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The Sulfur City: Chemoautotrophy and Facultative Coloniality in Two Species of Spiders of Vromoner Cave

Biology * Environment * Conservation

Introduction: The Anomaly in the Dark

In the canon of subterranean biology, deep caves are classically defined as oligotrophic deserts -- energy-limited environments where specialized troglobites subsist on sparse organic detritus filtering down from the sunlit surface. Sulfur Cave (Spilia tou Vromonerou), situated in the rugged Vromoner Canyon along the border of Greece and Albania, stands as a dramatic violation of these speleological norms.[1] Within an aphotic chamber saturated with hydrogen sulfide (H2S), researchers have documented an ecosystem of extraordinary density: a continuous, colonial spiderweb spanning more than 100 square meters (1,140 square feet) and housing an estimated 111,000 arachnids.[1] First encountered during a 2022 karst survey by the Czech Speleological Society under Marek Audy and quantitatively surveyed in 2024 by a multinational team led by Dr. Istv n Ur k of Sapientia Hungarian University of Transylvania, this subterranean "megacity" challenges foundational assumptions regarding arachnid territoriality, chemical ecology, and social evolution.[1][9][10]

Unlike evolved eusocial arachnids of the tropics, the Vromoner assemblage is constructed by two typically solitary and mutually predatory surface species: the barn funnel weaver, Tegenaria domestica, and the marsh dwarf sheet weaver, Prinerigone vagans.[1][11] In the pitch-black, sulfur-choked atmosphere of the cave, these competitors have abandoned intraguild predation to maintain a multi-tiered silk infrastructure that harvests millions of chironomid midges rising from the thermal stream below.[1]

Sulfuric Acid Speleogenesis and the Hypogenic Environment

Understanding the biological productivity of Sulfur Cave requires examining its geology. Whereas epigenic caves form from the top down as surface rainwater enriched with carbon dioxide (carbonic acid) dissolves limestone, Sulfur Cave is part of a hypogenic karst system shaped from below through Sulfuric Acid Speleogenesis (SAS), alongside the neighboring Atmos and Turtle caves.[1] Deep anoxic groundwater charged with geogenic H2S -- derived from hydrocarbon reservoirs and evaporitic sulfate reduction -- ascends through bedrock faults along the Sarandaporo River canyon.[1] Where these sulfidic waters intersect the water table and oxygenated cave atmosphere, H2S oxidizes with oxygen into sulfuric acid (H2SO4), which rapidly reacts with calcium carbonate (CaCO3) bedrock to form soluble gypsum (CaSO4 * 2H2O) and CO2:[3]

H2S + 2O2 -> H2SO4

As structural gypsum crusts spall from the walls and dissolve into the stream, the void continuously enlarges.[3] This active chemical reactor produces a warm, humid

microclimate that acts as a year-round metabolic incubator for ectotherms while excluding unadapted surface predators.[2]

| Parameter | | Measurement | | Ecological Significance | | Source |

| Location | | Vromoner Canyon, Albania/Greece | | Active hypogenic karst zone along the Sarandaporo River | | [1] |

| Cave Genesis | | Sulfuric Acid Speleogenesis (SAS) | | Ongoing carbonate dissolution via H2SO4 | | [2][3] |

| Stream Temperature | | ~26 deg C (Constant year-round) | | Eliminates winter dormancy; stabilizes ectotherm metabolism | | [1][9] |

| Air Temperature | | Up to 29 deg C | | High-humidity thermal buffer across cave walls | | [2] |

| Dissolved H2S | | Up to 65 mg/L | | Primary inorganic electron donor for microbial biofilms | | [1] |

| Atmospheric H2S | | Up to 14 ppm | | Chronically toxic barrier to non-adapted fauna | | [2] |

The Chemoautotrophic Engine and Trophic Bridge

In the total absence of sunlight, photosynthesis cannot occur; instead, primary production in Sulfur Cave is driven entirely by chemoautotrophy.[1] Along the turbulent sulfide-oxygen interface of the thermal stream, filamentous sulfur-oxidizing bacteria (SOB) -- predominantly Beggiatoa and Thiothrix -- employ specialized enzymes to oxidize dissolved H2S into intracellular elemental sulfur granules and sulfate, using the liberated chemical energy to fix inorganic carbon into thick, white mucilaginous mats.[2][9] On upper walls where degassing H2S condenses on rock surfaces, extreme acidophiles such as Acidithiobacillus form pendulous microbial draperies ("snottites") dripping with sulfuric acid at pH 0-1.[3][4][5]

Stable isotope profiling (13C and 15N) of the cave biota confirms that this microbial biomass is the sole foundation of the food web.[2] The invertebrates exhibit strongly depleted ("light") carbon and nitrogen isotopic signatures diagnostic of chemoautotrophic carbon fixation rather than surface photosynthetic detritus.[2][9]

The critical trophic bridge connecting bacterial mats to the arachnid canopy is the non-biting chironomid midge Tanytarsus albisutus.[1][9] Equipped with high-affinity hemoglobin-like pigments that scavenge oxygen in hypoxic, sulfidic water (65 mg/L H2S), aquatic T. albisutus larvae graze directly on the regenerating Beggiatoa mats, reaching benthic densities of ~45,000 larvae per square meter.[1][9] Upon metamorphosis, adult midges emerge in dense convective clouds -- maintaining a standing airborne population exceeding 2.4 million individuals -- that drift upward into the silk curtain lining the cave ceiling and walls.[1][17]

Architecture and Dual-Species Dynamics of the Megacity

Beginning roughly 50 meters inside the cave entrance, the colonial web forms a thick, spongy "living curtain" covering over 100 m2 of rock wall.[14][15] Rather

than a single communal structure built by an obligate social species, the megacity is an integrated composite woven by ~111,000 individuals across two distinct spider families (exceeding 1,100 spiders per m2).[1][12]

| Species / Trophic Guild | | Family | | Estimated Population | | Mean Density | | Functional Role in Megacity |

| Tegenaria domestica | | Agelenidae (Funnel weavers) | | 69,000 | | ~690 per m2 | | Primary structural architect; builds basal sheet-and-funnel framework[1][12] |

| Prinerigone vagans | | Linyphiidae (Sheet weavers) | | 42,000 | | ~420 per m2 | | Interstitial tenant; spins fine capture meshes between major funnels[1][16] |

| Combined Arachnid Assemblage | | Dual-Family Complex | | 111,000 | | ~1,110 per m2 | | Multi-layered aerial filtration of emerging T. albisutus midges[1][12] |

In surface habitats, Tegenaria domestica is a fiercely territorial solitary predator that constructs isolated funnel retreats and readily cannibalizes conspecific intruders.[12] In Sulfur Cave, 69,000 robust individuals occupy tightly packed, overlapping funnels, exhibiting seasonal peaks in egg clutch size during early summer despite the constant 26 deg C thermal regime.[1][12] Even more remarkably, 42,000 diminutive Prinerigone vagans spiders inhabit the interstitial spaces of the Tegenaria framework without triggering predation.[1][11] This commensal or mutualistic partitioning allows the two species to harvest different aerodynamic trajectories and size fractions of the midge swarm while reinforcing the shared silk matrix.[1]

The structural longevity of the web in an acidic, humid cave atmosphere also highlights the biochemical resilience of spider silk proteins. Natural spinning in spiders relies on carbonic anhydrase-driven acidification (dropping duct pH from ~7 to ~5) to lock spidroin amino acid terminal domains into insoluble fibers, making the polymerized silk inherently tolerant of acidic condensation.[7][8] Furthermore, T. domestica silk restricts nitrogen accessibility to inhibit bacterial and fungal degradation (such as Bacillus subtilis), preventing microbial rot across the multi-layered curtain.[6]

Behavioral Mechanisms and Comparative Speleobiology

Why have two solitary, territorial spider species suspended agonistic hostility and intraguild predation? Three complementary mechanisms explain this transition to facultative coloniality:[1][13]

* Resource Superabundance: Territorial defense and combat carry high energetic costs and injury risks that are adaptive only when prey is scarce. With over 2.4 million midges continuously emerging from the stream, prey capture is passive and effectively unlimited, reducing the selective payoff of aggression to zero.[1][17]

* Sensory Masking in the Aphotic Zone: In complete darkness (0 lux), visual agonistic displays are eliminated. Simultaneously, the acoustic roar of the thermal river, dense midge swarms, and thousands of moving neighbors create continuous vibrational background noise across the silk sheet, habituating mechanoreceptors and masking discrete territorial intrusion signals.[1][15]

* Genetic Isolation and Plasticity: Molecular comparisons demonstrate that the

Sulfur Cave populations of both T. domestica and P. vagans are genetically diverged from outside surface populations, indicating restricted gene flow and rapid local selection favoring docile phenotypes that allocate energy toward fecundity rather than agonistic conflict.[1][12]

When compared to other landmark chemoautotrophic caves -- such as Romania's sealed Movile Cave (where Agraecina cristiani hunts solitarily) or Italy's Frasassi Caves -- Vromoner is uniquely defined by its open fluvial connection combined with extreme thermal and trophic stability, enabling surface species to undergo real-time behavioral reorganization.[1][2]

Conclusion: Conservation of a Subterranean Metropolis

The "Sulfur City" of Vromoner Canyon demonstrates that behavioral categories such as "solitary" and "territorial" are not fixed constraints, but plastic ecological strategies shaped by resource economics.[1][13] Fueled entirely by H2S oxidation, this 111,000-spider assemblage offers a striking terrestrial analogue for chemoautotrophic ecosystems beneath the icy crusts of Europa or Enceladus.[1] Because the colony sits just 50 meters inside a transboundary canyon between Greece and Albania, its survival depends on protecting the Sarandaporo watershed and regulating cave tourism.[1][14]

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