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INITIAL STEPS OF INSECT FOSSILISATION IN CAVE FLOWSTONE

ZAČETNE STOPNJE FOSILIZACIJE ŽUŽELK V JAMSKI SIGI

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Abstract

Tone Novak, Peter Kozel, Luka Gale, Ljuba Slana Novak & Katja Adam: Initial steps of insect fossilisation in cave flowstone

In a small, abandoned coal mine in northeastern Slovenia, there is an area with intensive flowstone deposition. We found about two hundred carcasses of the mosquito *Culex pipiens* s. l., as well as a few remains of a winter crane fly *Trichocera* sp., a rove beetle *Atheta* cf. *spelaea*, and a false diamondback moth *Digitivalva pulicariae* on the wall, partly or entirely embedded in the flowstone. We describe the initial taphonomic steps in these carcasses and discuss the probable reasons why the insect remains disintegrate completely, interrupting the process of fossilisation.

Keywords: actualistic approach, parietal association, sandstone, taphonomy.

Izvleček

Tone Novak, Peter Kozel, Luka Gale, Ljuba Slana Novak & Katja Adam: Začetne stopnje fosilizacije žuželk v jamski sigi

V majhnem, opuščenem rudniku v severovzhodni Sloveniji je predel z intenzivnim odlaganjem sige. V njej smo našli okrog dvesto delno ali v celoti zasiganih navadnih komarjev *Culex pipiens* s. l., nekaj zimskih košeninarjev *Trichocera* sp., kratkokrilcev *Atheta* cf. *spelaea* in mikrometulja *Digitivalva pulicariae*. Opisujemo tafonomske stopnje njihovih kadavrov in razpravljamo o verjetnih razlogih za njihov popolni razkroj v sigi, kar onemogoči nadaljnjo fosilizacijo.

Ključne besede: aktualistični pristop, parietalna asociacija, peščenjak, tafonomija.

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1. INTRODUCTION

Originally established as a palaeontological subdiscipline (Efremov, 1940), taphonomy has gained broad acceptance in palaeontology, archaeology, and forensic science, with all these fields applying its principles in research. Summarising these perspectives (Benton & Harper, 2009; Lyman, 2010; Domínguez-Rodrigo et al., 2011; Pokines, 2013; Behrensmeyer, 2021; Rust & McCoy, 2025; Trombley and Agarwal, 2025), taphonomy is the study of the transition of living organisms, their products, and traces – organic or inorganic – from the ecosphere to the lithosphere, or their destruction. The death of an organism, usually followed by partial or complete decomposition of organic matter (necrolysis), is the initial step in the process of fossilisation. This is accompanied and followed by biostratinomy, the phase between death and burial, during which the organism's remains may be disarticulated, transported, fragmented, abraded, or otherwise modified by the environment. After final burial in a preserving medium, diagenesis occurs. This last phase involves structural and mineralogical transformation of the skeleton, its partial or complete dissolution, and deposition of new or additional minerals (ibid.). The initial two steps in fossilisation are usually studied in present-day environments, and the principle of paleoactualism is followed to interpret fossilised remains (Martin, 1999).

Caves are important habitats for the preservation of paleontological resources, as their relatively stable environmental conditions, compared to the surface, enable the long-term preservation of fossils (Schubert and Mead, 2019). Although the abundance of remains of animal groups other than vertebrates in cave deposits is comparable to that of mammals (Schubert and Mead, 2019), research is biased especially towards the latter due to researchers' interests and expertise (ibid.). Invertebrates are studied much less frequently, as only a few have strongly mineralised body parts, such as serpulid tubes (e.g., Mihevc et al., 2002, 2025) and molluscan shells (e.g., Zupan Hajna et al., 2021), which are comparatively well preserved. Most invertebrates, such as oribatid mites, cladocerans, and insects (e.g., Moldovan et al., 2011), are much smaller and more difficult to find, even though many surface-dwelling species use caves and similar subterranean habitats, such as mines, tunnels, and cellars, as winter hibernacula, while many others seek temporary shelter there during unfavourable environmental conditions on the surface in summer (Novak et al., 2010; Zittra et al., 2019). These so-called parietal associations – assemblages of species on the cave walls, and in most caves also ceiling – form a significant part of the cave communities and differ greatly from those dwelling on the cave floor (Mammola and Isaia, 2018). However, only highly decay-resistant organic matter, such as pollen, charcoal (McGarry & Caseldine, 2004), and tapeworm eggs (Lartigot-Campin et al., 2022), have been found fossilised in speleothems, while there are no reports of fossilised soft animals or arthropods in cave flowstone or dripstone.

To our knowledge, no cases of arthropod fossilisation in cave flowstone have been reported. In the abandoned Pekel jama coal mine in northeastern Slovenia, we surveyed the parietal fauna in winter and documented a massive entombment of arthropods in cave flowstone, with their ultimate decay. We describe the initial taphonomic steps of fossilisation and discuss probable reasons for the subsequent complete disintegration of the insect remains during diagenesis. We hope that this contribution will encourage further search for subfossils or chemical fossils in flowstone.

2. MATERIALS AND METHODS

The Pekel jama mine (46.48844° N, 16.20258° E, 237 m a.s.l.) (Figure 1A) in Gresovščak near Ljutomer, NE Slovenia, is located within the Haloze–Ljutomer graben, a smaller basin filled with Miocene conglomerates or debrites and quartz-rich sandstones and siltstones (Horvat, 2009). Local coal miners excavated this mine just before or during the First World War, but due to the small quantities of low-calorie coal, further activities were abandoned (Dobrajc and Panič, 2012). The mine is excavated mainly in quartz sandstone and partly in siltstone. Spring water from Pekel jama creates an anthropogenic hypotelminorheic in front of the mine (Figures 1B–C), which mimics a typical hypotelminorheic habitat, as it supports typical spring-dwelling species but no *Niphargus* or other stygobionts (Pipan et al., 2012). On the walls of the mine, the drips branch in micro-drips (Figure 1E). At the end, there are small areas of pebbles up to 3 cm in size on the floor (Figure 1F), likely carried into the gallery by dripping water from loose conglomerates in the main rock. Although these pebbles are noncarbonate, they are most likely cemented together with carbonate binding. This is concluded as the percolating water emerging in the mine

is carbonate-oversaturated, resulting in abundant flowstone deposition in a section about 3 m long near the end of the mine (Figures 1D–E). After heavy rain, percolating water (drips of up to about 0.1 L/s) washes a giant *Niphargus goricae* Delić, Trontelj & Fišer, 2017 into floor puddles. The temperature of the dripping water is relatively high (9.8–10.3°C) throughout the year. We visited Pekel jama in all seasons, between the years 2012 and 2025. Here, we focus on parietal fauna in the flowstone section in winter (16 Dec. 2012, 7 Feb. 2018, 10 Dec. 2025), as insects were entrapped in the flowstone only during this season. We conducted a census of the fauna on the flowstone and photographed selected areas with entrapped insects to document all successive stages of their initial fossilisation. Living mosquitoes were collected with an aspirator and kept in refrigerator until identification.

3. RESULTS

In winter, the following parietal species have been recorded in Pekel jama: the gastropods *Limax cinereoniger* Wolf, 1803 (Limacidae) and *Campylaea illyrica* (Stabile, 1864) (Helicidae); the spiders *Metellina merianae* (Scopoli, 1763) (Tetragnathidae) and *Nesticus cellulanus* (Clerck, 1757) (Nesticidae); the millipedes *Polydesmus collaris* C. L. Koch, 1847 (Polydesmidae) and unidentified Julida; the coleopterans *Choleva* cf. *sturmi* Brisout de Berneville, 1863 (Leiodidae) and *Atheta* cf. *spelaea* (Erichson, 1839) (Staphylinidae); the dipterans *Trichocera* sp. (Trichoceridae), *Culex pipiens* s. l. Linnaeus, 1758 (Culicidae), *Speolepta leptogaster* (Winnertz, 1863), two unidentified species of Mycetophilidae, and a Brachycera species; the hymenopteran *Diphyus quadripunctorius* (Müller, 1776) (Ichneumonidae); the lepidopterans *Scoliopteryx libatrix* Linnaeus, 1758 (Geometridae) and *Digitivalva pulicariae* Klimesch, 1956 (Acrolepiidae); and the trichopteran *Stenophylax permistus* McLachlan, 1895 (Limnephilidae).

Speolepta larvae and both spiders were active throughout the year, while all others underwent winter dormancy. Although short, three zones can be distinguished in the Pekel jama with respect to the resting places of the parietal species. Close to the entrance, up to about 5 m inside the mine, *Speolepta* larvae, both gastropods, and spiders were common. About 5–10 m from the entrance, *Polydesmus* (Figure 2A) and *Choleva* built overwintering chambers from silt-mud, and *Scolyopterix*, *Stenophylax*, unidentified julids, and remnants of a brachyceran fly, probably Muscidae, were recorded. Deeper inside, there was a gradually denser assemblage of *Culex* (35 to 150 per winter) and Mycetophilidae (30 to 110 per winter), along with a few *Trichocera*, *Atheta*, and *Digitivalva*. Excitable Mycetophilidae were only exceptionally found on flowstone walls and moved whenever disturbed by the presence of a person. In contrast, the others established their diapausing sites on the walls without selecting resting places with respect to water drips. In this way, numerous *Culex* (Figures 2B–H), and sparce *Atheta* (Figure 2G), *Trichocera* (Figure 2H) and *Acrolepia* (Figure 2I) rested on the flowstone and became entrapped by the forming flowstone. All these animals died in situ and were not exposed to any post-mortem transport or scavengers. By far the most numerous remains in the flowstone were from about 200 *Culex* specimens. There were also a few *Atheta*, *Digitivalva*, and the remains of one *Trichocera*. No mycetophilid cadaver has been identified in the flowstone. Mosquito bodies can be found collapsed on the surface of the flowstone, in some cases already partly decayed (Figure 2I). In other cases, only parts of the body can be found in various stages of decay. Deeper in the flowstone, only beige-yellowish spots in semi-transparent areas are visible to a depth of about 1 cm below the surface. These spots apparently disappear in the deeper, older calcareous deposits.

4. DISCUSSION

Single dead arthropods and other small organisms, together with plant and humus remains, are readily transported by drips on flowstone surfaces and rarely attract the attention of biologists, palaeontologists, or karstologists. The same applies to animals such as *Atheta*, *Trichocera*, *Digitivalva*, and *Culex*, which occasionally settle on forming flowstone and die there. However, the mass deaths of *Culex pipiens* in Pekel jama warrant special comment, as they attract the attention not only of speleobiologists and palaeontologists, but also epidemiologists.

This is because mosquitoes and other blood-sucking insects are a global epidemiological concern due to their role as vectors in transmitting disease agents, such as viruses, parasitic protozoans, and nematodes from infected humans and animals to new hosts, and many of them temporarily inhabit caves (Obame-Nkoghe et al., 2016; Zittra et al., 2019; Knap et al., 2020). The widely distributed *C. pipiens* in Europe (Marcolin et al., 2025) has been reported to transmit two members of the Flaviviridae family, *West Nile Virus* and *Usutu Virus*, which threaten public and vertebrate animal health (Brugman et al., 2018). In Austria (Zittra et al., 2019) and Germany (Dörge et al., 2020), caves and artificial galleries serve as resting and overwintering sites for the most common *C. pipiens pipiens* and *C. torrentium*, as well as, more rarely, other mosquito species. Most probably, mosquitoes in the Pekel jama belong to *C. pipiens pipiens*, blood-feeding on avian hosts (Brugman et al., 2018), which are by far the most abundant mosquitoes in European caves (Zittra et al., 2019; Dörge et al., 2020). *Culex* embedded in flowstone have been found also in Austria (E. Christian, in lit.).

During the fossilisation of an organism lacking biomineralised tissues, burial mineralisation must occur before the microbial decay of an organism is completed. The taphonomic sequence of the studied culicids is as follows. The first, ecological step involves a mosquito landing on the flowstone surface, which is covered by a thin layer of carbonate-saturated dripping water. As the mosquito remains immobile during winter diapause, newly formed carbonate deposits from the oversaturated water eventually entrap its tarsi. When the mosquito dies, its body collapses onto the surface and begins to decay, while the remains are gradually covered by carbonate deposits. This marks the beginning of the second taphonomic step, equivalent to burial. This process is largely random, depending on micro-drips around each specimen. Occasionally, a crust forms rapidly over the entire body – probably within a few days – before the soft tissues disintegrate and the chitinous sclerites at least partly detach from each other. Such carcasses appear nearly untouched (Figure 2F). Ongoing carbonate deposition then covers either the whole body or specific disintegrated chitinous remains. The expected third taphonomic step, mineralisation and diagenesis, which usually follows in semi-fossils (subfossils?), does not occur, as the chitinous remains continue to decay until completely decomposed. Although some insect carcasses were covered with flowstone in a relatively short time, and the high pH of the flowstone-depositing water hindered the decay of organic matter (Wang and Kuzyakov, 2024), the carcasses continued to decay. This was likely due to a sufficient oxygen supply (cf. Benton & Harper, 2009; Heidke et al., 2021) through the porous flowstone cover over the dead body, as well as the relatively high, constant temperature of the water. Microbial activity within animal remains, even in otherwise decay-resistant chitin (Schimmelmann et al., 1986), was not inhibited, leading to gradual and complete disintegration of the remains. The final recognisable stage of mosquitoes was a beige-yellowish spot in the flowstone.

Fossilisation processes in amber (Viertler et al., 2024), tar and flowstone are similar in that, in most cases, they predominantly entrap living animals and usually enclose them completely. However, there are notable differences. In amber, larger, more vigorous beetles are more likely to struggle and escape from resin than smaller arthropods, resulting in a taphonomic bias towards smaller arthropods (Song et al., 2022). Taphonomic studies in resins reveal a wide range of fossilisation outcomes, from fossils with perfectly preserved internal organs to empty casts (Viertler et al., 2024). This variation is due to different burial histories and maturation scenarios in various resins (Bojarski et al. 2025). A perfectly preserved body indicates the inclusion of an animal alive or very soon after its death. Poorly preserved bodies, by contrast, may result from the inclusion of a dead, decomposed body or from inclusion in a type of resin that does not prevent decomposition after sealing, due to the chemical properties of the resins (McCoy et al., 2017, 2018; Seyfullah et al., 2018; Viertler et al., 2024). In contrast, insect size had no role in entrapment in the studied flowstone. Instead, entrapment was the consequence of a behavioural bias. Due to their avoidance of wet surfaces and immediate displacement when disturbed, Mycetophilidae were not susceptible to entrapment, while the insensitivity of mosquitoes to wet surfaces and their long-term immobility enabled their massive entrapment. Moreover, flowstone likely never prevents oxygen supply, causing ongoing decay (cf. Rousseau et al., 1995) until complete microbial disintegration of the remains.

The fossilisation process described also resembles encrustation by tufa and travertine. While tufa is deposited in creeks and riverbeds, travertine forms from carbonate-laden hydrothermal waters (Ford and Pedley, 1996; Golubić et al., 2008; Capezzuoli et al., 2014). Like flowstone, tufa and travertine are calcium carbonate deposits that form crusts over pre-existing surfaces; however, whereas flowstone is a cave deposit, tufa and travertine are mainly precipitated under subaerial conditions (Capezzuoli et al., 2014). Both tufa and travertine frequently contain subfossils and fossils, with remains of photoautotrophs predominating – micro- to macrophytes in tufa, cyanobacteria in travertine (Pentecost, 2005; Sanders et al., 2011; Capezzuoli et al., 2014; Rott et al., 2021). A much more intensive incrustation is re-

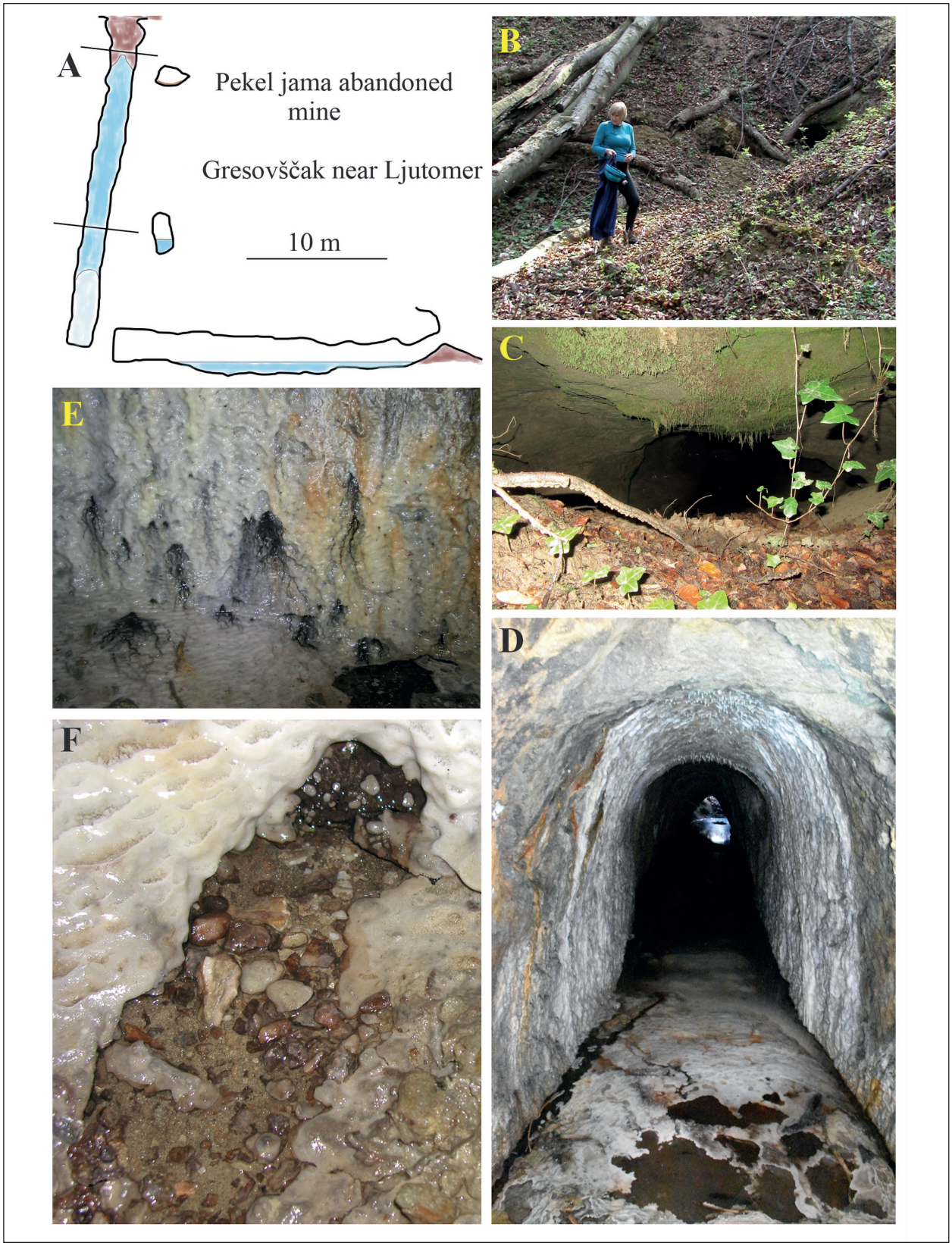

Figure 1: Pekel jama abandoned charcoal mine. A. Mine map. B–C. Entrance. D. The passage from inside outwards, with remarkable flowstone (white) section. E. Charcoal traces showing dispersion of seeping water on the walls. F. Pebbles in the bed of a minor inflow rivulet.

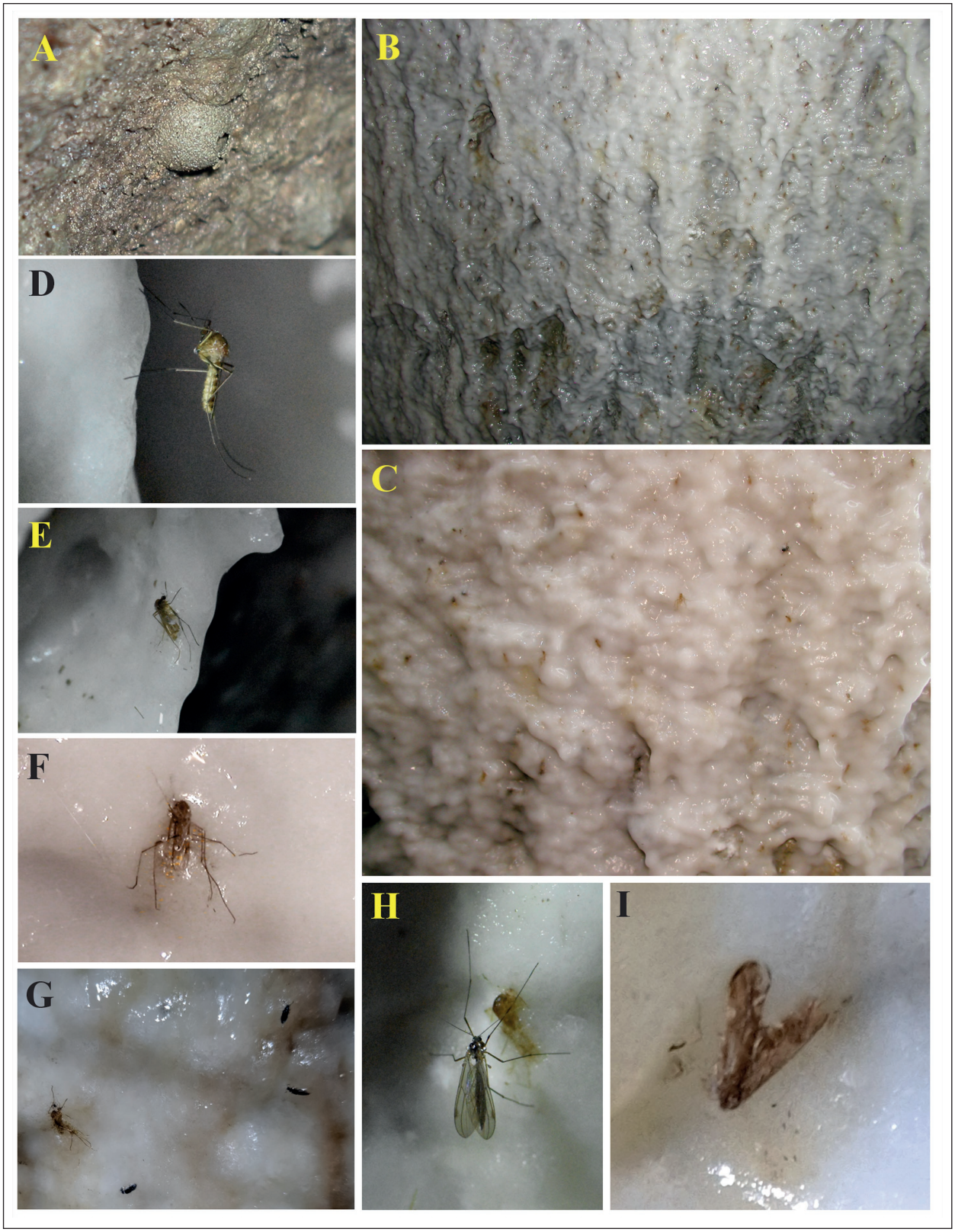

Figure 2: A. Overwintering chamber of Polydesmus collaris. B, C. Flowstone with numerous insects, predominantly mosquito remains at various stage of decay. D–F. Culex pipiens alive, dead on the flowstone surface, partly embedded in flowstone. G. Remains of a Culex and three Atheta specimens. H. Trichocera on flowstone with embedded Culex. I. Remains of Digitivalva embedded in flowstone.

ported for oversaturated, hot springs that deposit the onyx-marble with numerous arthropod fossils, as animals that fall in water trigger crystallisation as nuclei (Pierce, 1951; Rowland & Sissom, 1980). Due to their porosity, tufa and travertine almost never preserve organic remains (Golubić et al., 2008), and only biomineralised structures, such as vertebrate bones and mollusc shells, are preserved (Dabkowski, 2014). Rapid burial by very fine tufa may create anaerobic conditions, allowing preservation of organic matter, but only for a few years (Pentecost, 2005). So far, only pollen grains have been recovered from tufa deposited during the Holocene (Dabkowski, 2014). Similarly, the short-lasting preservation of arthropod remains embedded in flowstone is evident, and besides, extensive deposition of flowstone in cave sections where mosquitoes take hibernacula are rare.

Mosquito thanatocoenoses in caves may benefit future epidemiological studies. Although flowstone does not allow long-term preservation of organic mosquito remains, the repeated formation of such death assemblages provides indirect evidence of species composition, abundance, and overwintering behaviour at specific sites over time. Caves that serve as hibernacula for large numbers of mosquitoes may therefore represent spatially predictable reservoirs of vector populations, even if their remains are only transiently preserved. Together, these observations underscore the value of cave environments as relatively understudied yet noteworthy habitats for future mosquito research.

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