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Occurrence of Taeniidae in a Middle Pleistocene speleothem of the Basura cave (Toirano, Liguria, Italy)

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ABSTRACT

Objective: This study aims to (i) analyse whether speleothems may contain fossil parasitic worm eggs and, if so, (ii) identify the pathogens involved, and (iii) place them in geological, palaeontological, and chronological contexts to know the zoonoses that could affect human and animal populations during the Middle Pleistocene.

Materials: A sample of calcite dated to the beginning of MIS 9 and MIS 8 from the Basura cave (Liguria, Italy) was analysed.

Methods: The chemical protocol applied is characterised using hydrochloric acid, the reduction of hydrofluoric acid application time, and by the absence of the use of base, dense liquor or acetolysis. **Results:** An embryophore of a taeniid was recovered.

Conclusions: Endoparasitic worm eggs can be found in speleothems. A taeniid embryophore was found in a calcite level dated to MIS 9. Zoonoses related to the Taeniidae family existed 300,000 years ago in the northern Mediterranean region and may have affected Middle Pleistocene predators, carnivores, or humans. Speleothems are good tools for paleoparasitological studies.

Significance: This is the oldest taeniid recovered and identified.

Limitations: A more precise determination of the genus of this taeniid is not possible in the absence of more precise palaeontological data.

Suggestions for further research: An application of this approach to other Pleistocene speleothems could broaden the spectrum of parasites and their zoonoses over remote Pleistocene periods.

KEYWORDS

Paleoparasitology ; Taenia/Echinococcus ; Marine isotopic stage 9 ; Calcite

1. INTRODUCTION

Since the beginning of the 20th century, the field of paleoparasitology has studied the remains of parasites from ancient human and animal populations and the evolution of host-pathogen relationships over time. This subdiscipline of bioarchaeology aims, among other things, to obtain information on the behaviour and lifestyle of ancient human populations (Reinhard, 1992; Bouchet et al., 1995, 1999; Araújo and Ferreira, 2000; Bouchet et al., 2003; Harter et al., 2003). Remains of gastrointestinal parasites are commonly found in archaeological or palaeontological contexts, and the eggs of endoparasitic helminths can be found in remains such as mummies (Cockburn et al., 1975; Horne and Lewin, 1977; Jones, 1982; Aspöck et al., 1995; Cockburn et al., 1998; Mitchell, 2013), human or carnivore coprolites, and in sediments containing faeces, such as latrines and ruminant stalling areas (e.g., Reinhard et al., 1986; Bouchet, 1995; Bouchet and Paicheler, 1995; Bouchet et al., 1995; Jouy-Avantin et al., 1999; Lartigot-Campin and Moné, 2017; Le Bailly et al., 2017; Barbera et al., 2020).

Until now, paleoparasitological examination of speleothems have not been undertaken. These carbonate concretions in caves are formed from run-off water, which seeps through the epikarst (Moore, 1952). This water, which feeds the concretions, is known to carry many minerals and biogeochemicals (e.g. McDermott, 2004; McDermott et al., 2006; Fairchild et al., 2006; Blyth et al., 2008; Lachniet, 2009; Błaszczuk et al., 2021; Luetscher et al., 2021) along with organic elements, such as sporopollen material from the surface (e.g. Bastin, 1978; Renault-Miskovsky and Girard, 1978, 1988; Davis, 1999; McGarry and Caseldine, 2004; Lebreton et al., 2007). These elements are trapped in calcium carbonates as they precipitate. The data derived from speleothems are considered reliable, as they are subject to very few taphonomic processes after the formation of the calcite. This is because the calcite gangue forms a stable, closed system that alters little after formation and is protected by the cave from external environmental variations (Wigley and Brown, 1976). For this reason, speleothems are excellent sources of information for multidisciplinary analyses, allowing the reconstruction of paleoenvironmental and paleoclimatic variation within a precise chronological framework.

Based on this information, it is conceivable that calcite could contain fossil eggs of endoparasitic worm eggs. This study aims to (i) analyse whether speleothems may contain fossil parasitic worm eggs and, if so, (ii) identify the pathogens involved and (iii) place them in geological, palaeontological, and chronological contexts to explore the zoonoses that could affect human and animal populations during the Middle Pleistocene.

This analysis was carried out on a calcite core, drilled in a stalagmitic flowstone from the Italian Basura cave, created between at least 625 kya and 225 kya (Pozzi et al., 2019).

2. MATERIAL AND METHOD

2.1. The site

The Basura Cave (Grotta della B`asura) is in north-western Italy, in western Liguria, about 1 km north of Toirano (Province of Savona) and 4.5 km from the Mediterranean coastline (Fig. 1A). It opens at 186 m above sea level (44°08'16.8"N; 8°12'07.3"E) in the dolomitic limestones of Mount San Pietro and forms a vast, tortuous karst system, 890 m long (Fig. 1B).

Known since the end of the 19th century (Morelli, 1889, 1890), the Basura cave was explored from 1950. Traces of charcoal on the walls, associated with bare foot, finger and knee prints were discovered, attesting that a human group composed of five people moved through these corridors, over at least 400 m, during the Upper Pleistocene, 12, 340 ± 160 years ago (Chiapella, 1952; Tongiorgi and Lamboglia, 1954; Chiapella, 1955; Blanc, 1960; Lamboglia, 1960; Molleson et al., 1972; Molleson, 1985; Citton et al., 2017; Romano et al., 2019). The cave was also visited by the cave bear, *Ursus spelaeus*, 24,230 ± 290 years ago B.P. (Molleson et al., 1972), as evidenced by the numerous scratches and footprints found there and the thousands of bones amassed in the "Bear Cemetery" room. These dates have been confirmed by additional cross-dating studies using ¹⁴C (Délíbrías, 1985), as well as U/Th and U/Pa methods (Shen, 1985; Yokoyama et al., 1985). The cave system is covered with speleothems formed during the Middle and Upper Pleistocene. Multiple dating campaigns have been carried out on the entrance stalagmitic cone, dated between

205,000 ± 24,000 years (205 ± 24 kya) and 12.34 ± 1.16 kya (Molleson et al., 1972), on the concretions of the Cibele Hall, dated between at least 600 kya and 179.7 ± 4.1 kya (Columbu et al., 2021), and those of the Fascio Hall (Fig. 1B), dated by Thermal Ionisation Mass Spectrometry (TIMS) between at least 625 kya (Marine Isotope Stage (MIS) 13) and about 225 kya (MIS 7) (Pozzi et al., 2019).

This analysis was carried out on the calcite of the Fascio Hall.

2.2. Material

The Fascio Hall hosts a vast stalagmitic flow 2.30 m thick, covering an area of about 100 m² (Fig. 2A). An initial radiometric study had previously been carried out on this limestone formation, on a core named “BF1” (Bahain et al., 1994). Research was continued by carrying out several non-destructive drillings using a 4-cm diameter diamond-headed corer (Fig. 2B). Two cores were taken, “BF2” for radiochronological and palaeomagnetic studies (Fig. 2C – Pozzi et al., 2019), and “BF Palyno” for palynological analyses. They are located approximately 90 cm apart. An association of samples, and therefore dates, is possible given the proximity of the two drillings.

The core “BF Palyno”, 240 cm long (Fig. 2D), is characterised by alternating coloured strata rich in humic acids (Rousseau, 1992), and particularly white strata indicating, in this case, the presence of pure calcite.

2.3. Method

In the laboratory, the core was cut into sections using a circular saw, the disc of which is 3 mm thick. These were then drawn on millimetre paper to a scale of 1:1 and scanned before being subdivided into smaller samples. Sampling was carried out by following the sedimentation gaps, forming natural breakage zones, and/or by cutting the main laminae, following the colour and/or appearance of the calcite.

Before starting the chemical etching, the speleothem fragments were brushed under a stream of distilled water to avoid contamination by actual elements. As the calcite was drilled, further cleaning with HCl was not applied, except for the top sample.

Parasitological studies use a protocol based on medical coprology, consisting mainly of rehydration of the sample, and derived from that initially proposed by Callen and Cameron (1960). But this protocol, used on organic matter, is not suitable for calcite.

Parasitic worm eggs are part of palynofacies (Diot, 1991). Eggshells are particularly hearty, which allows them to be preserved in sediments and to withstand the physico-chemical protocol of pollen analysis, although the use of strong bases and acids can damage them and reduce their biodiversity (Dufour and Le Bailly, 2013). Thus it is common to observe parasitic worm eggs associated with recovered sporopollen material (Reinhard et al., 1987; Warnock and Reinhard, 1992; Florenzano et al., 2012; Brinkkemper and van Haaster, 2012; Dufour and Le Bailly, 2013; Bosi et al., 2011).

A protocol allowing the preservation of the organic matter while destroying the mineral matter was applied, inspired by that proposed by McGarry and Caseldine (2004) using hydrochloric acid (HCl) at 37.5% cold, to eliminate the calcite. As the resulting pellets were extremely small, the cold 70% hydrofluoric acid (HF) etch was limited to 3 h rather than the 12–20 h recommended in standard pollen analysis in order to remove any sand particles and ensure that the slides were legible. Fluorosilicates, formed during the HF etch, were removed by a hot 18.25% HCl etch for 10 min. The pellets were then rinsed with distilled water, dried, preserved in glycerol, and placed between a slide and coverslip. Neither potassium hydroxide (KOH – 10%), nor sorting with a dense liquor (ZnCl₂) or acetolysis, was used to preserve the palynofacies and its biodiversity.

3. RESULTS

A parasitic worm egg was observed in the calcite. This egg, more precisely, this embryophore, was round and slightly oval, with a dark brown, slightly pitted shell (Fig. 3A) and measured 33.99 µm wide by 39.29 µm long, with a striated

wall (internal shell) 5.93 μm thick. These characteristics allowed it to be attributed to the Taeniidae family (see Bour'ee et al., 2012).

The embryophore was found in calcite sample P5.1 from core 'BF Palyno', which is less than one metre from the recently dated core "BF2" (Pozzi et al., 2019). As this sample lies between 23 cm and 26 cm from the top of the core, its age is estimated to be between 278 and 315 kya for the top, and between 300 and 334 kya for the base of the sample, that is, during MIS 9 and the beginning of MIS 8 (Fig. 3B).

4. DISCUSSION

An endoparasitic worm egg was found in the analysed calcite. It is the first evidence of the presence of a helminth egg in speleothems. The morphological characteristics of this embryophore allow it to be assigned to the Taeniidae family.

Preservation of this embryophore can be explained by two parameters. First, the eggshells of endoparasitic worms allows them to resist attack from the external environment. The observation of this taeniid embryophore was made possible because the chemical extraction protocol used here was minimally aggressive and included a reduction in the application of hydrofluoric acid, the non-use of base, and the absence of acetolysis, which damage parasitic worm eggs in samples and reduce their biodiversity (Dufour and Le Bailly, 2013). Secondly, calcite, after crystallisation, forms a stable and closed system, altered little and protected by the cave from fluctuations of the external environment (Wigley and Brown, 1976). It is therefore not subject to post-depositional taphonomic processes and is not contaminated by recent material. In addition, before carrying out the chemical protocol, the calcite fragments were carefully brushed under a stream of distilled water, purified of all minerals and organisms, to avoid contamination of the samples. The embryophore found does not show the characteristics observable in recent tapeworm eggs, such as an outer membrane or an embryo, whose hooks are sometimes visible under the microscope. The hypothesis of external contamination by recent material can therefore be ruled out. All this information attests to the antiquity of this embryophore whose environmental calcite has been dated between 278 and 325 ka (Pozzi et al. 2019).

The discovery of the Taeniidae embryophore in a calcite sample forms the oldest evidence of this Cestode in the world. The discovery is even more remarkable since paleoparasitological data for such ancient periods are rare. Indeed, the oldest traces of endoparasitic worms in prehistory date from the Lower and Middle Pleistocene, with the discovery in coprolites of nematode larvae dated to 1.5 mya B.P. (Ferreira et al., 1993) and trematode eggs (Dicrocoelidae) dated to 550 kya B.P. (Jouy-Avantin et al., 1999). It was not possible to attribute the embryophore discovered in Basura to a particular taeniid genus. Indeed, most ancient taeniid eggs belong to the genus *Taenia* sp. or *Echinococcus* sp. Morphological examination of the embryophores under the light microscope alone does not allow them to be differentiated, as the shape and size ranges overlap. Indeed, these embryophores are morphologically very similar, with ellipsoid shapes, thick shells, and a characteristic radial striations. The ellipsoid embryophores of *Taenia* sp. are 35–40 μm in length and 30–35 μm in width. *Echinococcus* embryophores are more rounded, with a diameter between 30 and 35 μm (Belding, 1965; Flisser et al., 2004; Cot'ee et al., 2016).

The presence of tapeworms has previously been found on archaeological materials of anthropic origin (Reyman et al., 1977; Dommelier et al., 1998; Gonç'aves et al., 2003; Harter, 2003; Le Bailly, 2005; Sianto et al., 2009; Slepchenko et al., 2016). Various infections related to the Taeniidae family and caused more particularly by *Echinococcus* sp. and *Taenia* sp., have been recorded in archaeological contexts, as well. *Taenia* sp. has been geographically and chronologically widespread since the Neolithic period. Embryophores of this parasite have been found in European (Harter, 2003; Harter-Lailheugue et al., 2005), the Middle East (Cahill et al., 1991; Harter, 2003; Mitchell and Tepper, 2007; Langgut, 2022), Asian (Yeh et al., 2016; Zhan et al., 2020), African (Harter, 2003; Harter et al., 2003; Bruschi et al., 2006; Le Bailly et al., 2010 e.g.), and American (Horne and Tuck, 1996; Beltrame et al., 2010) archaeological sites, over time periods ranging from 10,000 B.P. to the present (Sianto et al., 2009). The oldest embryophores of *Taenia* sp. were identified in a skeleton from Cyprus, dated between 8300- and 7000-years B.C. (Harter-Lailheugue et al., 2005). Embryophores or bone lesions associated with *Echinococcus* sp. have been reported from Europe (Weiss and

Møller-Christensen, 1971; Kristjansdóttir and Collins, 2011; Florenzano et al., 2012), the Middle East (Perry et al., 2008) and North America (Williams, 1985). The earliest record of *Echinococcus* sp., a recovered hydatid cyst, was found in Siberia in the burial of a woman, dating from the Early Neolithic (Waters-Rist et al., 2014). The discovery of this Taeniidae embryophore in a calcite sample considerably extends the chronological evidence known to date for this Cestode.

The discovery of the Taeniidae embryophore in a calcite sample offers new perspectives for paleoenvironmental reconstruction. Taeniidae belong to the Platyhelminthes (flatworms) phylum and the Cestodes class. This family includes 4 genera, *Taenia*, *Echinococcus*, *Versteria* and *Hydatigena* (Nakao et al., 2013). Their life cycle is heteroxenous, with two obligatory mammalian hosts, including humans (Rausch, 1994). Each species has a characteristic cycle, involving an intermediate host, herbivorous or omnivorous, and a final host, carnivorous or omnivorous (Abuladze, 1964; Hoberg et al., 2000; Loos-Frank, 2000). This cycle takes place in two phases, the first being based on this predator-prey relationship and the second on a free stage in the external environment in the form of eggs, consisting of the embryophore protected by a fragile external membrane. All predators, the definitive hosts of taeniids, become infected through their hunted or scavenged prey. In light of the life cycles of present-day taeniids, it is possible to hypothesise about the composition of the groups of animals affected by the predator-prey relationships necessary for the development of these parasites. In Europe today, two species of *Taenia* have humans as their definitive host. These are *T. solium* (or *T. porcini*) and *T. saginata* (*T. bovine*). Other species of *Taenia* (e.g. *T. crassiceps*, *T. gonyamiai*, *T. pisiformis*) mainly parasitise canids (foxes, wolves, coyotes), using rodents, ruminants (cattle, deer) or lagomorphs as intermediate hosts. *Versteria* prefers mustelids as definitive hosts and *Hydatigena* prefers felids, using rodents as intermediate hosts. Humans are rarely affected by the latter forms (García et al., 2003; Dorny and Praet, 2007; Spickler, 2020). It is also possible that omnivores, such as bears, badgers, raccoons, or primates, may become intermediate hosts after ingesting eggs (Spickler, 2020). There are also several species of *Echinococcus*, but the best known in Europe today are *E. granulosus* and *E. multilocularis*. The definitive host, a carnivorous mammal (most often a canid, and to a lesser extent a felid) becomes infected by ingesting parasitized viscera, from deer, horses, and also bison and wild boar. However, humans can be accidentally infected (Ammann and Eckert, 1996; Rahman et al., 2015; Romig et al., 2017). Phylogenetic analysis showed that during the Lower Pleistocene, 1–2.5 million years ago, the first African hominins became the definitive hosts of *Taenia* sp., which then only parasitised carnivores, such as hyenids, canids and felids. The cysticerci contained in the meat of hunted or scavenged bovids, such as antelopes could not be destroyed in the absence of fire (Hoberg et al., 2001). In the Middle Pleistocene, between 781 kya and 126 kya, humans and carnivores, such as canids, felids, hyenids or ursids, were social predators. They hunted the same prey in the same ecological niches and thrived in the same environments (Brain, 1981; Payne, 1983; Stiner, 1994). Based on their development cycles, which are reliant upon a predator-prey relationship, taeniids could possibly infect Middle Pleistocene hominids. The presence of humans is noted on the northern Mediterranean edge in the Middle Pleistocene and in the Italian peninsula in the sites of Polledrara de Cecanibbio (Ceruleo et al., 2019), Torre in Pietra (Villa et al., 2016) and Castel di Guido (Michel et al., 2008). The composition of the faunal assemblage at isotopic stages 8 and 9 has been noted at Torre in Pietra and Vitinia (Petronio et al., 2019). Animals likely to act as reservoirs for *Taenia* sp. were, among predators, ursids (*Ursus spelaeus* and *U. arctos*), canids such as wolves (*Canis lupus*) or red foxes (*Vulpes vulpes*) and among mustelids, the European polecat (*Mustela putorius*). Herbivorous intermediate hosts would include equids (*Equus ferus* and *E. hydruntinus*), cervids (*Megaloceros giganteus*, *Cervus elaphus* ssp., *Dama clactoniana* and *D. dama tiberina*), as well as rodents such as the vole (*Arvicola mosbachensis*). All these archaeological data are contemporary with the period of crystallisation of the calcite sample in which the embryophore was found. However, none of these data are available in the Basura cave, whose infilling consists exclusively of calcite. The only trace of life from this period is our embryophore.

The discovery of this embryophore also provides insight into human behaviour. In the environment, taeniid eggs can be found in soil, where they can be retained for long periods of time, but also in waterways, or on plants soiled by the faeces of wild carnivores (Jansen et al., 2021). Although the parasite cycle may have changed from the current

baseline known during ancient times (Bouchet et al., 2003), it is conceivable that humans could have been infected with *Taenia* sp. by eating raw or undercooked infected meat from hunted or scavenged prey (Dorny et al., 2009) or by drinking contaminated water (Hadi and Makawi, 2013). They could also have acquired zoonotic infection from carnivores that became infected by drinking water contaminated with *Echinococcus* eggs, as water plays an important role in parasite transmission (Slifko et al., 2000; Lass et al., 2019). These carnivores would then act as a reservoir and release new eggs into the environment through faeces, contaminating plants (leaves or berries) and fungi, which hunter-gatherers also fed on (Lass et al., 2015). Studies have shown that, today, wolves and foxes are particularly parasitized by taeniids in Liguria (Di Cerbo et al., 2008; Gori et al., 2015; Citterio et al., 2021), with echinococcosis being one of the most widespread zoonoses in the Mediterranean region (Dakkak, 2010; Alvarez Rojas et al., 2018), creating an important public health problem.

Eggs of endoparasitic worms are transported into caves, and thus in calcite, by air currents and water, but also in the hair or on the feet of humans, animals or insects visiting the cave (Leroi-Gourhan, 1965; McGarry and Caseldine, 2004; Lebreton et al., 2007; Kinfu and Erko, 2008; Alvarez Rojas et al., 2018). However, the calcite sample studied here contained only a very small amount of pollen grains (Lartigot, 2007). This may be explained by the remoteness of the sampling area and the complexity of the cave system, which made it unlikely for air currents or insects to transport particles. As percolating water is responsible for the formation of calcite (Fairchild et al., 2006), it could have carried the taeniid embryophore from the surface where it would have been deposited in a proglottid or excreta, the contents of which would then have been dispersed. Indeed, Taeniidae eggs are released into the environment in proglottids and each of these segments is likely to contain 100–1500 eggs in *E. granulosus* and up to 88,000 eggs in *T. ovis* (Alvarez Rojas et al., 2018). As the embryophore found in Basura is isolated, it cannot be the direct deposition of a gravid proglottid on calcite. However, the lack of pollen grains in the sample suggests that particles such as pollen and embryophores may have been retained by anfractuosités in the epikarst (McGarry and Caseldine, 2004; Lebreton et al., 2007). The hypothesis of indirect deposition in the cavity, by a human or an animal, cannot therefore be ruled out. In this case, it cannot be excluded that humans, long before *Homo sapiens*, ventured into deep karst networks, into a room far from the entrance and light, as demonstrated in the Bruniquel cave, in France (Jaubert et al., 2016).

5. CONCLUSION

This study shows that calcite is likely to preserve fossil parasitic worm eggs, giving paleoparasitology new material to study and providing more data on zoonotic diseases affecting human and animal populations in ancient times. The application of a light chemical analysis protocol, with a short hydrofluoric acid attack and without the application of base, dense liquor and acetolysis, allows the observation of endoparasitic worm remains. Calcite is a promising medium for interdisciplinary analysis, being little affected by post-depositional taphonomic processes and potentially well-dated.

The application of this method to a speleothem in Basura cave has allowed the observation of a taeniid embryophore in calcite levels that crystallised between 278 kya and 315 kya. This discovery constitutes the oldest traces of Taeniidae in the world and attests to the presence of this zoonosis in the Middle Pleistocene on the northern edge of the Mediterranean.

The discovery of a parasite egg in calcite, which is the only trace of animal life in the absence of any other palaeontological data, such as bones or coprolites, opens new perspectives, both in terms of reconstructing biological palaeoenvironments and in human or animal behaviour. Indeed, although the attribution of this embryophore to a genus of Taeniidae is not possible, it testifies to the presence of pathogens likely to infect human or animal populations during MIS 9 as part of their subsistence behaviour. Indeed, this embryophore could represent a type of parasite, such as *Taenia* (*T. saginata* or *T. solium*), which, if infected raw or undercooked meat was consumed, could infect and harm humans. However, the embryophore could also be a parasite specific to carnivorous predators, such as *Echinococcus*, which poses no direct risk to humans unless consumed through contaminated plants.

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Fig. 1.

The Basura cave.

A) Geographical location (white star);

B) Map of the cave.

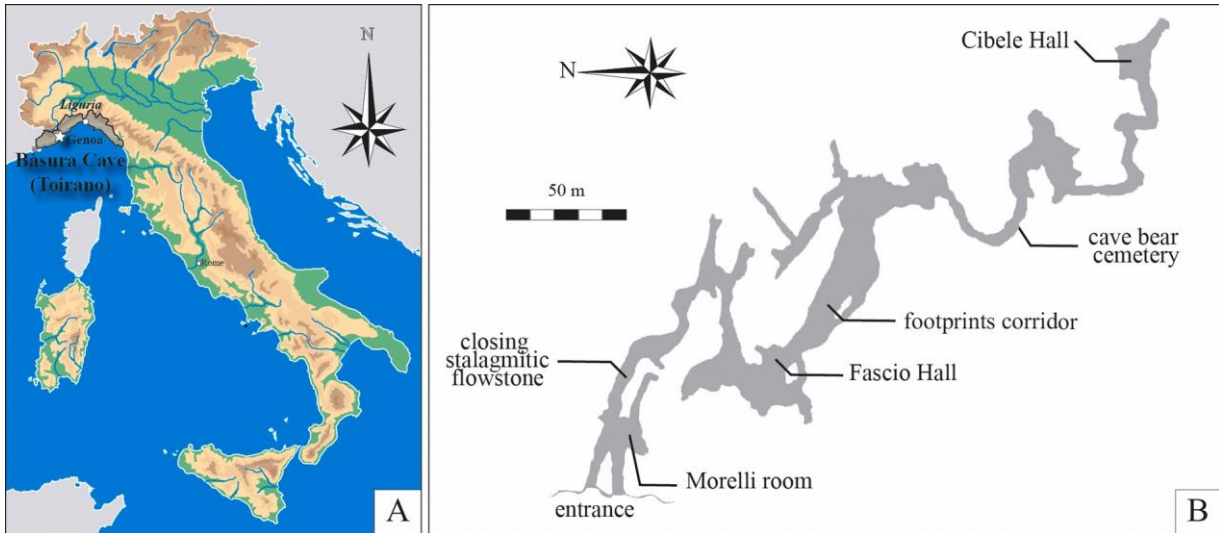


Fig. 2.

The “BF Palyno” core:

A) Overview of the sampling area in the Fascio room;

B) Core barrel used for drilling;

C) U-Th dates and age model of “BF2” core. The blue curves show the minimum (left) and maximum (right) calcite precipitation ages. (after Pozzi et al., 2019); D) “BF Palyno” core.

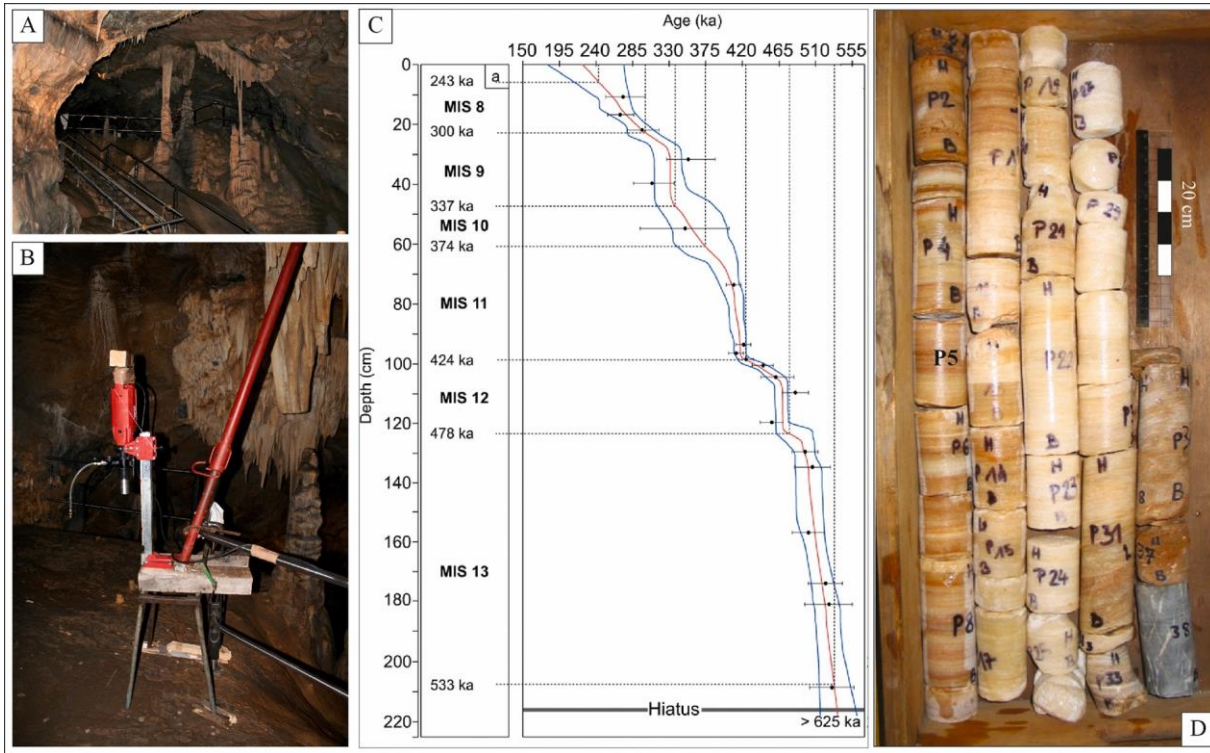


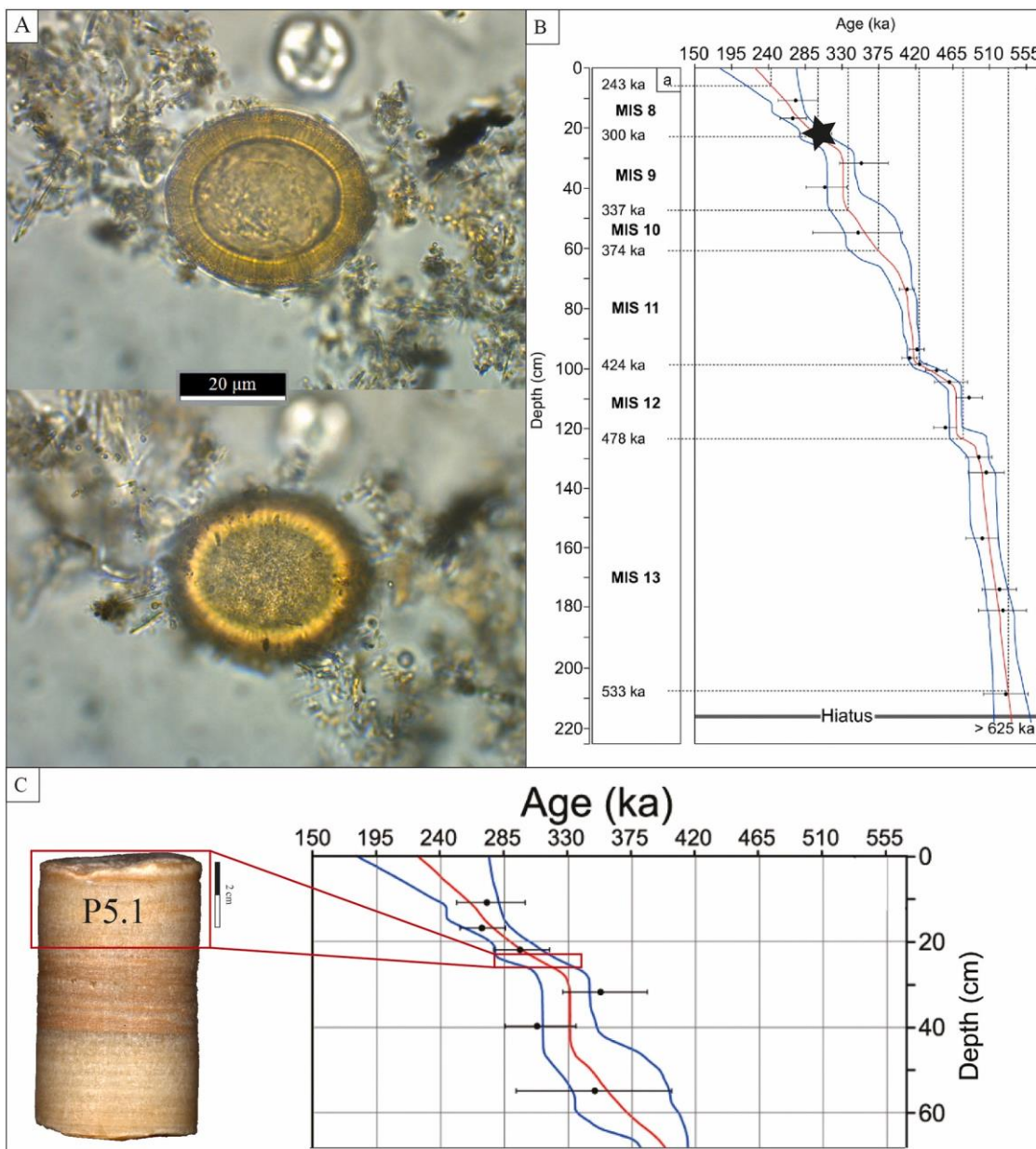
Fig. 3.

Taeniidae embryophore found in calcite sample P5.1.

A) Overview of the radiated (up) and punctate (down) internal shell of the embryophore;

B) Position (black star) of sample P5.1 from core “BF Palyno” with the dating curve from core “BF2” (after Pozzi et al., 2019);

C) Presentation of the crystallisation dates of the top and bottom of the calcite sample P5.1 with the dating curve from core “BF2” (after Pozzi et al., 2019).



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