization for high humidity environments. With temperature at a constant 12 °C (as in their cave habitat), no beetles in any treatment outside of the 100 % RH control (i.e., 80 %, 65 %, and 50 % RHs) survived longer than three days (Fig. 1). There were significant differences in survival across all four relative humidities, with each having a significantly lower average survival than the next highest humidity (Fig. 2). The narrow humidity threshold in which troglobionts can survive is apparently a much more limiting factor than temperature in adapting to future abiotic shifts within their cave habitat.

Preference for high humidities is not uncommon in epigeal beetle species (Neve, 1994; Šustek et al., 2017; Kirichenko-Babko et al., 2020), and only a physiological comparison of *D. kentuckensis* and an epigeal sister species could reveal if the lack of desiccation resistance is a cave adaptation and not an ancestral trait shared by other trechines. According to Maddison et al. (2019), an epigeal trechine beetle closely related to *D. kentuckensis* is the genus *Trechus* Clairville. Physiology research conducted on any epigeal relatives of *D. kentuckensis* is lacking, but ecological studies indicate that at least one *Trechus* species (*T. quadristriatus* Schrank) has a preference for relatively dry conditions that may indicate a high tolerance for low humidities (Kriegel et al., 2021).

The limited dehydration resistance observed in *D. kentuckensis* is consistent with previous studies focusing on troglotic desiccation tolerance. Cave cricket species in the eastern United States with increased troglomorphic adaptation have much lower desiccation tolerances than species closely related but less troglomorphic (Yoder et al., 2011). Troglotic carabid beetles in Australia are completely absent in caves with low or varying relative humidity, whereas caves with adequate moisture hold abundant populations (Humphries and Collis, 1990). Even in vertebrates, the

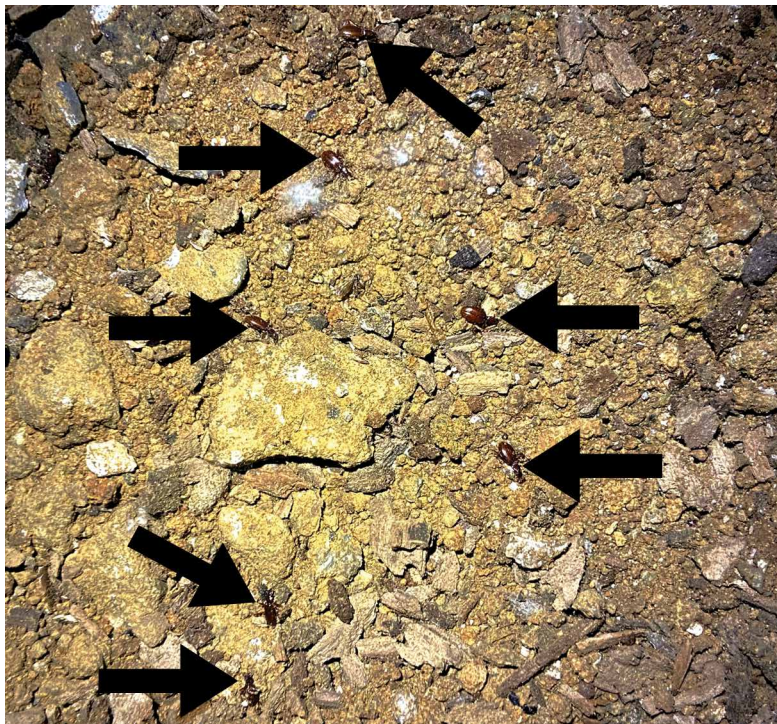


Figure 5. Apparent “death zone” discovered in Climax Cave, Rockcastle Co., Kentucky, where conditions were notably drier than areas of the cave containing live individuals. Arrows indicate remains of dead *D. kentuckensis*.

cave adapted coqui frog species, *Eleutherodactylus cooki* Grant, demonstrates higher rates of water loss than its close epigeal relative *E. coqui* Thomas (Rogowitz et al., 1999). Lastly, a pattern of high humidity dependency by *D. kentuckensis* may have been observed by the authors in Climax Cave (Rockcastle County, Kentucky) in the eastern United States; an apparent “death zone” was discovered with noticeably drier conditions after climbing up to an elevated region deep in the cave. Here, numerous remains of beetles were discovered, and no live individuals were found (Fig. 5).

The wider-than-expected thermal tolerance breadth observed in *D. kentuckensis* suggests remnant physiological characteristics of ancestral troglomorphic carabids. In contrast, the narrow humidity tolerance suggests that a decrease in epigeal habitat moisture in the past could better explain the eventual restriction of now-troglobionts to a subterranean existence. In summary, a wide range of thermal tolerance may have been necessary for survival during the transition to cave life, while the necessary humid conditions could be found through microhabitat refugia.

Climate Change Implications

With obvious sensitivity to humidity differences in its environment, *D. kentuckensis* and presumably other troglobionts with similar evolutionary histories are under serious threat from altered conditions in their subterranean environment. Theoretical models (Badino, 2004; Covington and Perne, 2015) and direct field observations (Domínguez-Villar et al., 2015) suggest that the underground climate may be significantly influenced by anthropogenic climate change. The United States Environmental Protection Agency estimates that groundwater recharge in Kentucky is decreasing 2.5–5 % annually. Droughts in Kentucky are also expected to become increasingly frequent and severe from altered precipitation patterns due to climate change (US EPA, 2016).

Notably, the effect of epigeal climate change on the hypogean environment is not immediate; there is typically a time lag of up to several decades underground due to the thermal inertia properties of caves (Domínguez-Villar et al., 2015; Badino, 2004). Cascade effects on both physical and biological components of cave ecosystems are likely due to the accumulation of energy fluxes from the atmosphere to the underground. For example, the effect on air density gradients will modify air circulation in caves through small temperature changes, causing potential fallout in condensation and erosion processes, speleothem growth, and seasonal ventilation rates (Domínguez-Villar et al., 2015).

The stability of cave temperature is largely due to the insulation provided by the carbonate rock layer, which is at the thermal equilibrium of the water running through it from precipitation. As climate change increases temperatures above ground, the warmer water flowing through the karst will eventually cause a rise in cave temperature (Badino, 2010). Although a concern, this may not be dramatic enough to cause population declines in *D. kentuckensis* compared to the effect of lower humidity.

We predict that changes in temperature, groundwater availability, and humidity will expose cave fauna to unprecedented novel environmental conditions. Changes in the physical properties of the cave air (both temperature and humidity) are understood to be the most important aspects that humans will impact within these unique terrestrial ecosystems. In addition to climate change, agriculture, oil and gas extraction, expanding transportation corridors, and urban development are all leading threats to the south central Kentucky Karst ecosystem (Romero, 2009).

Behavioral thermoregulation through microhabitat selection is reduced in troglobionts due to their restriction to cave habitats. Further issues for species endemic to caves and other isolated habitat fragments such as islands and mountain summits are limited distributions, low recolonization potential, and reduced vagility that all hinder dispersal to new habitat (Hedin, 1997; Snowman et al., 2010; Yao et al., 2016; Cardoso et al., 2011a; Cardoso et al., 2011b). Based on this research, the climate crisis with its current trajectory could result in the irreversible failure of hypogean ecosystems including high levels of troglobiont extinction.

SUMMARY

The results from exposing populations of *D. kentuckensis* to different relative humidities suggest highly evolved specialization for high humidity environments. The narrow humidity threshold in which these beetles can survive is a much more apparent limiting factor than increasing temperatures in adapting to climatic shifts within a cave environment. The wider-than-expected thermal tolerance in *D. kentuckensis* suggests remnant physiological characteristics of ancestral troglophilic carabids. Changes expected in temperature, groundwater availability, and humidity within caves are predicted to expose this fauna to unprecedented novel environmental conditions as the climate crisis continues to pose an existential threat to this small but unique part of global biodiversity.

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